Large-scale ecology

I. Landscape ecology (Ch. 21)
   A. Introduction to landscape ecology
   B. Landscape structure includes the size, shape, composition, number, and position of ecosystems within the landscape
   C. Landscape structure affects landscape processes
      1. Many species exist as populations inhabiting spatially isolated habitat patches, but with significant movement of individuals among patches
      2. Studying/understanding the relationship between patch structure and biological processes is especially important now because human activity is increasingly fragmenting natural landscapes
      3. the size, number, and isolation of habitat patches influences movement of organisms
      4. patch size and isolation affects population density
      5. demographic differences among patches affect metapopulation dynamics
   D. Climate, geology, organisms, and other factors interact to produce dynamic landscapes
   E. Landscape restoration is an increasingly important conservation activity

II. Geographic ecology (Ch. 22)
   A. Introduction to geographic ecology
   B. On islands and habitat fragments on continents, species richness increases with area and decreases with isolation
   C. The equilibrium model of island biogeography (MacArthur and Wilson, 1967) is based on the idea of species richness on islands resulting from the dynamic interaction between colonization, extinction
   D. For most groups of organisms, species richness increases from the poles to the equator, although the reason(s) for this are not yet clear
   E. Long-term historical and regional processes can produce exceptional patterns of species diversity

III. Global ecology: deforestation (Ch. 23)
   A. Human activity has altered 1/3 to ½ of the ice-free land surface of the earth
   B. Tropical deforestation illustrates several problems with anthropogenic alteration of landscapes
      1. Background on tropical forests and deforestation
      2. Deforestation in the Brazilian Amazon has been well documented
      3. The consequences of deforestation include direct effects of forest loss, edge effects, and additional effects of fragmentation
      4. Specific results of deforestation will vary among forest types and regions

I. Landscape ecology

A. Introduction and background

1. Landscapes are heterogeneous areas composed of multiple ecosystems
    a. ecosystems form a mosaic of **patches** = **landscape elements**
    b. e.g., elements of a mountain landscape might include forests, meadows, bogs, streams, ponds, wet meadows, rock outcrops, etc.
2. Landscape ecologists study landscape structure, landscape processes, and changes in landscape, with special attention to the interaction between the spatial patterns in a landscape and various ecological processes

B. Landscape structure includes the size, shape, composition, number, and position of ecosystems within the landscape

1. To compare landscapes and to answer many questions about landscape function, need to be able to quantify landscape structure
2. Example of kinds of patterns that can be quantified using Ohio landscapes (OH/fig 18.4)
    a. diagrams show forest patches surrounded by other types of ecosystems (other kinds not distinguished)
    b. visual examination shows that landscapes clearly differ in several attributes, including
        i. total cover
        ii. number of patches
        iii. average size of patches
        iv. shapes of patches
    c. quantifying those attributes reveals patterns that might not be completely apparent to visual examination:
        i. total cover
            a) clearly is least in Concord (2.7% cover)
            b) pretty clear that Washington has most (43.6% cover)

c) how much greater is cover in Somerset than in Monroe? Somerset actually has double the cover of Monroe – which isn't really obvious visually

ii. patch size – comparing median patch size

a) surprise? Concord has slightly larger median patch size (4.1 ha) than does Monroe (3.6 ha)

b) Washington has greatest

iii. patch density = number of patches per unit area

a) Somerset clearly has more patches than Monroe – but how many? 244 vs. 180 (~ 35% more)

b) Monroe has more than twice as many patches as Boston (180 vs. 86)

iv. patch shape – it's often important to know how much perimeter a patch has compared to its total area (we'll see why in the next section of this unit)

a) investigators used a measure S calculated in such a way that

i) S = 1 is a circular patch

ii) as S becomes greater than 1, patch becomes longer, narrower

b) Concord had the most circular patches; Washington had the least

c) note that Boston patches are less circular than are Somerset – again not necessarily clear to the naked eye

3. Scale is important in landscape ecology in two different ways

a. different ecological processes operate at different spatial and temporal scales – need to be sure that the extent of a study in space and time is appropriate to the process being studied: compare, e.g., the amount of space and time needed to study:

i. speciation/extinction vs. population dynamics

ii. secondary succession on intertidal boulders vs. primary succession in Glacier Bay

iii. competitive replacement of a native tree by an exotic tree on an island vs.

competitive replacement of a native annual plant by an exotic annual plant in a community park

b. studying the same landscape using different scales of resolution can produce very different results
   i. this was key insight of Benoit Mandelbrot, who developed a type of mathematics called fractal geometry to help explain/quantify how different scales of resolution produce different measurements of complex objects
   ii. e.g.: Milne's measurements of the perimeter of Admiralty Island (off coast of SE Alaska – fig. 18.7)
      a) measuring the perimeter with a 1-km "ruler" produces estimate of ~ 800 km
      b) measuring the perimeter with a 10-km "ruler" produces estimate of ~ 400 km
         i) note that this is a smaller estimate because the larger "ruler" misses a lot of the nooks/crannies that the shorter ruler measures
      c) from the perspective of actual organisms:
         i) eagles nests are ~ .78 km apart: so measuring with an "eagle ruler" (= .78 km), eagles perceive the coastline as ~ 760 km
         ii) barnacles range only about 2 cm in lifetimes after settlement; measuring with a "barnacle ruler", barnacles perceive the coastline as ~ 11,000 km!
         iii) so how long would the coastline be for a molecule of crude oil? that's the scale that matters for cleanup of Exon Valdez oil spill . . .
   iii. e.g., differences in satellite resolution
      a) earliest Landsat satellites (used to collect data about earth from space) collected data at a resolution of 90m x 90m (i.e., each 90m x 90m plot would be recorded as having a single value – e.g., a single vegetation type – elements smaller than that would be missed)

b) later satellites have resolutions of up to 10m x 10m, so much smaller elements are detected

c) practical question: how can we use data from two such different scales of resolution to compare changes in landscapes using satellite data? very difficult to do!

C. Landscape structure affects landscape processes – we'll look at just a few examples of the interaction between structure and process

1. Many species exist as populations inhabiting spatially isolated habitat patches, but with significant movement of individuals among patches
   a. spatially isolated populations "connected" by migration of individuals = **metapopulations**
   b. e.g., desert bighorn sheep exist as populations inhabiting separate mountain ranges in the desert SW, but individuals move among ranges,
2. Studying/understanding the relationship between patch structure and biological processes is especially important now because human activity is increasingly fragmenting natural landscapes
3. The size, number, and isolation of habitat patches influences movement of organisms among suitable patches: e.g., Diffendorfer et al.'s study of patch size and movement in small mammals
   a. investigators created an experimental landscape in a natural prairie
      i. divided study area into 5000 m^2 plots
      ii. each plot was mowed to create a different patch structure – small, medium, and large patches of intact vegetation
   b. used livetrapping over 8 years to monitor presence and movement of three species of small mammals: cotton rats, prairie voles, and deer mice
   c. made two major predictions:
      i. animals would move farther in more fragmented landscapes (because distance from any point to "next suitable patch" is greater)

ii. animals would remain longer in each patch in the more fragmented landscapes (because, having found a good patch, the benefit of living in a better patch is less than the cost of trying to find one) – so proportion of individuals moving would be less in fragmented landscapes

d. predictions were confirmed for at least some species:
   i. deer mice and prairie voles in the more fragmented landscapes moved farther than did conspecifics from less fragmented landscapes
   ii. for all three species, the proportion of individuals moving was less in the most fragmented landscapes
e. so important finding is that patch structure influences movement – which can have significant consequences for the population as a whole (see below)

4. patch size and isolation affects population density
   a. e.g. 1, Hanski et al.'s study of Glanville fritillary butterflies in Finland
      i. habitat is landscape of farms, agricultural fields, pastures, meadows, and woods
      ii. suitable habitat patches for butterflies are patches of larval food plant (*Plantago lanceolata*)
      iii. within the landscape, investigators recorded variation in
         a) patch size: patches ranged from 12 - 46,000 m^2
         b) isolation of patches: found that patches could be a close together as 30m or as far apart as 1.6 km
         c) population size: patches had from as few as 0 individuals to as many as 2,190
      iv. investigators found several correlations between population size/density and patch structure:
         a) population size increased with patch size, but density decreased (i.e., large patches had large numbers of individuals, but at lower density overall than smaller patches)

b) population density decreased as isolation from other patches increased: increasing isolation decreased the number of individuals migrating into the isolated patches
c) local extinction was more likely on small patches than on large patches
d) local colonization was more likely on small patches than on large patches

v. think about the importance of these kinds of patterns for conservation!

b. e.g. 2: Merriam et al.'s study of chipmunks and white-footed mice (information from Dobson et al., Ecology 1/e pp. 92-93)

i. study site was agricultural landscape in Canada: mosaic of crop fields, scattered woodlands, and fencerows
a) woodlands = suitable habitat patches for chipmunks
b) fencerows = migration corridors animals use to move from one woodland patch to another

ii. study focused especially on connectivity of patches – two techniques were used
a) livetrapping and experimental removal of animals from woodlots
b) computer models to simulate effects of different patterns of connectivity among woodlot patches

iii. important patterns found were
a) after local extirpation of chipmunks (experimentally induced by trapping and removing chipmunks from experimental patches; naturally occurring because of winter mortality), recolonization was more rapid in more connected than in isolated woodlands
b) computer simulation showed that patches with the greatest "connectedness" had the larger population sizes and longer persistence of white-footed mouse populations over time

5. demographic differences among patches affect metapopulation dynamics

a. a key insight from these kinds of studies is that habitat patches within a landscape can vary dramatically in demographics (birth, death, immigration, emigration rates)
b. patches with an excess of births over deaths may become **source patches** = populations from which surplus individuals emigrate to colonize other patches
c. patches with an excess of deaths over births will be **sink patches** in which populations can only be maintained if immigration from source patches offsets deaths
d. result of this type of structure is that loss of a few key patches (i.e., source patches) may cause major decline of entire metapopulation
e. conservation implications pretty obvious!

D. Climate, geology, organisms, and other factors interact to produce dynamic landscapes – selected examples:

1. Climate and geology interact to produce mosaic of soil types – which in turn produces mosaic of vegetation types – in Tucson Mountain bajadas (studied by McAuliffe)
   a. Sonoran desert mountains consist of long, narrow ranges separated by basins/valleys
      i. mountains formed by uplift 12-15 mya
      ii. basins formed by subsidence at same time
      iii. erosion of sediment from mountains deposited in basins, producing sloping plains called bajadas at base of mountains
   b. although bajadas appear (from distance) to be uniform environments, can be quite variable over distances of a few km; differences largely a function of differences in soils (fig. 18.17, 18.19)
      i. McAuliffe found soils of at least four different ages – each corresponding to a time when the local climate produced extensive flooding and erosion
      ii. soils of different ages also have different structural properties because of

the effects of climate on the soils themselves – especially the effects of water transport on clays, calcium carbonate (caliche)

c. so landscape mosaic is a function of the interaction of geological events (uplift, subsidence, erosion) and climate variation over time

2. Plants and animals can have a major influence on landscape structure, including causing landscape structure to change
   a. examples of the effects of plants on landscape structure include, e.g., the effects of exotic legumes: legumes increase soil nitrogen content, which changes soil fertility and decomposition – which in turn can change the types of plants found in an area
   b. many animals have major effects on landscape structure – e.g.
      i. elephants control the extent of tree cover in some African landscapes
      ii. alligators dig "wallows" that become isolated ponds during the dry season – these are critical landscape components for many species in a variety of wetland habitats
      iii. feeding and burrowing by kangaroo rats and other rodents add patchiness to desert landscapes
      iv. termites build large mounds that are prominent landscape features important for a variety of other organisms
   c. one well-studied example = effect of beaver (*Castor canadensis*) on NA landscapes
      i. note that, historically, beavers ranged across North America from arctic tundra to Chihuahuan and Sonoran deserts – modified nearly all temperate stream valleys in the Northern hemisphere!
      ii. basic activities of beavers:
         a) dam streams to create ponds
         b) maintain systems of streams to/from ponds to surrounding areas
         c) cut vegetation (trees) for use as food and for building materials

d) general effects on landscapes include
   i) increasing extent of wetlands
   ii) changing hydrologic (water flow) regime
   iii) trapping sediments
   iv) increasing patchiness of plant communities
   v) reducing population size of preferred tree species

e) taken together, effect = addition of whole new ecosystems to landscapes

iii. e.g. effects of beaver on landscape structure in Voyageurs National Park (MN) – studied by Johnston et al.
   a) beavers reinvaded park ~ 1925 after being locally extirpated
   b) by 1988, changes included
      i) addition of 834 ponds (density of 3 ponds/km^2)
      ii) area of new ecosystems (ponds, wet meadows, moist meadows) increased to ~ 13% of peninsula
      iii) foraging altered an additional 12-15% of upland areas
      iv) landscape changed from predominantly spruce forest to more complex mosaic of habitat types (fig. 18.24)
      v) nutrient retention increased 20-72% (depending on nutrients)

3. Disturbances such as fire are an important determinant of landscape structure
   a. fire contributes to landscape structure in at least three different types of environments
      i. temperate grasslands
      ii. Mediterranean chaparral communities
      iii. boreal and other types of coniferous forests
   b. in general, fires do not burn uniformly across a landscape, so general effect of fire is to create/maintain patchiness within the landscape
   c. e.g., stand-replacing fires (fires that kill trees and initiate ecological

succession) in boreal forests

i. these are large, infrequent fires with return intervals of 80-400 years
ii. happen only when severe burn conditions prevail – note that most fires in such forests are small and burn themselves out
iii. effect of fires is, in part, to generate a mosaic of different stand ages across landscapes
    a) note that different age stands will often have different understory structure/composition – so patches differ more than just in age of overstory trees

E. Landscape restoration is an increasingly important human activity – the Kissimmee River restoration

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:
        i. floods affect landscape structure by
            a) depositing silt on floodplains
            b) isolating oxbow lakes
            c) creating new river channels
        ii. Floods influence nutrient cycling and decomposition
        iii. many species of river fish use flooded floodplains as spawning and nursery grounds
        iv. many species of plants require flooding for germination and establishment
        v. 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. growing recognition that flood management efforts result in loss of water quality and biodiversity has led to efforts to restore riverine systems

2. The Kissimmee river
   a. flows from headwaters in Lake Kissimmee south into Lake Okeechobee.
   b. historical landscape included
      i. highly braided, meandering channel ~ 166 m long
      ii. floodplain 1.5 to 3 km wide included 35,000 ha of wetland
      iii. variety of ecosystems, including oxbow lakes and four types of marshes
      iv. 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
   c. because of extent, duration of inundation, river “acted” much like large tropical river – tight linkage between river and floodplain very important to organisms living there
   d. Before modification, landscape supported
      i. 48 species of fish
      ii. 16 species of wading birds
      iii. 22 species of ducks and other water birds
      iv. 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 river: river converted into system of
      i. 5 reservoirs connected by
      ii. canal 9 m deep, 100 m wide, 90 km long
   b. eliminated 14,000 ha of wetlands within the landscape
   c. filled in former river channels
4. Effects on the river include:

a. reduced winter waterbird populations by 92%
b. large mouth bass populations replaced by non-game species that tolerate low oxygen concentrations
c. populations of riverine inverts replaced by inverts typical of ponds and lakes
d. reduction of exchange of nutrients, organic matter, and organisms between river and floodplain
e. loss of spawning and foraging habitat for adult fish
f. loss of refugia and nursery areas for larval/juvenile fish

5. By mid-1980s, people realized that effects of channelization were, on balance, negative; restoration was mandated and test project begun 1984 –
   a. project included
      i. building weirs to divert water from canal into remnant river channels
      ii. fluctuating water levels within one of the reservoirs to restore flooding
   b. results were fairly quick and impressive:
      i. native vegetation returned; exotics declined
      ii. flow through remnant channels cleared detritus and restored channels
      iii. riverine inverts recolonized remnant channels
      iv. fish moved into flooded areas
      v. fish requiring high dissolved oxygen returned
      vi. wetlands attracted more waterfowl
6. Consequence is that 15-year project is now underway to restore a large portion of the system; major features will include
   a. restoring historical landscape structure by
      i. restoring complex channel network
      ii. reestablishing floodplain marshes
   b. restoring flood pulses to “reconnect” river with floodplain

II. Geographic ecology

A. Introduction to geographic ecology

1. MacArthur defined geographic ecology as the “search for patterns of plant and animal life that can be put on a map”
2. Geographic ecology really began with early naturalists (Humboldt, Darwin, Wallace, Merriam, many others) who described large-scale distributions of plants and animals
3. started becoming more quantitative/predictive in mid-1900's, especially with work of MacArthur and students such as E.O. Wilson
4. current applications include trying to predict consequences of long-term climate and habitat change (anthropogenic and otherwise)

B. On islands and habitat fragments on continents, species richness increases with area and decreases with isolation

1. The general pattern of increasing species richness with increasing area holds for numerous groups of organisms on both land and habitat islands.
   a. remember, “land” island is surrounded by water
   b. habitat island = patch of habitat isolated from other, similar patches – e.g., lakes, forests on isolated mountain peaks, etc.
2. This relationship was generalized into an equation for the “species-area curve” or species/area relationship:
   a. $S = CA^z$, where S = number of species, A = area, C is a constant measuring the number of species per unit area^2, and z is a parameter that varies predictably among types of organisms and types of habitats examined
   b. an easier way to see the relationship is to convert to log-scale; z is then the slope of the line expressing the log # of species against the log area
   c. for the wide range of organisms for whom z has been measured, z ranges from around .15 - .35
      i. in practical terms (don’t worry about the math), z = .30 means that the number of species will double with a 10x increase in area
      ii. or, conversely (think about conservation implications), when z = .30, a 10x

decrease in area will cut the number of species in the area in half

d. z varies in fairly predictable ways across organisms, habitats – e.g.,
   i. low z = a shallow species-area line
   ii. occurs when small "islands" have nearly as many species as large "islands"
   iii. low z is characteristic of organisms with good dispersal ability (easily able to reach all islands within their range)
   iv. low z is also characteristic of continental habitats (compared to land islands of comparable ranges of areas) because continents present fewer barriers to dispersal – so species that go extinct in a small area may be rapidly replaced
e. Species-area curves are one tool used to predict extinction patterns due to anthropogenic habitat loss – e.g., due to deforestation in Brazil (from E.O. Wilson, *The Diversity of Life*)
   i. in 1989, area of Brazilian rain forests was declining by 1.8% annually
   ii. if that trend continues until 2022, ½ of the remaining forest will be gone
   iii. using species-area curves with range of z values, can predict that:
      a) 10% of species with low z (0.15) will become extinct
      b) 22% of species with high z (0.35) will become extinct
      c) note that, if rainforests are as species rich as most biologists think, the loss of 10-22% of their species could = 5-10% of total species on earth.

3. Species richness on islands decreases with increasing isolation (from source populations)
   a. e.g., fig. 22.5 – species richness as a function of isolation in New Guinea
   b. cause is intuitive: as isolation increases, chances of colonization from a source decrease
   c. note that, because of differences in dispersal ability, an individual island may appear more isolated to some organisms than to others – e.g., Williamson's comparison of Azores, Channel Islands

i. Azores lie ~ 1600 km west of Iberian Peninsula; Channel Islands very close to coast of France
ii. both groups have similar climates, biotas, so differences in species richness should be (at least largely) due to isolation
iii. compared two groups – birds and pteridiophytes (ferns and fern allies)
   a) birds had lower richness on Azore islands of similar size because of greater difficulty of dispersal to Azores
   b) pteridiophytes showed no effect of distance – they produce huge numbers of very small, very light spores that can easily disperse across long distances

d. The same pattern of decreasing species richness with increasing isolation occurs on continental habitat islands – e.g., Lomolino et al.'s work on montane mammals in southwest US:
   i. in southern NM, numerous isolated mountain ranges form "islands" in a "sea" of desert habitat
   ii. two sources for colonization = southern Rocky mountains (extending into NM) and Mogollon Rim (of Arizona/NM)
   iii. found strong negative relationship between richness, isolation
   iv. findings imply that migration continues to occur – if colonization only happened once (or if faunas left from glacial eras), would see greater richness on large mountains regardless of distance to source
   v. means that species richness on islands is maintained by dynamic process of ongoing colonization, extinction

C. The equilibrium model of island biogeography (MacArthur and Wilson, 1967) is based on the idea of species richness on islands resulting from the dynamic interaction between colonization, extinction
   1. The basic model (22.8) predicts species richness based on immigration and extinction, where

a. immigration = the number of new species added to the island from some source
    i. note that, on a new island with 0 species, immigration will be high because all species arriving will be new at first
    ii. as species accumulate, immigration declines
        a) the number of individuals arriving at the island stays the same
        b) but, because most "new arrivals" will be members of species already present, they don't add new species to island
b. extinction increases as species richness increases for 3 reasons:
    i. statistical: the greater the number of species, the greater the number of "candidates" for extinction
    ii. population dynamics: as the number of species increases, the population size of each must decline, which increases extinction risk
    iii. species interactions: as the number of species increases, interspecific competition increases, which will place poor competitors at greater risk of extinction
c. on a graph of immigration/extinction rate vs. number of species, the point at which the two curves cross = the equilibrium number of species – it's an equilibrium because shifting the number in either direction will return the number to the equilibrium point:
    i. at lower numbers of species, immigration exceeds extinction and the number of species increases
    ii. at higher numbers of species, extinction exceeds immigration and the number of species decreases

2. Next, MacArthur and Wilson added the effects of island size and isolation to the basic model (22.9)
    a. immigration rate is primarily a function of distance: far islands will have lower rates than near islands

  b. extinction is primarily a function of island size (large islands support more species)
  c. adding new curves for immigration to near and far islands and extinction on large and small islands, get 4 potential equilibria – most importantly:
    i. species richness will be lowest on far, small islands
    ii. species richness will be greatest on near, large islands
3. Note that this model <u>describes</u> basic patterns of species richness; it also <u>predicts</u> that species composition should change over time
  a. immigration and extinction are ongoing processes
  b. on a particular island, no reason to expect that immigration will replace extinct species exactly
  c. prediction met: e.g., Diamond's study of CA Channel Island birds (22.10)
    i. A. B. Howell's 1917 survey provided baseline for number of species on most islans
    ii. Diamond surveyed in 1968
    iii. found that species richness on most islands stayed constant due to balance of immigration and extinction
    iv. found that species composition had changed
4. Wilson and Simberloff used an experimental study of mangrove islands in Florida to test the model (22.11):
  a. mangrove islands were good model system because of
    i. the variety of sizes and distances to source populations available
    ii. the islands are relatively small (11-18 m in diameter), so could manipulate whole faunas
  b. on experimental islands, most animals = arthropods (primarily insects, spiders) – 20-40 insect species and 2-10 spider species per island
  c. established 2 control and 6 experimental islands
    i. surveyed all islands and identified insect, spider species

ii. defaunated experimental islands by enclosing in plastic tents and fumigating
iii. checked experimental islands to be sure arthropods had been killed
iv. followed recolonization over ~ 1 year

d. findings met predictions (22.12):
   i. number of species on control islands stayed the same, but composition varied over time
   ii. following defaunation:
      a) number of species increased on all islands
      b) near islands had greater richness than far islands
      c) in all, species composition varied over time

5. ON YOUR OWN: study the “natural experiment” of colonization of new islands formed in Lake Hjälmaren, Sweden p. 504. How did the islands form, what did investigators study, what did they find?

D. For most groups of organisms, species richness increases from the poles to the equator, although the reason(s) for this are not yet clear

1. No one hypothesis (yet) seems to explain the pattern
2. Some of the major hypotheses (and their weaknesses) include:
   a. **time since perturbation**: proposes that high species richness is due to the age and long-term climatic stability of the tropics
      i. mid and high-latitude regions have been repeatedly disrupted by glaciers
      ii. with greater long-term stability, tropics have had more time for speciation and fewer causes of extinction
      iii. problem: at smaller scales, at least, moderate levels of disturbance increase species diversity – so how do we reconcile this?
   b. **productivity**: this hypothesis notes that the two most species rich environments on earth (coral reefs, tropical rainforests) both have extremely high productivity

i. with more energy to "divide" among organisms, highly productive systems may allow
   a) niche partitioning leading to more specialized consumers
   b) large population sizes (which decreases extinction risk)
ii. problem: at smaller scales (as we've seen), increasing nutrient availability (which leads to increased productivity) decreases species richness – so how do we reconcile this?

c. **favorableness**: this hypothesis is based on the fact that the tropics have relatively stable and favorable abiotic conditions (especially temperature, moisture)
   i. a very wide range of organisms can tolerate these kinds of conditions
   ii. far fewer organisms are adapted to harsher abiotic conditions

3. One hypothesis that may explain a large portion of the pattern is the land-area hypothesis developed most recently by Rosenzweig
   a. contrary to intuition (and the Mercator projections used for most maps), the tropics (defined as the area between the Tropic of Cancer and the Tropic of Capricorn) include greater land and water area than do regions at higher latitude
   b. in addition to greater land area, temperature is more uniform across the tropics than across comparable ranges of temperate latitudes:
      i. Terborgh found that temperatures are relatively stable +/- 25^o N and S of equator (so across a total range of 50^o latitude)
      ii. above 25^o N and S, temperature decreases linearly with latitude
      iii. this means that tropical organisms can disperse across a very large area (into and out of refugia) and still face the same general conditions
   c. Rosenzweig proposed that increasing land area decreases extinction rates two ways:
      i. large areas of similar habitat lead to large species distributions and large

total population sizes

ii. large areas increase the number of refugia in which populations can survive local environmental disturbances

d. He also proposed that larger species ranges increase allopatric speciation, because large ranges are more likely than small ranges to be interrupted by geographic/climatic barriers

e. Testing the land area hypothesis:

i. The hypothesis predicts that the relationship between area and species richness holds at continental scales as well as "island" scales – e.g., Brown's study of non-volant mammal diversity in continental areas and continent-sized islands (22.20)

ii. The hypothesis also predicts that, within the tropics, regions with greater area should have greater species richness – e.g., Rosenzweig's study of tropical plants and frugivores (22.21)

4. Summary: so far, no one hypothesis explains the entire latitudinal gradient of species diversity; "real answer" is probably a combination of land area, productivity, favorableness, and other factors

E. Long-term historical and regional processes can produce exceptional patterns of species diversity (area and isolation aren't the only important factors!)

1. Cape Floristic Region of S. Africa

a. has a Mediterranean climate similar to CA, SW Australia

b. exceptional pattern: CFR has ~ 2x the species diversity in spite of a much smaller area (~90,000 km^2 vs. ~ 320,000 km^2 in Australia, 324,000 km^2 in CA)

c. several historical and geographic factors have increased its diversity:

i. selection for arid-adapted plants likely began well north of the CFR during the late Tertiary (26 mya) – so larger area of origin, at least, than might expect based on current distribution

ii. as Africa drifted northward, arid adapted plants migrated S to Cape region

iii. speciation in the Cape region was promoted by geographic and climatic features:
   a) highly dissected landscape (many barriers to gene flow)
   b) diversity of soils
   c) expansion and contraction of species ranges during climate fluctuations of Pleistocene promoted speciation
   d) many refugia reduced extinction rates

2. Temperate forest trees
   a. E. Asia, Europe, and North America have ~ equal areas of temperate forest
   b. exceptional pattern: E. Asia has ~ 3x as many species as North America and ~ 6x as many species as Europe
   c. historical component of pattern: most temperate tree taxa originated in Asia and migrated to Europe and NA (when NA was connected to Europe, forming the Laurasian supercontinent)
      i. so, even with ongoing dispersal, still expect greater diversity in Asia (not all species will successfully disperse)
      ii. barriers to dispersal have formed, while speciation in Asia has continued, producing genera (and species) endemic to Asia (and increasing its species richness)
   d. mountain ranges are the primary geographic influence on this pattern:
      i. during Pleistocene glaciation, climate distributions shift N, S
      ii. in Europe, E-W mountain ranges are major barriers to tree dispersal – extinction rates have been much higher there
      iii. in NA, Appalachians run N-S, so don’t act as barrier to dispersal
      iv. in E. Asia, few mountain ranges present, and those that are run N,S
      v. also note that E. Asian species can migrate farther south than they can in NA

III. GLOBAL ECOLOGY: DEFORESTATION

(Note: additional information comes from Meffe et al., *Principles of Conservation* Biology 2/e and web sites listed on the “notes” page of the course web site)

A. Human activity has altered 1/3 to 1/2 of the ice-free land surface of the earth

1. Conversion of land for agriculture and urbanization are the most important causes of habitat alteration
2. The problem is global and includes non-forest habitat types: from Meffe et al., e.g.:

Country/region	**Habitat type**	**% remaining**
North America	Tallgrass prairie	1
Sri Lanka	Thorn scrub	25
United Kingdom	Heathland	27
Nigeria	Mangrove	50
Paraguay	Chaco	57
South Africa	Fynbos	67

3. Deforestation is a global problem
   a. World wide, global deforestation rates in developing countries is currently about 13.7 million ha/year, according to the UN FAO Forestry division
      i. this means that global deforestation rates average ~ 2% annually
      ii. total loss is ~ equivalent to losing the total heavily forested land in Virginia annually
   b. Rates of deforestation vary among forest types: in Costa Rica, e.g.,
      i. > 99% of dry deciduous, lowland moist, premontane moist, lower montane moist, and montane wet forests have been lost, compared to 32% of montane rainforest and 35% of lower montane rainforest
   c. Deforestation isn’t a problem only of developing countries
      i. in US, severely depleted forest types include
         a) Mature red spruce in Appalachians

b) Old-growth Douglas Fir in Pacific Northwest

c) Longleaf pine in southeast US

ii. problem exists in our own region – study by American Forests (see web site) found that

a) heavily forested land in the SE Chesapeake Watershed was reduced from 25,5000 km^2 in 1973 to 17,747 km^2 in 1997

b) estimated that loss of forest cover in the Baltimore-Washington corridor has had significant economic costs:

i) loss of stormwater retention capability worth $1.08 billion

ii) loss of pollution removal worth $24 million annually

B. Tropical deforestation illustrates several problems with anthropogenic alteration of landscapes

1. Background on tropical forests and deforestation

a. extent of tropical forests globally:

i. tropical forest occurs in 73 countries and once covered 11,610,350 km^2

ii. of that total, 75% occurs in only 10 countries (in SA, Indonesia, Africa, India – see fig. 20.15 in text)

iii. of that total, just over 30% occurs in Brazil

b. the primary causes of deforestation are (in approximate order of importance)

i. conversion to subsistence farming (especially in Africa, Asia)

ii. conversion to large-scale ranching (especially SA, Asia to a limited extent)

iii. other types of economic development (dams, roads, mining, etc.)

2. Deforestation in the Brazilian Amazon has been well documented in a study by Skole and Tucker:

a. measured rates of deforestation using satellite imagery from 1978, 1988

i. satellites showed deforested areas

ii. images converted to GIS maps that allowed quantitative analysis

b. major findings were that

i. by 1978, ~ 78,000 km^2 of intact rain forest had been lost
ii. from 1978 - 1988 loss was ~ 15,500 km^2 annually
iii. by 1988, a total of ~ 230,000 km^2 of rain forest had been lost

3. On global scale (from E.O. Wilson, *The Diversity of Life*, p. 275): *"By 1989 the tropical rain forests of the world had been reduced to about 8 million square kilometers, of slightly less than half of the prehistoric cover. They were being destroyed at the rate of 142,000 square kilometers a year, or 1.8 percent of the standing cover, nearly double the 1979 amount. The loss is equal to the area of a football field every second. Put another way, in 1989 the surviving rain forests occupied an area about that of the contiguous forty-eight states of the United States, and they were being reduced by an amount equivalent to the size of Florida every year."*
4. The consequences of deforestation include direct effects of forest loss, edge effects, and additional effects of fragmentation
   a. direct effects of forest loss include
      i. loss of "ecosystem services" – many of which we've talked about: deforestation typically results in
         a) loss of nutrients and nutrient retention (remember Hubbard Brook!)
         b) change in the hydrological regime
            i) reducing tree cover reduces the amount of water returned to the atmosphere via transpiration – which, in turn, reduces rainfall (in tropical rainforest, this can amount to a significant climate change)
            ii) loss of trees decreases the water-retaining capacity of the soil, causing an increase in surface runoff and flooding
            iii) so total effect is, ironically, an increase in severity of both floods and droughts!
      ii. loss of species, especially endemics with limited ranges (not uncommon in

the tropics) – e.g.

a) Centinela Ridge in Ecuador lost ~ 90 species of endemic plants (no one knows how many endemic animals – most likely arthropods – that were dependent on the plants) when it was cleared for agriculture

b) Cerro Tacarcuna, a mountain in Panama, has 71 species of angiosperms (24% of total flora) with ranges of only 5-10 km^2

b. edge effects (result from changes in the abiotic conditions along the edge of clearcuts and other disturbances)

i. edge of a clearcut has different abiotic conditions than are found in forest interiors; regardless of forest type, edges of clearcuts typically

a) are exposed to increased solar radiation, wind

b) consequently tend to be sunnier, warmer, and drier than interiors

ii. because of abiotic differences, edges are typically more susceptible to specific kinds of disturbance, including

a) fire

b) disease

c) tree fall

iii. also because of abiotic differences, structure and function of vegetation differs along edges – edges typically are

a) dominated by early successional “weedy” species

b) typically “shrubbier” and more densely vegetated

iv. changes in plant community along edges, in turn, change the abundance and distribution of animal species – in NA forests, e.g., edges typically attract opportunistic predators such as raccoons, jays, crows, foxes, etc.

v. the “real” problem with edge effects is that they’re not confined just to the edges of clearcuts: they can extend well into the interior or “core habitat”:

a) the physical effects (changes in abiotic conditions) may extend from a few 10s to as many as 1000 m into the interior, depending on the type of forest, the aspect of the edge, climate, etc.

b) in one study of a forest in Queensland, investigators found increased rates of canopy and subcanopy damage + proliferation of disturbance-adapted plants extending 500 m from forest edge

c) Janzen found evidence of invasive weedy plants 5 km into a forest in Costa Rica

d) in NA forests, opportunistic predators living in edge habitats may extend hunting/foraging hundreds of meters into forest interior, causing significant nest predation on interior bird species

vi. note that the severity of edge effects will be strongly influenced by the shape of "core patches" left after cutting: patches with high perimeter:core will have stronger edge effects than patches with lower perimeter:core (more circular patches)

vii. note also that, because of edge effects, patches of forest below some threshold size will have no unaffected core habitat – so even though trees may still be standing, the core habitat may be eliminated

viii. Skole and Tucker extended their analysis of Brazilian deforestation to include edge effects –

a) including edge effects, they concluded that 588,000 km2 of forest had been affected by deforestation

b) note that that's more than double the area directly affected

c. Deforestation has additional consequences resulting from fragmentation of intact forest into more or less isolated patches:

i. large-scale deforestation often has the effect of simplifying landscape elements: process often results in

a) fewer different kinds of patches

b) patches that are, themselves, less complex than were originally present

ii. insularization (patches act as habitat islands): patches may lose species richness simply because of the effects of patch size and increased isolation from other patches

iii. competitive replacement by exotics: fragmentation often results in "corridors" of disturbed habitat that allow dispersal of exotics (including pests and pathogens) into patches, where they may outcompete "natives"

5. Specific results of deforestation will vary among forest types and regions, so predicting specific outcomes is very difficult – some of the reasons are
   a. variation expected due to differences in climate, forest type, surrounding habitat matrix
   b. variation resulting from differences in type of logging and post-logging practice
   c. our own lack of detailed information, especially in tropics and other remote areas