Ecology of communities and ecosystems

I. General introduction

II. Species abundance and diversity (Ch. 16)
   A. Most species are moderately abundant in their communities
   B. Species diversity is a function of both number of species and their relative abundance
   C. Species diversity often increases with environmental complexity
   D. Species diversity is often greatest in communities with moderate levels of disturbance
   E. Environmental complexity and disturbance aren't necessarily mutually exclusive

III. The trophic structure of communities: food webs (Ch. 17)
   A. Food webs summarize feeding relationships within a community; they provide a basic and important description of community structure and function.
   B. The feeding activities of a few keystone species may control the structure of communities, but their effects depend on a number of important variables
   C. Exotic predators can collapse and simplify the structure of food webs.
   D. Humans can be keystone species

IV. Primary productivity and energy flow within an ecosystem (Ch. 18)
   A. Concepts and definitions
   B. Terrestrial primary productivity is generally limited by temperature and moisture
   C. In aquatic systems, primary productivity is generally limited by nutrients
   D. Consumers can increase or decrease primary productivity
   E. Energy flow within ecosystems results in trophic pyramids

V. Nutrient cycling and retention
   A. Nutrient cycling is a key ecosystem service that is affected by human activity.
   B. The rate of nutrient cycling is affected by both biotic and abiotic factors.
   C. Nutrient cycling in streams is complicated by water flow

VI. Community succession and stability
   A. Succession is the gradual change in plant and animal communities in an area following a disturbance
   B. Community-level changes during succession include changes in species richness and composition
   C. Ecosystem-level changes during succession include changes in productivity, respiration, biomass, and nutrient retention
   D. Species turnover within a sere is a function of
      1. biotic interactions among species
      2. extrinsic factors that influence composition of the pioneer community
   E. Although details of species turnover vary among communities, both early and late successional species have common characteristics across communities
   F. Stability in communities and ecosystems may be due to a lack of disturbance or to resisitance and resilience in the face of disturbance

I. General introduction

A. Some definitions:

1. **Ecological community** = an association of interacting species inhabiting a defined area
   a. communities actually studied are often subset of the “complete” community of an area
   b. subsets may be defined many different ways, depending on questions being asked -- e.g.:
      i. **place/habitat**: benthic vs. pelagic stream communities; soil communities
      ii. **taxon**: small mammal community; invertebrate community
      iii. **guild or lifeform**: shrub community; granivore community
      iv. of course, combinations possible as well (benthic marine invertebrate community; desert ant community; etc.)
2. **Ecosystem** = an ecological community and its abiotic components
   a. note that distinction between ecosystem and community often fuzzy
      i. most community ecologists incorporate components of the abiotic environment in their concept of “community”
      ii. few ecosystems ecologists would consider a termite mound with its associated abiotic features an ecosystem (but it would fit the above)
   b. common approach = consider ecosystem a higher level of organization:
      i. = multiple communities linked by patterns of energy and nutrient flow
      ii. e.g., forest, meadow, riparian communities within the same watershed

B. In this unit, we’ll move back and forth between these levels; much of what we’ll discuss is applicable to both

1. First we’ll look at some basic features of community structure: species abundance, diversity, trophic relationships
2. Then we’ll move on to important processes: productivity, nutrient cycling, succession

II. Species abundance and diversity

One of the most obvious kinds of difference among communities is the abundance and diversity of species in those communities -- what is species diversity, and why are some communities more diverse than others?

A. Across communities, most species are moderately abundant; few are very abundant or extremely rare
   1. Pattern first documented by Preston (1948 +)
      a. he looked at the relative abundance of species = relative number of individuals by defining "abundance classes", each of which was twice as "big" as the one before it (i.e. -- abundance class 1 = 0-2 individuals; class 2 = 2-4 individuals; etc.)
      b. then plotted frequency distributions: number of species in each community that fall into each abundance class
      c. resulting plots were almost always bell-shaped:this type of frequency distribution called **lognormal** because it's a normal distribution with one logarithmic axis
      d. pattern has several important implications:
         i. indicate that most species are moderately abundant
         ii. each community will have a very few highly abundant and extremely rare species
         iii. practical application: rare species will be hard to document unless communities carefully sampled -- so serves as "reminder" to watch for the rare ones
   2. Pattern is interesting for several reasons
      a. One of the best established, most consistent patterns in all of community ecology, yet the underlying causes aren't fully understood!
         i. one possibility: statistical models indicate that this is the pattern we'd expect if lots of random environmental variables were acting simultaneously on

many populations at same time

a) for a very few species, all variables would be positive => those would be the few highly abundant species

b) for a very few species, all variables would be negative => those would be the very few extremely rare species

c) for the rest, would have some positive, some negative effects leading to moderate abundance

ii. May be the result of specific kinds of interactions (especially, some suggest, interspecific competition)

iii. Or some combination of both -- still lots of debate about this

b. Regardless of underlying mechanism, pattern is very useful because it lets us predict/estimate the number of species in a community even when we don't have a complete sample:

i. we can "plot" the abundances of the species in the sample

ii. this will give us part of the lognormal distribution; we can mathematically extrapolate to "fill in" the rest of the curve

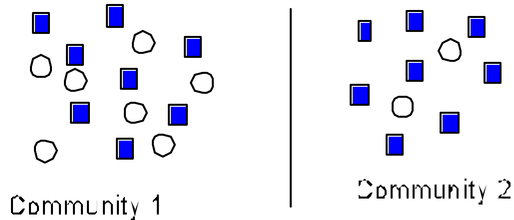
iii. because complete sampling often very difficult, this is extremely useful!

B. Species diversity is a function of both the number of different species in community and their relative abundances

1. This idea is based on a largely intuitive sense that both factors are important --e.g. (OH): two "communities" with different patterns of number, abundance:

a. both "communities" have two species

b. imagine walking through both communities -- in #1, you're more likely to encounter both species than in #2; we perceive that as more diverse



c. from a more ecological perspective, both species in Community 1 are likely to have important effects on community; in Community 2, the rare species is likely to have relatively little effect

2. So, ecologists recognize two components to diversity:
   a. **species richness** = number of species
   b. **species evenness** = relative abundance of species
3. These two components can be combined into a number of different mathematical models of diversity, allowing quantitative comparisons among communities. One of the most common is the **Shannon-Wiener diversity index**
   a. $H' = -\sum_{i=1}^{s} p_i \log_e p_i$ where s = number of species

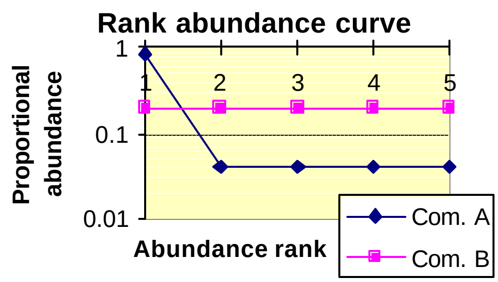
      p = proportion of total # individuals represented by each species

      H' = index of diversity
   b. H' will increase with both species number and with species evenness
   c. e.g.: two communities, five species each with numbers of individuals as follows (table 16.1):

Community A		Community B	
Species	#	Species	#
1	21	1	5
2	1	2	5
3	1	3	5
4	1	4	5
5	1	5	5

   d. work sample problem (end of notes)
   e. note weakness: only one number used, so can't tell how much of the difference in diversity between communities is due to differences in richness and how much to difference in evenness

4. Diversity can also be compared among communities graphically using **rank-abundance curves**
   a. plot log proportional abundance against abudance rank (from most abundant to least)
   b. e.g. from above table:
      i. number of ranks = number of species = richness
      ii. slope reflects evenness: more shallow = more even



      iii. community 2 more diverse because more even
   c. examples from actual studies: (OH, HO)
      i. Caddisfly communities in Portugal: stream communities are more diverse than coastal pond communities due to greater richness and greater evenness
      ii. Reef fish communities in the central Gulf of California are more diverse than are communities from the northern Gulf primarily because of greater evenness.
5. So, question now is why some communities are more diverse than others – this question doesn't have a simple answer, and ecologists are still working to figure it out!

C. Species diversity often increases with increases in environmental/habitat complexity
1. Basic reasoning fairly intuitive:
   a. to coexist, species need to occupy different niches
   b. more complex environments offer more niches
2. e.g., famous studies by Robert MacArthur (and others) show that bird species diversity increases with increasing forest complexity
   a. first studied warblers coexisting in same forest; birds feed by gleaning insects from bark, leaves
   b. reasoned that the critical niche dimension was foraging zone in tree

i. predicted that coexisting spp. used different parts of the tree to forage

ii. prediction confirmed by observation

c. then extended reasoning to more general hypothesis about bird species in whole forests:

i. quantified relationship between bird species diversity and vegetation stature (volume of tree canopy) on Mt. Desert Island, Maine: increasing stature increased the number of warbler species present

ii. compared relationship between species diversity and foliage height diversity among 13 forest communities from North and Central America: found positive correlation across communities

3. Similar results found in many studies of many kinds of animals in a variety of communities -- but there are also lots of exceptions

a. note that in this kind of study, investigators need to identify appropriate elements of environmental variability for the species they're looking at: variation that "matters" to one group of organisms might be irrelevant to another

4. Algae and terrestrial plant diversity also seems to be correlated with environmental complexity/heterogeneity

a. Hutchinson (of n-dimensional hypervolume fame) articulated the "paradox of the phytoplankton"): aquatic communities have high levels of plankton diversity in spite of

i. plankton competing for same nutrients

ii. apparently uniform habitats

b. so heterogeneity doesn't seem to explain phytoplankton diversity – and same holds for terrestrial plant communities

c. In fact, though, soil, water chemistry (nutrients, etc.) do vary enough on a local scale to help account for plant, algae diversity

i. Nitrate, silicate abundance in the surface waters of Pyramid lake, Nevada show high heterogeneity (contrary to intuitive sense of surface waters as being relatively uniform!)

ii. Nitrate and soil moisture highly variable over relatively small distances even in an agricultural field (where plowing etc. tends to make soil more uniform)

d. Does heterogeneity also explain(at leat in part) high levels of terrestrial plant diversity in tropics? Yes – because of subtle differences in soil characteristics -- e.g. from Jordan's study

i. studied plant communities in Amazon forest

ii. identified six distinct communities (each with its own combination of species) over a distance of <500 m and < 8m elevation, based on subtle differences in soil properties (water, particle size primarily)

e. Both plant and algal species diversity decline with increased fertility (nutrient availability)

i. e.g., Ghana rainforest: highest number of species found in soils with lowest fertility

ii. Park Grass experiment in England: grass has been fertilized on experimental plots since 1856; control plots left alone -- both species richness and evenness have declined over time!

iii. same pattern has been found in many studies of diatoms

iv. seems surprising -- but actually makes sense:

a) increasing nutrient availability actually makes environments more uniform (think of soil map from earlier)

b) with nutrient saturation, only limiting resource = light; one or a few species will be able to overgrow others and exclude them (competitive exclusion)

D. Species diversity is often greatest in communities with moderate levels of disturbance

1. Until now, have discussed habitats as though conditions changed relatively little; conditions more or less stable and in equilibrium. In fact, all habitats are susceptible to various kinds of **disturbance**

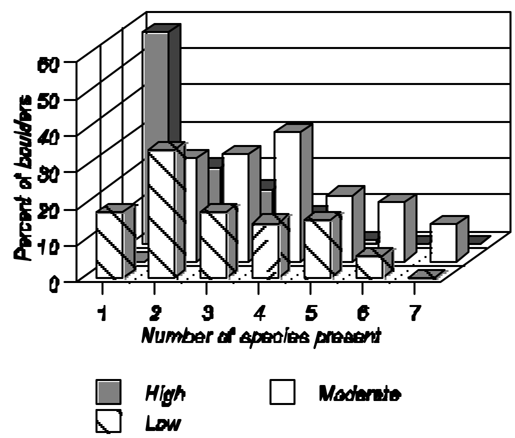
a. broadly defined as any discrete event that disrupts population, community or ecosystem structure and function

b. note that an event that constitutes a disturbance to one population/community might have no effect on another -- e.g., salt fluctuation would be disturbance to coral community, but not to estuary
c. many different kinds of biotic and abiotic events/processes can cause disturbance
d. we'll talk about effects of disturbance again when we talk about stability and succession; for now, we'll just note that disturbances can range in severity by ranging in
    i. frequency (how often)
    ii. intensity (how strong)

2. Connell (1975 +) was one of first ecologists to actually develop hypotheses about community structure based on the assumption that disturbance would be the norm (prior to that, most assumed equilibrial conditions made interspecific competition "driving force" behind much of community structure/function).
3. Proposed "intermediate disturbance hypothesis" of species diversity: species diversity will be highest under moderate levels (frequency or severity) of disturbance: reasoned that
    a. at high levels of disturbance, relatively few species would be present
        i. disturbed habitats often have harsh physical/chemical conditions; relatively few organisms have necessary physiological tolerances
        ii. if disturbance frequent, relatively few species would have adaptations necessary to colonize and complete life cycles before next disturbance
    b. at very low levels of disturbance, relatively few species would be present
        i. equilibrial conditions allow lots of interspecific competiton
        ii. communities will become limited to a few excellent competitors
    c. at intermediate levels, diversity will be greatest:
        i. sufficient time between disturbances to allow many species to colonize
        ii. not enough time for competition to reduce diversity
        iii. also possible (depending on type of disturbance) that moderate levels don't

produce conditions as severe as high disturbance

4. Test 1: disturbance and diversity in the intertidal zone (Sousa 1979):
   a. studied invertebrate communities on boulders
   b. disturbance = wave action overturning boulders, burying existing organisms and exposing new surface for colonization by new individuals
   c. measured force required to turn over boulders of different sizes in six study plots and the frequency with which waves turned boulders over the course of two years
   d. using that information, classified boulders into low, moderate, and high frequency disturbance classes and measured species diversity on each one
   e. results conform to prediction:
      i. majority of “high frequency disturbance” boulders had only 1 species; none had more than 5
      ii. modal frequency for low disturbance was 2 species; none had more than 6
      iii. intermediate disturbance had modal frequency of 4 species, substantial number had 5, 6, or 7



5. Test 2: disturbance and diversity in temperate grasslands (Whicker and Detling 1988)
   a. studied temperate grasslands, where historically important disturbances have been grazing, fire, and burrowing by mammals
   b. focused on effects of prairie dogs (Cynomys) at Wind Cave National Park
      i. squirrel relatives living in colonies of 10-55 individuals/ha
      ii. as late as 1919, occupied 40 million ha of NA grasslands; now reduced to tiny fraction of that (populations down to about 2% of original)
      iii. build extensive burrow systems: 1-3 m deep, 15m long, requiring removal and dumping of 200 kg of soil, usually deposited as mound 1-2m diameter

around the entrance

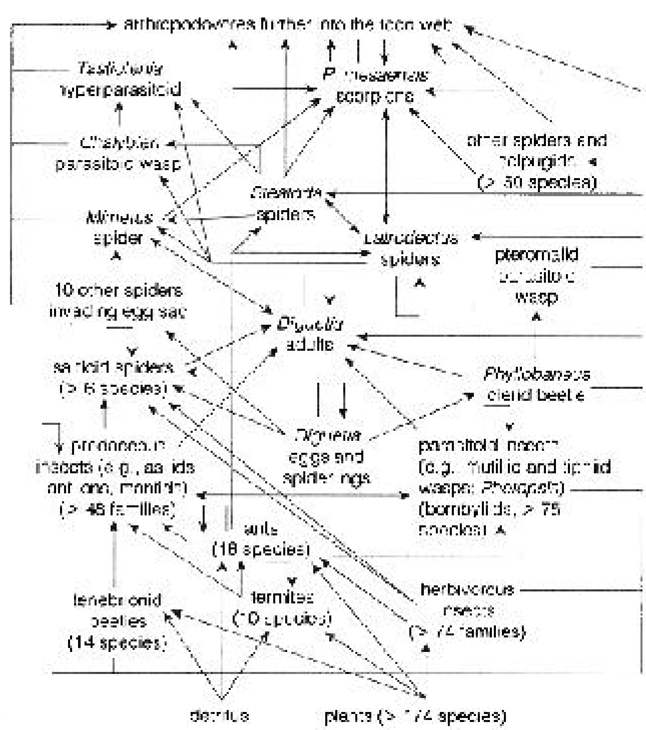
c. found that prairie dog colonies had vegetation communities much different from surrounding (undisturbed) prairie, with greatest diversity at intermediate levels of disturbance (= intermediate densities of prairie dogs)
   i. "bare surface" of newly-excavated soil good habitat for good colonizers
   ii. over time, early colonizers displaced by better competitors
   iii. at intermediate levels of burrowing, get complex mixture of "patches" of different age, plant composition (old ones with good competitors, young ones with good dispersers)

E. Prairie dog example illustrates that environmental complexity and disturbance aren't necessarily mutually exclusive; in many communities, disturbance creates the environmental complexity/heterogeneity that promotes species diversity
1. In forests, e.g., blow-downs create open patches that are structurally and functionally distinct from closed-canopy patches
2. In grasslands, fire and grazing important for keeping "best competitors" from excluding other species
3. conservation implications:
   a. if we're trying to restore a community or ecosystem and want to preserve optimal species diversity, may need create or simulate appropriate disturbance conditions
   b. also means that, for some communities, moderate human use (e.g., logging, grazing) may still be compatible with conservation goals -- just need to be careful.
4. ON YOUR OWN: Read about human disturbance and diversity of chalk grasslands (pp. 388-39=89); what evidence suggests that high levels of diversity result form human activity? Answer review question #8 p. 390.

III. The trophic structure of communities: food webs

A. Food webs summarize feeding relationships within a community; they provide a basic and important description of community structure and function.

1. This is a huge and complex area of ecology – we're just going to introduce a few basic concepts and identify a few common patterns without going into detail.
2. The earliest work on food webs (1920's) was qualitative and focused on relatively simple communities; we'll use an example to illustrate basic vocabulary:
   a. autotrophs vs. heterotrophs
   b. producers vs. consumers
3. Even in relatively impoverished communities, trophic relationships complex; when studied in more detail, level of complexity becomes huge
   a. Winemiller's study (fig. 17.4) of food web consisting only of 10 of the most common species in a community of 20 fish species (leaving out all other species!) -- clearly, huge amount of complexity!
   b. level of complexity can be reduced several ways:
      i. **aggregation**: combine species according to taxonomy, trophic position e.g., food web of just species at soil surface of desert in the Coachella Valley, CA: 174 species of plants, 138 species of inverts, 55 arachnids, over 2,000 species of microorganisms reduced to (relatively) simple diagram:



      ii. focusing on **interaction strength** (measured, usually, by amount of energy flow), with or without removing "weak" links (those involving less than some threshold value of energy flow).
         a) e.g., simplified Winemiller web easier to follow
         b) e.g. <u>Phragmites</u> food web: by focusing on interaction strength, can make better predictions about the

effects of different species in the web -- e.g., blue tits have strongest effects along "left side" of web

4. Food web structure can be quantified so that comparisons can be made among communities
   a. three factors commonly quantified; all relate to complexity:
      i. **connectance** = measure of relative complexity = actual number of "connections"/total possible connections (e.g., Coachella has connectance of .49 -- fairly high)
      ii. **linkage density** = # of links/species (# links/# species)
      iii. **chain length** = # of links between producer and top consumer (often averaged for entire web)
   b. unfortunately, although tons of studies have been done comparing communities, general patterns have been very elusive
      i. major problem is with the data themselves:
         a) virtually all published webs involve some sort of aggregation; kind and degree can make big difference in resulting patterns (in one study, Paine showed that connectance values ranged from ~ .30 to .60 for same community studied by different investigators!)
         b) even carefully detailed webs are often over-simplifications of actual relationships:
            i) food habits (position in web) may change over time (because of changes in organism, changes in environment)
            ii) migrating species may be very important elements of web at some times, but absent at others
            iii) strengths of interactions almost never known
      ii. one pattern that seems to hold with at least some consistency is that chain length seldom exceeds 4 -- but reasons unclear!
         a) early hypothesis was that chain length was related to productivity (amount of energy at "bottom" of web);

b) Pimm et al. disproved by experiments on tree-hole communities supplemented with external energy sources: no change in chain length over 4-fold increase in energy inputs

iii. one pattern that doesn't hold is relationship between community stabilityand food web complexity

a) this was early hypothesis of MacArthur and others

b) idea was that communities "connected" by complex food webs wouldbe less susceptible to disturbance and/or recover from disturbance more quickly than would simpler communities

c) field, laboratory and modeling studies fail to bear this out -- but why isn't really known

5. Conclusion: food web structure, even when qualitative, does give us important insights into community function; although general patterns still not clear, very active area of research

B. The feeding activities of a few keystone species may control the structure of communities, but their effects depend on a number of important variables

1. We've mentioned keystone species already (Paine's starfish *Pisaster*); now we'll define and distinguish from dominant species:
   a. **keystone species** = species that have large impacts on their community structure in spite of low biomass
   b. **dominant species** = species that have large impacts on their community's structure because of their large biomass
2. *Pisaster* = classic example: because of its trophic relationships with other tide pool invertebrates, it largely controlled species diversity within tidepools
3. Jane Lubchenko (1978) was one of first investigators to demonstrate that theeffects of keystone herbivores on trophic structure depended on several important factors, and that those effects can vary among communities.
   a. also studied tidal communities, but worked on snail-algae interactions
      i. snail = *Littorina littorea*, a grazer on a variety of tidepool macroalgae

ii. previous studies of the effects of herbivores on species diversity had mixed results: some found herbivory increased diversity, some found it decreased diversity

b. proposed that three major factors interacted to determine the effect of keystone species on trophic structure:
   i. food preferences of the consumer (herbivore)
   ii. competitive interactions among the plant species
   iii. variation in both food preference and competition across environments
c. did a series of experiments in lab and field:
   i. in lab studies, demonstrated that *Littorina* had definite food preferences (*Enteromorpha* > *Chondrus*)
   ii. in field studies, found strong relationship between presence of snail and densities of algae:
      a) where snail present, preferred algae absent and least preferred algae present
      b) where snail absent, preferred algae outcompetes least preferred algae (preferred species is best competitor)
      c) so snail has effect on algae similar to *Pisaster* on prey species: consumption reduces competitive exclusion of least preferred by most preferred
d. Found that species richness in tide pools related to snail density: highest species richness in tide pools with intermediate snail densities
   i. at low snail densities, preferred alga outcompetes others
   ii. at high snail densities, snail eats most species; least palatable only onesthat persist
   iii. so, in tidal communities, effect of herbivory is to increase species diversityat intermediate herbivore densities (herbivory ~ disturbance)
e. Found different effect of snails on algal diversity in emergent (above-water) habitats:

i. different combination of species present
ii. preferred prey species = <u>least</u> competitive of species present
iii. increasing snail density decreases algal species richness across all densities: effect of snail is to speed up competitive replacement

f. conclusion from these and other studies:
i. consumers can definitely be keystone species in a wide range of communities/ecosystems
ii. effects of consumers on food webs depends on several factors, including
a) consumer food preferences
b) local population densities of consumers
c) relative competitive ability of prey species
iii. because a-c above can vary over time and among environments, <u>effects of keystone consumer can also vary over time and among communities</u>

C. Exotic predators can collapse and simplify the structure of food webs
1. In our earlier discussion about competition, we noted that the introduction of exotic species can reduce biodiversity through competitive replacement
2. another <u>major</u> problem with exotics (probably even greater than #1) is that they reduce biodiversity through their effects on food webs: net effect is reduction insize, complexity of food webs
a. e.g., Nile perch in Lake Victoria
i. historically, Lake Victoria had over 400 species of fish, many endemic
ii. introduction of Nile perch and Nile tilapia around 1954; population really exploded beginning in 1980's (possibly as consequence of other changes in surrounding environments)
iii. fish catch now dominated by only 3 species: perch, tilapia, and one native sp.
iv. effect of perch may well be largest mass extinction of vertebrates in modern times!
b. unfortunately, similar processes happening all over, especially with introduction

of game fish in freshwater systems

c. ultimate consequences unclear: we don't know whether or not changes in trophic structure will have effects on communities beyond the obvious reduction in biodiversity

D. Humans can act as keystone species – e.g. from tropical South America (Kent Redford)

1. Amazonian subsistence hunteres take ~ 1.4 million mammals + 5 million birds and reptiles annually
2. Commercial hunters take ~ 4 million (for meat, skins, feathers, etc.)
3. Both activities produce "indirect kills"; Redford estimates ~ 60 million killed annually
4. Is this an example of keystone predation? One test = examine which species are affected: usually, large animals are disproportionately hunted
   a. at one national park in Peru, the 18% of mammal species actually hunted constitute over 75% of available mammal biomass
   b. similarly, the 9% of bird species actually hunted constitute over 52% of bird biomass
   c. total hunting impact = 80-93% reduction in mammal biomass, 70-90% of bird biomass
   d. so clearly humans have an effect disproportionate to our own biomass!
5. ON YOUR OWN: are the animals that humans hunt keystone species? What's the evidence? (pp. 407-408).
6. ON YOUR OWN: read section on keystone predators and pest control (pp. 408-410); be able to describe the basic elements and interactions of the citrus ant food web and the role of ants as pest control agents.

V. Primary productivity and energy flow in ecosystems

A. Concepts and definitions

1. In this unit, we'll look briefly at how energy "moves" through ecosystems, with special attention to
   a. factors affecting the amount of energy available within systems

b. effects of energetics on trophic structure

2. Energy for most ecosystems comes from the sun:
   a. **Primary productivity** = solar energy converted by plants to chemical energy in the form of fixed carbon
   b. **Gross Primary Productivity (GPP)** = total amount of solar energy converted (or total amount of carbon fixed, as surrogate measure)
   c. **Net Primary Productivity (NPP)** = total amount of chemical energy (fixed carbon) left after plant respiration
      i. = GPP - energy "burned" by plant for own uses
      ii. = amount of energy available to "fuel" the rest of the system
3. Primary productivity is influenced by multiple factors:
   a. Abiotic factors affect physiological processes in individual plants (including PSN) -- often referred to as "bottom-up control" of PP
   b. Biotic factors affect plant population size, which in turn affects total PSN -- these often referred to as "top-down control" of PP
4. To evaluate the effects of energy on trophic relationships, organisms are assigned to **trophic levels** based on position in food webs relative to plants – e.g.
   a. plants = producers
   b. plant-eating animals = primary consumers
   c. animals eating plant-eating animals = secondary consumers
   d. etc. – up to ~ 4' consumers (almost never more – why?)

B. Terrestrial primary productivity is generally limited by moisture, temperature
   1. Early investigation by Rosenzweig (1968) related PP to **annual evapotranspiration**
      a. AET = total amount of water that evaporates and transpires (from plants) off a landscape in one year
      b. AET will increase with both precipitation and temperature
      c. (OH): found very strong, positive relationship between PP an AET: productivity is highest in warmest, wettest environments (think about why)

2. Although relationship to AET is very strong, there's still some variation in PP not explained by variation in AET (i.e., within a given AET level, can still get differences in PP)
    a. subsequent experimental work shows additional correlation between PP and soil fertility (nutrient availability)
    b. not surprisingly (given how we treat our lawns, gardens, and agricultural fields!), nitrogen and phosphorous are generally the important nutrients

C. In aquatic systems, primary productivity is generally limited by nutrients
1. For freshwater systems (especially lakes), there's a very strong and well-documented pattern of increasing PP with increasing nutrient levels –
    a. increasing nutrient concentrations -->increases algal biomass -->increases NPP
    b. for freshwater systems, phosphate is most often the critical nutrient
2. In marine systems, PP is highest along continental margins
    a. these areas have the greatest nutrient concentrations as a consequence of
        i. runoff from terrestrial systems
        ii. mobilization due to disturbance of bottom sediments
        iii. upwelling
    b. for marine systems, nitrogen seems most often to be the limiting nutrient

D. Consumers can increase or decrease primary productivity
1. Consumers (primary or higher) affect NPP via their effects on food webs – similar to the effects of keystone species, but the effects are on productivity rather than on species diversity
2. E.g. #1: piscivorous fish depress primary productivity in some lake systems
    a. Important trophic links are: piscivorous fish -->planktivorous fish -->large herbivorous inverts -->plankton
    b. increasing piscivore abundance ultimately decreases plankton abundance; decreasing piscivore abundance has opposite effect
3. E.g. #2: Moderate densities of grazing increase productivity in Serengetti

grasslands

a. grasses exhibit phenomenon of **compensatory growth**
   i. = increased growth rate following grazing
   ii. results from effects of grazing on leaf area, shading, and other properties
b. at moderate grazing levels, NPP is greatest
   i. at low levels, no compensatory growth occurs
   ii. at high levels, grazing damage is too severe for plants to compensate
   iii. at intermediate levels, get net increase in PP because compensatory growth gives net gain in grass biomass

E. Energy flow within ecosystems results in trophic pyramids

1. In any ecosystem, only a very small fraction of incoming solar radiation is "converted" by plants
   a. e.g., Hubbard Brook -- NPP = ~ 1% of total incoming solar radiation
   b. means that all other food webs are based on only tiny fraction of total energy!
2. As energy is "transferred" through the food web, only a relatively small amount is actually available for transfer from one trophic level to the next
   a. review energy use in organisms: only a very small amount is used for the production of biomass (growth, reproduction), but that's the only energy available for transfer to next trophic level
   b. in addition to energy "lost" at each level, energy is also lost in the transfer from one level to another due to inefficiency of assimilation (think about "waste" not consumed)
   c. the general rule of thumb is that no more than ~10% of the energy available in one organism (or one trophic level) will be available to the next
   d. the consequence is that when the total energy content of each trophic level is calculated and plotted, get trophic pyramid:
      i. generally, trophic pyramids have 4 levels or less (remember chain length!)
      ii. consider implications for conservation of top predators!

V. Nutrient cycling and retention

A. Nutrient cycling is a key ecosystem service that is affected by human activity.

1. The major biogeochemical cycles (e.g., C, N, P) make key nutrients available to organisms; they depend on complex interactions between abiotic and biotic components of the environment.
2. The carbon cycle is our source of structural carbon:
    a. The major pool of activlely-cycled carbon is atmospheric CO_2.
    b. Although most carbon is rapidly cycled, some becomes sequestered for long periods of time in the forms of peat, fossil fuels, and carbonate rock.
    c. Overview of carbon cycle (fig. 19.4)
    d. The major anthropogenic effects on the carbon cycle are
        i. burning fossil fuels, increasing atmospheric CO_2
        ii. large-scale deforestation has the same effect (directly by burning and/or decomposition of wood; indirectly by reducing PSN)
    e. The main consequence of concern is effects of increasing CO_2 on global climate -- see the IPCC climate change report for possible consequences.
    f. Changing CO_2 levels may also have complex consequences for everything from individual plants (carbon availability affects energy allocation patterns, which can lead to changes in life history) to whole ecosystems (as atmospheric carbon levels change, competitive relationships among plants may change) – very hot topic!
3. The nitrogen cycle provides nitrogen for proteins, nucleic acids
    a. The major source of cycled N is N_2 gas in the atmosphere.
    b. The N cycle is complex:
        i. consists of “inner” and “outer loops”: cycling among organisms and cycling between organisms and the atmosphere
        ii. uptake by primary producers requires complex chemical conversions fromN_2 gas to ammonia, nitrite, nitrate; conversions require specialized organisms (bacteria primarily)

   c. note that nitrate is negatively charged; nitrate not assimilated by plants will be rapidly leached from soils
   d. Overview of the N-cycle
   e. major anthropogenic effects include
      i. burning fossil fuels returns N to atmosphere as nitrous oxides -- this is a greenhouse gas and a source of acid precipitation
      ii. deforestation precipitates nitrogen loss from forest systems:
         a) after trees cut, N returned to soils through decomposition
         b) nitrifying bacteria convert to nitrate
         c) with less vegetation to assimilate nitrate, it’s leached from the soils and lost via streams, rivers
      iii. use of nitrogen fertilizer increases nitrogen availability in aquatic systems, leading to nutrient pollution, eutrophication, changes in algal species diversity, and fish kills
4. The phosphorous cycle provides P for structural compounds (bone), ATP, and nucleic acids
   a. in contrast to C, N cycles, the P cycle is mostly sedimentary: the major pool of phosphate is in phosphate-bearing rock/sediment
   b. cycle is relatively simple, with release via erosion and simple cycling among organisms
   c. cycle is complicated by the chemistry of phosphate: pH limits its availability in both aquatic and terrestrial systems:
      i. at $pH < 5.5$ and > 7.0, phosphate combines with iron, aluminum (low pH), calcium (high pH) and other elements to form insoluble compounds
      ii. only soluble compounds can be assimilated by plants
   d. overview of cycle
   e. major anthropogenic effects:
      i. acid precipitation/mine drainage may have long-term effects on phophate availability in affected systems

ii. mining phosphorous-bearing rock for fertilizer harms local environments
iii. use of phosphate-rich fertilizers has same effects as using nitrogen fertilizers

B. The rate of nutrient cycling is affected by both biotic and abiotic factors.
1. Rates of nutrient cycling depend on rates of decomposition
a. decomposition converts nutrients from organic to inorganic form **mineralization**); assimilation usually requires inorganic forms of major mineral nutrients
b. decomposition rates increase with AET
c. in both terrestrial and aquatic systems, decomposition rates depend on chemical composition of litter; in general
i. rates increase with increasing N content
ii. rates decrease with increasing lignin content
2. Plants and animals have complex effects on nutrient cycling and availability –e.g.
a. prairie dogs (and other burrowing mammals) increase the nitrogen content of the grasses on their colonies (through complex processes)
b. large grazers speed up turnover of plant biomass in grassland systems; this requires an increase in decomposition
c. leguminous plants increase soil nitrogen:
i. directly through action of root symbionts and indirectly through the production of nitrogen-rich detritus
ii. changes in soil nitrogen availability can have effects on plant community structure
iii. cause of concern when exotic legumes imported for, e.g., erosion controlinto “naive” communities (Africa, Hawaii, eastern US)

C. Nutrient cycling in streams is complicated by water flow
1. In contrast to terrestrial systems (where nutrients are retained on site in soils), nutrients in streams may be transported from their “place of origin”
2. The pattern of uptake, release, downstream movement, reuptake, etc., is better described as a spiral than as a cycle

3. Spiraling dynamics are summarized in a quantity called **spiraling length (S)**
   a. **S = VT** where
      i. S = spiraling length
      ii. V = velocity of nutrient flow (not necessarily the same as the velocity of the stream!) downstream
      iii. T = time for nutrients to complete one cycle of uptake/release/reuptake
   b. so, S is low when V, T are small and
   c. low S implies high nutrient retentiveness (nutrients are staying in one place for longer) within a stream
4. Factors that affect nutrient retention will affect S (and vice-versa) – e.g., study by Grimm on aquatic invertebrates in Sycamore Creek, AZ (fig. 19.14):
   a. System basics:
      i. like many streams in arid southwest, this stream has high densities/biomass of aquatic invertebrates
      ii. > 80% of macroinvertebrate biomass = organisms in the category of "collector-gatherers" = detritus feeders
      iii. as in many systems, primary productivity in this stream is limited by N availability – so N retention is of particular interest
   b. Grimm found that macroinvertebrates increased N retention:
      i. quantified N budgets (measured amount of N at each level and the rate of movement among trophic levels)
      ii. measured N retention as the daily difference between N inputs and outputs
      iii. set daily difference at 100% of budget & expressed components as proportion of that 100% – found that
         a) ingestion rates = 131% (macroinvertebrates, like many other detritus/plant feeders, consume feces to improve extraction of nutrients)
         b) 15-70% of nitrogen excreted and recycled in the form of ammonia – these high feeding and excretion rates reduce T (fast cycling)
         c) ~ 10% of N at any one time is in the biomass of the invertebrates (which

stay in place) – this reduces V (rate at which nutrients are transported)

d) so together, inverts reduce V, reduce T, and therefore reduce S: short spiraling length = increase nutrient retention

D. ON YOUR OWN: read Plants and Nutrient Dynamics of Ecosystems (pp. 443-444); what effects have exotic legumes had on nutrient availability (and how); what are some of the potential consequences of those changes (think about what you know about species interactions)?

VI. Community succession and stability

In this unit, we'll look at how communities change following disturbance. Those changes have effects both at the community and at the larger ecosystem scale; we'll introduce the ecosystem changes here, then look at those processes in more depth in the next units (as time permits)

A. **Succession** is the gradual change in plant and animal communities in an area following a disturbance

1. Use example of old-field succession in the Piedmont Plateau to illustrate basic concepts: (check this out next time you drive rt 13 through northern North Carolina!)
    a. the disturbance, in this case, is conversion of forest to agricultural land --remove trees, plant crops, etc.
    b. because we often have a good idea of when fields were abandoned, we can look at fields abandoned for different lengths of time to chronicle patterns of change
    c. typical sequence (there is always some variation from community to community, even within the same general habitat type) is from community dominated by annuals through "shrubbier" communities, to final hardwood forest
2. Some definitions:
    a. **primary succession** = succession following disturbance severe enough to remove soil (so includes soil formation); e.g., following glacial retreat, volcanic eruption, severe dune erosion, etc.
    b. **secondary succession** = succession following disturbance that leaves soil

more or less intact (note that extreme disturbance of soil may be virtually the same as destruction/removal of soil); e.g., following fire, deforestation

c. specific sequence of community types formed during succession = **sere**
d. each stage in a sere = **seral stage**
e. first seral stage (first after disturbance) = **pioneer community**
f. latest seral stage = community that will persist without further change until further disturbance = **climax community**
    i. as a general rule (but exceptions exist!), climax communities tend to be similar within geographic regions with similar climates, soils (they are, in fact, the "biomes" we looked at at the beginning of the semester)
    ii. within geographic regions with similar climates, soils, can still get variation among climax communities depending on many factors, including:
        a) local variation in climate, soils, aspect, topography, etc.
        b) nature, frequency, and severity of disturbance

3. Succession has been well-studied in several especially important "model systems"; we'll use some to illustrate processes, patterns
    a. Glacier Bay, Alaska: first described in 1700's; we have a good, continuous record of changes as glaciers in the bay have retreated inland (beginning with John Muir's documentation from 1879)
    b. dunes of Lake Michigan formed as lake levels have fallen; distance of dunes from current shoreline is a rough measure of age (we can also use other dating methods)
    c. Hubbard Brook experimental forest (NY) -- large forest system where investigators have been able to experimentally log and treat large areas and follow for 30 years
    d. new: Mount St. Helens has been intensively studied since eruption 20 years ago
    e. old: Park Grass site in England, continuously studied for 100+ years!
    f. focus is usually on plant species -- but animals follow comparable kinds of patterns

B. Community-level changes during succession include changes in species richness and composition

1. Species composition changes identify seral stages; we'll look at mechanisms of change later
   a. note that change in composition includes changes in absolute presence/ absence as well as in relative abundance
2. Regardless of community, common pattern of change in species richness holds:
   a. species richness increases as succession proceeds
   b. rate of change is rapid initially, then slows to 0 at/near climax
   c. note that pattern holds in a variety of communities over 3 orders of magnitude difference in total time:
      i. 1.5 years in intertidal communities (boulders)
      ii. 150 years in Piedmont plateau communities
      iii. 1500 years in Glacier Bay (why does this one take so much longer?)
   d. timing of change in richness within a community is not necessarily the same for all growth forms: e.g. from Glacier Bay: (OH)
      i. mosses, liverworts reach max. richness after ~ 100 years
      ii. low shrubs and herbs increase in richness throughout

C. Ecosystem-level changes during succession include changes in productivity, respiration, biomass, and nutrient retention (we'll look at some of these processes in more detail next section)

1. Like community-level changes, ecosystem changes are often rapid initially, then conditions stabilize at/near climax
2. Changes in soil properties are especially important in primary succession (but also happen in 2' succession), e.g. Glacier Bay pattern = (OH)
   a. increases in soil depth at all horizons
   b. increases in , nitrogen, soil moisture, organic content
   c. decreases in phosphorous, pH, bulk density
3. As succession increases, biomass increases

a. biomass = dry weight of organisms =~ fixed carbon
b. an increase in biomass can only happen if PSN > respiration -- i.e., plants are fixing more energy as stored carbohydrate than plants and animals are “burning” as fuel
c. (for this reason, early successional communities are often called carbon sinks)
d. as succession proceeds, rates of PSN stabilize; rates of respiration increase then stabilize; at climax, the two are generally ~ balanced and total biomass is ~ stable (but there are exceptions to this!)

4. Hubbard Brook experiments demonstrate that soil nutrient retention increases as succession proceeds:
   a. very important, because (as we’ll see later) soil nutrients are often lost rapidly following disturbance
   b. experimenters logged one watershed, then experimentally suppressed succession by applying biocides: results pretty clear (OH)
      i. after succession allowed to proceed, biomass increased
      ii. immediately after clearcut, nutrients were lost rapidly
      iii. as succession proceeded, nutrient loss declined to control levels

D. Species turnover (which species replace which species over time) within a sere depends on many factors:
1. biotic interactions = mechanisms of replacement:
   a. **facilitation** = presence of one species changes the environment, making it less favorable to original species and more favorable to a second sp.
      i. e.g., light-tolerant species create shade -- reducing suitability for own seedlings but improving conditions for shade-tolerant sp.
      ii. e.g., cedars prefer limestone soils; own needles make soils more acidic, favoring species that prefer acidic soils
   b. **inhibition** = one species makes the environment unfavorable for other species
      i. e.g., many plants use allelopathic chemicals to inhibit growth of other plants (oaks, walnuts, e.g.)

ii. competition and predation (for animals) can also be inhibitory mechanisms

c. **tolerance** = lack of effect of one species on another

d. e.g., effects of dominant plants on spruce seedlings during succession at Glacier Bay: note that any one species can have both facilitory and inhibitory effects on another!

e. lesson from Mount St. Helens: commensalisms can also be important: salamanders were able to survive/recolonize affected areas by living in/moving through pocket gopher burrows via openings left by elk!

2. abiotic conditions before and during succession can influence species composition within seral stages, particularly by affecting the species composition of the pioneer community:

   a. <u>size of the disturbed area</u>: in general, increasing distance from the "edge" to the "core" of the disturbed area will increase the difference in abiotic conditions between undisturbed and disturbed areas -- so the larger the disturbance, the more harsh the abiotic conditons in the "most disturbed" portion and the more different the pioneer community will be from the original

   b. <u>distance from disturbed area to source populations</u> (sources of new seeds and animals):

      i. increased distance favors plants adapted for long-distance dispersal;

      ii. decreased distance allows less dispersal-adapted plants to become part of pioneer community

   c. <u>severity of disturbance</u>: this can have two kinds of effects:

      i. severity determines new abiotic conditions, which help determine which species can colonize

      ii. more severe disturbances may kill portions of seed bank (seeds and propagules present in the soil), making it less likely for those species to be included in the pioneer community

3. Mount St. Helens demonstrates complexity of succession:

   a. disturbance itself was highly complex – included landslides, pyroclastic & debris flows, ash depositions

b. recovery process did not proceed as simple pattern of seral stage replacement from early successional pioneer to late successional forest
c. instead, got complex recovery processes that owed as much to chance as to deterministic processes
    i. except in areas of lava/hot pumice, lots of organisms (plant and animal) survived, either as complete individuals or as reproductive parts
        a) e.g., moles, gophers, salamanders persisted underground
        b) roots, bulbs of some flowering plants were "tumbled" along the surface of avalanches (rather than being buried 600 feet deep) – so could re-establish themselves quickly
    ii. many saplings and shrubs were protected intact by late-lying snowbanks (chance = eruption happened while snowcover was still present to protect vegetation) – these immediately resumed growth
    iii. structural legacies played big role:
        a) structural legacy = organic structures like blown-down trees, standing snags, etc.
        b) these have big effect on succession:
            i) moderate abiotic conditions through shading, trapping moisture, limiting erosion, etc.
            ii) provide protective cover, habitat, food & other nutrient sources for lots of species – so help those species recolonize earlier than might otherwise be expected.
d. ON YOUR OWN: is lupine a facilitator or inhibitor of succession on Mount St. Helens? Describe the experiments and evidence discussed on pp. 465-466.

E. Although details of species turnover vary among communities, both early and late successional plant species have common characteristics across communities

1. Early successional species will be those that can
    a. disperse rapidly over long distances

b. tolerate relatively harsh abiotic conditions

2. Late successional species will tend to be those that are good competitors over time (note that these species are often present as seeds/seedlings in early stages and only come to dominate later stages as they grow)
3. General scheme of characters (think about equilibrial vs. non-equilibrial species!):

characteristic	early successional spp.	late successional spp.
number of seeds	many	few
seed size	small	large
dispersal	wind, passive animal	gravity, active animal
seed viability	long; can stay latent in soil	short
root:shoot	low	high
growth rate	rapid	slow
mature size	small	large
shade tolerance	low	high

F. Stability in communities and ecosystems may be due to a lack of disturbance or to resisitance and resilience in the face of disturbance

1. In lay terms, “stability” implies lack of change -- some ecological communities may exhibit relatively little change simply because of lack of disturbance
2. More interesting to ecologists is stability even when disturbance occurs (which is the case for most ecosystems!) -- **stability** can be defined as perisistence of a community or ecosystem in spite of disturbance.
3. This type of stability can be a consequence of two different community or ecosystem properties:
   a. **resistance** = ability to maintain structure and/or function in the face of a disturbance -- eg.,
      i. chaparral communities are resistant to fire (at least normally!)
      ii. riparian communities may be resistant to flooding

b. **resilience** = ability to recover original structure/function after a change following a disturbance; succession is the process that lets this happen

4. Stability remains very poorly understood:
   a. ecologists would like very much to understand correlates -- why some communities are more stable than others; what features of community structure/function enhance resistance and resilience
   b. no general patterns yet
   c. three things we do know:
      i. our perception of stability may be scale-dependent: a community or ecosystem that seems stable at one spatial, temporal, or structural scale may be less stable at other scales:
         a) e.g., Park Grass experimental site in England: from 1910 to 1948
            i) at the coarsest level of resolution, fertilized and unfertilized plotswere very stable: all began as meadows and persisted as meadows
            ii) at the scale of growth forms, also get good stability: the relative proportion of grasses, legumes, and other plants stayed very consistent on most plots
            iii) at the level of individual species abundances, found lots of variation: some species had no change, some much, and lots in between
         b) important implication: if this kind of pattern holds following human disturbance, how easy/hard would it be to recognize changes at the finer levels of resolution? would that matter?
      ii. communities/ecosystems that are resistant to or resilient following one kind of disturbance might be badly affected by another
      iii. stability is a function of complex interactions between biotic and abiotic factors -- e.g., Sycamore Creek , Arizona
         a) ecosystem <u>resilience</u> (species composition following flooding) is a function of nitrate levels -- portions of the creek with high nitrate levels

have greatest resilience

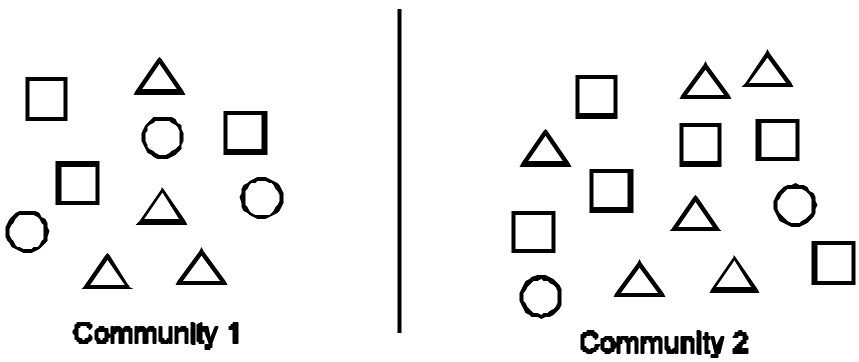
b) nitrate levels are a function of the strength and direction of flow between surface water and water flowing through sediments along the streambed -- upwelling increases nitrate levels

c) spatial arrangement of upwelling, stationary, and downwelling regions is highly resistant to flooding; it's a function of the geomorphology of the streambed (especially the depth of bedrock).

d) so here, geology of the streambed provides stability in one component of community/ecosystem function; that component increases resilience in other components (species composition)

Biology 205 - Principles of Ecology
Shannon-Weiner diversity index sample problem
Dr. Kilburn

In the illustration, each shape represents a different species; each individual figure represents an individual organism. Using the table provided, calculate H' for both communities. Which has the greater diversity? Which has the greater species richness? Which has the greater species evenness?



Community 1				
Species	Number	Proportion (p_i)	$\log_e p_i$	$p_i \log_e p_i$
Community 2				
Species	Number	Proportion (p_i)	$\log_e p_i$	$p_i \log_e p_i$