ENVIRONMENTAL STUDIES 30 -- THE GLOBAL ECOSYSTEM
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LECTURES 11 and 12: The Temperate Forest Biomes: Warm-Temperate Evergreen Forest, Cool-Temperate Deciduous Forest, and Boreal Forest.

Introduction

Huge areas of the Earth between 30° and 60° latitude are forested (or were before human disturbance). (Figure 11.1 gives the distribution of these biomes.) Most of the land mass in the temperate zones of the world is either close enough to the ocean, or cool enough if continental, to bring the PE ratio down to one or less. The area of desert sclerophyll woodland and steppe in the temperate zone is large, but the forest biomes occupy still larger areas. The main environmental variation within these forests is temperature, particularly winter temperature (See Figure 11.2 for climate diagram).

The more southerly biomes lack freezing winters (months with mean minima of 0°C or less), although they have at least some frosty weather. These climates support coniferous or broadleaved evergreen forests. Except for the higher rainfall and lack of sclerophyllous plants, the Warm-Temperate Biomes resemble the Mediterranean; before the Pleistocene the same forest species dominated the regions of the modern Mediterranean Biome. The Warm-Temperate Forest Biome can be subdivided into two rather different sub-biomes: 1) Broadleaf Evergreen Forests, typically on the east sides of continents and 2) Coniferous Forests, typically on the west sides of continents (they now only exist in western North America).

The middle latitudes of the temperate zone, with a few months of freezing winter weather, support the Cool-Temperate Deciduous Forest biome. This biome is absent in the Southern Hemisphere. Southern continents have very little area at high latitudes, and the small bits of cool-temperate climate are very maritime. In the Northern Hemisphere, this biome is differently distributed in Eurasia and North America. In Eurasia Temperate Deciduous Forests occur on both sides of the continent, in Europe and again in China. In North America they are confined to the east side of the continent.

As winters become longer and colder (6 months of below 0°C mean minimum), deciduous forests give way (usually) to evergreen conifers of the Boreal Biome. This biome is present only in the Northern Hemisphere, where it is distributed as a globe-girdling band at 50-65° N latitude. This is the only biome in the world in which the west, middle and east parts of continents have the same biome. But there are some differences even here; species composition changes across the continent, and the Boreal Forest is displaced northward on the west sides of the continents.

Warm-Temperate Evergreen Forest Climates

See Figure 11.2 for climate diagrams representative of the coniferous and broadleaved variants of this biome.

A. The coniferous variant is semi-mediterranean, having a summer rainfall minimum, but without a conspicuous drought in the summer. Often these forests are very humid indeed, and the communities are described as "temperate rain forest," such as the Olympic Peninsula of Washington or the low elevation areas of Southern Chile. This variant is in the core area of the westerly wind belt, and the climates are very maritime. Frosts are mild, and cold-sensitive trees reach quite high latitudes.

B. The broadleaved variant exists under a continental climate with an even distribution of rainfall, or a summer peak. These climates usually receive tropical storms in the summer, and cyclonic rains in the winter. The usual location of these forests is on the eastern side of continents where continental polar air sometimes penetrates quite far south in the winter. The southeastern part of the U.S., for example, has mean winter temperatures only a little cooler than California at equivalent

latitude and altitude, but the extreme minima are a good deal cooler; the occasional snowstorm penetrates practically to the Gulf of Mexico. The difference is reflected in the distribution of citrus, which will tolerate only mild frost. We can grow citrus in California almost to 40° N latitude. The east coast industry is restricted to Florida, no further north than 30°, in the ecotone between the Deciduous Tropical Forest Biome and the Temperate Evergreen Forest Biome.

Temperate Deciduous Forest Climates

A. Typical east coast version

The large northern continents have quite continental climates on their eastern sides. The Evergreen Forests give way to deciduous ones as the winter weather comes to be dominated by continental Polar air masses. The Deciduous Forest Biome climates are characterized by a few months of below 0°C mean minimum temperatures and most winter precipitation as snow. Winter snow cover is continuous for a few months in the more northerly and continental examples of the biome.

B. The Anomalous Cool-Temperate Climates of Western Europe.

Because of the presence of the very warm Gulf Stream, the Temperate Deciduous Forest Biome reaches the west coast in Europe at a fairly high latitude. Europe lacks a coastal mountain range and becomes mildly continental, but humid, away from the immediate influence of the open Atlantic. Thus, here the climate has short freezing winters on its western side. Perhaps it is more correct to say that North and South America are the anomalies because they have coastal mountain ranges. Before the uplift of the Sierras and the Cascades, the Western United States had Temperate Deciduous Forests in what is now Steppes and Steppe Desert in Eastern Washington, eastern Oregon and Nevada.

Boreal Forest Climate

The climates of this biome have long, cold winters, but reasonably warm summers. the total rainfall is moderate in an absolute sense, with annual totals in the 400-500 mm range. In a warmer climate these areas would be semi-arid, but cool temperature reduce evaporation to the point that the biome has ample rainfall for plant growth. Rainfall has a summer maximum; winter temperatures are so low that the air can carry only a limited amount of moisture that falls as very dry snow.

The climates of this biome vary considerably. All are very strongly seasonal climates, but in the continental interiors they become very seasonal indeed. Eastern Siberia includes climates that have both the coldest mean temperatures in the Northern Hemisphere and the greatest range of monthly means (see the climate diagram of Oimekon, Figure 11.2). Now you know why the Russians send people to Siberia for punishment.

Soils of the Temperate Forest

Each of the temperate forest biomes has a characteristic kind of soil development pattern. Since rainfall exceeds evaporation in the forests, soil formation is dominated by downwardly percolating water. Most Temperate Forest soils develop pronounced layers or horizons as the percolating water moves or removes different soil constituents. Figure 11.3 shows several soil profiles typical of moist to semi-arid temperate climates. Tropical soils generally lack conspicuous horizons because they are thoroughly weathered from top to bottom. The arid-zone soils also have weakly developed horizon structures, but this is because they are not weathered by the steady downward percolation of moisture. Even in the Steppes, rainfall is not sufficient to move clay particles, although $CaCO_3$ is leached from the upper layers. In the more moist temperate forests, a process called podsolization occurs. The damp climate and humid forest floor promote the decay of the leaf litter before it becomes incorporated into the mineral soil layer. Water rich in CO_2 and organic acids percolates downward, moving clays downward and chemically degrading them. In the warmer Evergreen Forest the clays are quite heavily degraded and loamy to sandy red topsoil layers result. In the cooler forests the clays are less weathered, but may be entirely removed from the surface layer of the soil (the A horizon) and redeposited 30 to 40 cm below in a second layer (the B

horizon). In the most extreme cases, the A horizon may contain only bleached white sand, and the B horizon may be quite compact, even cemented with iron precipitates to form a hardpan. All the forest soils tend to be acid in reaction, often very acid, unless the parent material is limestone.

Where podsolization is not too severe, these soils can be farmed, and as usual, younger soils derived from loess or alluvial deposits are the best. In the U.S., forest soils were farmed (with difficulty) as far north as New England. After the Prairie Steppe soils of the Midwest were opened for settlement in the 1830s, agriculture disappeared from much of the Deciduous Forest, and eventually the Evergreen Forest Biomes. This process continued into recent decades in the Deep South where cottonlands gradually gave way to pastures and pine plantations. The 20th Century exodus of rural Southerners to the North, Midwest, and West resulted from this process. Country music and the blues were brought to us Yankees courtesy of those red Southern soils! Much of the eastern half of the U.S. has reverted to secondary forest; it is quite common to stumble across abandoned homesteads in what now seems like virgin forest.

Plant Adaptations

A. Deciduous vs. Evergreen Leaves

The delicate balance between the costs and benefits of retaining vs. shedding leaves are nicely exhibited by the Temperate Forest Biomes. In the areas where neither drought nor cold is severe, trees are evergreen. However, the two variants of the Warm-Temperate Forest are quite different in North America: the eastern variant is dominated by broadleaf evergreens (magnolias are a good example), and the western variant is dominated by conifers, such as Redwood, Douglas Fir and various other cold-sensitive firs, spruces, and cedars. In Europe, where this type of conifer was lost during the glacial episodes, and in South America and New Zealand, where conifers are rare due to historical effects, the climatic analogs of our Pacific Northwest have a broad-leafed vegetation. The advantage of the conifer in western variant where they are biogeographically "available," is apparently their superior drought resistance. The needle leaves of conifers are sclerophylls in effect, well able to resist water loss. (We have already met the pines in the Mediterranean Biome, where they are well adapted to drought. Pines are also common in the Eastern Warm Temperate Evergreen Forest, and in the Cool-Temperate Deciduous Forest, but they usually occur only on sandy, well drained soils where drought is a problem for edaphic reasons.) The west-coast variant of the Warm-Temperate Forest, with its summer rainfall minimum, must experience sufficient drought stress, at least occasionally, to favor the conifers over the broadleaves.

When winters are cold but fairly short, the dominant vegetation is winter deciduous. Summers are still long enough for trees to bear the cost of elaborating leaves that must be shed annually. When winters become longer still, but summers reasonably warm, the conifers become the dominants. The short summers give a considerable advantage to being ready to photosynthesize as soon as the temperatures exceed freezing. The drought-adapted leaves of the conifers are suited to withstand the long cold period, because the most severe effect of freezing conditions is, paradoxically, to expose plants to severe water loss. Remember from Lecture 3 that frozen roots and trunks cannot translocate water to make up even the small winter losses. Christmas trees work because conifer needles are rather effective in this regard. It takes 5-6 weeks for them to shed their leaves even after they are cut from the stump, and perhaps a couple of these weeks are spent in a warm, dry house to boot.

In those areas of the Boreal Forest where winters are exceedingly severe (Eastern Siberia) the trees are again winter deciduous, this time a conifer, or a larch. Only the fairly warm summer of this extremely continental area permits trees to exist at all. The tundra beyond the treeline actually has higher mean temperatures, but with less severe winters and cooler summers. A certain minimum growing season warmth is necessary to provide sufficient photosynthesis to support the large standing biomass of a tree.

B. Shade-adapted Understory Plants

The amount of leaf biomass in Temperate Forests is seldom quite as great as the Tropical Forests. Hence, a thin understory often develops. Understory shrubs and shade tolerant trees, with flat sprays of very thin leaves, can live with as little as 1 or 2% of full sunlight (Dogwood is a good example). Some evergreen shrubs live in the understory of the deciduous forest. Their leaves are protected by snow in winter and can photosynthesize in good light conditions for a few weeks until the overstory trees are in full leaf.

Tree succession in the forest is partly determined by the shade tolerance of seedlings. In the Eastern United States, birch is often the pioneer species in clearings, but its seedlings cannot grow in the shade of their own parents. The birch is replaced by sugar maple, which is in turn replaced by highly shade tolerant beeches. Beech seedlings can grow with only a little more than 1% of full sunlight.

Many perennial herbs exploit the early spring in the deciduous forest in a manner similar to the evergreen shrubs; they display their leaves for a few weeks in the spring before the trees leaf out.

C. Bog and Heath Plants

The humid climate and intense nutrient leaching of the temperate forests open a niche for plants with very low nutrient requirements. Very humid Temperate Forests are much like the Tropical Rain Forests, much of the nutrient reserves are tied up in the biomass. Logging or other repeated human disturbances may badly degrade this habitat by allowing the stored stock of nutrients to wash away.

The coastal parts of Ireland and Britain are covered with heath, a low shrubby vegetation, dominated by N-fixing brooms or Calluna shrubs very tolerant of acid, low nutrient soils. This anthropogenic climax can be reversed by reforestation only with difficulty.

Bog formation can also occur in humid coastal areas of the Deciduous Forest after forest clearance. Trees transpire a great deal of water. When they are cut, the water table often rises nearly to the surface, inhibiting the regrowth of the trees. Spagnum mosses then invade, partly because of the high water table and partly because they are tolerant of poor acid soils like the heaths. But low growing Spagnum does not transpire much water and trees are never able to recolonize the landscape. Rather the bog grows upward on a spongy mat of dead, partly decomposed Spagnum. If the climate is rainy enough, raised bogs develop over several feet of peat. Eventually the peat becomes so compact that it can be drained and cut for fuel. In the past, coal deposits formed from peat deposited in a similar way.

Spagnum bogs are particularly prevalent in the Boreal Forest on flat topography. Here the low evapotranspiration rate of the cool climates rather than human disturbance is the villain. Even with fairly low absolute rainfall, surplus water is abundant and the water table tends to be high. If impeded, drainage raises it to 50 cm of the surface or so, the trees die and are replaced by bogs. Once started, the bogs can spread because they further reduce transpiration and cause water tables to rise at their edges. Western Siberia contains the World's biggest bog, 800 km x 1800 km in size, a little larger than the area of California. A few small bogs can be found in our mountains above 6,000 feet.

Animal Adaptations

The Temperate Forests have many analogies to the Tropical Forests. Big herbivores are scarce. The big game of the forests either exploit successional habitats (deer, moose) or forage for roots, nuts, berries and small animals (pigs and bears). Seed-eating rodents are common and their carnivores form some of the fur species so important in the history of the boreal forest (mink, martens, sables). Insects are relatively important, but generally consume only a small part of each year's primary production. Thus the detritivore community is more important than the herbivorous one.

The arboreal fruit-eating and pollination guilds, so common in the tropics, are much reduced. Fewer temperate trees produce edible fruit and many of the dominants are wind pollinated. Among the birds, insectivores and seed eaters are relatively much more important in the temperate than in the tropical zones. Migratory species also rise as a percent of the fauna. Reptiles and amphibians gradually drop out of the fauna as low temperatures reduce their ability to be active.

Animals of the same or similar species often become much larger and more compact in the more poleward biomes. Large animals with a minimum of body surface area keep warm more easily than small ones. (This effect is quite noticeable in California's big-game species. Our deer and elk average half to two-thirds the weight of their counterpart subspecies in the Rockies).

Ecosystem Characteristics

The gross primary production of Temperate Forests is much less than that of Tropical Forests, perhaps half as much. However, respiration is also much lower as a result of lower temperatures. Thus, as far north as the Cool-Temperate Deciduous Forest Biome, net production values are roughly comparable to the tropics, say 13 tons/ha/yr. or so. In the colder Boreal Biome, production falls to perhaps 5 tons/ha/yr.

The diversity of plant and animal species falls drastically in all the temperate biomes. In fact, the Warm Temperate Forest is in the middle of a global diversity gradient that, for most components of the earth's biota, falls with increasing latitude (**Figure 11.4** [from slide in lecture] shows several of these gradients for North America). Ecologists and evolutionary biologists have argued for many years about the causes of this gradient. There are six or so other prominent hypotheses. I am a proponent of a favorableness hypothesis, which says simply that as the absolute limits of life are approached, plants and animals must devote an increasing fraction of their adaptive repertoire to coping with the extremes, and are forced to generalize on other traits. Hence niches are broader and fewer species can be packed into a given habitat. Warm, wet habitats are diverse and very cold or very dry ones become lifeless.

Whatever the correct explanation, the result is that by the Boreal Forest, the number of important tree species is reduced from hundreds in the tropics to less than ten. Individual communities are often strongly dominated by a single species in the Boreal Forest, in contrast to the hundred species per hectare of the Evergreen Tropical Forest. The whole flora of the Boreal regions is reduced from tens of thousands of species to a few hundred.

Human Adaptations

A. Hunting and Gathering

Forests are not ideal habitats for hunters, as we have observed before. Most likely, hunters were largely confined to forest edges and other open communities within the Temperate Forests, where game was more abundant and easier to hunt.

B. Agriculture

We have already spoken of the moderate suitability of the Warm Temperate Forests and Deciduous Forest for agriculture. Horticulture and agriculture penetrated into temperate Europe and North America fairly early, but was for a very long time confined to lighter soils. Forest clearance and the working of heavy soils was impossible without heavy plows and strong draft animals (the heavy horse). In Europe the invention of these in the Medieval Period resulted in a renewed episode of forest clearance that lasted until the 18th century. Some historians attribute the industrial revolution to the shift from wood to coal as a fuel in Europe as forest products for the first time became scarce. At least the first use of steam engines was for mine pumps, and the steam engine was the key invention of the industrial age.

The Temperate Evergreen and Deciduous Forest Biomes are relatively tolerant of human

disturbance. Much of rural Europe displays a stable, productive agricultural complex that does not seem to be causing progressive denudation of its land base. Industrial pollution is a problem, however, as is the excessive application of nitrogen fertilizer. Heath and bog formation are the conspicuous exceptions; these degraded communities are favored by deforestation in more humid and poorly drained sites.

In North America, aboriginal horticulturalists were also c[illegible]fined to better soils and population sizes were quite modest compared to the favorable a[illegible]nd semi-arid subtropical regions in Mexico and Peru.

The Boreal Forest marks the limits of cultivation. Poor [illegible] and short growing seasons do not permit [illegible]riculture. Even today, these biomes are among t[illegible]ast affected by human activities. Fur trappin[illegible]and forestry are the main uses of the Boreal Fores[illegible] large fraction of the world's newsprint comes from Boreal Forests: the trees are often too small to compete with saw-timber. Still, only those areas close to transportation and markets are heavily exploited (Southeastern Canada, Finland, Europe, Russia).

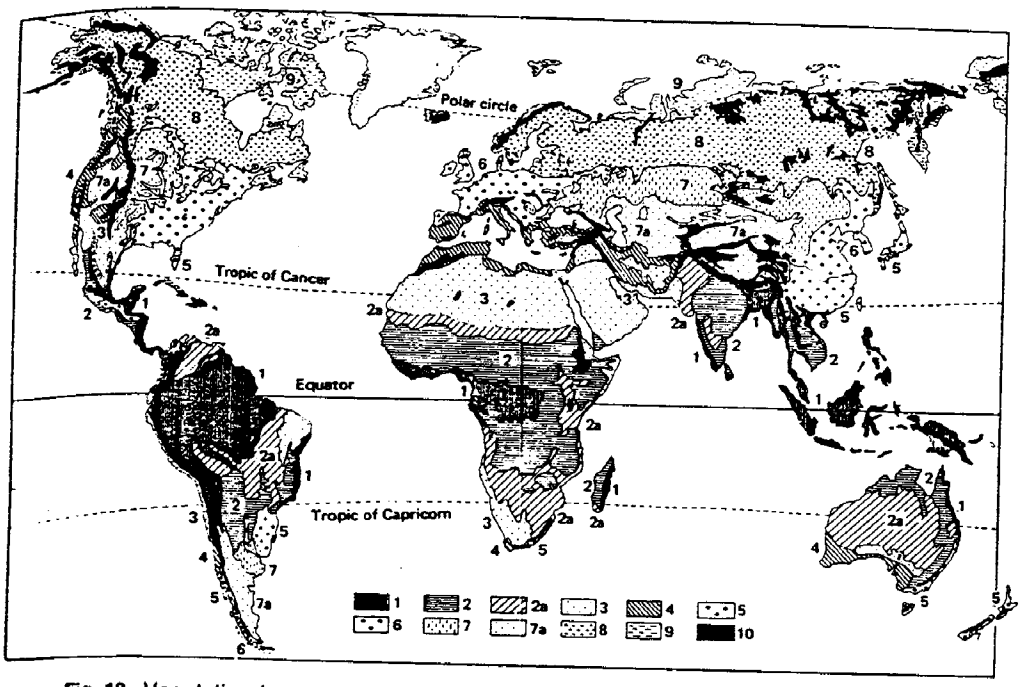


Fig. 19. Vegetational zones (much simplified, without edaphically or anthropogenically influenced vegetational regions). I. *Tropical and Subtropical Zones:* (1) Evergreen rain forests of the lowlands and mountainsides (cloud forests); (2) semievergreen and deciduous forests; (2a) dry woodlands, natural savannas or grassland; (3) hot semideserts and deserts, poleward up to latitude of 35° (see also 7a). II. *Temperate and Arctic Zones:* (4) sclerophyllous woodlands with winter rain; (5) moist warm temperature woodlands; (6) deciduous (nemoral) forests; (7) steppes of the temperate zone; (7a) semideserts and deserts with cold winters; (8) boreal coniferous zone; (9) tundra; (10) mountains. (From Walter, 1964/68.)

Figure 11.1

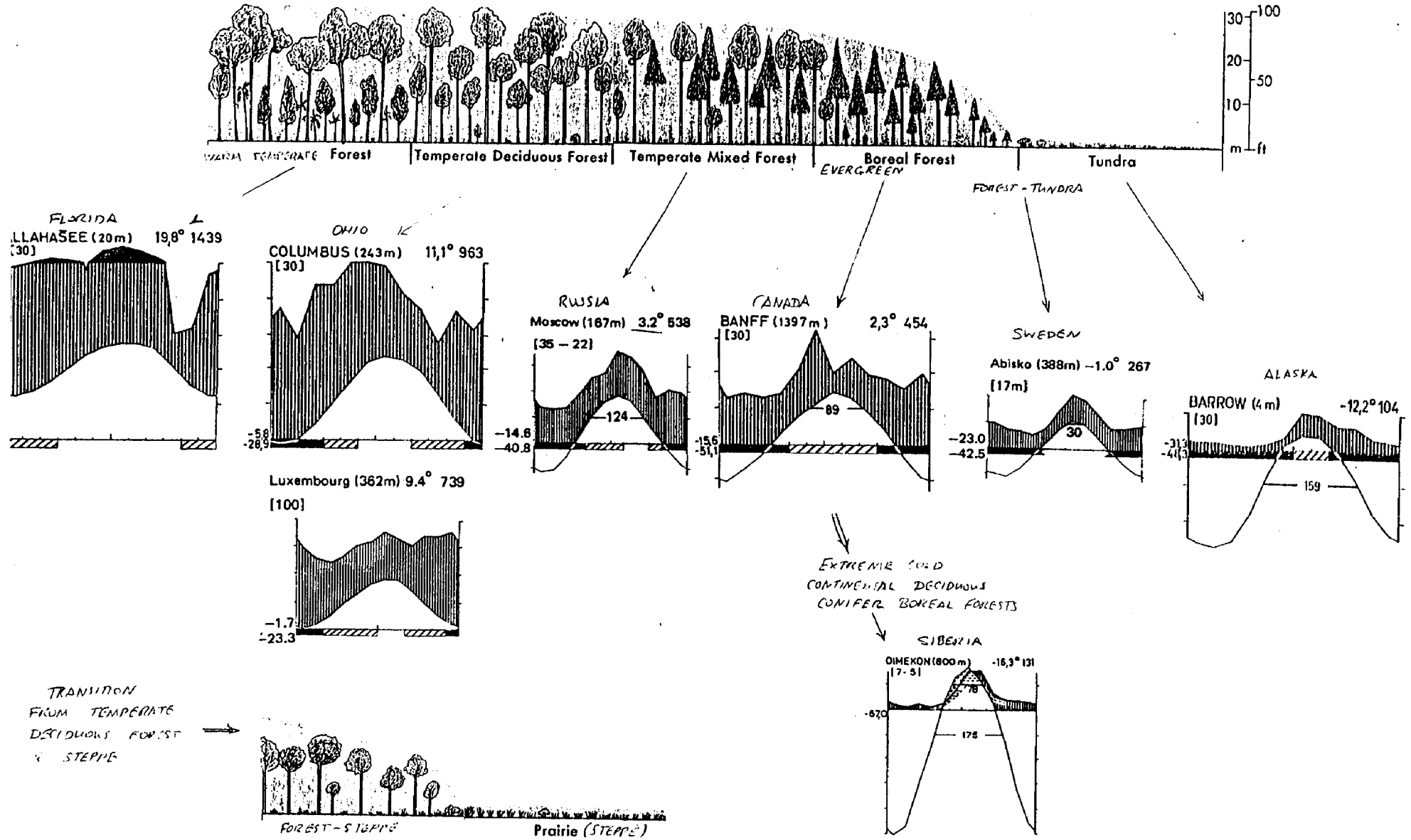
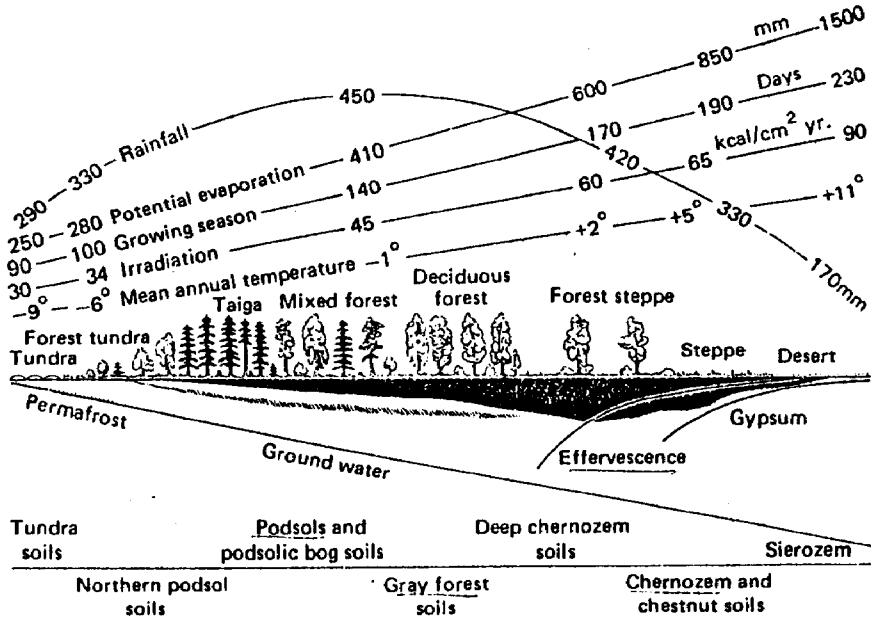

Temperate Deciduous Forest
Temperate Mixed Forest
Boreal Forest
EVERGREEN
Tundra
FOREST - TUNDRA
30
20
10
m
100
50
ft
FLORIDA
LLAHASEE (20m) 19,8° 1439
[30]
OHIO
COLUMBUS (243m) 11,1° 963
[30]
-5.8
-26.9
Luxembourg (362m) 9.4° 739
[100]
-1.7
-23.3
RWSLA
Moscow (167m) 3.2° 538
[35 – 22]
124
-14.6
-40.8
CANADA
BANFF (1397m) 2,3° 454
[30]
89
-15.6
-51.1
SWEDEN
Abisko (388m) -1.0° 267
[17m]
30
-23.0
-42.5
ALASKA
BARROW (4 m) -12,2° 104
[30]
159
EXTREME COLD
CONTINENTAL DECIDUOUS
CONIFER BOREAL FORESTS
SIBERIA
OIMEKON (800 m) -16,3° 131
[7-5]
78
-67.0
175
TRANSITION
FROM TEMPERATE
DECIDUOUS FOREST
& STEPPE
FOREST-STEPPE
Prairie (STEPPE)
Uman (216m) 7.0° 463
[30 – 34]
160
-9.5
-33.0
Chkalov (114m) 3.8° 385
[30 – 26]
-19.1
-41.7

FIGURE 11.2

Fig. 90. Schematic climate, vegetation, and soil profile of the east European lowlands from northwest to southeast: Black, humus horizon; diagonal shading, illuvial B-horizon. Vegetational season in the tundra corresponds to the number of days with a mean temperature above 0°C, elsewhere to the number of days with a mean temperature above 10° C. (From Schennikov; Walter, 1964/68.)



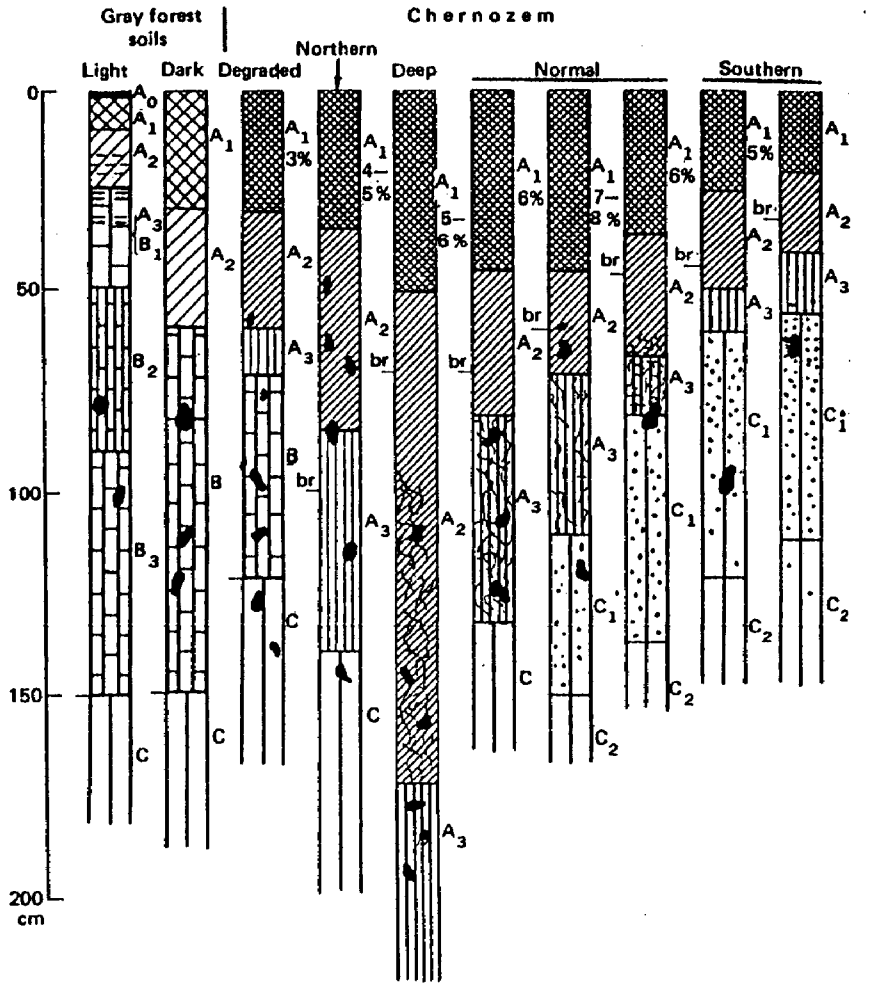


Fig. 91b. Schematic representation of the soil profiles of the forest-steppe and steppe zones (west of the Dnieper), from north to south. Percentages, humus content of the A_1-horizon; br, effervescence horizon; wavy lines, pseudomycelia ($CaCo_3$); small dots, $CaCO_3$ nodules; large black spots, krotovinas (abandoned ground squirrel burrows); horizontal dashes, laminated structure in forest soil. (From Walter, 1960.)

FIGURE 11.3

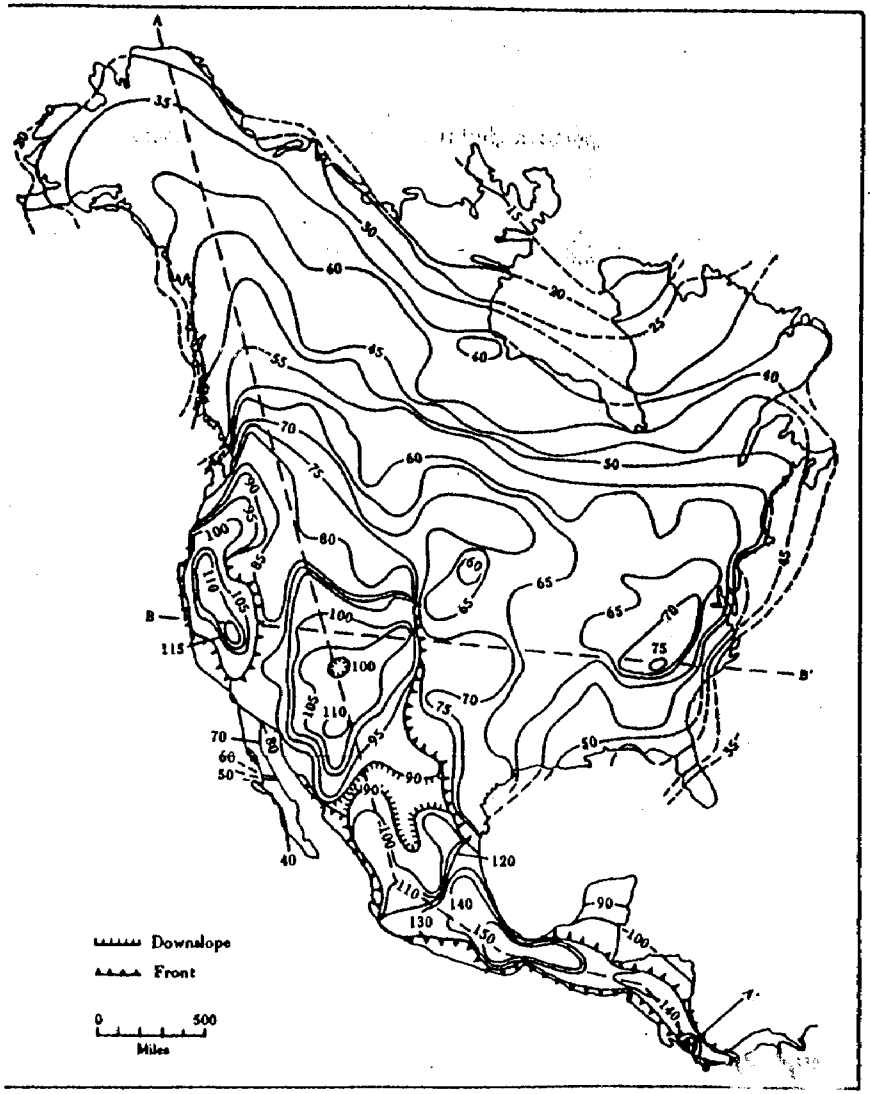


FIGURE 291

Species density contours for Recent mammals of continental North America. The contour lines are isograms for numbers of continental (nonmarine and noninsular) species in quadrats 150 miles square. The "fronts" are lines of exceptionally rapid change that are multiples of the contour interval for the given region. (After Simpson 1964.)

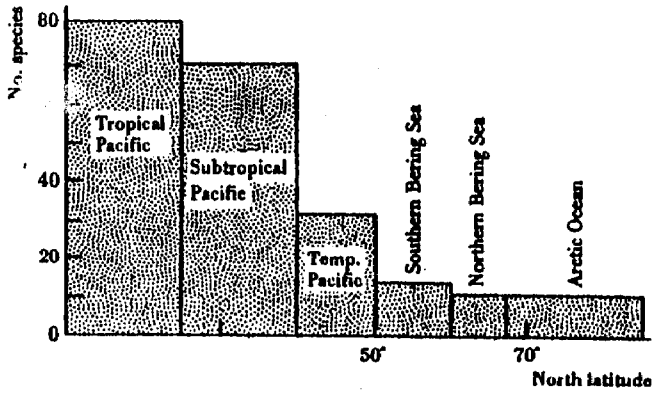


FIGURE 290

Tropical to polar gradient in species diversity for the calanid copepods of the upper 50 m of the Pacific Ocean. (After Fischer 1960.)

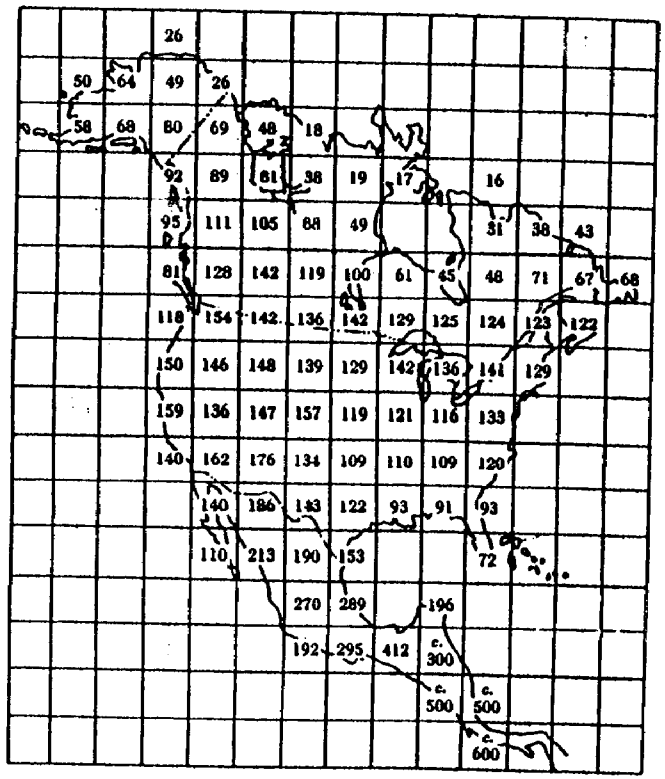


FIGURE 289

Numbers of breeding land-bird species in different parts of North America. (After MacArthur and Wilson 1967.)

FIGURE 11.4