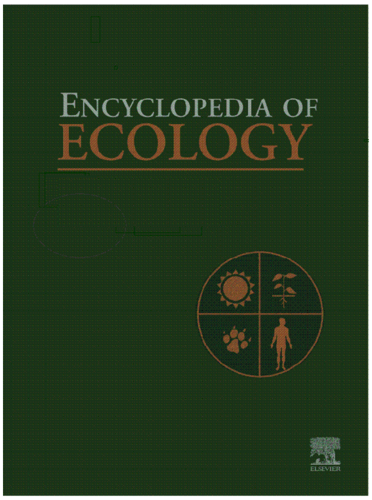

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Temperate Forest

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Introduction

The temperate forest biome is characterized by a distinct seasonality that includes a long growing season together with a cold winter season in which much of the vegetation may be dormant. The strong seasonality drives physiological events to occur at regular annual intervals for plant species. These include bud break, flowering, and foliar and shoot extension. As the growing season ends, marked by dropping temperatures and shortening photoperiod (day length), trees and shrubs undergo seasonal physiological changes that include the senescence and abscission of foliage (although in evergreen species some foliage is also retained) and the setting of buds for the next growing season. Because of the cold winters, the dominant woody vegetation is characterized by freeze-hardy species. During the winter season, the air temperature drops below freezing and soils are frozen or cold and wet, impeding decomposition of plant litter and promoting the accumulation of an organic layer on the soil surface.

The temperate forest is distributed over portions of five regions of the globe: North America, South America, Europe, Asia, and Australia–New Zealand (Figure 1). Within this biome, distinct biogeographic units are recognized, particularly the mixed-deciduous temperate forest (the largest in terms of area), the mixed-evergreen temperate forest (sometimes called subtropical evergreen), and the temperate rainforest. Major taxa include pines (*Pinus* spp.), maples (*Acer* spp.), beeches (*Fagus* spp., *Nothofagus* spp.), and oaks (*Quercus* spp.) in the mixed-deciduous and mixed-evergreen temperate forests; spruces (*Picea* spp.), Douglas-fir (*Pseudotsuga menziesii*), and redwoods (*Sequoia sempervirens*, *Sequoiadendron giganteum*) in the Northern Hemisphere temperate rainforests;

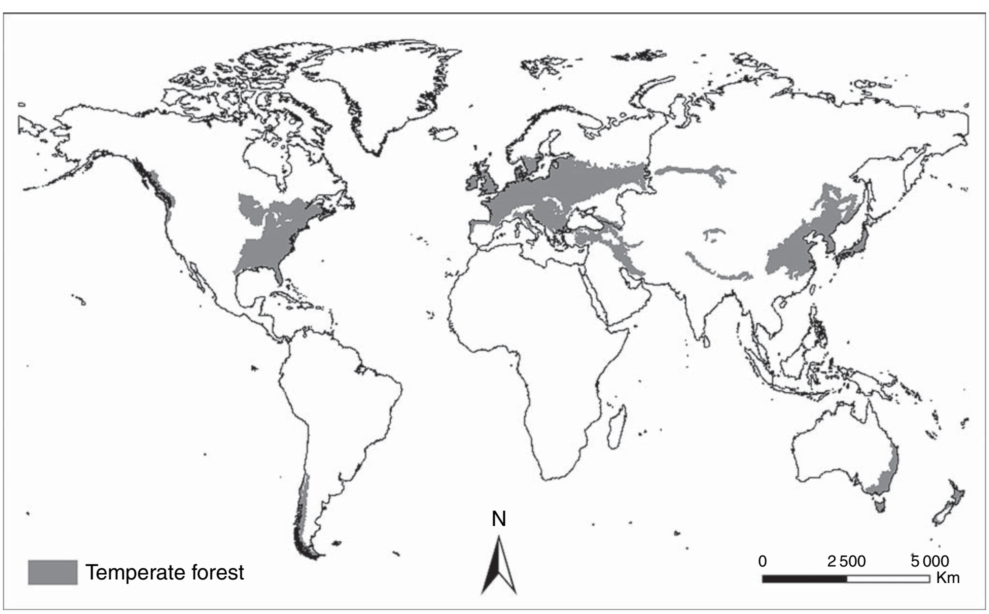

Figure 1 The distribution of temperate forests of the world. Map data: Olson DM, Dinerstein E, Wikramanayake ED *et al*. (2001) Terrestrial ecoregions of the world: A new map of life on earth, *BioScience* 51: 933–938. Map prepared by the Environmental Spatial Analysis Laboratory, University of Michigan, USA, 2006.

and southern beeches (*Nothofagus* spp.) and eucalyptus (*Eucalyptus* spp.) in Southern Hemisphere temperate rainforests.

Within a continent, forests in the temperate biome grade into subdivisions based on latitude, elevation, and large-scale patterns of precipitation. In North America, for example, the predominant natural vegetation in the eastern United States and the southern reaches of eastern Canada is mixed-deciduous temperate forest. This forest grades to the south through broad-leaved-coniferous mixtures to the mixed-evergreen forest along the Atlantic coastal plain (**Figure 2**). Temperate rainforests in North America are found in the coastal Pacific Northwest where marine climates together with orographic lifting produce high rainfall. In South America temperate forests are found in Chile and parts of Patagonia. In Europe, within the temperate forest biome the mixed-deciduous forests dominate in the western continent, Great Britain, southern Eastern Europe, and southern European Russia. In Near-East Asia, the temperate forest occurs in Turkey and Iran and a narrow band is found in Central Asia as a transition between the boreal forest to the north (see Boreal Forest) and steppe to the south. The temperate forests in East Asia occur predominantly in northern and central China, but also over most of Japan, Korea, and of the southern tip of Siberia. Temperate forests, including rainforests, are also found in parts of New Zealand, the southeast coast of Australia, and Tasmania.

Temperate forests are distinguished from boreal forests by having a 4–6-month (140–200 days) frost-free growing season with on average at least 4 months at 10 °C or above and mean annual temperatures from 5 °C to 20 °C. At higher latitudes, the temperate forest transitions to the boreal forest (see Boreal Forest), a biome of evergreen cold-tolerant forests with much shorter growing seasons.

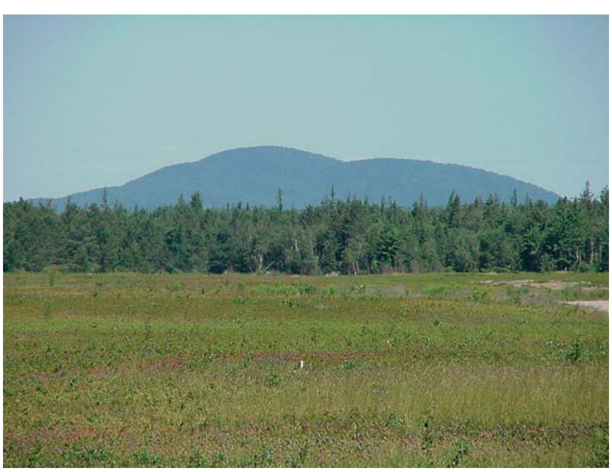

Figure 2 The edge of a mixed coniferous–deciduous forest in southeastern Maine, USA. Photo by W. S. Currie.

The latter are also found in middle latitudes as montane forests at high elevations and are often closer, floristically and functionally, to boreal than to temperate forests.

The occurrence of frost (at 0 °C or colder) differentiates the extratropical (including temperate) from tropical regions (see Tropical Rainforest and Tropical Seasonal Forest). Moisture also distinguishes temperate regions from drier forested regions, such as chaparral (see Chaparral) and wetter forested regions such as tropical rainforests (see Tropical Rainforest). In temperate regions, precipitation exceeds potential evaporation and water is available at approximately 50–200 cm yr^{-1}. Precipitation in most temperate regions is fairly evenly distributed throughout the year in contrast to the tropics where there are typically pronounced wet and dry seasons.

Physiography, Climate, and the Temperate Forest Biome

Climatic and Physiographic Controls on the Distribution of Temperate Forests

The geographic distributions of the different vegetation biomes of the world are dependent on the physical environment and climate in the form of light, temperature, and moisture. In middle latitudes (30°–60° N and S), these controls result in a temperate forest biome within each hemisphere that is discontinuous, separated by the oceans and the tropics, and by moisture and physiographic barriers. The present-day distribution of temperate forests derives not only from present climatic controls but also from paleoclimates and past connections among the continents. Climates during the Pleistocene (*c.* 1.8 million to 10 000 years ago) set the stage for the present-day distribution. During glacial maxima, ice sheets covered large parts of Europe and North and South America as well as isolated areas in East Asia. In North and South America, plants migrated to unglaciated refugia and re-migrated, as glaciers receded, to their present-day distributions. Evidence suggests that many genera of forest trees that remain in North America and unglaciated East Asia were extirpated from Europe because the east–west running Alpine range blocked migrations to refugia during Pleistocene glaciations. Similarly important were continental connections between North America (the Nearctic), East Asia, and Europe (the Palearctic) at different points in geologic history. As a result, floristic differences are relatively small across the Holarctic, which spans from the west coast of North America to the east coast of Asia and includes the majority of the world's temperate forests.

Temperate forests occur across a wide range of local physiographic landforms, from rocky slopes to rolling plains and river floodplains, although generally under non-extreme physiographic conditions. Trees that occupy slopes or well-drained substrates with low organic matter such as sandy outwash plains (e.g., pines and some oaks) are adapted for drier (xeric) sites low in nutrients. Trees adapted for moderate (mesic) sites are found on plains, glacial moraines, or low hills with greater stocks of soil organic matter. Nutrient- and moisture-demanding broad-leaved species, for example, maples and beeches, thrive in mesic landscapes. Trees occupying river floodplains, wetlands, or bogs have environments that can be very moist to wet (wet-mesic to hydric). These soils are relatively rich in organic matter but trees in these landscapes must be adapted to withstand flooding, including long periods with wet, anoxic soils with low nutrient availability.

Climatic and Physiographic Subdivisions

Given the great geographic extent of temperate forests it is not surprising that regional differences are observed. Systematic classifications of ecoregions and climates describe subdivisions within the biome (**Table 1**). The extensive temperate mixed-deciduous forest occurs primarily in Bailey's warm continental division (210), hot continental division (220), and marine division (240); these are Köppen–Trewartha classes *Dcb*, *Dca*, *Do,* and *Cf.* The warm continental division has snowy cold winters, while the hot continental division has warmer, wetter summers and milder winters. In the marine division (240) winters are mild, summers relatively cool, and precipitation occurs most of the year.

The temperate mixed-evergreen forests occur primarily in Bailey's temperate and rainy subtropical division (230) which is most analogous to the Köppen–Trewartha mid- and lower-latitude *Cf* (humid subtropical) class (**Table 1**). These climates have no dry season, with even the driest months having at least 30 mm of rain, and have hot summers with the average temperature of warmest month greater than 22 °C.

Temperate rainforest conditions largely occur where ocean moisture is abundant and prevented from moving inland by mountain ranges. These conditions occur in particular continental placements within Bailey's marine division (240) and Köppen–Trewartha *Do* class in higher latitudes and within Bailey's subtropical division (230) and Köppen–Trewartha *Do* and *Cf* classes in lower latitudes (**Table 1**).

Disturbance and Forest Structure

Major disturbances occur naturally in temperate forests, although particular locations vary in the types, frequencies, and severities of disturbance. Major natural disturbances include fires, windthrow during severe storms, ice storms, flooding, disease, and irruptions of defoliating or wood-boring insects. The array of natural disturbances that occur at a particular location constitutes its disturbance regime, a strong force in shaping forest structure and composition. Smaller-scale disturbances also shape forests over long time periods in the absence of a major disturbance. These include the production of

Table 1 Temperate forest biome types and corresponding geographic regions, Bailey ecoregions, and Köppen–Trewartha climate classes

Temperate forest type	*Geographic region*	*Bailey ecoregion*	*Köppen–Trewartha[a] climate class*
Temperate mixed-deciduous forest	• Eastern North America • Asia • Europe • South America • Australia/New Zealand	Humid temperate domain (200) • Warm continental division (210) • Hot continental division (220) • Marine division (240)	*Dcb*: Temperate continental, cool summer *Dca*: Temperate continental, warm summer *Do*: Temperate oceanic *Cf*: Humid subtropical
Temperate mixed-evergreen forest	• Southeast North America • Asia • South America • Australia/New Zealand	Humid temperate domain (200) • Subtropical division (230)	*Cf*: Humid subtropical
Temperate rainforest	• Northwestern North America • South America • Southeast Australia/New Zealand	Humid temperate domain (200) • Marine division (240)	*Cf*: Humid subtropical *Do*: Temperate oceanic

[a]*Dc*: Temperate continental: 4–7 months above 10 °C, coldest month below 0 °C; *Cf*: Humid subtropical: 8 months 10 °C, coldest month below 18 °C, no dry season; *Do*: Temperate oceanic: 4–7 months above 10 °C, coldest month above 0 °C.

forest gaps from the mortality of one to a few large trees. In some cases, idiosyncratic combinations of processes may produce repeated disturbance. An example is 'fir waves' that occur only in Japan and the northeastern US. In these waves of mortality that pass through the forest repeatedly, a fungal pathogen weakens the roots in mature trees while wind gusts cause the weakened roots to break as they rub against sharp gravel in the rocky soil. Because of the repetitive nature of natural disturbances and the long lifetimes of temperate forest trees, trees are often adapted (through what is termed 'vital attributes') to withstand particular disturbances or to regenerate following disturbance. Some examples are trees that re-sprout from stumps following fire or from branches following windthrow, cones that require fire to open, and seeds that germinate best on exposed soil.

Human activities have substantially altered the disturbance regimes in many temperate forests. The large-scale harvesting of trees for timber, whether cutting selected sizes or species of trees or cutting all of the trees in a stand, are relatively new forms of disturbance that now affect forest structure and community composition throughout much of the temperate biome. Human activities also cause large-scale chronic disturbances, including polluted rainfall (e.g., acid rain) that causes soil acidification and nitrogen enrichment over large regions of the US, Western Europe, and increasingly in eastern Asia. Still another category of human-induced disturbance is in the introduction of invasive species. In the eastern US, the introduction of a fungal pathogen in the early twentieth century caused the chestnut blight, essentially eradicating one of the dominant trees (the American chestnut, *Castanea dentata*) from a large region.

Structural Layers of Vegetation

Disturbances in temperate forests vary not only in their type and frequency but also in their intensity or severity, the latter gauged by the percentage of vegetation mortality. A major disturbance that causes widespread or near total mortality of trees in a forest stand, followed by the development of a new (secondary) forest stand, is known as a stand-initiating event. Following such an event, but mediated by the occurrence and severities of subsequent disturbances, the vertical structure of a forest stand tends to grow more complex over time. More favorable site conditions such as organic-rich, fertile soils and ample moisture also promote structural complexity. With full development, the vertical structure includes a canopy overstory, understory, a shrub layer, and an herbaceous layer. In achieving such development the forest passes through several stages. These include a stand initiation stage in which seedlings and saplings dominate and new species may continue to arrive; a stem exclusion stage in which the canopy closes, shading out shorter individuals; an understory re-initiation stage in which shade-tolerant species grow as seedlings and saplings; and finally an old-growth or steady-state stage. In the old-growth stage, the overstory typically includes both canopy dominants and subdominants (the latter with crowns only partially in sunlight) together with understory and shrub layers made up of mature, shade-tolerant individuals. Old-growth stands can be identified through a few key characteristics, including a distribution of age and size classes of trees, the absence of saw-cut stumps, and the presence of decaying logs the size of overstory trees.

The understory in a structurally complex temperate forest stand comprises trees and shrubs that spend their entire life cycle there as well as young or suppressed individuals of potential canopy-dominant species. Understory-tolerant species are those that can survive in, or even require, the shade of a forest canopy (e.g., sugar maple, *Acer saccharum*). In old-growth stands or those not recently disturbed it is common to see shade-tolerant species in both the understory and overstory because the overstory trees are those that regenerated in the shade of the canopy. Some temperate forests have a dense layer of understory shrubs, for example *Kalmia* spp., *Rhododendron* spp., and *Vaccinium* spp. (blueberry). The herbaceous layer of a temperate forest commonly contains mosses, lichens, vines, and forbs. Many shrubs and herbs are adapted to low-light environments or grow before canopy leaf extension in the spring or after overstory leaf abscission in fall; in summer only about 10% of full sunlight reaches the herbaceous layer, but this figure can rise to 70% in deciduous stands in winter. Shrubs and herbs that require more light grow in well-lighted gaps or extend their crowns into openings. Vines grow into forest canopies to access light and may be plentiful following a disturbance that kills canopy trees but leaves the dead trees standing.

Soils and Woody Debris

Soils provide a physical rooting medium, the capacity to store and release water, and the capacity to store and release nutrients for growing trees. The soils of the temperate forest regions occur in five orders of the system of soil taxonomy, namely Spodosols, Alfisols, Ultisols, Entisols, and Inceptisols. They range from somewhat infertile (Spodosols) to quite fertile (Alfisols). Spodosols are characterized by a heavily leached surface mineral horizon and a deeper accumulation of Al and Fe-rich organomineral complexes. Spodosols form under coniferous or mixed forests in relatively cool regions with substantial hydrologic leaching, particularly at the northern borders of the biome in the Northern Hemisphere. Further toward the subtropical in cooler areas of eastern North America, Europe, and parts of

Asia and Australia, Alfisols form, characterized by organic-rich mineral soil horizons throughout the soil profile, moderate leaching and high fertility. Ultisols, the oldest and most highly weathered soils in temperate zones, are located in the unglaciated and warmer portions of the biome, including southern North America, Asia, Australia, and New Zealand. Because of their advanced age and weathering, these can be deep soils with relatively poor fertility. Inceptisols and Entisols, the youngest soils characterized by less weathering and poor horizon development, are widely distributed in temperate forests. In particular, these form in areas where glaciers left behind new parent material either as till or outwash.

A characteristic that distinguishes temperate from tropical forest soils is the much larger stores of soil organic matter typically present in temperate soils. In temperate regions, litter in various stages of decomposition from fresh litter to humified matter often accumulates atop the mineral soil, forming the forest floor. This organic layer is key in retaining water, retaining and releasing nutrients, and providing animal habitat. It varies in thickness from a few centimeter to tens of centimeters, depending on the age of the stand, the soil pH, the inherent decomposability of the species of litter, the amount of rainfall, and the presence or absence of earthworms.

An additional important category of organic detritus found in many temperate forests is coarse woody debris. This includes standing dead trees and downed, decomposing logs. Rotting woody debris provides a rooting medium, a habitat for soil fauna, a substrate for the saprotrophic flow of energy to the food web, and a means for returning nutrient elements to soils, as well as important structural material for forest streams. Logs undergo a wide range of decay rates, from relatively rapid (a few years) where logs are small and wetting–drying cycles are rapid, to very slow (lasting to a century) where logs are large and the environment is wet and cool. In harvested or managed forests, coarse woody debris may be absent because logs are removed for timber. In unmanaged temperate forests, the long time periods needed for large logs to be produced and decomposed produces a U-shaped curve in the mass of woody debris over time (Figure 3). After a stand-initiating disturbance, woody debris from the previous stand accumulates rapidly and then decays slowly. A lag time of several decades typically exists before woody debris from the new stand begins to accumulate. If the new stand remains even-aged, a second peak may occur as the new stand passes through the stem exclusion stage of development and widespread mortality occurs in smaller trees that compete unsuccessfully for light after the canopy has closed.

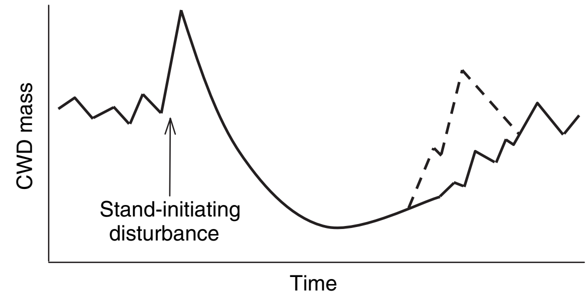

Figure 3 Dynamics in the mass of coarse woody debris (CWD) before, during, and after a major stand-initiating disturbance in a temperate forest. The solid line represents a U-shaped curve in CWD mass over time. The dashed line represents a secondary peak that may occur if the newly initiated stand remains even-aged and undergoes a self-thinning stage.

Ecological Communities and Succession

Vegetation Communities

Temperate forest vegetation communities span the range from single-species stands to mixed-species stands as well as the range from even-aged to all-aged stands. Which type of community is present at any point in space and time depends on the site physiography, soil, and climate together with its disturbance history. Species such as pines, eucalyptus, cottonwoods (*Populus* spp.), and others may form natural single-species, even-aged stands (Figure 4). Pioneer species such as aspens (*Populus* spp.) and some pines may initially form even-aged monocultures which eventually diversify in composition and vertical structure as growth, self-thinning, or succession proceeds. Long-lived hardwoods and other conifers also form stands where, increasingly with forest age, great diversity exists in tree ages and sizes. An example of the latter are hemlock-northern hardwood forests of the Great Lakes region of the United States. If horizontal structure and heterogeneity are taken into account, small patch mosaics of even-aged forests of varying ages form larger landscapes of mixed-aged stands, known at the landscape scale as a shifting-mosaic steady state.

It is easy to observe apparent associations of forest trees that occur at certain scales, for example old-growth hemlock–sugar maple (*Tsuga canadensis–Acer saccharum*) stands that form at the scale of square kilometers, or the oak–hickory (*Quercus–Carya*) associations that form more loosely in secondary forests over hundreds of thousands of square kilometers. However, a longstanding debate concerns whether forest communities represent organized associations or simply continuously varying associations as tree species respond individualistically to environmental gradients.

Temperate forest tree species form apparent associations with one another and with the abiotic environment not only across space but also over time at a particular

Figure 4 The canopy of an even-aged red pine plantation, aged about 75 years, in Massachusetts, USA. Photo by W. S. Currie.

location. A key organizing principle in understanding such temporal associations is the concept of succession, or the replacement of one dominant species or set of dominant species with another, over time, on a particular soil. Primary succession refers to the replacement of species over time occurring in the first forest stand to grow on a newly exposed soil, for example, following the retreat of a glacier. Secondary succession refers to species replacement over time following a major disturbance such as massive windthrow, mortality, or forest harvest. Early-successional species, termed pioneers, are those that are able to fix nitrogen from the atmosphere (see the section titled Nutrient cycling) or those that grow rapidly under high-light conditions but cannot tolerate shade. Late-successional forest species are typically those that can tolerate low-light or low-nutrient conditions as understory trees, while continuing to grow over long time periods, eventually reaching the overstory. Forest ecologists have long sought general principles of succession – for example, the identification of a deterministic sequence leading to a particular stable endpoint or 'climax' vegetation community in a particular climate and physiographic landform. Current understanding, however, emphasizes that while certain successional mechanisms exist, the particular sequences and possible endpoints of succession at a particular location are typically numerous, ultimately depending on a complex interplay among competition, species arrival, regeneration, disturbance regimes, and species' modification of the environment.

Temperate Forest Fauna

Faunal biodiversity in temperate forests is not as great as that in tropical forests (see Tropical Rainforest), but is greater than in boreal forests (see Boreal Forest). Because temperate forests are highly seasonal in their climate and cycles of vegetation physiology and production, faunal life cycles, ecology, and populations are often tied strongly to the seasons. Animal habitats within temperate forests are numerous and heterogeneous, including soils, the forest floor, woody debris, woody stems, and the layers of vegetation canopies. Although some animals depend on particular tree species, many are more dependent on certain aspects of forest structure.

In the temperate forest, the greatest concentration of fauna is on and just below the forest floor, in the litter, humus, and soil. Animals not only inhabit these strata, but through their activities drive soil carbon and nutrient cycling. Also within these strata are gradients of moisture, temperature, gases, and organic matter. Soil microhabitats are pore spaces, water film on soil particles, plant remains, the rhizosphere, and tunnels and burrows. Together, soil fauna and saprophytic flora contribute to the decomposition of organic matter. While most decomposition and nutrient release take place in the warm, humid summers, coinciding with the growing season of the vegetation, microorganisms and invertebrates can remain active below the insulating winter snowpack. Some animals occupy the litter in summer and move to the mineral soil in winter.

Because of the moist soil conditions, many temperate forest floors are home to reptiles (turtles and lizards) and amphibians (toads, frogs, newts, and salamanders). In the mixed-deciduous temperate forests there are over 230 species of reptiles and amphibians. These animals live on the forest floor close to streams, depressions, or lakes where there is available moisture. Lizards are found in moist woods and also in disturbed areas. Turtles live in or near bodies of water and toads and frogs are widespread, needing only shallow water. Temperate forest streams and rivers can support abundant fish populations, particularly under less-disturbed conditions and in coastal temperate rainforests.

Mammal populations in temperate forests tend to be comprised of scattered individuals or groups, and their habitat ranges from the forest floor to the canopy layers. Examples of small mammals are squirrels, rabbits, mice, chipmunks, skunks, and bats. Very large mammals are the exception and in temperate forests may include bear, mountain lions, deer, and other ungulates such as moose and elk. These mammals depend on the herb and shrub layers of the forest in addition to the litter and woody debris for food and habitat. Edge areas form transition zone habitats; for example, deer and other large animals usually live near the edges of forest openings with the trees providing shelter while edible ground vegetation is available in the openings all year.

Trunks are also habitats for spiders, beetles, and slugs. Birds are especially versatile across habitat structures; they are found on the forest floor and in several of the vegetation layers depending on nesting and foraging preferences. Types of birds that breed in mixed-deciduous forests include bark foragers (woodpeckers, flickers), canopy gleaners and pursuers (chickadee, vireo, flycatchers), ground species (thrushes, ovenbirds), and warblers. Deciduous forest are also breeding habitat for larger avian species including turkeys, vultures, owls, and hawks. In addition, moths, butterflies, and other flying insects feed and reproduce in the canopy, the understory, and the forest floor.

Water and Energy Flow, Nutrient Cycling, and Carbon Balance

Water, Evapotranspiration, and Energy

Water enters temperate forests as rainfall, snowfall, fog, and the direct condensation of water vapor onto plant or soil surfaces. Some water, amounting to less than 10% of rainfall under most conditions, is lost immediately to the atmosphere through evaporation. Depending on the season, water drips from the forest canopy to enter soils or accumulates as snow until a mid-winter thaw or spring snowmelt. Entering the soil, water is stored, taken up by plant roots, or moves to groundwater or surface water. Water taken up by plants moves upward through the xylem and exits as water vapor through leaf stomates in the process of transpiration. Typically, through the combined processes of evaporation and transpiration, less than half of the annual precipitation is passed directly back to the atmosphere as water vapor. Somewhat more than half of the annual precipitation passes through the rooting zone of the soil to enter groundwater or surface water such as streams and lakes.

Evapotranspiration, or evaporation and transpiration taken together, makes a large contribution to the ecosystem energy budget and to the regulation of temperature. In the conversion of liquid water to gas, evapotranspiration carries away large amounts of heat as latent heat. This cooling effect combines with other terms in the energy budget of a forest canopy to regulate the temperature of leaves and of the forest as a whole. Other major terms in the energy budget include the absorption or reflection of short-wave (sunlight) and long-wave radiation (from sunlight and from the atmosphere), the emission of long-wave radiation, and the gain or loss of sensible heat from the atmosphere. On a typical summer day the vegetation canopy absorbs energy in short-wave radiation from the Sun and dissipates the energy as sensible and latent heat to the atmosphere, heating the troposphere from below. On warm days with strong sunlight, the ability of forest tree canopies to dissipate heat allows the trees to maintain leaf temperatures closer to the photosynthetic optimum while also minimizing plant respiration. The opening and closing of stomates, governing transpiration, is under plant physiological control and is an important aspect of plant adaptation to life in a particular environment. During prolonged periods of drought, when trees are less able to use water to cool the canopy and maintain leaf turgor, foliar wilting and tissue damage can occur. Some temperate forest trees can be unexpectedly drought-deciduous, dropping their foliage during a late summer drought.

The photosynthetic conversion of light energy to stored chemical energy is a minor term in the physical energy budget of a forest, amounting to no more than 2% of the energy in sunlight. At the same time, this energy conversion represents the largest term in the ecological energy budget of a forest. The energy stored in photosynthate drives the life processes of all of the plants and animals in the ecosystem. A large portion of this energy is consumed by the vegetation itself through plant respiration, supplying energy for growth, metabolism, and reproduction. Another large flow of energy enters the food web through herbivory; herbivores eat seeds, fruits, and living plant tissues. The consumption of living leaves by insects, while normally minor, can grow during insect irruptions to encompass virtually the entire forest canopy over large areas. Similarly, the consumption of living leaves by forest ungulates including deer and moose are typically small energy fluxes at the ecosystem scale (although the browsing of seedlings and saplings can have a strong impact on forest regeneration and the future composition of the vegetation community). The chief means of energy flow to the faunal food web is through the saprotrophic pathway. Fungi and bacteria (often called soil flora) decompose dead and senesced plant material including leaves, roots, and woody debris. The soil flora is grazed upon by soil microfauna, which are in turn preyed upon by other fauna including arthropods, amphibians, and birds.

Nutrient Cycling and Carbon Balance

To achieve the high levels of productivity typical of temperate forests, trees require ample and reliable supplies of nutrient elements. Those required in the largest supplies include N, P, K, Ca, Mg, S, and Mn. Trees acquire most of their nutrients through root uptake from soils, which store nutrients in soil solution, on the surfaces of mineral grains, on the surfaces of organic matter, and in decomposing organic matter itself. A forest ecosystem receives inputs of nutrients from the atmosphere and from mineral weathering, experiences losses of nutrients via leaching (the water-driven movement of elements out of the rooting zone, ultimately to streams), and cycles nutrients internally (**Figure 5**). A key internal cycle is the plant–soil cycle in which an element such as calcium (Ca) is taken up by plant roots, used nutritionally by the tree, returned to the soil in foliar litterfall, and returned to the pool of soil-available nutrients during decomposition of the litter. Temperate forests are characterized by the fact that, for most nutrient elements required for plant growth, the internal cycling is greater than the ecosystem inputs and losses of these elements.

While most of the required nutrient elements can be released through mineral weathering, a notable exception is nitrogen (N). Temperate forests rely on inputs of N from the atmosphere. Combined with the fact that trees have a high demand for N, and with the fact that N is strongly retained in unavailable forms in soil organic matter, this makes N the most limiting nutrient for plant growth in most temperate forests. Trees have a high demand for N because photosynthesis and plant metabolism require enzymes, which are made of N-rich amino acids. Amino acids are also one of the primary needs of herbivores that consume plant tissues, including defoliating insects, deer that browse saplings, and beavers that girdle trees by eating the cambium around the tree base. Given the high demand for N by forest trees, it is somewhat ironic that trees in temperate forests are surrounded by two large, potential sources of N that are limited in availability because of the chemical form of the N. The first is N_2 gas, which is the primary constituent of the atmosphere. Most forest trees cannot access gaseous N_2, although a few exceptions include red alder (*Alnus rubra*) and black locust (*Robinia pseudoacacia*) in the USA, which access atmospheric N_2 through the process of N fixation (**Figure 5**). In this process, symbiotic bacteria living in root nodules fix the N_2 into plant-available forms. The second large pool of poorly available N occurs in humus and soil organic matter, made up of partially decayed and humified plant and microbial detritus. Typically, large accumulations of N are bound in this material in large, polyfunctional macromolecules that form during litter decomposition. Temperate forests are characterized by the combined facts that (1) cold, wet winters impede microbial decomposition and allow these pools of organic matter to accumulate, and (2) warm, humid summers promote decomposition by fungi, causing these soil organic matter pools to turn

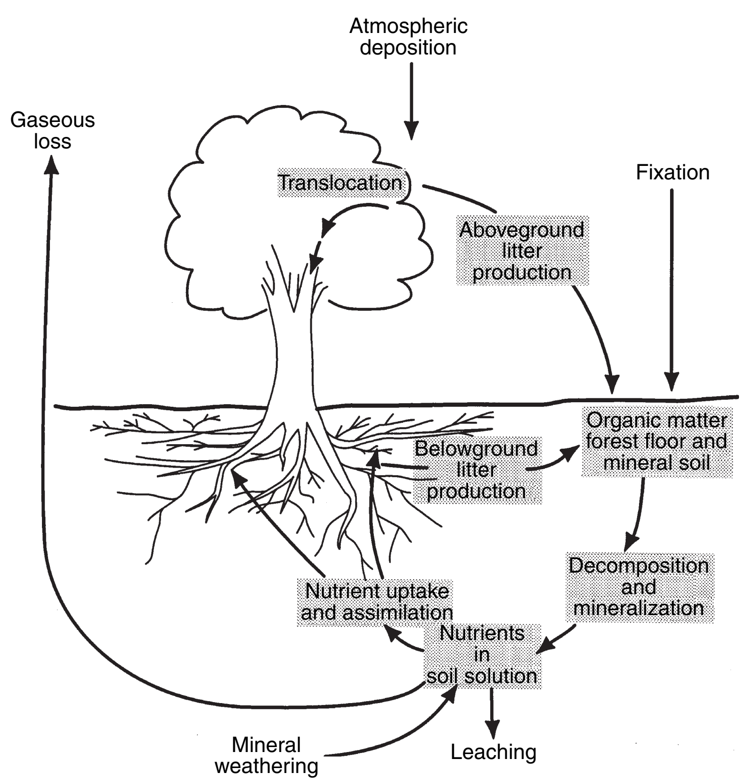

Figure 5 Schematic diagram of generalized nutrient cycling in temperate forests. Shaded terms represent nutrient cycling fluxes within the system, while unshaded terms represent ecosystem inputs or losses. From Barnes BV, Zak DR, Denton SR, and Spurr SH (1998) *Forest Ecology*, 4th edn. New York, USA: Wiley.

over and release nutrients at slow but continuing rates. Nutrient release during decomposition is termed mineralization because N is converted from organic to the inorganic forms of nitrate (NO_3) and ammonium (NH_4) which are easily taken up and used by plants (Figure 5).

Carbon is the primary elemental constituent of both forest vegetation and the organic matter in forest soils. Carbon (C) is not considered a nutrient element *per se* because a C atom passes through a forest once, in a single direction, closely linked to the flow of energy; unlike nutrients, carbon does not cycle between plants and soils repeatedly. Forests are highly open systems with respect to carbon, exchanging large quantities of CO_2 with the atmosphere. The carbon balance of a temperate forest arises from the interplay among processes controlling forest sources and sinks of atmospheric CO_2. Photosynthesis, or primary production, converts atmospheric CO_2 to reduced organic compounds, storing energy and C in the forest. Autotrophic respiration, the conversion of organic compounds to CO_2 by plants, provides energy for plant metabolism. Heterotrophic respiration, the conversion of organics to CO_2 by herbivores, microorganisms, soil fauna, and other animals in the food web, releases energy for animal life processes. Fire, the rapid oxidation of organics, also releases CO_2 to the atmosphere. Depending on the balance among these processes, temperate forests can either store or release large quantities of carbon. The primary storage pools include growing trees (particularly the woody stems), the forest floor, standing and downed woody debris (Figure 6), and soil organic matter. The transfer of carbon among these pools is linked to forest disturbance and stand dynamics including aggradation and succession. The flows of carbon into and out of the ecosystem are closely coupled to the availability of water, flows of energy, and the cycling of nutrients.

Figure 6 An old-growth sugar maple–birch–hemlock forest showing a large piece of downed woody debris. This forest is located in northern Michigan, USA. Photo by W. S. Currie.

Temperate Forest Land Cover

Historical Land Cover and Land-Cover Change

Temperate forests in all regions of the globe have been significantly altered by human activities for thousands of years. Their moderate climates, fertile soils, and vegetation productivity have been favorable to human settlement and clearing for agriculture, as well as direct use of trees themselves for lumber and fuels. Agricultural and settlement activities have included development of urban areas, widespread grain and other crop (e.g., corn, vegetables) cultivation, livestock grazing, gathering of mulch, and alteration of natural water drainage. Under these historical pressures, it is estimated that only 1–2% of the original temperate forest remains as never-harvested remnants scattered around the globe. The vast majority of temperate forest land cover is in secondary forest responding to human harvest or other human-induced disturbance.

The longest histories of substantial forest clearing have been in Asia and Europe. In China clearing for agriculture probably began some 5000 years ago, where the Chinese civilization is believed to have begun around the Huang He (Yellow River). The primary sociopolitical factor contributing to deforestation of China over the centuries has probably been the focus on an agriculture-based economy. At present, there is negligible large-scale reforestation in temperate China and significant soil erosion problems hampering reforestation.

Forest clearing for agriculture in Europe began over 5000 years ago starting in present-day Turkey and Greece and moving northwest through Middle Europe to Northern Europe. Forests of Britain were substantially cleared for agriculture and grazing. Woodlands regained some area in the Middle Ages; however, even remaining European temperate forests were degraded, being used for fuelwood, woodland pasture, and later for charcoal. Coppice practices promoted species that re-sprouted more quickly than beech – including maples and oaks, and this activity altered the natural floristic composition. Tall trees in Britain and Western Europe were removed for shipbuilding. Manorial estates provided some of the few refuges for natural forests. Reforestation in recent centuries in Europe began subsequent to reduction in the use of woodlands for pasture and fuel; reforestation has also occurred through the introduction of planted managed forests and scientific forestry. However, spruce, pine, and larch have been widely planted on areas previously occupied by once deciduous temperate forests.

North American indigenous populations cleared or burned small areas for some agriculture, but land-cover change in North American temperate forests began at large scales in the late sixteenth century with the European settlement. Eastern North American was rapidly cleared as the population moved westward in the nineteenth century. By the start of the twentieth century only a small amount of the original North American temperate forest remained. When the richer soils of the topographically level Midwest and Great Plains were found to be more productive for agriculture than those of eastern North America, eastern farms were abandoned and natural forests began to re-grow. At present, secondary forests are regrowing in the eastern and central United States.

In the Near East the temperate forest occurs in a narrow belt including in Turkey and Iran. This area probably served as a plant refugium during the Ice Ages and the floristic composition is more diverse than that in Europe. Some forests have been exploited for coppice, timber, or grazing and others transformed into agriculture and fruit-tree plantations. Beech forests are the most significant of the present-day broad-leaved forests in the region. In the small area of temperate deciduous forest in South America, forests have been moderately altered since the arrival of the Spaniards in the sixteenth century; the further south one goes the more recently the vegetation has been undisturbed and wooded areas remain. Australia first saw introduction of European agricultural practices only approximately 150 years ago.

Present-Day Land Cover and Rates of Change

The global temperate forest continues to be changed by a combination of long-term effects of historical land-cover change and by present-day change agents. Present-day drivers of land-cover change in temperate forests include accelerated population growth, continued industrialization, and changes in agricultural practices. These are expressed on the landscape as continued clearing for settlement and agriculture in some regions, abandonment of agriculture and reforestation in other regions, and widespread alteration in landscape spatial structure and biodiversity.

While rates of tropical deforestation increased between 50 and 90% in the 1980s, the area of temperate forests has remained constant or increased in the last 50 years in the form of new second-growth forests. In some areas, in eastern North America and parts of Northern Europe, farming is less economically viable than in other parts of the temperate region, leading to reforestation in these areas. Preservation in the form of parks has expanded by active conservation efforts worldwide. Managed forestry has maintained existing temperate forest lands by re-planting after harvest, and sustainable forestry practices are receiving increasing attention.

While the temperate forests may have stabilized or increased in terms of total area, most regions continue to experience other alterations manifested in the landscape spatial patterns and forest biodiversity. Today the temperate forest biome is a mosaic of settlements, patches of forest, and agriculture. Large expanses of unbroken forests from past centuries have been replaced by considerable landscape-scale heterogeneity and fragmentation. Temperate forest communities have changed compositionally, as disturbance regimes have shifted from natural to a combination of natural and human-caused, producing different patterns of regeneration and succession. While some recently established nature preserves have a natural forest structure, reduced biodiversity characterizes many temperate managed and secondary forests. Considerable present-day challenges lie in understanding and addressing the impacts of land-use change and other aspects of global environmental change in the temperate biome on forest biodiversity and forest ecology.

See also: Boreal Forest; Chaparral; Tropical Rainforest; Tropical Seasonal Forest.

Further Reading

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