Boreal and Temperate Forests

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The Earth's latitudinal gradient of forests encompasses boreal to temperate deciduous to temperate evergreen forests (as well as tropical forests). In addition, there are several variants of the temperate evergreen forest and there are montane forests at high elevations. Boreal and temperate forests differ in environment, structure, composition and disturbance.

Introductory article

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Introduction

The Earth has a wide range of forests, from wintry boreal forests to colourful temperate deciduous forests to humid temperate evergreen forests to diverse tropical forests and others. The Earth's forests encompass many tree growth forms, including needle-leaved evergreens such as pines (*Pinus*), and spruces (*Picea*), broad-leaved deciduous trees such as beeches (*Fagus*), and maples (*Acer*), and broad-leaved evergreens such as some species of oak (*Quercus*), and mahogany (*Swietenia*). These growth forms and the forests they characterize occur along gradients of environment, particularly climate. The major gradient in the Earth's forests is latitudinal, from high latitude boreal regions to equatorial tropical regions. This gradient – better developed in the northern hemisphere which has larger land masses – encompasses changes in environment, composition, structure and diversity.

Latitudinal Gradient in Forests

Environment and composition

The latitudinal gradient includes increasing length of the growing season from the short growing season of the boreal region to the year-long growing season of the wet tropics. This factor has dramatic effects on species composition, as boreal forests tend to be dominated by needle-leaved evergreen trees, while temperate deciduous forests are characterized by broad-leaved deciduous trees and temperate evergreen forests and tropical rainforests are dominated by broad-leaved evergreen trees, all adapted to the length of the growing season in their geographic region.

Structure

Along with the changes in composition, the latitudinal gradient parallels changes in forest structure as forests become increasingly complex toward the equator. The boreal forest tends to be relatively simple with four layers of plants of different heights: a surface layer of mosses and lichens on the forest floor (and often on tree trunks and limbs), a somewhat taller herb layer, a shrub layer, and a canopy layer of trees. The temperate deciduous forest and some temperate evergreen forests have five layers, as a second tree layer, the subcanopy, is present and consists of trees that have not reached their full height or are genetically restricted to being short. Other temperate evergreen forests and the tropical rainforest have six layers, with scattered taller trees extending above the canopy layer, producing an emergent (protruding) layer.

Species diversity

Another latitudinal gradient is the increase of species diversity (richness) from high latitudes to the equator. Consider, for example, the number of tree species likely to be found in an area of 1 ha (10 000 m^2). In typical boreal forest, 1 ha contains only two to four different tree species (plus of course additional plant, animal and microbial species). A hectare of temperate deciduous forest is likely to have twice as many tree species, and a temperate evergreen forest a few more. In contrast to boreal and temperate forests, 1 ha of tropical rainforest is likely to have 50 to 100 tree species. An astounding fact about tropical rainforest diversity is that scientists have found a Peruvian rainforest where a hectare contained 621 tree species – only slightly fewer than the 652 in all of Canada and the continental United States combined (an area of nearly 2×10^9 ha).

Boreal Forest

Boreal forest, sometimes called taiga, is characterized by needle-leaved evergreen coniferous trees. It covers much of northern North America and Eurasia, with the arctic tundra to the north and deciduous forest (or grassland, where drier continental climates prevail) to the south. Boreal forest is especially common in Canada, Sweden,

Figure 1 Landscape view of boreal coniferous forest in central Finland.

Finland (**Figure 1**) and Russia, where it dominates most landscapes and flavours human cultures. Of the Earth's great forests, this has been least altered by humans. No comparable forest exists in the southern hemisphere.

Environment

Boreal landscapes are gently rolling to flat, as a result of glaciation. They also tend to be wet, as many areas have extensive lakes and bogs (acidic mires).

The boreal environment is dominated by an extremely seasonal climate. Summer growing seasons are brief (2–3 months) and cool (highs usually $< 30^{\circ}C$), and winters are long and harsh (lows commonly near $-15^{\circ}C$). Despite the wetness of much of the landscape and the popular perception of snowy winters, total annual precipitation is low (generally 400–500 mm, peaking in summer). The anomaly of wet landscapes and low precipitation is explained by slow rates of evaporation (caused by low temperatures) and flat, poorly drained topography.

Boreal soils tend to be thin, acidic, and low in nutrients, but with a thick organic layer resulting from slow rates of decomposition.

Another important environmental factor in the boreal region is fire. Naturally occurring fires tend to be infrequent in any location (one per century) and, because fuels such as tree trunks, limbs and dead needles accumulate between fires, the fires are also high in intensity. Therefore, the forest is characterized by expansive crown fires that kill most canopy trees.

Structure and composition

With the harsh climate, trees of the canopy layer tend to be small (typically under 15 m height and 0.5 m diameter) – and as old as the previous crown fire. Most boreal trees are needle-leaved, cone-shaped evergreens; however, broad-leaved deciduous trees also occur, particularly following disturbance. The shrub and herb layers are generally sparse, but the surface layer of mosses and lichens covers tree trunks, limbs, and much of the forest floor, especially in more open forests toward the north and where human land use has opened the forest canopy.

Boreal forests of North America and Eurasia are similar in appearance and composition, although North American and Asian forests have more species than European boreal forests. The most characteristic trees are conifers, especially spruces, (*Picea*), followed by firs (*Abies*), pines (*Pinus*) and, especially in Asia, larches (*Larix*). Broad-leaved deciduous trees are mostly birches (*Betula*) and aspens (*Populus*).

Evergreen coniferous tree species are well adapted to the boreal climate. They retain leaves throughout the year and therefore are able to photosynthesize during the early weeks of the growing season when deciduous trees are forming new sets of leaves. However, evergreens have the disadvantage of being in leaf during the severe winters. Their needle leaves have a thick cuticle (protective layer of wax) and sunken stomata (leaf pores that are invaginated and less exposed to the atmosphere). These adaptations, which are also present in plants of some arid areas, prevent leaf desiccation and death in winter when tree roots cannot absorb water from the frozen soil.

The boreal forest dramatically changes in structure from north to south. At treeline (the northern-most limit of tree growth), trees are small and widely spaced. Tree size and density increase southward, first forming an open-canopy forest resembling savannah or woodland and eventually forming a closed-canopy forest of larger trees.

Disturbance

Natural disturbance in the form of crown fires was – and in many remote areas remains – common in the boreal forest. These fires can be exceptionally large, covering many square kilometres.

Human disturbance, except near populated areas, has been more limited than in other forests. Reasons include the boreal forest's geographic isolation, challenging environment, small tree size, and soil and climate poorly suited for agriculture. When logging is done, many trees are used for pulp in the making of paper products.

Where large-scale disturbance occurs, forest regrowth or succession is dominated by broad-leaved deciduous trees of *Populus* and *Betula* along with some needle-leaved species of *Pinus*. Seeds of these species tend to be wind-dispersed, allowing them to reach disturbed sites. They also are well adapted to the light of open sites, but are physiologically intolerant of shade. Therefore, they are replaced by other more shade-tolerant trees, although some species of *Pinus* can persist in drier more open areas. Some boreal species root sprout after disturbance or have closed cones that open only with heat produced by forest fires.

With logging expected to increase in extent and frequency in the future, early successional species will dominate more landscapes. In the long term, repeated logging may deplete soil nutrients and thereby reduce forest productivity.

Temperate Deciduous Forest

South of the boreal forest is the temperate deciduous forest (**Figure 2**), which is dominated by broad-leaved species that are leafless in winter. This type of temperate forest is common only in the northern hemisphere and is most extensive in Europe, eastern Asia and eastern North America. Given extensive human habitation in these regions, much of the land has been converted from forest to agriculture.

Environment

Temperate deciduous forest is found in flatter to more rolling landscapes – flat where glaciated and rolling where unglaciated. In Europe, this forest occurs in both maritime and continental climates, but most of eastern Asia and eastern North America has continental climate. An important aspect of the climate is its seasonality, with freezing temperatures during the cold season alternating with a warm, moderate-to-long growing season (120 to 250 days). Precipitation typically averages 750–1500 mm and in some areas is greater in summer. Temperature, growing season and precipitation increase southward.

Soils also show latitudinal variation. They are relatively acidic and nutrient poor in the north, reach maximum richness and productivity in central regions, and are strongly leached and less productive in the south. Fire, in the form of frequent, low-intensity surface fires, was an important naturally occurring factor in many regions; however, human habitation has dramatically altered natural fire patterns.

Figure 2 Interior view of temperate deciduous forest in southern Indiana, USA.

Structure and composition

Large broad-leaved deciduous angiosperms with dome-shaped crowns form a continuous canopy in most areas. Trees reach 35–40 m height, >1 m diameter, and several hundreds of years age. The subcanopy layer is more open and also consists of broad-leaved deciduous angiosperms. The deciduous growth form is well adapted to the seasonal climate, as plants are leafless during the most stressful time of year. Growing seasons are sufficiently long for these trees to produce entire sets of leaves in the spring and yet have adequate time for growth during the summer.

The shrub layer has broad-leaved deciduous and evergreen angiosperms and is variable in density. The herb layer is well developed in most areas and dramatically changes in species composition in response to shading by trees. 'Spring season' herbs grow before trees are in leaf and utilize bright spring light. 'Summer season' species growth after trees are in leaf and therefore are shade tolerant. 'Full season' species grow both before and after trees are in leaf and thesrefore are highly flexible with regard to light. The surface layer is dominated by mosses and lichens, but it is more abundant on trunks and limbs of trees than on the forest floor, where it may be covered by tree leaves in the autumn.

Although broad-leaved deciduous species are abundant throughout, species composition depends on latitude. In the north near the boreal forest, birches (*Betula*), aspen (*Populus*) and maples (*Acer*) are common, but so are needle-leaved conifers, especially pines (*Pinus*). Conifers decline in abundance southward to the central portion of the temperate deciduous forest, although some *Pinus* species may be found in drier sites and, at least in North America, were maintained by frequent surface fires in the south.

The central temperate deciduous forest is almost entirely composed of broad-leaved deciduous species. In Europe,

the major trees are oaks (*Quercus*), European beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*). Elsewhere, forests are more diverse. Common trees in North America include sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), basswoods (*Tilia*), *Quercus*, hickories (*Carya*), and American chestnut (*Castanea dentata*; now nearly extinct because of an introduced fungal disease). Common trees in Asia include Japanese beech (*Fagus crenata*), *Quercus*, *Acer*, ashes (*Fraxinus*) and *Tilia*.

In the south, broad-leaved deciduous species from the central region are joined by broad-leaved evergreen angiosperm trees, such as some species of *Quercus*. In Europe, this reflects proximity to dry-season broad-sclerophyll forest (see below) near the Mediterranean Sea. In eastern North America it reflects the longer growing season in the south, and in eastern Asia it reflects the growing season and proximity to temperate evergreen forest.

Disturbance

Natural disturbances in the temperate deciduous forest include fire and wind. Surface fires have been important in maintaining *Pinus* species as part of the northern and southern portions of the temperate deciduous forest. The effects of wind range in scale from single tree falls that produce small gaps in forest canopies to large-scale blowdowns following hurricanes and typhoons that remove the forest canopy over large areas near coastlines.

Human disturbances have been very extensive. Deforestation for agriculture became widespread in eastern Asia several millennia ago, in Europe in the Middle Ages, and in North America in the nineteenth century. Today, many areas have only small, scattered patches of forest.

Other important large-scale human disturbances include air pollution, which is believed to have resulted in reduced growth rates and deaths of trees, and the introduction of non-native diseases and insect pests, which have killed individuals of susceptible species (including *Ca. dentata* in North America). Moreover, forest fragmentation has the potential to have a negative impact on species migrations.

Following large-scale but short-term disturbances such as large windstorms, reforestation is rapid where species regenerate by sprouting. However, following longer-term disturbances such as conversion to agriculture, reforestation may take two or more centuries as succession begins with short-lived herbs and these are replaced by longer-and longer-lived herbs, shrubs, shade-intolerant trees, and shade-tolerant trees. However, in some areas of Europe, for example, where forest clearing was followed by ongoing disturbances such as repeated burning and livestock grazing, forest has been replaced by grasslands in drier areas and by heathlands in wetter areas such as in the British Isles.

Temperate Evergreen Forest

Temperate evergreen forest occurs at the warm, moist end of the latitudinal gradient of boreal and temperate forests. It is dominated by broad-leaved evergreen angiosperms. This forest occurs only in the northern hemisphere, primarily in eastern Asia, but most of it has been replaced by agriculture. The forest is uncommon in southern Europe, which has a Mediterranean climate with dry-season broad-sclerophyll forest (see below), and in south-eastern North America, where the extent of forests is limited by the Gulf of Mexico.

Environment

Temperate evergreen forest occurs in rolling landscapes. The climate is nearly subtropical, being characterized by long hot, humid growing seasons and mild winters. Precipitation is high (1000–1750 mm), and soils are well leached and therefore relatively low in productivity. The role of naturally occurring fire is unknown, but fire frequency may have been limited by moist conditions.

Structure and composition

Because most of the forest has been replaced by agriculture, details of its structure and composition are not well known. Two or three tree layers can be present, with large broad-leaved, dome-shaped evergreen angiosperms forming a somewhat continuous canopy, sometimes with taller emergent trees present. Evergreen leaves are well adapted to a climate with mild winters, as photosynthesis can occur throughout the year. The presence of many epiphytes and vines resembles wet subtropical and tropical forests.

The forest is generally richer in species than temperate deciduous forest. In eastern Asia, forests are dominated by oaks (*Quercus*), and *Castanopsis*, but there are many other species including laurel (*Machilus*).

Disturbance

Little is known about the natural disturbance regime of this forest; however, periodic blowdowns by typhoons are likely, especially in coastal areas. As indicated above, human disturbance has been widespread, especially in China where much of the forest has been cleared for agriculture. Some disturbed areas of Japan now have pine (*Pinus*) forests.

Variants

Temperate evergreen forest has several variants that occur in regions of maritime and dry-season climates. These

forests cover more land area than the temperate evergreen forest itself.

Maritime broad-leaved forest

Maritime broad-leaved forest is best developed in the southern hemisphere, where it extends for 800 km south of Valdivia, Chile, and occurs in New Zealand and small areas of southeastern Australia, including Tasmania. The forest is dominated by tall, broad-leaved evergreen angiosperms and narrow-to broad-leaved conifers.

The climate is maritime, with mild temperatures and very high precipitation (2000–3000 mm). Soils are well leached and organic matter accumulates on the soil surface because of slow decomposition rates. The role of fire is not well known.

The forest is dominated by huge trees and has complex structure. It often has a subtropical or tropical character, with an emergent layer of tall trees and high species richness.

In South America, the dominant canopy tree is the broad-leaved evergreen angiosperm southern beech (*Nothofagus dombeyia*). Other trees include *Laurelia*, *Eucryphia* and *Aextoxicon*. In New Zealand, narrow-to broad-leaved conifers of *Podocarpus* and related genera often dominate an open emergent layer above a canopy of broad-leaved evergreens such as southern beech (*Nothofagus*). In southeast Australia and Tasmania, the dominant is the broad-leaved evergreen angiosperm myrtle beech (southern beech), *Nothofagus cunninghamii*.

Natural disturbance factors are fires and landslides. Fires are especially important in limiting the extent of the forest in drier areas, while landslides are more common in areas of steep topography. Human disturbances have included widespread logging and clearing for agriculture and for plantations of fast-growing non-native conifers.

Maritime needle-leaved forest

Maritime needle-leaved forest occurs only in the northern hemisphere in a narrow band along the coastline of North America from central California to southeastern Alaska. The forest is dominated by needle- and scale-leaved evergreen conifers of enormous size (**Figure 3**).

Much of this region is hilly as a result of proximity to coastal mountains. The maritime climate results in mild temperatures (rarely dropping below $-15^{\circ}C$ even in southeast Alaska), long growing seasons, and high precipitation (650–4000 mm or more). Precipitation is seasonal in the south where there is little rainfall in the summer, but drought is alleviated by coastal fog, which reduces evaporation and also condenses on tree leaves and drips to the ground.

Soils are well leached, acidic, and, as in maritime broad-leaved forests, have an accumulation of organic matter. Fire has been important in drier regions.

Figure 3 Interior view of temperate evergreen forest (maritime needle-leaved forest variant) in northern California, USA.

Canopy trees can exceed 50 m height, 1.5 m diameter, and centuries in age. Unlike most coniferous forests, there is a subcanopy layer of trees; however, the forest is less rich in species than the maritime broad-leaved forest. In the south, the forest is dominated by California redwood (*Sequoia sempervirens*); some individuals are the tallest organisms on Earth at nearly 120 m. Douglas fir (*Pseudotsuga menziesii*) is common in the southern and central portions. Further north, the dominant species is western hemlock (*Tsuga heterophylla*). Other important trees are spruce (*Picea*) and red cedar (*Thuja*).

Fire is the most common natural disturbance, at least in drier areas, and crown fires lead to dominance by *Ps. menziesii*, which can persist for several centuries. Major human disturbances are logging and fire suppression. *Sequoia sempervirens* regenerates by sprouting.

Dry-season broad-sclerophyll forest

Another variant of the temperate evergreen forest occurs in areas with periodic drought. The best known of these

climates is the 'Mediterranean', a summer dry–winter wet climate named after the region of the Mediterranean Sea, but areas with drought at other times of year may also have dry-season broad-sclerophyll forest. This forest occurs in the northern hemisphere around the Mediterranean Sea, eastward into Asia, and in the southwestern United States (particularly California) and northern Mexico. In the southern hemisphere it is largely restricted to parts of southwestern and southeastern Australia. The forest is dominated by angiosperm trees with thick, hard, often waxy, evergreen leaves of medium width.

Landscapes with this forest are frequently hilly if not mountainous. The Mediterranean climate of most regions is characterized by hot dry summers and cool wet winters when most of the annual precipitation (of 300–1000 mm) falls. Other climates have periodic seasonal drought such as in winter or spring. Soils are low in nutrients and fires are common.

Forests in the northern hemisphere tend to be relatively short, with a canopy of 10 m trees dominated by oaks (*Quercus*). Forests in the southern hemisphere are generally taller, up to 30 m or more, and are dominated by *Eucalyptus*.

Natural disturbances are primarily fire, especially during the dry season. Human disturbance in the form of logging has been especially extensive around and east of the Mediterranean Sea, as these areas were cleared hundreds to thousands of years ago. Logging has been less extensive in North America and Australia, and Australia has the greatest extent of dry-season broad-sclerophyll forest remaining.

Montane Forests

Tall mountains such as the Rocky Mountains and Sierra Nevada of North America and the Alps of Europe provide spectacularly beautiful landscapes for a complex array of forests. Mountains in the boreal and temperate zones are usually dominated by needle-leaved evergreen conifers, although broad-leaved deciduous angiosperms also occur. Mountains of the subtropics and tropics are not covered in this article, although they may have temperate forest vegetation at mid to higher elevations.

Environment

The complexity of montane forests is the result of steep gradients in environment, especially the elevational gradient, which result in large changes in short distances. In the central Rocky Mountains, for example, with every 100 m increase in elevation, mean annual temperature decreases about 0.6°C and the growing season decreases by about a week. Moreover, precipitation increases to a maximum somewhat above mid-elevation where it is much greater than in surrounding lowland areas. Overall, the combined effects of precipitation and evaporation (largely based on temperature) produce increasingly moist environments with higher elevation.

Another key environmental gradient in mountains is a topographic moisture gradient related to slope aspect, i.e., the compass direction a mountainside or hillside faces. In the northern hemisphere, south-facing slopes tend to receive more solar energy than north-facing slopes. Therefore, south- (and west-) facing slopes tend to have drier soils, warmer temperatures and longer growing seasons. As a result, lower elevation forests adapted to warmer, drier conditions tend to extend to higher elevations on south-and west-facing exposures. Of course it is the opposite in the southern hemisphere.

The elevational and topographic moisture gradients, particularly as they affect moisture levels, have a dramatic influence on fire, another key aspect of many montane forest environments. Warmer, drier areas – such as low-elevation south- and west-facing slopes – tend to have higher fire frequencies. This allows little fuel accumulation between fires, so fires tend to be surface fires which burn along the ground surface where they kill tree saplings but few canopy trees. In contrast, cooler, wetter areas – such as high elevation north- and east-facing slopes – tend to have lower fire frequencies and higher fire intensities resembling the crown fires of the boreal forest.

In general, soils of mountains tend to be less well developed than lowland soils because erosion on slopes tends to remove soil particles.

Although these generalizations hold for many mountains, there can be large differences between mountain chains of different regions. In North America, for example, the Sierra Nevada has a summer-dry, winter-wet climate, but summer precipitation is common 1000 km to the east in the Rocky Mountains.

Structure and composition

Given the broad range of montane environments, montane forests are complex. High elevation forests resemble boreal forest. Structurally, both have four layers and small trees (especially toward treeline where the forests grade into tundra). Compositionally, both are dominated by genera such as *Picea* and *Abies*, whose needle-leaved evergreen foliage is well adapted to the cold high-elevation climate and whose cone shape and flexible limbs effectively shed the several metres of snow common in mountain areas (**Figure 4**). In mountains between North America's Sierra Nevada and Rocky Mountains, these high elevation forests include bristlecone pine, *Pinus longaeva*, which has the world's oldest organism, 4767 years.

Down slope, montane forests are more diverse and consist of taller, larger trees. Tree height often exceeds 75 m, with diameters > 1 m. Perhaps the most unusual tree

Figure 4 Montane coniferous forest in eastern British Columbia, Canada.

of the mid-elevations is the giant sequoia, *Sequoiadendron giganteum*, which has the world's largest (by volume) organisms. This species occurs in scattered areas of California's Sierra Nevada. More common are species of *Pinus*, *Abies*, *Picea* and *Larix*, as well as *Pseudotsuga* in the western United States and *Fagus* and other broad-leaved deciduous trees in the Alps. Mountains in coastal areas tend to have species of genera found at lower elevations in maritime forests.

Where drier conditions are found at lower elevations, such as in mountains of the western United States, canopy trees tend to be nearly as large as at mid-elevations; however, the forest canopy and understorey is much more open, at least in old-growth forests. The openness is the result of frequent surface fires which rarely kill canopy trees with thick, somewhat fire-resistant bark, but kill many sapling trees, which are too young to have thick bark.

Disturbance

Major natural disturbance factors in montane forests include avalanches and crown fires. Avalanches, which occur on steep slopes subject to high snowfall, remove forest trees and thereby open sites for succession. Crown fires also kill most canopy trees and initiate succession.

The obvious human disturbance is logging, which has been widespread in all mountain chains, except perhaps at the highest elevations. Logging in mountains is a special problem because of erosion. Natural revegetation and tree planting are problematic on steep, eroded slopes. In Europe, montane conifers have been planted down slope in tree plantations that replace deciduous forests.

Another major human disturbance is the suppression of naturally occurring fires. In North America, fire suppression began in the early twentieth century when many forests of western mountains remained uncut. Suppression was generally highly successful in eliminating fire as a natural environmental factor; however, suppression increased the risk of fires by increasing tree densities and fuels. Today, even forests formerly characterized by surface fires are susceptible to crown fires.

A third important human disturbance in montane forests is air pollution. Tree deaths associated with air pollution have been particularly widespread in portions of central Europe, where entire forests have been killed and converted to treeless meadows.

Where the forest canopy is opened by disturbance, the site is invaded by early successional tree species such as broad-leaved deciduous trees of *Betula* and *Populus* and coniferous trees of *Pinus*. These species are adapted to an early successional role by having effective seed dispersal by wind, shade intolerance, resprouting from roots, and cones that open and disperse seeds only with the heat from fire.

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