Chapter 55

Ecosystems

Lecture Outline

Overview: Observing Ecosystems

- An **ecosystem** consists of all the organisms that live in a community as well as all the abiotic factors with which they interact.
  - An ecosystem can encompass a large area, such as a forest, or a microcosm, such as the area under a fallen log.
  - Some ecologists view the entire biosphere as a global ecosytem.
- The dynamics of an ecosystem involve two processes that cannot be fully described by population or community phenomena: energy flow and chemical cycling.
- Energy enters most ecosystems in the form of sunlight, which is converted to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and dissipated as heat.
- Chemical elements are cycled among the abiotic and biotic components of the ecosystem.
  - Photosynthetic organisms assimilate chemical elements in organic form from the air, soil, and water, and incorporate them into their biomass.
  - Some of these chemical elements are consumed by animals.
  - The elements are returned in organic form to the environment by the metabolism of plants and animals and by decomposers such as bacteria and fungi, which break down organic wastes and dead organisms.
- Energy, unlike matter, cannot be recycled.
- An ecosystem must be powered by a continuous influx of energy from an external source, usually the sun.
- Energy flows through ecosystems, whereas matter cycles within and through them.

Concept 55.1 Physical laws govern energy flow and chemical cycling in ecosystems.

- Ecosystem ecologists view ecosystems as transformers of energy and processors of matter.
- We can follow the transformation of energy in an ecosystem and the movements of chemical elements through a community by grouping the species in a community into trophic levels of feeding relationships.

Ecosystems obey physical laws.

- The first law of thermodynamics states that energy cannot be created or destroyed but only transformed.

    - Plants and other photosynthetic organisms convert solar energy to chemical energy, but the total amount of energy does not change.
    - The total amount of energy stored in organic molecules plus the amounts reflected and dissipated as heat must equal the total solar energy intercepted by the plant.
- One area of ecosytem ecology computes such energy budgets and traces energy flow through ecosystems in order to understand the factors that control these energy transfers.
    - Transfers help determine how many organisms a habitat can support and the amount of food that humans can harvest from a site.
- The second law of thermodynamics states that every exchange of energy increases the entropy of the universe.
    - Some energy is lost as heat in any conversion process.
    - The efficiency of ecological energy conversions can be measured.
- According to the **law of conservation of mass**, matter, like energy, cannot be created or destroyed.
    - Because mass is conserved, we can determine how much of an element cycles within an ecosystem or is gained or lost by that ecosystem over time.
- Unlike energy, chemical elements are continuously recycled within ecosystems.
    - A carbon or nitrogen atom moves from one trophic level to another and eventually to the decomposers and back again.
- Chemical elements can move between ecosystems as inputs and outputs.
    - Nutrients enter a forest ecosystem as dust or as solutes dissolved in rainwater or leached from rocks in the ground.
    - Nitrogen is also supplied through the biological process of nitrogen fixation.
    - On the output side, gases return elements to the atmosphere and water carries materials away.
- Like organisms, ecosystems are open systems, absorbing energy and mass and releasing heat and waste products.
    - Most inputs and outputs are small compared to the amounts recycled within ecosystems.
- The balance between inputs and outputs determines whether an ecosystem is a source or a sink for an element.
    - If an element's outputs exceed its inputs, it will eventually limit production in that system.
- Human activities may change the balance of inputs and outputs considerably.

Trophic relationships determine the routes of energy flow and chemical cycling in ecosystems.

- Ecologists assign species to trophic levels on the basis of their main source of nutrition and energy.
- Autotrophs, the **primary producers** of the ecosystem, ultimately support all other organisms.
    - Most autotrophs are photosynthetic plants, algae, or prokaryotes that use light energy to synthesize sugars and other organic compounds.
    - Chemosynthetic prokaryotes are the primary producers in deep-sea hydrothermal vents.
- Heterotrophs are at trophic levels above the primary producers and depend on their biosynthetic output.

- Herbivores that eat primary producers are called **primary consumers**.
- Carnivores that eat herbivores are called **secondary consumers**.
- Carnivores that eat other carnivores are called **tertiary consumers**.
- Another important group of heterotrophs is the **detritivores**, or **decomposers**.
- Detritivores get energy from **detritus**, nonliving organic material such as the remains of dead organisms, feces, fallen leaves, and wood.
    - Many detritivores are in turn eaten by secondary and tertiary consumers.
- Two important groups of detritivores are prokaryotes and fungi.
- These organisms secrete enzymes that digest organic material and then absorb the breakdown products, linking the primary producers and consumers in an ecosystem.

Decomposition connects all trophic levels.

- Detritivores recycle chemical elements back to primary producers.
    - Detritivores convert organic materials from all trophic levels to inorganic compounds usable by primary producers, which then recycle these elements into organic compounds.
- If decomposition stopped, all life on Earth would cease as detritus piled up and the supply of chemical ingredients for the synthesis of new organic matter was exhausted.

Concept 55.2 Energy and other limiting factors control primary production in ecosystems.

- The amount of light energy converted to chemical energy by an ecosystem's autotrophs in a given time period is an ecosystem's **primary production**.

An ecosystem's energy budget depends on its primary production.

- Most primary producers use light energy to synthesize organic molecules, which can be broken down to produce adenosine triphosphate (ATP).
- The amount of photosynthetic production sets the spending limit of the entire ecosystem.
- A global energy budget can be analyzed.
- Every day, Earth's atmosphere is bombarded by approximately 10^{22} joules of solar radiation.
- The intensity of solar energy striking Earth varies with latitude, with the tropics receiving the greatest input.
- Most of this radiation is scattered, absorbed, or reflected by clouds and dust in the atmosphere.
- Much of the solar radiation that reaches Earth's surface lands on bare ground, bodies of water, or ice, which either absorb or reflect the energy.
- Only a small fraction of this solar radiation actually strikes algae, photosynthetic prokaryotes, or plants.
- Only certain wavelengths are absorbed by photosynthetic pigments; the rest is transmitted, reflected, or lost as heat.
- Thus, only about 1% of the visible light that reaches photosynthetic organisms is converted to chemical energy by photosynthesis.
- Despite this small amount, Earth's primary producers produce about 150 billion metric tons (150×10^{12} kg) of organic material per year.

- The total primary production in an ecosystem is known as **gross primary production (GPP),** the amount of light energy that is converted to chemical energy by photosynthesis per unit time.
- Plants use some of these molecules as fuel in their own cellular respiration.
- **Net primary production (NPP)** is equal to gross primary production minus the energy used by the primary producers for respiration (R):

  $$NPP = GPP - R$$

  - In many ecosystems, NPP is about half of GPP.
- To ecologists, net primary production is the key measurement because it represents the stored chemical energy that is available to consumers in the ecosystem.
  - Net primary production can be expressed as energy per unit area per unit time ($J/m^2 \cdot yr$), or as biomass of vegetation added to the ecosystem per unit area per unit time ($g/m^2 \cdot yr$).
  - Net primary production should not be confused with the *total* biomass of photosynthetic autotrophs present in a given time, which is called the *standing crop*.
  - Net primary production is the amount of *new* biomass added in a given period of time.
  - Although a forest has a large standing crop biomass, its primary production may actually be less than that of some grasslands, which do not accumulate vegetation because animals consume the plants rapidly and because grasses and herbs decompose more quickly than trees do.
- Different ecosystems vary greatly in their net primary production.
  - Tropical rain forests are among the most productive terrestrial ecosystems, and they contribute a large portion of Earth's overall net primary production.
  - Estuaries and coral reefs also have very high net primary production, but they cover only about one-tenth the area covered by tropical rain forests.
  - The open ocean has a relatively low production per unit area but contributes as much global net primary production as terrestrial systems because of its vast size.
- What limits primary production in ecosystems? What factors could we change to increase or decrease primary production for a given ecosystem?

In aquatic ecosystems, light and nutrients limit primary production.

- Light is a key variable controlling primary production in oceans and lakes because solar radiation can penetrate to only a certain depth known as the photic zone.
  - The first 15 m of water absorbs more than half of the solar radiation.
  - Even in "clear" water, only 5–10% of the radiation may reach a depth of 75 m.
- If light were the main variable limiting primary production in the ocean, we would expect production to increase along a gradient from the poles toward the equator, which receives the greatest intensity of light.
- There is no such gradient, however.
  - Some parts of the ocean in the tropics and subtropics exhibit low primary production, whereas some high-latitude ocean regions are relatively productive.
- More than light, nutrients limit primary production in aquatic ecosystems.
- A **limiting nutrient** is an element that must be added for production to increase in a particular area.
- The nutrient that most often limits marine production is either nitrogen or phosphorus.

    - Nitrogen and phosphorus levels are very low in the photic zone because these nutrients are rapidly taken up by phytoplankton and because detritus tends to sink.
    - Nutrient levels are higher in deeper water, where light does not penetrate.
- Nutrient enrichment experiments confirmed that nitrogen is limiting phytoplankton growth off the south shore of Long Island, New York.
    - This knowledge can be used to prevent algal blooms by limiting pollution that fertilizes phytoplankton.
    - Eliminating phosphates from sewage will not solve the problem unless nitrogen pollution is also controlled.
- Some areas of the ocean have low phytoplankton density despite their relatively high nitrogen concentrations.
    - For example, the Sargasso Sea has a very low density of phytoplankton.
    - Nutrient-enrichment experiments showed that iron availability limits primary production in this area.
    - Windblown dust from the land is the main input of iron to the ocean, but relatively little windblown dust reaches the centers of oceans.
- Marine ecologists carried out large-scale field experiments in the Pacific Ocean, spreading low concentrations of dissolved iron over 72 km^2 of ocean and measuring the change in phytoplankton density over a seven-day period.
- A massive phytoplankton bloom occurred, with increased concentrations in water samples from test sites.
    - Adding iron stimulates the growth of cyanobacteria that fix atmospheric nitrogen, and the extra nitrogen stimulates the proliferation of phytoplankton.
- In areas of upwelling, nutrient-rich deep waters circulate to the ocean surface.
- These areas have exceptionally high primary production, supporting the hypothesis that nutrient availability determines marine primary production.
    - Because the supply of available nutrients stimulates the growth of the phytoplankton populations that form the base of marine food webs, upwelling areas are prime fishing locations.
    - The largest areas of upwelling occur in the Southern Ocean (also called the Antarctic Ocean) and the coastal waters off Peru, California, and parts of western Africa.
- Nutrient limitation is also common in freshwater lakes.
- Sewage and fertilizer pollution can add large amounts of nutrients to lakes.
    - Cyanobacteria and algae grow rapidly in response to these added nutrients, ultimately reducing oxygen concentrations and visibility in the water.
    - This process is called **eutrophication** and has a wide range of ecological impacts, including the loss of most fish species.
- A series of whole-lake experiments identified phosphorus as the nutrient that limited cyanobacterial growth.
    - This research led to the use of phosphate-free detergents and other water quality reforms.

In terrestrial ecosystems, temperature and moisture are the key factors limiting primary production.

- Tropical rain forests, with their warm, wet conditions, are the most productive of all terrestrial ecosystems.

- By contrast, low-productivity ecosystems are generally dry (deserts) or dry and cold (arctic tundra).
- Between these extremes lie temperate forest and grassland ecosystems with moderate climates and intermediate productivity.
- These contrasts in climate can be represented by a measure called **actual evapotranspiration**, which is the annual amount of water transpired by plants and evaporated from a landscape.
    - Actual evapotranspiration increases with precipitation and the amount of solar energy available to drive evaporation and transpiration.
- On a more local scale, mineral nutrients in the soil can limit terrestrial primary production.
    - Nitrogen and phosphorus are the soil nutrients that most commonly limit terrestrial production.
- Adding more of a limiting nutrient to soil will increase production until some other nutrient becomes limiting.
- Studies relating nutrients to terrestrial primary production have practical applications in agriculture.
    - Farmers can maximize crop yields by using fertilizers with the right balance of nutrients for the local soil and type of crop.

Concept 55.3 Energy transfer between trophic levels is typically only 10% efficient.

- The amount of chemical energy in consumers' food that is converted to their own new biomass during a given time period is called the **secondary production** of an ecosystem.
    - In most ecosystems, herbivores eat only a small fraction of the plant material that is produced.
    - Moreover, herbivores cannot digest all the plant material that they *do* eat.
    - Thus, much of primary production is not used by consumers.
- We can measure the efficiency of animals as energy transformers using the following equation:

  Production efficiency = Net secondary production × 100% / Assimilation of primary production
    - Net secondary production is the energy stored in biomass represented by growth and reproduction.
    - Assimilation is the total energy taken in and used for growth, reproduction, and respiration.
- **Production efficiency** is thus the fraction of food energy that is *not* used for respiration.

Production efficiencies differ among organisms.

- Birds and mammals typically have low production efficiencies of 1–3% because they use so much energy to maintain a constant body temperature.
- Fishes, which are ectotherms, have production efficiencies of around 10%.
- Insects and microorganisms are even more efficient, with production efficiencies averaging 40%.
- **Trophic efficiency** is the percentage of production transferred from one trophic level to the next.
    - Trophic efficiencies must always be less than production efficiencies because they take into account not only the energy lost through respiration and contained in feces, but also the energy in organic material at lower trophic levels that is not consumed.

- Trophic efficiencies are generally about 10% and range from approximately 5% to 20%, depending on the type of ecosystem.
    - In other words, 90% of the energy available at one trophic level is typically not transferred to the next.
    - This loss is multiplied over the length of a food chain.
    - If 10% of energy is transferred from primary producers to primary consumers, and 10% of that energy is transferred to secondary consumers, then only 1% of net primary production is available to secondary consumers.

The progressive loss of energy along a food chain limits the abundance of top-level carnivores.

- Only about 0.1% of the chemical energy fixed by photosynthesis can flow all the way through a food web to a tertiary consumer, such as a snake or a shark.
- This limits most food webs to four or five trophic levels.
- *Pyramids of net production* represent the multiplicative loss of energy in a food chain.
    - The width of each tier in the pyramid is proportional to the net production of each trophic level, expressed in joules.
    - The highest level, which represents top-level predators, contains relatively few individuals.
    - Because populations of top predators are typically small and the animals may be widely spaced within their habitats, many predator species are highly susceptible to extinction.
- *Biomass pyramids* represent the ecological consequences of low trophic efficiencies.
    - Each tier represents the standing crop (the total dry mass of all organisms) in one trophic level.
    - Most biomass pyramids narrow sharply from primary producers to top-level carnivores because energy transfers are so inefficient.
- In some aquatic ecosystems, the biomass pyramid is inverted and primary consumers outweigh producers.
    - Such inverted biomass pyramids occur because the producers—phytoplankton—grow, reproduce, and are consumed by zooplankton so rapidly that they never develop a large standing crop.
    - Phytoplankton have a short **turnover time**, which means they have a small standing crop biomass compared to their production:

      Turnover time = Standing crop biomass (g/m^2) / Production ($g/m^2 \cdot day$)
    - Because phytoplankton replace their biomass at such a rapid rate, they can support a biomass of zooplankton much greater than their own biomass.
    - However, the *pyramid of net production* for this ecosystem is still bottom-heavy.
- The dynamics of energy flow through ecosystems have important implications for the human population.
- Eating meat is an inefficient way of tapping photosynthetic production.
- Worldwide agriculture could feed many more people if all humans fed as primary consumers, eating only plant material.
- Estimates of Earth's human carrying capacity depend greatly on our diet and on the amount of resources each of us consumes.

Herbivores consume a small percentage of vegetation: the green-world hypothesis.

- How green is our world?
  - 70×10^{10} metric tons of carbon are stored in the plant biomass of terrestrial ecosystems.
  - Global terrestrial primary production is about 6×10^{10} metric tons per year.
  - Herbivores annually consume less than one-sixth of the global net primary production.
  - Most of the rest is eventually consumed by detritivores.
- According to the **green-world hypothesis**, terrestrial herbivores consume relatively little plant biomass because they are held in check by a variety of factors.
  - Plants have defenses, such as spines or noxious chemicals.
  - Low nutrient concentrations in plant tissues force herbivores to process large quantities of biomass to extract small amounts of nutrients.
  - Abiotic factors such as temperature and moisture may limit the number of herbivores.
  - Biotic factors such as intraspecific competition, including territorial behavior, and interspecific competition, particularly from predators, parasites, and pathogens, may limit the growth of herbivore populations.

Concept 55.4 Biological and geologic processes cycle nutrients between organic and inorganic parts of an ecosystem.

- Chemical elements are available to ecosystems in only limited amounts.
- Life on Earth depends on the recycling of essential chemical elements.

Biogeochemical cycles involve both biotic and abiotic components of ecosystems.

- There are two general categories of **biogeochemical cycles:** global and local.
  - Gaseous forms of carbon, oxygen, sulfur, and nitrogen occur in the atmosphere, and cycles of these elements are global.
  - Elements such as phosphorus, potassium, and calcium are too heavy to occur as gases.
  - In terrestrial ecosystems, these elements cycle locally, absorbed from the soil by plant roots and eventually returned to the soil by decomposers.
  - In aquatic systems, these elements cycle more broadly as dissolved forms carried in currents.
- We will consider a general model of chemical cycling that includes the main reservoirs of elements and the processes that transfer elements between reservoirs.
- Each reservoir is defined by two characteristics: whether it contains organic or inorganic materials and whether or not the materials are directly available for use by organisms.
- **Reservoir a** includes the nutrients in living organisms and in detritus.
  - These nutrients are available to other organisms when consumers feed and when detritivores consume nonliving organic material.
- **Reservoir b** includes materials that move to the fossilized organic reservoir as dead organisms and are buried by sedimentation over millions of years.
  - Some fossilized organisms become coal, oil, or peat.
  - Nutrients in fossilized deposits cannot be assimilated directly but may move into the available reservoir of inorganic nutrients when fossil fuels are burned, releasing exhaust into the atmosphere.
- **Reservoir c** includes inorganic elements and compounds that are dissolved in water or present in soil or air.

- These materials are available for use by organisms.
- **Reservoir d** includes inorganic elements present in rocks.
  - These nutrients are not directly available for use by organisms, but they may gradually become available through erosion and weathering.
- Describing biogeochemical cycles in general terms is much simpler than trying to trace elements through these cycles.
- Ecologists study chemical cycling by adding tiny amounts of radioactive isotopes to the elements they are tracing and by following the movement of naturally occurring stable, nonradioactive isotopes through the various biotic and abiotic components of an ecosystem.

There are several important biogeochemical cycles.

- We will consider the cycling of water, carbon, nitrogen, and phosphorus.

The water cycle

- **Biological importance**
  - Water is essential to all organisms, and its availability influences the rates of ecosystem processes.
- **Biologically available forms**
  - Liquid water is the primary form in which water is used.
- **Reservoirs**
  - The oceans contain 97% of the water in the biosphere.
  - Two percent is bound as ice.
  - One percent is in lakes, rivers, and groundwater.
  - A negligible amount is in the atmosphere.
- **Key processes**
  - The main processes driving the water cycle are evaporation of liquid water by solar energy, condensation of water vapor into clouds, and precipitation.
  - Transpiration by terrestrial plants moves significant amounts of water.
  - Surface and groundwater flow returns water to the oceans.

The carbon cycle

- **Biological importance**
  - Organic molecules have a carbon framework.
- **Biologically available forms**
  - Autotrophs convert carbon dioxide to organic molecules that are used by heterotrophs.
- **Reservoirs**
  - The major reservoirs of carbon are fossil fuels, soils, aquatic sediments, the oceans, plant and animal biomass, and the atmosphere (CO_2).
- **Key processes**
  - Photosynthesis by plants and phytoplankton fixes atmospheric CO_2.
  - CO_2 is added to the atmosphere by cellular respiration of producers and consumers.
  - Volcanoes and the burning of fossil fuels add CO_2 to the atmosphere.

The nitrogen cycle

- **Biological importance**
  - Nitrogen is a component of amino acids, proteins, and nucleic acids.
  - Nitrogen may be a limiting plant nutrient.
- **Biologically available forms**
  - Plants and algae can use ammonium (NH_4^+) or nitrate (NO_3^-).
  - Various bacteria can use NH_4^+, NO_3^-, or NO_2.
  - Animals can use only organic forms of nitrogen.
- **Reservoirs**
  - The major reservoir of nitrogen is the atmosphere, which is 80% nitrogen gas (N_2).
  - Nitrogen is also bound in soils and the sediments of lakes, rivers, and oceans.
  - Some nitrogen is dissolved in surface water and groundwater.
  - Nitrogen is stored in living biomass.
- **Key processes**
  - Nitrogen enters ecosystems primarily through bacterial nitrogen fixation.
  - Some nitrogen is fixed by lightning and industrial fertilizer production.
  - *Ammonification* by bacteria decomposes organic nitrogen.
  - In *nitrification,* bacteria convert NH_4^+ to NO_3^-.
  - In *denitrification,* bacteria use NO_3^- for metabolism instead of O_2, thus releasing N_2.

The phosphorus cycle

- **Biological importance**
  - Phosphorus is a component of nucleic acids, phospholipids, and ATP and other energy-storing molecules.
  - Phosphorus is a mineral constituent of bones and teeth.
- **Biologically available forms**
  - The only biologically important inorganic form of phosphorus is phosphate (PO_4^{3-}), which plants absorb and use to synthesize organic compounds.
- **Reservoirs**
  - The major reservoir of phosphorus is sedimentary rocks of marine origin.
  - There are also large quantities of phosphorus in soils, dissolved in the oceans, and in organisms.
- **Key processes**
  - Weathering of rocks gradually adds phosphate to soil.
  - Some phosphate leaches into groundwater and surface water and moves to the sea.
  - Phosphate may be taken up by producers and incorporated into organic material.
  - Phosphate is returned to soil or water through decomposition of biomass or excretion by consumers.

Decomposition rates largely determine the rates of nutrient cycling.

- The rates at which nutrients cycle in different ecosystems are extremely variable as a result of variable rates of **decomposition**.

- Decomposition is controlled by the same factors that limit primary production in aquatic and terrestrial ecosystems: temperature, moisture, and nutrient availability.
- Decomposition takes an average of four to six years in temperate forests, whereas in tropical rain forests, most organic material decomposes in a few months to a few years.
    - The difference is largely due to the warmer temperatures and more abundant precipitation in tropical rain forests.
- In tropical rain forests, relatively little organic material accumulates as leaf litter on the forest floor. The woody trunks of trees contain 75% of the nutrients, and the soil contains 10%.
    - Thus, the relatively low concentrations of some nutrients in the soil of tropical rain forests result from a short cycling time, not from a lack of these elements in the ecosystem.
- In temperate forests, where decomposition is slower, the soil may contain 50% of the organic material.
    - The nutrients present in temperate forest detritus and soil may remain there for a long time before plants assimilate them.
- Decomposition on land slows when conditions are too dry for decomposers to thrive or too wet to supply them with enough oxygen.
    - Ecosystems that are both cold and wet, such as peat lands, store large amounts of organic matter.
    - Decomposers grow poorly most of the year there, and net primary production greatly exceeds decomposition.
- In aquatic ecosystems, decomposition in the anaerobic mud of bottom sediments can take 50 years or longer.
    - Algae and aquatic plants usually assimilate nutrients directly from the water.
    - Aquatic sediments may constitute a nutrient sink.
    - Interchange between the bottom layers of water and the surface increases aquatic productivity.

Nutrient cycling is strongly regulated by vegetation.

- Since 1963, Herbert Bormann and Gene Likens have been studying nutrient cycling in a forest ecosystem at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire.
    - The study site is a deciduous forest with several valleys, each drained by a small creek that is a tributary of Hubbard Brook.
    - Bedrock impenetrable to water is close to the surface of the soil, and each valley constitutes a watershed that can drain only through its creek.
- The research team first determined the mineral budget for each valley by measuring the input and outflow of several key nutrients.
    - They collected rainfall at several sites to measure the amount of water and dissolved minerals added to the ecosystem.
    - To monitor the loss of water and minerals, they constructed a small concrete dam with a V-shaped spillway across the creek at the bottom of each valley.
    - About 60% of the water added to the ecosystem as rainfall and snow exits through the stream, and the remaining 40% is lost by evapotranspiration.
- Preliminary studies confirmed that internal cycling within a terrestrial ecosystem conserves most of the mineral nutrients.

- Only about 0.3% more calcium (Ca^{2+}) left a valley via its creek than was added by rainwater, and this small net loss was probably replaced by chemical decomposition of the bedrock.
- During most years, the forest actually registered small net gains of a few mineral nutrients, including nitrogen.

- In one experiment, the trees in one valley were cut down and then the valley was sprayed with herbicides for three years to prevent regrowth of plants. All the original plant material was left in place to decompose.
- The inflow and outflow of water and minerals in this experimentally altered watershed were compared with those in a control watershed.
- Over the three years, water runoff from the altered watershed increased by 30–40%, with no plants to absorb and transpire water from the soil.
- Net losses of minerals from the altered watershed were huge.
  - The concentration of Ca^{2+} in the creek increased fourfold, for example, and the concentration of K^{+} increased by a factor of 15.
  - Most remarkable was the loss of nitrate, whose concentration in the creek increased 60-fold, reaching levels considered unsafe for drinking water.
- This study demonstrates that the amount of nutrients leaving an intact forest ecosystem is controlled mainly by the plants.
- The effects of deforestation occur within a few months and continue as long as living plants are absent.
- The 45 years of data from Hubbard Brook reveal other trends as well.
- In the last half-century, acid rain and snow have dissolved most of the Ca^{2+} in the forest soil, and the streams have carried it away.
- By the 1990s, the forest biomass at Hubbard Brook had stopped increasing, apparently because of a lack of Ca^{2+}.
- To test this idea, ecologists at Hubbard Brook began a massive experiment in 1998.
- They first established a control and an experimental watershed, which they monitored over two years before using a helicopter to add Ca^{2+} to the experimental watershed.
- By 2006, sugar maple trees growing in the Ca^{2+}-enriched location had higher Ca^{2+} concentrations in their foliage, healthier crowns, and greater seedling establishment than those growing in the control watershed.
- These data suggest that sugar maple declines in the northeastern United States and southern Canada are attributable at least in part to the consequences of soil acidification.
- The Hubbard Brook studies, as well as 25 other long-term ecological research projects funded by the National Science Foundation, assess natural ecosystem processes and provide important insight into the mechanisms by which human activities affect these processes.

Concept 55.5 Human activities now dominate most chemical cycles on Earth.

- Human activities and technologies have disrupted the trophic structure, energy flow, and chemical cycling of ecosystems worldwide.
- Human activities have greater influence on chemical cycles than natural processes do.

The human population moves nutrients from one part of the biosphere to another.

- Human activity intrudes in nutrient cycles.
    - Nutrients from farm soil may run off into streams and lakes, depleting nutrients in one area, causing excesses in another, and altering chemical cycles in both places.
    - Humans also add entirely new materials—some toxic—to ecosystems.
- In agricultural ecosystems, large amounts of nutrients are removed from the area as crop biomass.
- After a while, the natural store of nutrients can become exhausted.
    - Then the soil cannot be used to grow crops without nutrient supplementation.
- Nitrogen is the main nutrient lost through agriculture.
    - Plowing mixes the soil and increases the decomposition rate of organic matter, releasing usable nitrogen that is then removed from the ecosystem when crops are harvested.
    - Applied fertilizers make up for the loss of usable nitrogen from agricultural ecosystems.
    - As shown in the Hubbard Brook studies, without plants to take up nitrates from the soil, the nitrates are likely to be leached from the ecosystem.
- Recent studies indicate that human activities have approximately doubled the worldwide supply of fixed nitrogen, due to the use of fertilizers, cultivation of legumes, and fossil fuel combustion.
- A key measure of the amount of nitrogen in an ecosystem is the **critical load**, the amount of added nutrient that can be absorbed by plants without causing damage.
- Nitrogenous minerals in the soil that exceed the critical load eventually leach into groundwater or run off into freshwater and marine ecosystems, contaminating water supplies, choking waterways, and killing fish.
    - Nitrate concentrations in groundwater are increasing in most agricultural regions, sometimes exceeding safe levels for drinking.
- Agricultural runoff and sewage from northern Europe and the central United States contaminate many rivers that drain into the Atlantic Ocean.
    - The Mississippi River carries nitrogen pollution to the Gulf of Mexico, fueling a phytoplankton bloom each summer.
    - When phytoplanktons die, their decomposition creates an extensive “dead zone” of low oxygen availability along the coast.
    - Fish, shrimp, and other marine animals have disappeared from these economically important waters.
    - To reduce the size of the dead zone, farmers have begun using fertilizers more efficiently, and managers are restoring wetlands in the Mississippi watershed.
- Nutrient runoff can also lead to the eutrophication of lakes.
    - The bloom and subsequent die-off of algae and cyanobacteria in a lake and the depletion of oxygen are similar to what occurs in a marine dead zone.
- Eutrophication threatens the survival of organisms.
    - For example, eutrophication of Lake Erie coupled with overfishing wiped out commercially important fishes such as blue pike, whitefish, and lake trout by the 1960s.
    - Tighter regulations on waste dumping into the lake have enabled some fish populations to rebound, but many native species of fishes and invertebrates have not recovered.

Combustion of fossil fuels is the main cause of acid precipitation.

- The burning of fossil fuels releases oxides of sulfur and nitrogen that react with water in the atmosphere to produce sulfuric and nitric acids.
- These acids fall back to earth as acid precipitation—rain, snow, sleet, or fog with a pH less than 5.2.
- Acid precipitation lowers the pH of streams and lakes and affects soil chemistry and nutrient availability.
- Acid precipitation is a regional problem arising from local emissions.
    - The tall exhaust stacks built for smelters and generating plants export the problem far downwind.
    - In the 1960s, ecologists observed that organisms in eastern Canadian lakes were dying because of air pollution from factories in the midwestern United States.
    - Lakes and streams in southern Norway and Sweden were losing fish because of acid rain from pollutants generated in Great Britain and central Europe.
    - By 1980, the pH of precipitation in large areas of North America and Europe averaged 4.0–4.5 and occasionally dropped as low as 3.0.
- In terrestrial ecosystems, the change in soil pH due to acid precipitation causes calcium and other nutrients to leach from the soil. The resulting nutrient deficiencies limit the growth of plants.
- Acid precipitation can also damage plants directly, mainly by leaching nutrients from leaves.
- Freshwater ecosystems are particularly sensitive to acid precipitation.
    - Lakes with poor buffering capacity because of low bicarbonate levels are most vulnerable.
    - Fish populations have declined in many lakes in Norway, Sweden, and Canada, where pH levels have dropped below 5.0.
    - Lake trout, keystone predators in many Canadian lakes, die when the pH drops below 5.4.
    - When the fish are replaced by acid-tolerant species, the dynamics of food webs in the lakes change dramatically.
- Several large ecosystem experiments have been carried out to test the feasibility of reversing the effects of acid precipitation.
    - One is the Ca^{2+} addition experiment at Hubbard Brook.
    - Another is a 17-year experiment in Norway in which scientists built a glass roof over a forest and then showered the forest with precipitation from which acids had been removed.
    - This "clean" precipitation quickly increased the pH and decreased the nitrate, ammonium, and sulfate concentrations in stream water in the forest.
- Leaders of more than 40 European nations have signed a treaty to reduce air pollution.
- Environmental regulations and new industrial technologies have enabled many developed countries to reduce sulfur dioxide emissions during the past 40 years.
    - In the United States, sulfur dioxide emissions decreased 31% between 1993 and 2002.
    - As a result, precipitation in the northeastern United States is gradually becoming less acidic.
- Even if sulfur dioxide emissions continue to decrease, ecologists estimate that it will take decades for aquatic ecosystems to recover.
- Currently, emissions of nitrogen oxides in the United States are increasing, and emissions of sulfur dioxide and acid precipitation in central and eastern Europe continue to damage forests.

Toxins can become concentrated in successive trophic levels of food webs.

- Humans release many toxic chemicals, including thousands of synthetics previously unknown in nature.
- Organisms acquire toxic substances from the environment along with nutrients and water.
- Some of the poisons are metabolized and excreted, but others accumulate in specific tissues, especially fat.
- Fat-soluble toxins become more concentrated in successive trophic levels of a food web, a process called **biological magnification**.
    - Magnification occurs because the biomass at any given trophic level is produced from a much larger biomass ingested from the level below.
    - Thus, top-level carnivores tend to be the organisms most severely affected by toxic compounds in the environment.
- Chlorinated hydrocarbons, including the industrial chemicals called PCBs (polychlorinated biphenyls) and many pesticides, such as DDT, demonstrate biological magnification.
    - Many of these compounds disrupt the endocrine systems of a large number of animal species, including humans.
    - In the food web of the Great Lakes, the concentration of PCBs in herring gull eggs at the top of the food web is nearly 5,000 times the concentration in phytoplankton at the base of the food web.
- An infamous case of biological magnification that harmed top-level carnivores involved DDT, a chemical used to control insects such as mosquitoes and agricultural pests in the decade after World War II.
- By the 1950s, scientists were learning that DDT persists in the environment and is transported by water to areas far from where it is applied.
- One of the first signs that DDT was a serious environmental problem was a decline in the populations of pelicans, ospreys, and eagles, birds that feed at the top of food webs.
    - The accumulation of DDT (and DDE, a product of its partial breakdown) in the tissues of these birds interfered with the deposition of calcium in their eggshells.
    - When these birds tried to incubate their eggs, the weight of the parents broke the shells of affected eggs, resulting in catastrophic declines in their reproduction rates.
- Rachel Carson's book, *Silent Spring,* helped bring the problem to public attention in the 1960s, leading to the banning of DDT in the United States in 1971.
- After the ban, the populations of the affected bird species recovered. In the tropics, DDT is still used to control the mosquitoes that spread malaria.
    - Societies there face a trade-off between saving human lives and protecting other species.
    - The best approach seems to be to apply DDT sparingly and to couple its use with mosquito netting and other low-technology solutions.
- The complicated history of DDT illustrates the importance of understanding the ecological connections between diseases and communities.
- Many toxins that cannot be degraded by microorganisms persist in the environment for years or even decades.
- In other cases, chemicals released into the environment may be relatively harmless but are converted to more toxic products through reactions with other substances, by exposure to light, or by the metabolism of microorganisms.
    - For example, insoluble mercury has been routinely expelled into rivers and the sea.

- Bacteria in the bottom mud convert the waste to methylmercury, an extremely toxic soluble compound that accumulates in the tissues of organisms, including humans who consume fish from the contaminated waters.

Human activities may be causing climate change by increasing levels of atmospheric carbon dioxide.

- Since the Industrial Revolution, the concentration of CO_2 in the atmosphere has increased greatly as a result of burning fossil fuels and deforestation.
  - Before 1850, the average CO_2 concentration in the environment was 274 ppm.
  - Measurements in 1958 read 316 ppm and have increased to 380 ppm today.
- If CO_2 emissions continue to increase at the present rate, the atmospheric concentration of CO_2 will more than double from the start of the Industrial Revolution to 2075.
- Increased productivity by vegetation is one consequence of increasing CO_2 levels.
- Because C_3 plants are more limited than C_4 plants by CO_2 availability, one effect of increasing CO_2 levels may be the spread of C_3 species into terrestrial habitats previously favoring C_4 plants.
  - For example, corn may be replaced on farms by wheat and soybeans.
- To assess the effect of rising levels of atmospheric CO_2 on temperate forests, scientists at Duke University began the Forest-Atmosphere Carbon Transfer and Storage (FACTS-I) experiment in 1995.
- The FACTS-I study is testing how elevated CO_2 levels influence tree growth, carbon concentration in soils, insect populations, soil moisture, understory plant growth, and other factors over a ten-year period.
  - After ten years, trees in the experimental plots (with elevated CO2 levels) produced about 15% more wood each year than those in the control plots. This increased growth is far lower than predicted from the results of greenhouse experiments.
- The availability of nitrogen and other nutrients apparently limits the ability of the trees to use the extra CO_2.
  - Researchers at FACTS-I began removing this limitation in 2005 by fertilizing half of each plot with ammonium nitrate.
- In most of the world's ecosystems, nutrients limit ecosystem productivity and fertilizers are unavailable.
- The results of FACTS-I and other experiments suggest that increased atmospheric CO_2 levels will increase plant production somewhat, but far less than scientists predicted even a decade ago.

Rising atmospheric CO_2 levels are changing Earth's heat budget.

- When light energy hits Earth, much of it is reflected off the surface.
- Water vapor, CO_2, and other greenhouse gases are transparent to visible light, but they intercept and absorb infrared light, reflecting some of it back toward Earth.
- This process retains solar heat, producing the **greenhouse effect**.
  - If it were not for the greenhouse effect, the average air temperature on Earth would be −18°C.
- The increasing concentration of atmospheric CO_2 is a great concern because of its link to increased global temperature.
- For more than a century, scientists have studied how greenhouse gases warm Earth and how burning fossil fuels could contribute to the warming.

- Most environmental scientists are convinced that such warming has already begun and will increase rapidly during this century.
- Global models predict that by the end of the 21st century, the atmospheric CO_2 concentration will more than double and the average global temperature will rise by 3°C.
    - A correlation between CO_2 levels and temperatures in prehistoric times supports these models.
    - Climatologists estimate past CO_2 concentrations by measuring CO_2 levels in bubbles trapped in glacial ice, some of which are half a million years old.
    - Prehistoric temperatures are inferred by several methods, including analysis of past vegetation based on fossils and the chemical isotopes in sediments and corals.
- An increase of only 1.3°C would make the world warmer than at any time in the past 100,000 years.
- The ecosystems where the greatest warming has *already* occurred are those in the far north, particularly northern coniferous forests and tundra.
    - As snow and ice melt and uncover darker, more absorptive surfaces, these systems reflect less radiation back to the atmosphere and warm further.
    - Arctic sea ice in the summer of 2005 covered the smallest area on record.
    - There may be no summer ice in the Arctic by the end of this century, decreasing habitat for polar bears, seals, and seabirds.
- Higher temperatures increase the likelihood of fires.
    - In boreal forests of western North America and Russia, fires have burned twice the usual area in recent decades.
- A warming trend would also alter the geographic distribution of precipitation, making major agricultural areas of the central United States much drier.
- Various mathematical models disagree about the details of how the climate in each region will be affected.
- By studying how *past* periods of global warming and cooling affected plant communities, ecologists are trying to predict the consequences of *future* temperature changes.
    - Analysis of fossilized pollen indicates that plant communities change dramatically with changes in temperature.
    - However, past climate changes occurred gradually, and plant and animal populations could migrate into areas where abiotic conditions allowed them to survive.
    - Many organisms, especially plants that cannot disperse rapidly over long distances, may not be able to survive the fast rates of climate change projected to result from global warming.
    - Furthermore, many habitats today are much more fragmented than they were in the past, further limiting the ability of many organisms to migrate.
- Quick progress to slow global warming can be made by using energy more efficiently and by replacing fossil fuels with renewable solar and wind power and, more controversially, with nuclear power.
- Stabilizing CO_2 emissions will require concerted international effort and the acceptance of changes in both personal lifestyles and industrial processes.
- Many ecologists think this effort suffered a major setback in 2001, when the United States pulled out of the Kyoto Protocol, a 1997 pledge by industrialized nations to reduce their CO_2 output by 5% over a ten-year period.

Human activities are depleting atmospheric ozone.

- Life on Earth is protected from the damaging effects of ultraviolet (UV) radiation by a layer of O_3, or ozone, in the lower stratosphere.
- Studies suggest that the ozone layer has been gradually "thinning" since 1975.
- The destruction of ozone results mainly from the accumulation of CFCs (chlorofluorocarbons)—chemicals used in refrigeration and in manufacturing processes.
  - The breakdown products from these chemicals rise to the stratosphere, where the chlorine they contain reacts with ozone to reduce it to O_2.
  - Subsequent reactions liberate the chlorine, allowing it to react with other ozone molecules in a catalytic chain reaction.
- The thinning of the ozone layer is most apparent over Antarctica in the spring, where cold, stable air allows the chain reaction to continue.
  - Scientists first described the "ozone hole" over Antarctica in 1985.
  - The magnitude of ozone depletion and the size of the ozone hole have generally increased in recent years.
  - The hole sometimes extends as far as the southernmost portions of Australia, New Zealand, and South America.
- At middle latitudes, ozone levels have decreased by 2–10% during the past 20 years.
- As a result of decreased ozone levels in the stratosphere, increased amounts of UV radiation are reaching the surface of Earth.
- The consequences of ozone depletion for life on Earth may be severe for plants, animals, and microbes.
  - Some scientists expect increases in the incidence of skin cancer and cataracts, as well as unpredictable effects on crops and natural communities, especially phytoplankton.
- Ecologists have conducted field experiments in which they used filters to decrease or block natural UV rays.
  - An experiment performed on a scrub ecosystem near the tip of South America showed that, when the ozone hole passed over the area, the amount of UV radiation reaching the ground increased sharply, causing DNA damage in plants that were not protected by filters.
  - Scientists have shown similar DNA damage and less phytoplankton growth when the ozone hole opens over the Southern Ocean each year.
- The good news about the ozone hole is how quickly many countries responded to it.
  - Since 1987, approximately 190 nations, including the United States, have signed the Montreal Protocol, a treaty that regulates the use of ozone-depleting chemicals.
  - Many nations, again including the United States, have ended the production of chlorofluorocarbons.
- As a consequence of these actions, chlorine concentrations in the stratosphere have stabilized and ozone depletion is slowing.
  - Even if all chlorofluorocarbons were globally banned today, however, the chlorine molecules that are already in the atmosphere would continue to influence stratospheric ozone levels for at least 50 years.
- Destruction of Earth's ozone shield is one more example of how much humans have been able to disrupt the dynamics of ecosystems and the biosphere.
- It also highlights our ability to solve environmental problems.