TEMPERATE FORESTS

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GLOSSARY

evapotranspiration The process of transferring moisture from the earth to the atmosphere by evaporation of water and transpiration from plants: actual evapotranspiration as observed at a locality or potential evapotranspiration, given unlimited water availability.

neogene The Miocene and Pliocene Epochs, accorded the status of a period when the Tertiary is considered an era.

physiognomy The outward appearance or morphology of a community as determined by the growth forms of the dominant plants present.

sclerophyll A plant with tough, leathery, evergreen leaves, usually associated with drought resistance.

sere The series of stages in an ecological succession sequence.

temperate region Any locality with at least 1 month of frost (for continental areas) or with one or more months with a mean temperature lower than 18°C (for maritime-influenced areas), and with at least 4 months with a mean temperature higher than 10°C.

tertiary The earlier part of the Cenozoic Era, occurring from about 65 to 2 million years ago.

A COMPELLING CASE CAN BE MADE that the temperate forests are afforded less protection and are more at conservation risk than all other forest systems of the world. They are more altered and reduced in extent globally than any other forest type. Temperate forests currently cover only about 30–35% of their current potential extent versus about 45 and 65% respectively for tropical and boreal forests. Moreover, temperate forests are afforded less conservation protection on average than are tropical forests. Very few if any remaining temperate forests have avoided human impact. Only about 1% of the remaining Northern Hemisphere temperate broad-leafed forests is substantially unaltered and old growth; the vast majority are either managed for wood production, are in plantations, or they reflect the pervasive, long-term effects of human land use practices. Because some of the highest human population densities are found in the temperate forest biome, some of the lowest forest areas per capita globally occur in

a

Humid Temperate Domain

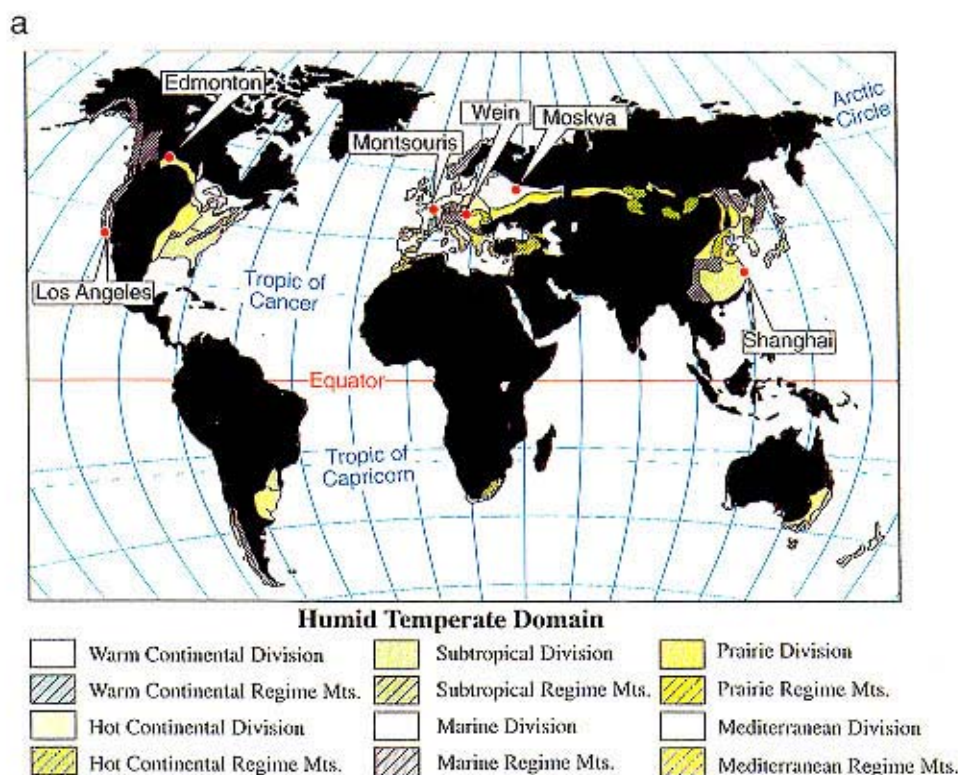|	Warm Continental Division		Subtropical Division		Prairie Division
	Warm Continental Regime Mts.		Subtropical Regime Mts.		Prairie Regime Mts.
	Hot Continental Division		Marine Division		Mediterranean Division
	Hot Continental Regime Mts.		Marine Regime Mts.		Mediterranean Regime Mts.

FIGURE 1   (a) Global distribution of the humid temperate ecoregions. These correspond to the potential distribution of temperate forest, grassland, and Mediterranean shrublands globally. (b) Representative climate diagrams for the various divisions of the humid temperate ecoregion domain [Reproduced with permission from R. G. Bailey, *Ecoregions: The Ecosystem Geography of the Oceans and Continents* (Figs. 6.2 and 6.3). © Springer-Verlag.]

this biome. Only the most isolated, inaccessible patches of forest remain unaltered by humans.

I. OVERVIEW

The temperate forests are globally important and unique. They host the largest and oldest organisms in the world. They serve as the world's major source of timber and wood products and are perhaps the only forests with some proven potential for sustainable management. The biomass of at least some temperate forests stands exceeds that of any tropical forest. The temperate forests of the world also provide critical ecosystem services locally and globally. Recent evidence indicates the global importance of carbon sinks in the temperate forest zone, especially in eastern North America. On a landscape level, temperate forests are critical to modulating hydrological, nitrogen, and carbon cycles. Although the biodiversity of temperate forests is typically much lower than that of tropical forests, some temperate forests approach the biodiversity observed at larger

spatial scales in the tropics. Temperate forest biodiversity hot spots with high levels of endemism rival in importance those anywhere. They have a unique evolutionary history divergent from either the tropics or the boreal regions. Moreover, Northern and Southern Hemisphere forests are as different from each other as either is from tropical or boreal forests. This contrast reflects striking differences in climate, biogeography, evolutionary history, and the impact of humans.

The objectives here are to provide an overview of the distribution of temperate forests globally; their structure and composition; evolutionary history; diversity, endemism, and rarity; ecosystems services provided; current conservation status; and current threats.

II. GLOBAL DISTRIBUTION PATTERNS OF TEMPERATE FOREST SYSTEMS

A global view of the forests of the world reveals everything from broad continuous expanses of trees to mosaics of small forest patches in the landscape and from
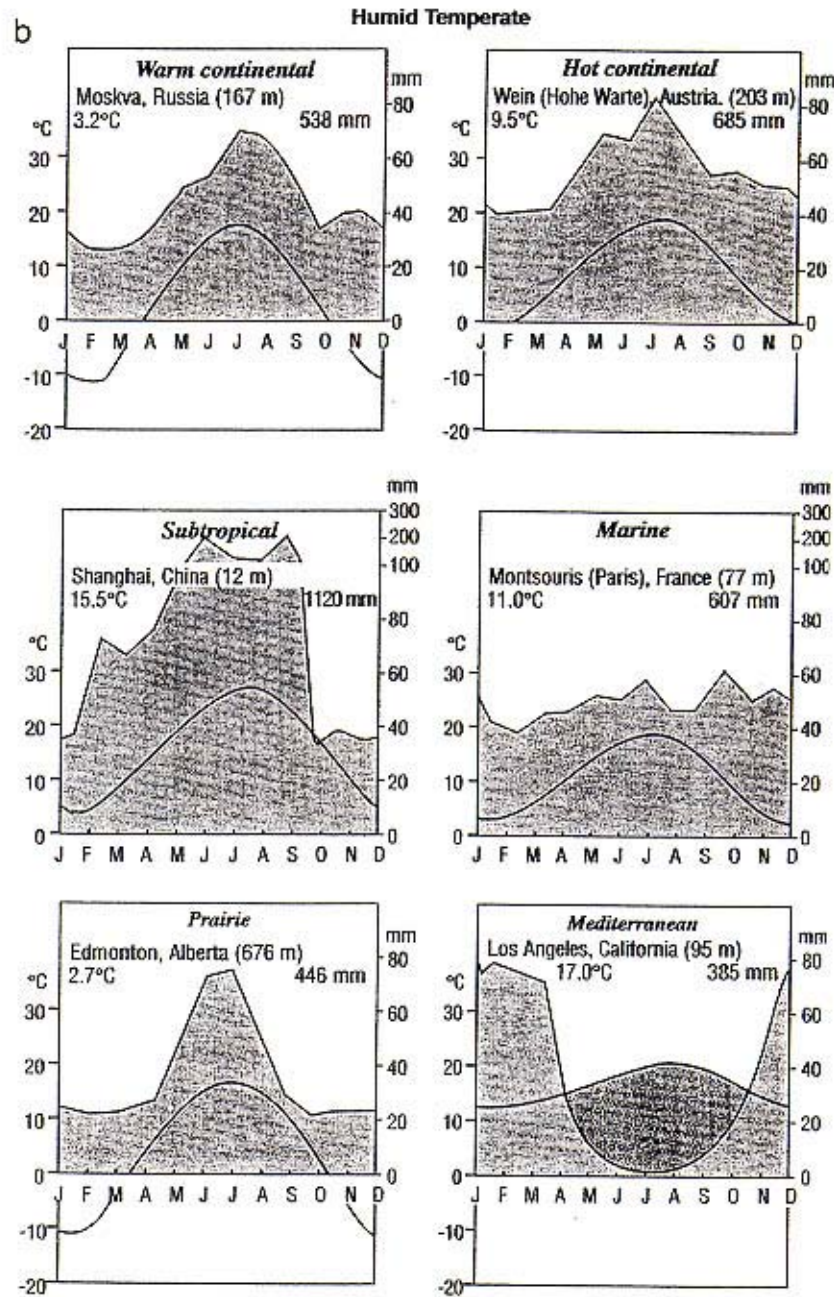
Humid Temperate

b

FIGURE 1   (continued)

dense, closed-canopy stands to open wooded parklands. As one progresses from the equator through the humid zones at midlatitude to tree line in the polar regions, changes in forest structure and composition typically occur gradually. Demarcating where the temperate forests begin and end along this continuum is difficult. Indeed, defining "temperate" is difficult. Of the many published maps portraying the extent of the temperate forest biome, few agree on boundaries. The broadest, most arbitrary definition of temperate forests includes all forested areas north or south of the tropics of Cancer and Capricorn, respectively. More common, general macroclimatic factors have been used to define boundaries. In such cases, the results are maps of the potential distribution of forests. Because of the pervasive effects of human and natural disturbances, such maps are considerably more extensive than those depicting extant forests (compare Figs. 1 and 2). Maps of existing forests

Global Distribution of Current Forests

Legend:
- Tropical Moist Forest
- Tropical Dry Forest
- Mangrove
- Temperate Broadleaf and Mixed Forest
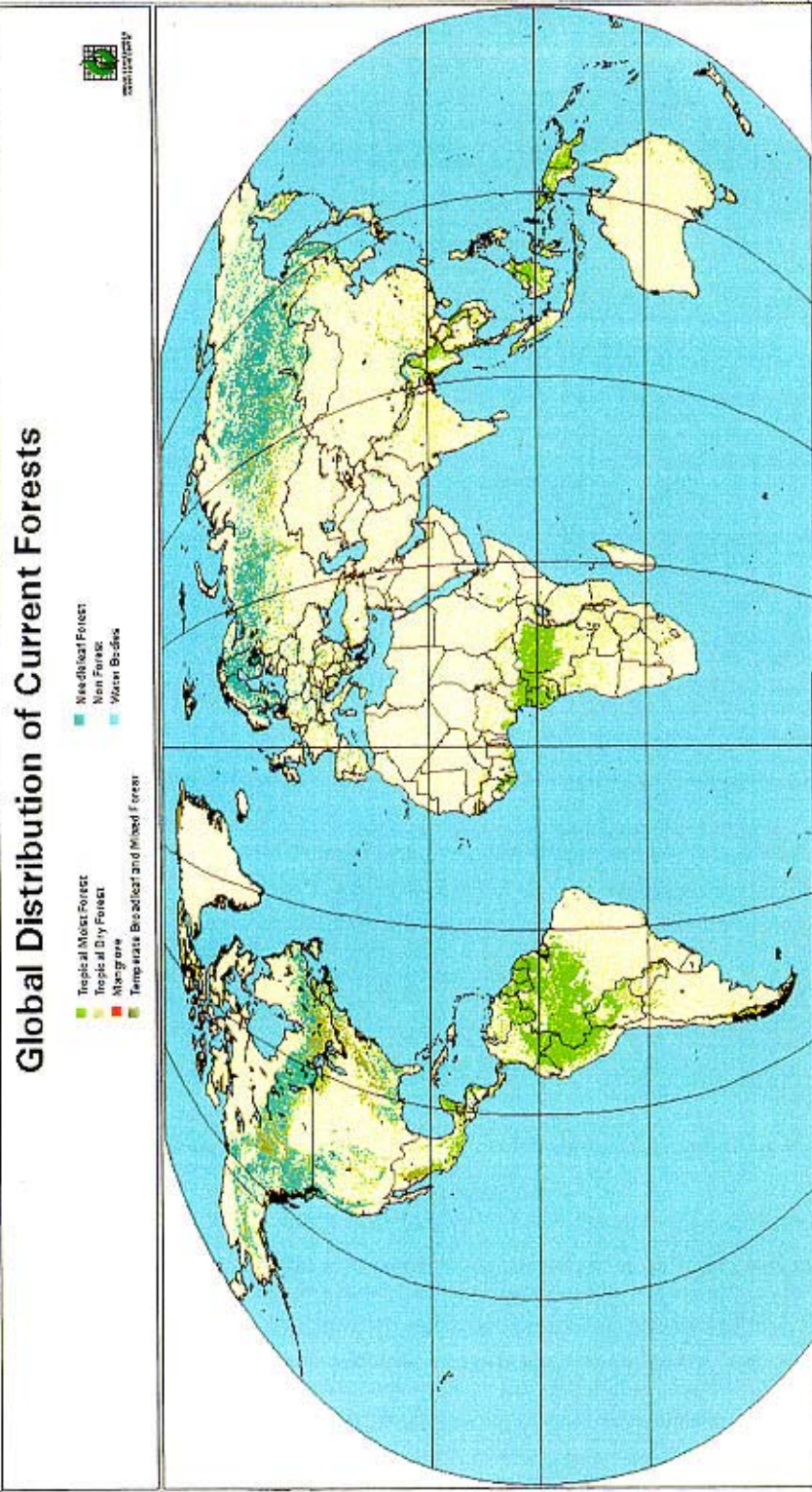- Needleleaf Forest
- Non Forest
- Water Bodies

FIGURE 2 The current distribution of forests globally. The data on which this map is based were assembled by the World Conservation Monitoring Centre in collaboration with the World Wide Fund for Nature and published on the World Wide Web (http://www.wcmc.org.uk/forest/data/wfm.htm).

are generally derived from remotely sensed images, but even these vary in what is portrayed as forest. In consequence, Fig. 2 does contain acknowledged, inherent errors in misclassification and omission.

Figure 1a shows where globally temperate forested landscapes may potentially be found, delimited by the humid temperate domain or ecoregion. The boundaries are based on macroclimate, which distinguishes this zone from the polar ecoregion with boreal forests, the humid tropical region with tropical forests, and the dry ecoregions dominated by arid grassland/savanna or desert vegetation. The latitudinal boundaries are set by thermal regime as modified from Köppen and Trewartha, who developed the most commonly used climate classification scheme. These zones are similar to those of Holdridge and Walter but differ in detail. The temperate region defined in Fig. 1 includes any locality with at least 1 month with frost (for continental areas) or with 1 or more months with a mean temperature lower than 18°C (for maritime-influenced areas) and with at least 4 months with a mean temperature higher than 10°C. Moisture availability sets the remaining boundaries, with the humid temperate domain bounded by where precipitation equals or exceeds potential evapotranspiration. Most other maps of temperate forest biomes employ variations on this theme.

Biome or community boundaries are only approximate, reflecting the difficulty inherent in delineating features that are fuzzy spatially and temporally. Boundaries are often either broad ecotones or a mosaic of patches. Moreover, these patterns will change as the climate, biotic composition, or disturbance regimes inevitably change over time. Consequently, any map will be at best an abstract representation of reality.

Within any biome or ecoregion, subdivisions of convenience may be designated. In Fig. 1, the humid temperate domain can be subdivided into subclimatic zones: marine (areas with temperature fluctuation moderated by oceanic influences and with elevated moisture availability, in some cases producing rainforests) and continental (areas with comparatively greater temperature fluctuation and greater probability of drought). Temperature zones are delineated as well: subtropical (defined as having 8 or more months with mean temperatures higher than 10°C), continental hot temperate (4–7 months with temperatures higher than 10°C, warmest month higher than 22°C, and coldest month lower than 0°C), and continental warm temperate (as for hot temperate, but with warmest month lower than 22°C).

The excess of annual precipitation over evapotranspiration becomes less as one moves away from oceanic influences on continents at midlatitudes. Thus, temperate forests tend to be replaced by grasslands in central North America, central and eastern Europe, central eastern Asia, and eastern South America. This may be augmented by fire and grazers or browsers. The boundary between forest and grassland may be a broad transitional, open wooded parkland with scattered trees, or a broad mosaic of forest and grassland patches with forests restricted to favorable soils, sites with more moisture, or sites protected from fire.

Forests may also be replaced as aridity increases in Mediterranean climates with winter rainfall–summer drought regimes. As fire becomes a pervasive element in the landscape, forests tend to be replaced by sclerophyllous shrublands, thickets, or sometimes open woodlands. Again, the transition may be abrupt or a gradual mosaic, with forest patches restricted to favorable soils and/or moist sites protected from fires.

The boundaries between the temperate forested regions and the adjacent boreal or tropical regions are often imprecise. In both cases, there can be a very broad transition zone with considerable overlap in species composition. The subtropical–tropical boundary set by the 18°C mean monthly isocline is quite arbitrary. Some have attempted to show that this boundary approximately corresponds to the natural poleward limits of the distribution of palms.

Boreal forests are distinguished only for the Northern Hemisphere as typically conifer-dominated forests within specified climate regimes (i.e., monthly mean temperatures all lower than 22°C but 1–3 months with means higher than 10°C). This boundary approximately corresponds with the mean position of the summer polar front in the Northern Hemisphere.

Confusion remains regarding the classification of conifer-dominated forests. The boreal forests of the Northern Hemisphere and the conifer forests of the North American Pacific Northwest, the Asian Pacific northeast, and the Southern Hemisphere are treated differently by different authors. Using the previously mentioned temperature criteria, all of the Southern Hemisphere forests, except perhaps the southern tip of South America, would be classified as temperate, as would most of the Pacific forests of Asia and North America. The climatic definition for the temperate zone forests will be used here.

There are parallel inconsistencies in classifying certain subtropical forest regions. For example, northern Indian forests, which are climatically subtropical, are usually classed as tropical. The same is true for forests with some temperate affinities in subtropical regions of southern Brazil.

Dealing with mountainous areas is problematic since they typically contain multiple ecoregions (tropical or temperate to boreal and alpine depending on elevation and latitude). In the Americas, Africa, eastern Asia, and Australasia, one can find discontinuous bands of forest with temperate affinities extending from sea level in the temperate zone well into the tropics at higher elevations. The most common resolution is to classify all forest elements as part of unclassified mountainous regions, as part of the surrounding domain, or as separately classified biome units within the domain. One consequence of this inconsistent classification is to obfuscate biotic patterns in some of the most important global hot spots of biodiversity.

The temperate forest biomes, thus defined, comprise about 14,600,000 ha (estimates vary). By far the largest actual or potentially forested landscapes occur in the Northern Hemisphere (80% or more) (cf. Fig. 1 and Table II). The regional biomes include (i) eastern North America from the Atlantic coast west to about 95° latitude and from about 45° latitude south to about 28°; (ii) western North America from about 35° north to about 60° (and mainly from the Sierra–Cascade ranges, west); (iii) western and central Europe from the Atlantic coast north to about 60° and east through eastern Europe, but excluding the Mediterranean coastal zone and much of Spain, and then extending in a narrow strip around 55° east across Russia to west central Asia; (iv) a small, discontinuous temperate forest zone in the Middle East, especially along the south coast of the Black Sea, to the southern Caucasus and to the southern Caspian Sea; (v) eastern Asia from about 50° south to about 25° in southern China and from Japan and the Pacific coast northwest to about 120° and southwest to about 100°; and (vi) northern south Asia (India) and adjacent areas.

In the Southern Hemisphere the extent of temperate forests is much more restricted in extent: (i) eastern, coastal Australia from about 25° south to Tasmania, plus the southern tip of Western Australia; (ii) most of New Zealand; (iii) southern Chile and adjacent Argentina from about 40° south to about 55°; (iv) a small area of southern Brazil just below the tropic of Capricorn, plus adjacent Paraguay and Argentina; and (v) small patches of coastal and interior forest in south and southeastern South Africa.

Table I summarizes the potential and current extent of forested areas within each of the 11 temperate forest biomes, from World Conservation Monitoring Centre (WCMC, see Fig. 2), World Wide Fund for Nature (WWF), and the Food and Agriculture Organization data based on approximately 25 forest types. The more

TABLE I

Temperate Forest Cover by Regions

Forested region	Potential extent of temperate (mesic) forest cover ($km^2 \times 10^6$)	Maximum potential forest extent (including dry forests, woodlands, and thickets) ($km^2 \times 10^6$)	Current estimated extent of temperate forest cover ($km^2 \times 10^6$)	Conservation areas (IUCN classes I–VI) ($km^2 \times 10^3$)
Europe (including Mediterranean)	3.30	3.91	0.85–1.1	44.0–54.0
Russia	1.12	1.13	0.26–0.36	11.0–36.0
East Asia	3.21	3.79	0.62–0.75	24.0–26.0
North America	4.26	4.72	2.13–2.17	117.0–132.0
Eastern north	3.56	3.72	1.63–1.57	—
Western (Pacific)	0.7	1.0	0.5–0.6	—
Middle East	0.36	0.61	0.05–0.11	1.0–4.0
South Asia	0.87	1.34	0.20–0.31	20.0–34.0
South America	0.7	1.8	0.4–0.52	45.0–69.0
Southern (Chile and Argentina)	0.60	0.8	0.25–0.30	51.0–54.0
Southeastern (Southern Brazil and adjacent countries)	0.14	1.0	0.12–0.22	12.0–15.0
Australia	0.45	1.64	0.03–0.66	4.0–44.0
New Zealand	0.23	0.25	0.04–0.08	17.0–18.0
Southern Africa	0.1	0.4	0.01–0.1	4.0–6.0
Total	14.6	19.6	4.7–6.2	287.0–423.0

TABLE II

Worldwide Forest Cover

Forested biome	Potential extent of mesic forest cover ($km^2 \times 10^5$)	Maximum potential extent (including dry forests, woodlands, and thickets) ($km^2 \times 10^6$)	Current estimated extent of forest cover ($km^2 \times 10^6$)
Boreal forests	12.2	18.5	8.0–11.5
Tropical forests	29.0	40.0	14.2–15.6
Temperate forests	14.6	19.6	4.6–6.8
Total	55.8	78.1	26.8–33.9

conservative estimate of potential forest (Table 1, column 2) is for mesic forest coverage only. Maximum potential extent (column 3) includes all types of dry forest, woodlands, and thickets but not savannas or other sparsely treed landscapes (i.e., forest cover <30%). The corresponding ranges under current forest extent are shown in the fourth column. These data are only approximate. The base data were obtained from different sources, with different categories or forest type classes reported for different regions. In some cases, conflicting information on forest cover is reported from different sources.

Almost 80–90% of the temperate forest biome types are found in the Northern Hemisphere. For current forest cover, the data are only slightly less for northern dominance. The major northern forest biomes of Europe, eastern North America, and east Asia all cover about the same potential area. However, eastern North America has by far the largest cover remaining (40–45%). The Middle East has the smallest percentage of potential forest cover (13–18%), followed by east Asia (<20%) and Europe (25–30%); western North America has the highest percentage of remaining forests (60–75+%). Estimates for western North America are only approximate (estimated from WCMC forest type information and other data), with the eastern and southern boundaries for this system fuzzy and disjunct. Similarly, the estimates for forest cover in south Asia are only approximate. For some regions these data can be deceptive. Much of the forest covering Europe, especially in western Europe, is intensively managed plantation or seminatural forest. The same is true for Japan, even though it retains more than one-third of its potential forest cover. China retains almost 12% of its original forest, but most of this is in the boreal to northernmost, mixed conifer forests.

Southern temperate forests are fragmented into six or more regional biomes, all much smaller in extent than their northern counterparts. The extreme ranges in

forest cover tabulated for some of the southern biomes reflect the large contribution of dry forest systems within the regions. The largest of the southern biomes comprises the forests of southern Chile and adjacent Argentina. The smallest of all temperate forest biomes is that found in South Africa, perhaps rivaled in size only by the forests of Western Australia. Most significantly, the South African forests are the richest of all temperate forests in tree families, genera, and possibly species (certainly if the complete tree flora is included).

Compared to other forest system globally, the temperate forest biomes covers a slightly greater area than boreal forests. Boreal and temperate forests together approximate the tropical forests of the world (Table II).

III. GENERAL CHARACTERIZATION OF TEMPERATE FORESTS

A. Physiognomic Features

Each of the previously discussed 11 temperate forest regions may be characterized by general physiognomic features (i.e., the outward appearance and structure of the dominant vegetation):

1. Eastern North America: dominated by broadleaf deciduous forests, mixed with conifers to the north, locally dominated by conifers under drier, successional conditions or in fire-prone areas in the southeast and northwest, plus small patches of broadleaf evergreen forests in the south. Closed forest systems predominate.

2. Western North America: dominated by evergreen conifers with broadleaf trees contributing little to the forests; some northwestern coastal areas support rainforests (i.e., rainfall in excess of 2000–3000 mm per annum). The eastern edge of this biome is discontinuous and grades to open conifer woodlands and montane

boreal forests. To the south it grades to a mosaic of conifer or broad-leafed evergreen forests and woodlands or shrublands.

3. Europe: mainly broadleaf deciduous forests, mixed with conifers to the north and in mountainous areas, and to the south grading to a mosaic of broadleaf evergreen forests (many sclerophyllous leafed), conifer-dominated forests, and shrublands under Mediterranean climate influence.

4. Middle East: mainly broadleaf deciduous forests with a mosaic of broadleaf evergreen, sclerophyllous, and conifer forests and woodlands. Rainforests occur very locally near the southeastern Black Sea coast.

5. Eastern Asia: mainly broadleaf deciduous forests mixed with conifers to the north and broadleaf ever-green forests to the south; mostly mesic closed forests. Evergreen broad-leafed rainforests occur locally in southeastern Japan, one of the rarest forest types found in the Northern Hemisphere.

6. South Asia: dominated by broad-leafed evergreen to semievergreen monsoonal forests; temperate mixed forests (locally rainforests) occur in the foothills of the Himalayas.

7. Australia: dominated by broadleaf evergreen for-ests (mostly sclerophyllous); small patches of closed forest (<70% cover) and extensive areas of open forests grading to woodlands. Very restricted patches of rain-forest are found in southeastern Australia and western Tasmania.

8. New Zealand: dominated by conifers and mixed with broadleaf evergreen forest patches, especially on the north island and locally on the south island. The western forests in New Zealand are rainforests.

9. Southern South America: dominated by broadleaf evergreen forests with some conifers. Broadleaf decidu-ous forests prevail in the southernmost areas and at higher elevation in the Andes; rainforests are restricted to the Pacific slope south of about 40° latitude.

10. Southern Brazil: characterized by the presence of southern conifer forests; elsewhere in this zone the forests are dominated by evergreen or semideciduous angiosperms with patches of open forest and thicket to the west.

11. South Africa: mixed broadleaf evergreen (many sclerophyllous leafed) with some conifers forming a very patchy mosaic in the landscape with thickets, shrublands, and savannas.

B. Dominant Floristic Features

The community dominance and floristic affinities for these regions as they exist today can be characterized very broadly. Detailed descriptions and characteriza-tions may be found elsewhere. There are broad floristic affinities among the forested biomes in the Northern Hemisphere with many shared families and genera both now and in the fossil record. These include older lin-eages from the Tertiary flora of Asiamerica and recent lineages that evolved under cooler and/or drier cli-mates. The Southern Hemisphere forests are very differ-ent floristically, with few important families or genera shared with the north. There are some Gondwanan lineages in common now or in the fossil record. How-ever, the floras today reflect considerable divergence with many tropical affinities and many fewer common links than are seen in the north.

In eastern North America, in the northeast birch, maple, beech, and hemlock (*Betula*, *Acer*, *Fagus*, and *Tsuga*) dominate the landscape, with the latter two tend-ing to form monodominant stands late in succession. Farther south and west the forests tend to be dominated by oaks (*Quercus* spp.) or hickories (*Carya* spp.). The central sections, especially in the central to southern Appalachians, tend to be the richest, with a diminished tendency toward dominance by one or a few canopy species, although the highest regional tree diversity is found in the southeast. In the extreme south, small patches of evergreen forest are found in protected areas dominated by evergreen oaks and *Magnolia*. Much of the southeast is now dominated by pine (*Pinus taeda*) plantations. Fire successional pines also dominate parts of the northwest. Drier sites throughout tend to be dominated by oaks or conifers, especially pines; wetter sites are dominated by conifers (e.g., *Tsuga* to the north and *Taxodium* to the south) or by locally adapted broad-leafed deciduous species (e.g., *Ulmus*, *Nyssa*, and *Acer*).

Western North American forests are dominated by a small number of large, long-lived conifer species; de-ciduous angiosperms are only minor components. The Pacific Coast rainforests are dominated by hemlocks (*Tsuga*), firs (*Abies*), spruce (*Picea*), and/or cedar (*Thuja*) from Alaska south to Washington State. Doug-las fir (*Pseudotsuga*) becomes important in the central coast. Timber industries in these zones tend to actively manage the landscape for monospecific stands of native species (e.g., Douglas fir). Fragmented stands of red-woods (*Sequoia*), which globally are the tallest trees, occur more southerly extending to central California. On the drier eastern slopes of the coastal mountains (central sections), pines, Douglas fir, and sometimes poplars (*Populus*) dominate the landscape. Further south in the Sierras one finds local dominance by *Sequoiadendron*, the most massive tree globally, and *Pinus aristata*, the longest lived tree. Drier, lower eleva-

tion landscapes in the south (California) may be dominated by broad-leafed evergreen forests of tanoaks (*Lithocarpus*) and madrone (*Arbutus*) or open oak, pine, or mixed woodlands, which grade into Mediterranean shrublands or grasslands.

European forests are highly disturbed and fragmented following centuries of human habitation. Central European forests tend to be dominated by beech (*Fagus*) on many intermediate sites and by various oaks (*Quercus*) on drier and slightly wetter sites or very acidic sites. The wettest sites tend to be dominated by birches (*Betula*). Many of these forests have been converted to *Picea* or *Pinus* plantations. For example, German forests have gone from 90% deciduous broadleaf domination to 80% *Picea* plantations. To the south there is a transition to dominance by evergreen oaks and pines under Mediterranean influence. To the north and throughout much of the central uplands, conifers (*Pinus*, *Picea*, *Abies*, and *Larix*) can locally dominate the landscape or there are mixed forests with beech and birch. Many of the European forests not in plantation are still actively managed for timber products.

The Middle Eastern forests of northern Turkey to the Caucasus and the southern Caspian Sea are probably the poorest known and least studied of temperate forests. In the western Mediterranean-influenced zone, one finds sclerophyllous forests and woodlands dominated by pines and oaks. Along the coast of the Black and Caspian Seas and the southern Caucasus (Colchian and Hyrcanian regions) one finds highly diverse, mesic deciduous forests with oaks, maples, beech, chestnut, and many other species. At higher elevations the forests are dominated by beech with conifer-dominated or mixed stands above. Drier sites in the landscape are dominated by open oak forests or woodlands. Many of these forests have experienced a long history of human occupation and associated agriculture with overgrazing.

East Asia has the most diverse forests in the Northern Hemisphere. Along the Pacific coast in northern Japan, southern Russian, and China, one finds forests similar to those of the North American Pacific Northwest, with conifer dominance but also mixed with broad-leafed species of maples, birches, limes (*Tilia*), and elms. Central China has been extensively cultivated for centuries, and there is very little forest cover left. Remnant tracts here indicate a rich diversity of mixed deciduous trees mentioned previously plus many other genera, including oaks, elms, poplars, ash (*Fraxinus*), and rowan (*Sorbus*), with a rich understory. Locally, the understory may be dominated by bamboos. The same pattern is seen in Korea and Japan. In southern Japan, much of the forest is managed for native *Cryptomeria*, and in

the north it is managed for *Abies* or *Picea*. South of the Yangtze River in China and in eastern and southern Japan the broad-leafed evergreen species increase in dominance as one approaches subtropics. These are the most diverse temperate forests in the Northern Hemisphere, with many of the same genera listed previously. However, these have become highly fragmented through human disturbance. In southern China there is a shift to forests with strong tropical affinities.

The temperate forests of south Asia are difficult to categorize. Most of the lowland and premontane remnant forests of northern India are climatically subtropical but the flora has strong tropical affinities. There is local strong dominance by Sal (*Shorea robusta*) and bamboos. In the northern hill forests there is a transition to strong temperate affinities with high species diversity. Oaks mixed with Lauraceae dominate the forest, but maples, *Castanopsis*, and *Magnolia* occur. In the montane zone diverse oak forests are mixed with conifer (*Abies*, *Picea*, and *Pinus*) forests and patches of *Rhododendron*. As is the case in much of Asia, these forests have been long affected by human disturbance. Throughout the lower elevations small stands of *Eucalyptus*, teak, pine, or *Populus* plantations are common.

The subtropical forests of the eastern mountains and coastal areas of Australia and the small areas of forest in Western Australia are dominated by the numerous sclerophyllous *Eucalyptus* species. Locally, stands tend to be dominated by one or only a few species. The eucalypt forests tend to form open-canopy stands grading to woodlands. The tallest angiosperm trees are found here. Only on Tasmania and in scattered pockets along the eastern mountain chain is there local dominance by closed-canopy or temperate rainforest species, including the southern beech (*Nothofagus*) and various southern conifers (*Dacrydium*, *Phyllocladus*, *Arthrotaxus*, or *Araucaria*). Throughout much of southeastern Australia plantations of Monterey pine (*P. radiata*) have become a pervasive component of the landscape.

The forests of New Zealand tend to be either multistoried mixed conifer–broadleaf with species composition varying across the landscape or low-diversity southern beech (*Nothofagus*) forests. The mixed forests dominating in the lowlands have a scattered overstory of *Agathis* in the north or various podocarps (e.g., *Podocarpus*, *Dacrycarpus*, and *Phyllocladus*), with a subcanopy of Lauraceae (*Beilschmeidia*), Myrtaceae (*Metrosideros*), Cunoniaceae (*Weinmannia*), and many other families and genera. Evergreen *Nothofagus* forests may form pure dense canopies in subalpine areas and may be a component in the lowland forests along with other broad-leafed species.

The forests of southern South America are confined to Chile and adjacent areas of Argentina. They vary from small remnants of sclerophyllous forests and woodlands in the Mediterranean zone to the species-rich Valdivian rainforests, the species-poor but still extensive north Patagonian and Magellanic forests, and depauperate deciduous *Nothofagus* forests at higher elevations and the interior south. The sclerophyll forests were dominated by *Acacia caven* and other species, with deciduous *Nothofagus* forests at high elevation. The Valdivian forests may be either broadleaf dominate, with *Nothofagus*, *Eucryphia* (Eucryphiaceae), *Laurelia* (Monimaceae), *Weinmannia*, and other species, or mixed with conifers [*Podocarpus*, *Araucaria*, or *Fitzroya* (Cupressaceae)]. The north Patagonian/Magellanic forests are dominated by evergreen *Nothofagus* mixed with *Podocarpus*, *Weinmannia*, and *Drimys* (Winteraceae). To the south, one of the deciduous *Nothofagus* species (*N. pumilo*) forms a pure stand or is mixed with *N. betuloides* at timberline. Many of the remaining Chilean forests are being clear-cut for chips and converted to *P. radiata* or *Eucalyptus* plantations.

The southeastern forests of Brazil have many south temperate affinities. These forests are characterized by the presence of *Araucaria*. However, other south temperate components include *Podocarpus*, *Weinmannia*, and *Drimys*, plus Sapindaceae, Proteaceae, and Myrtaceae. These forests have been largely cleared for agriculture. The subtropical forests to the west in adjacent Paraguay and Argentina have more tropical affinities.

The forests of South Africa are some of the richest in tree species of any in the temperate zone. However, this is also the smallest of all temperate forest biomes, and it is highly fragmented into many small forest patches. It is not clear how forest cover has changed during the Pleistocene. These forests do have south temperate affinities, with the presence of *Podocarpus*, Cunoniaceae, and Proteaceae, but the majority of the temperate forest flora have tropical affinities. Despite these tropical affinities, the level of tree endemism is high for a continental area contiguous with tropical forests. The "Afromontane" forest elements extend from southernmost South Africa at sea level to the mountains through northeastern Africa. The coastal, Indian Ocean (Maputaland/Pondoland) forests are quite different floristically, with high diversity and many local endemics. The vast majority of the forested landscape is now in *P. radiata* or *Eucalyptus* plantation.

IV. TRENDS IN BIODIVERSITY

Comparing trends in biodiversity within and among regions is fraught with difficulties. The results can differ depending on the scale of the sample unit compared (i.e., 0.001 vs 1, 1000, or 100,000,000 ha). For many regions of the world, data are available only for a limited scale range. For example, in east Asia there are very few accessible data records for small plots (0.1–100 ha). In other regions (e.g., the Middle East), species diversity numbers are either estimates for large areas or entirely lacking. For many records the number of tree species may be accurately reported but the number of herbaceous, especially ephemeral, plants may be significantly undercounted or not reported at all. Even simply listing tree species numbers can be misleading because authors vary widely in delimiting the threshold size for what constitutes a tree. Likewise, authors vary in classifying vegetation type with which tree taxa may be associated (closed forest to sparsely treed parkland). Nevertheless, some trends appear robust.

Table III summarizes regional tree taxon richness from a variety of different sources, and Fig. 3 plots tree richness tallies against area for 75 forest sample sites throughout the temperate zone (spanning 10^{-2} to 10^8 ha). Despite this large range in areas and the inherent variation in estimates and counts, there are significant differences in tree richness among biomes and between hemispheres. For these data, greater tree species richness occurs in the Southern Hemisphere across the full range of areas surveyed (Fig. 3). This is also reflected
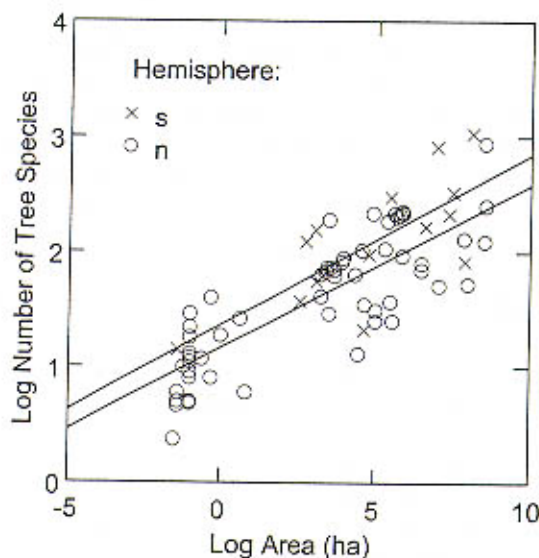

FIGURE 3 The relationship between tree species numbers and area sampled is shown, log transformed for both variables. The samples are from a wide range of different sources for most of the temperate zone forest biomes. These are simply classified here as Northern (n) and Southern (s) Hemisphere localities with best fit linear regression lines. There were significant differences between hemispheres ($p = 0.024$, $n = 75$, $r^2 = 0.695$) and among regions ($p < 0.001$, $r^2 = 0.916$).

TABLE III

Tree Species Diversity Patterns across the Temperate Forested Region

Region	Families	Genera	Species	Genus:family	Species:genus	Forest biome maximum extent (km² × 10³)
Europe	21	43	124	2.0	2.9	3300–3910
East Asia	67	177	876	2.6	4.9	3210–3790
Eastern North America	46	90	253	2.0	2.8	3560–3720
Western (Pacific) North America	24	47	131	2.0	2.8	700–1000
Chile	29	40	83	1.4	2.1	330–370
Southern Brazil	25	45	77	1.8	1.7	<100
Southeast Australia	37	78	331	2.1	4.2	300–700
New Zealand	47	74	212	1.6	2.9	230–250
Southeast South Africa	88	280	598	3.2	2.1	20–50

in the absolute number of families and genera. For species, the totals are similar, but the tabulated survey covers only a small part of the diverse tree flora for Australia and South Africa, respectively, and only part of southeastern Australia and Tasmania and Kwazulu-Natal province and adjacent Transkei. If all the tree species are included for South Africa alone (well over 1000 species in 370 genera and 97 families), the species numbers would be higher in the Southern Hemisphere despite the fact that southern forests only cover 10–20% of the area of northern forests. On an area basis, the taxon richness of the southern forests is at least an order of magnitude greater than that of the north.

This high southern diversity is contributed largely by the flora of South Africa, arguably one of the richest per unit area of any biome globally. Australia and New Zealand also contribute to this southern richness, each having a taxon richness per unit area of 4–10 or even 100 times that of northern forested regions. Just the rainforests of New South Wales and Victoria, covering less than 200,000 ha, have more than 250 tree species (not all included in Table III). Even the Chilean forests, perhaps the most depauperate in tree species of any temperate forest biome, have more taxa per unit area than any northern biome (except for total species in east Asia).

Among northern temperate forest biomes, east Asia has by far the richest tree flora. Europe and western North America are the most depauperate, with Europe having the lowest tree taxon diversity per unit area globally.

Figure 4 shows analogous species area data for all vascular plants tallied for about 200 plots or regions (spanning 10^{-5} to 10^8 ha) across all temperate forest biomes. Here, the hemisphere trends are reversed. The north has a slight but significantly higher total vascular

flora than the south across the range of sample areas. East Asia and the Middle East (the latter, a smaller sample size) tend to have the highest vascular plant diversity, and New Zealand, South America, and western North American forests tend to have the lowest vascular plant diversities. Forested systems in eastern North America, Europe, Australia, and South Africa tend to be intermediate across areas sampled. There is a dramatic decrease in species diversity toward the pole, more so in the Southern Hemisphere. In pairwise comparisons at intermediate sample areas the trends tend to hold. The vascular plant flora for east Asia at 0.5–10
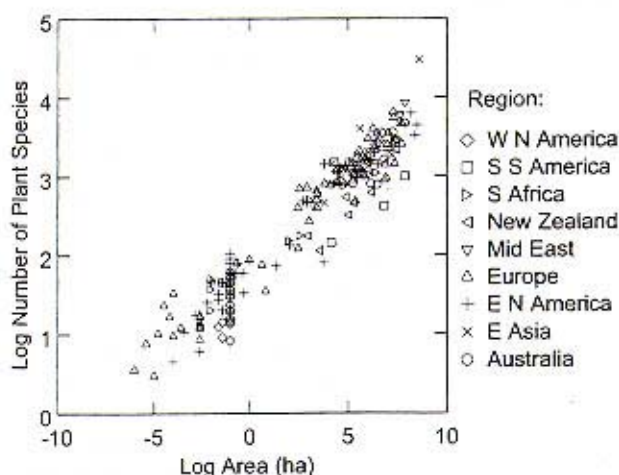

FIGURE 4 The relationship between total vascular plant diversity and area samples is shown, log transformed for both variables. The samples are from a variety of different sources covering most of the temperate zone forest biomes. The samples are classified by the biome region from which they were obtained. Significant differences are found between hemispheres ($p = 0.005$, $r^2 = 0.924$, $n = 198$) and among regions ($p < 0.001$, $r^2 = 0.938$).

ha is significantly richer than that of Europe or eastern North America. However, few differences can be seen among regions at the smallest plot sizes (<0.01 ha).

Trends in alpha, beta, and gamma diversity vary considerably within and among regions. Some of the large- to intermediate-scale patterns in species richness are undoubtedly related to spatial landscape heterogeneity. Regionally, high levels of species richness are associated with mountains [e.g., the Smoky Mountains (east North America), the Pyrenees, Alps, or Balkan Mountains (Europe), and the Sichuan Mountains or Mount Halla (east Asia)]. Complex mosaics of vegetation types [e.g., southeast Australia or Pondoland (South Africa)] or multiple successional states (e.g., Indiana Dunes National Seashore) all tend to support significantly higher diversity than adjoining areas. Even for the United Kingdom, with an exceptionally small flora overall, regional or county floras that encompass a diversity of habitats and seral stages may have as many species as are found in many similar-sized temperate regions elsewhere. Within Europe there many more tree species in the southern, Mediterranean-influenced region with complex spatial heterogeneity (almost 100 versus 12 common and 25 uncommon species in northern and central Europe). Perhaps the high tree and overall species diversity in South Africa is related to the extreme spatial heterogeneous and natural fragmentation of the vegetation (forest and otherwise). Locally or regionally, lower species diversity tends to be found under closed conifer forests and late successional stands dominated by trees that cast deep shade. Often, the highest diversity will be found in intermediate successional stage forests or in a landscape with a mosaic of seral stages. Locally, higher diversity will tend to be found on richer, fine-textured soils with circum neutral pH with higher cation exchange capacity and more humus. This contrasts with diversity trends elsewhere. For example, higher diversity tends to be found on poorer soils in Mediterranean shrubland biomes.

Compared to tropical forests, the species richness (of trees or all vascular plants) in the temperate zone will usually be smaller than that of comparable areas in the tropics, especially at the 0.05- to 10-ha scale. Most temperate forest stands tend to be dominated by one or a few species, with the other tree species being uncommon or rare. In the majority of tropical forest stands local dominance by one or a few species is rare; greater evenness is common. Perhaps only on a regional basis may floristic diversity of temperate forests (e.g., southern China and South Africa) begin to approach those observed in the tropics.

An alternative measure of global richness patterns may be obtained by focusing on clades or higher taxonomic richness. The data from Table III show more genera and families in the Southern Hemisphere forests sampled. Also, the ratios of species to genus and genus to family tend to be lower in the south. These trends indicate a potentially richer phylogenetic diversity (using higher taxa in lieu of cladistic information) in the south. A complementary, global perspective is provided by the British Natural History Museum (NHM) global mapping of plant family richness (395 in total) on 10° latitude/longitude grids. The trends reveal higher family diversity on average in the tropics, with the richest cell in Southeast Asia, and a dramatic decline poleward. However, family richness is as high in southern China as it is anywhere else in the world (other than Southeast Asia), and about as high in the central southern United States as in most of South America (including Amazonia) and southern Africa versus tropical Africa. Centers of plant family richness in the temperate zone at the 10° grid cell included southern east Asia, southern North America, and southern Africa, with lower diversity in Europe and temperate Australia and South America.

V. ENDEMISM AND RANGE SIZE RARITY

Endemism (species restricted to specific localities) and taxon rarity have received a similar amount of attention as has biodiversity. How do levels of plant endemism compare among temperate forested regions and with other biomes? Statistics on plant endemism tend to be available for only a limited range of spatial scales (often countywide, occasionally for states or provinces, and infrequently for localities) and are often incomplete or lacking for poorly known regions such as the tropics. Nevertheless, there are some trends in the data that are available. Boreal and cold temperate forested regions in the Northern Hemisphere tend to have very low levels of endemism based either on absolute numbers or the percentage expected on average per unit area [e.g., northern and western European countries (0–2%) and the eastern United States (0 to <1%)]. Regions that include warm temperate to subtropical regions with topographically heterogeneous landscapes (and therefore heterogeneous climates and vegetation types), and especially with isolated mountain ranges, tend to have higher than expected endemism per unit area [e.g., Bulgaria (9%), Turkey (31%), western North America, and countrywide for China (56%)]. Larger islands and

peninsulas tend to have higher than expected species diversity [e.g., Korea (14%), Florida (12%), Japan (37%), and New Zealand (82%)]. The Southern Hemisphere forested regions tend to have some of the highest levels of floristic endemism globally (50–80% for Australia, New Zealand, Chile, and South Africa). In part this reflects their geographic isolation. The previous data are for species endemism for the entire flora. Tree species endemism is more difficult to determine and likely to be much lower. For example, in South Africa about 25% of the more than 1000 tree species are confined approximately to the borders (and enclaves) of the country and about 40% to southern Africa (versus 70–80% for the entire flora). Regional tree endemism is much lower (e.g., about 8% for Pondoland and 15% for Maputaland forest regions). However, very high levels of tree species continental endemism are found in southern South America: 85% of woody species and 34% of genera are endemic.

Compared to tropical forests, the absolute numbers of endemics are generally lower in the temperate zone, except perhaps for some of the Southern Hemisphere temperate zone. This reflects the larger floras in the tropics, which are still poorly known for many localities. However, on the basis of expected percentage endemism per unit area the trends are less clear. For example, although Venezuela (38%), Panama (13%), and the Congo (29%) have higher than expected levels of plant endemism, Columbia (4%), Nicaragua (<1%), and Nigeria (4%) have lower than expected endemism. On a subregion or local basis the tropics may well have substantially higher levels of endemism than equivalent localities in the temperate zone, but this pattern remains to be shown conclusively.

Species endemism is only one way to assess rarity or the geographical restrictions of taxa for conservation purposes. Range size rarity of taxa or clades evaluated in the absence of political or other arbitrary boundaries may be a more consistent and robust means of judging rarity. A global survey by the British NHM of range size rarity was done on a 10° grid for selected plant taxa. This showed that there were no clear trends between warm temperate and tropical regions in range size rarity. Many, perhaps the majority of the prime hot spots, are in temperate grids that include forested regions (e.g., southern South Africa, central China, southeastern Australia, and central to south-central Chile, with secondary centers in southern Chile, northern New Zealand, elsewhere in China, and the southeastern United States). Clade rarity and endemism need evaluation as an alternative to enumerating species endemism or range size rarity.

VI. EXPLANATIONS FOR PATTERNS OF DIVERSITY AND ENDEMISM

A variety of hypotheses have been put forward to explain local and global patterns of species distributions and therefore richness. One author lists as many as 120 named hypotheses for variation in species richness. Geological and biogeographic history provides one set of important related explanations for observed trends in richness and endemism. This may well explain some of the patterns within and between hemispheres.

A. Historical and Geological Explanations

In the Triassic period global plate tectonic activity had united major landmasses of the world to form a single supercontinent (Fig. 5) which created the potential for a common biota. However, by the beginning of the Cretaceous this landmass began to break up, forming northern and southern landmasses. This, together with the formation of a broad sea, effectively isolated the northern Asiamerica continent from the southern Gondwanaland. The angiosperm and gymnosperm floras on these separate landmasses thus began to evolve independently. This history is reflected in both the Tertiary floras of the fossil record and the floras we see today. Until approximately 40 million years into the Tertiary the climate was warm, moist, and relatively stable. In the Northern Hemisphere forests spanned North America and Eurasia into the present-day Arctic. In the mid-Cretaceous [100 million years ago (mya)] these forests were dominated by both conifers (Pinaceae, Ginkgoaceae, and Taxodiaceae) and angiosperm taxa. Early examples of widespread flowering plant genera include *Magnolia*, *Betula*, and *Platanus*. Many modern northern genera soon followed in the fossil record (e.g., *Quercus*, *Castanea*, *Carya*, *Ulmus*, *Juglans*, and *Acer*), also spanning the Northern Hemisphere.

By the beginning of the Neogene, approximately 25 mya, the climate began to change, becoming cooler and drier in certain regions as a consequence of mountain building and shifts in ocean currents. In the cold northern regions, conifers were favored, giving rise to the boreal forests. At midlatitude, summer drought and/or winter cold favored deciduous angiosperms. Midcontinent aridity also gave rise to the temperate steppe grasslands and deserts. This, together with Pleistocene glaciation, undoubtedly contributed to divergence in the north temperate forest floras and their biodiversity.

In Europe and central Asia, east–west trending mountain ranges and arid zones blocked the southward

a
Late Carboniferous–Early Permian

b
Late Permian–Triassic

c
Mid–Jurassic

d
Early Cretaceous
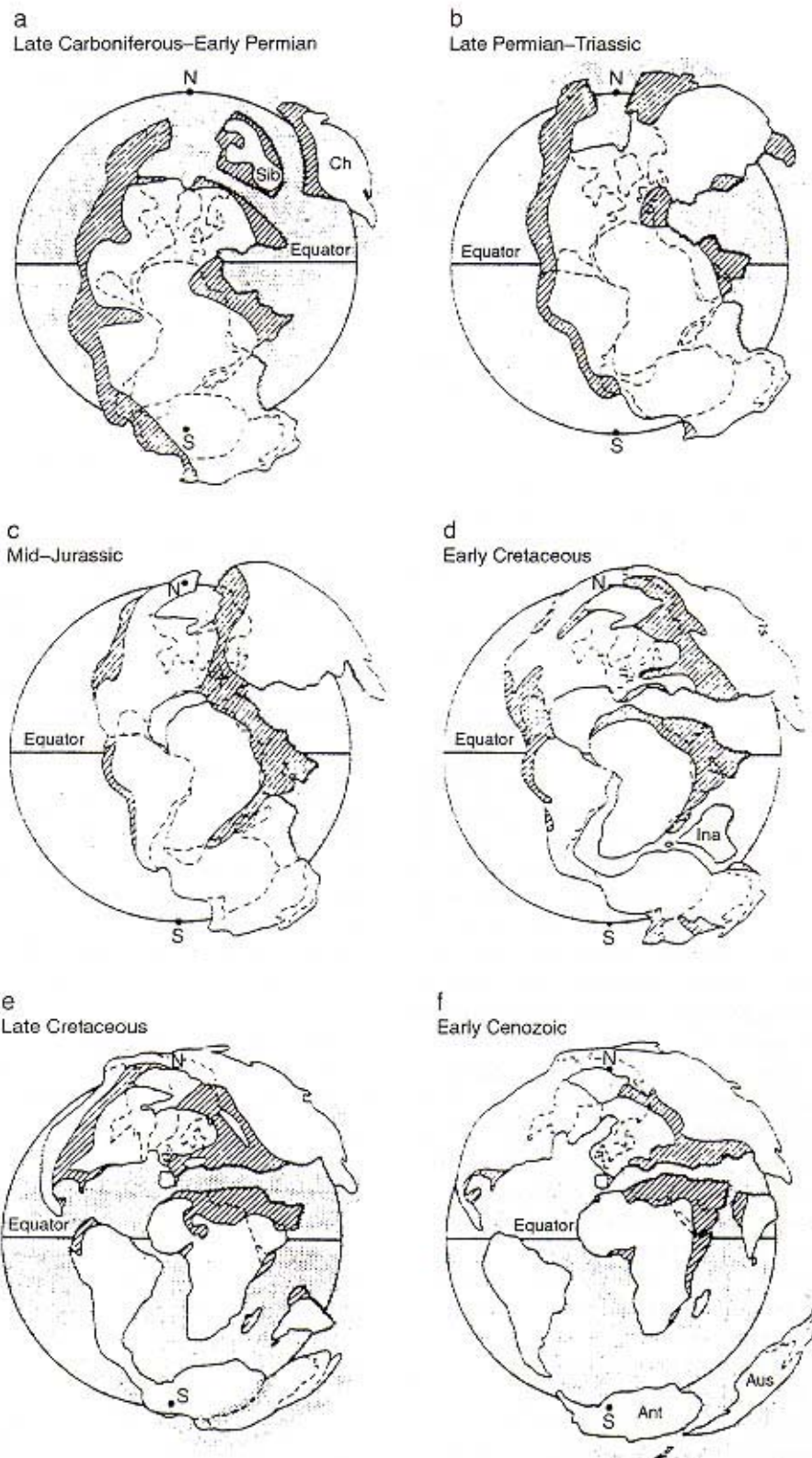
e
Late Cretaceous

f
Early Cenozoic

FIGURE 5   Changes in the locations of continental landmasses are shown from the Mesozoic to the early Tertiary in Lambert equal area projections. Areas on the back projection of the spheres are folded out for view. Dashed lines indicate shoreline of modern continents, hatched areas are epicontinental seas, and stippled areas are oceans (reproduced with permission from Cox and Moore, 1985).

retreat of the forests as the glaciers advanced. In consequence, there was apparently greater species extinction here than elsewhere in the Northern Hemisphere, and geographic isolation prevented recolonization from temperate or tropical locations elsewhere. In contrast, in east Asia, continental glaciation was less extensive and continuous connections with tropical wet forests permitted temperate forest species to retreat south and advance north with climate oscillations; there were many fewer extinctions and thus greater retention of an older phylogenetic diversity. This tropical connection undoubtedly accounts for the greater tropical affinities seen in the flora of east Asia today. In eastern North America the mountains trend north–south and thus migrations with the glacial oscillations were possible. However, the tropical connections were largely blocked by seas or arid zones. Compared to Asia, there were more extinctions with fewer opportunities for recolonizations by taxa with tropical affinities. In eastern North America the phylogenetic lineages have a more recent and more northerly balance. Western North America suffered the greatest extinctions. Extensive mountain building, accompanying aridity, and the development of a Mediterranean climate to the south favored conifers or sclerophyllous trees with divergent evolutionary lineages from those of the mesic Tertiary forests. To the north, cool, wet climates favored conifer forests (many with tertiary affinities) at the expense of angiosperms.

The forests of the Southern Hemisphere began similarly in the Cretaceous. Warm, mesic, mixed conifer and angiosperm forests spanned Gondwanaland. These were dominated by southern conifers, including Auracariaceae and Podocarpaceae, and southern angiosperms, including Cunonaceae, Proteaceae, Myrtaceae, and Sapindaceae. In addition to these, Casurinaceae and the genus *Nothofagus* were present throughout, except on what became Africa. Gondwanaland began to break up early in the Cretaceous (Fig. 5) well before Asiamerica. Southern Africa and India had become isolated by the early Cretaceous. This undoubtedly accounts for Africa's greater dissimilarity with the rest of the southern temperate flora. India eventually joined Asia and today it has primarily north temperate or Asian tropical floristic affinities. Not until early in the Tertiary did South America, Antarctica, and Australia finally separate. Climate changes in the Southern Hemisphere were less dramatic during the Neogene and Pleistocene than they were in the north. Aridity and glaciation were more localized; the climate remained less continental. In consequence, the forest flora retains more characteristics of the warm, mesic Tertiary flora than is the case in the north.

During the Neogene, temperate southern Africa experienced increased aridity. With climatic oscillations the forests expanded and contracted. Many of the Gondwanan elements became extinct, leaving only a couple of species of Podocarpaceae and a minor contribution of Cunonaceae and Proteaceae to the forest flora today. Connections along the east coast of southern Africa allowed connections with the tropical forest flora, and today the temperate South African forests have the strongest tropical affinities of any temperate region and the greatest tree diversity. Exceptionally high levels of spatial and temporal environmental heterogeneity may contribute to speciation here as well. With substantial tropical affinities also found in Australia and New Zealand, the southern forests as a group have a much stronger representation of tropical plant families than do the northern forests.

During the Pliocene the southern temperate forest region of Chile and adjacent Argentina became isolated from the rest of South America by the Andes and arid zones to the north and east. The isolation and relatively small extent of these forests undoubtedly account for the low diversity and high endemism found here. Only in the extreme south of Chile and at high elevations with lower mean and absolute temperatures are deciduous (*Nothofagus*) forests found in the Southern Hemisphere.

Australia and New Zealand retain much of their Tertiary flora. The maritime climate of New Zealand has changed relatively little during the Tertiary. Its long isolation from other landmasses is responsible for the high level of endemism. Increased aridity in Australia in the Neogene substantially affected the temperate forest structure and composition. Explosive radiation occurred in the genus *Eucalyptus* (Myrtaceae) and *Acacia* (Mimosaceae). Unique among temperate forests, there are more than 500 species of *Eucalyptus* in Australia (many restricted to temperate forests). These are sclerophyllous-, drought-, and fire-tolerant tree species that dominate most of the temperate forest and woodlands in the east and west. Only in moist, cool patches in the southeast or at higher elevations are remnants of the tertiary flora found. *Nothofagus*, Araucariaceae, Podocarpaceae, and other groups are part of the rich tree flora.

The previous account indicates that it is not simply history or geology but a complex process that incorporates the role of temporal and spatial heterogeneity, geographic isolation, recent Pleistocene effects, and the role of climate stability that jointly affect the patterns of taxon distributions, diversity, and endemism we see today. What about other explanatory variables?

B. Productivity

The differential effects of solar radiation figure prominently as an explanatory hypothesis, measured either directly or indirectly via actual or potential evapotranspiration (i.e., AET or PET) or productivity. There is conflicting evidence on the relative importance of this as an explanatory variable versus historical factors, at least at the regional scale. Examined at the plot level (~1 ha) across regions, correlations are found between diversity and AET. There are also correlations at the regional and latitudinal scales (boreal vs temperate vs tropical forests). However, other evidence shows that differences at regional and local scales can be well explained by historical factors after taking into account AET. Global joint correlations between species richness and productivity were examined by the British NHM for plant family diversity on a 10° grid scale. This study showed higher family richness than expected from productivity in southern Africa, southern North America, and southern east Asia and lower or expected diversity elsewhere in the temperate zone. Undoubtedly both sets of factors may be involved, but these remain only correlates; cause–effect relationships have not been demonstrated.

C. Spatiotemporal Heterogeneity and Other Explanations

The roles of disturbance regimes and environmental or habitat heterogeneity at local and regional levels have figured prominently as explanatory hypotheses for richness patterns. Higher diversity is predicted under intermediate levels of disturbance. On a local or landscape level there is considerable evidence to support this idea. Midsuccessional forests and successionally diverse landscape support a richer flora. For example, in northeastern North America many of the extinct or threatened species are those that occurred in open or early successional landscapes that were common 100 years ago but have since disappeared with the homogenizing reforestation of the landscape.

The predominant natural disturbances in temperate forest zones include fire and windstorm. Fires are most prevalent in the drier forests of western North America, Australia, South Africa, and the Mediterranean Basin. In many of these systems, periodic fires contribute to higher landscape biodiversity. The role of fires in other forest systems is less clear. Large cyclonic storms affect mainly eastern coastal, midlatitude regions in the

Northern Hemisphere (eastern North America and Asia). Tornadic events are most prevalent in midcontinental North America. Such storms contribute to heterogeneous successional stages in the landscape and thus higher diversity. Occasionally, human activity can contribute to higher landscape diversity. Historically, Europeans husbanding the landscape for diverse forest products undoubtedly increased the local diversity over what it would have been naturally. Humans creating a moderate spatially and temporally heterogeneous landscape ironically may contribute slightly to increased regional diversity. The higher regional species richness in mountainous areas associated with the manifold habitats was discussed previously. Another example is the extremely rich South African forests (and other biomes). The high local and regional richness has been largely attributed to the environmental heterogeneity found at this scale.

In addition, there are many other explanatory variables for patterns in species richness, some of which were intimated or included in the topics discussed previously: environmental stability or predictability, abiotic rarifaction, land area, seasonality, aridity, range limits and geometric constraints, and many more. For many of these factors it is easy to establish correlation and much more difficult to establish cause–effect relationships.

VII. ECOSYSTEM SERVICES

Temperate forests provide important ecosystem services globally, regionally, and locally. Temperate forests contribute about 17% to global net primary productivity (versus about 49% for tropical forest systems and 8% for boreal forests). However, recent evidence from atmospheric and oceanic CO_2 data point to temperate forests, especially those in eastern North America, as globally important carbon sinks. The magnitude and causes of the net carbon uptake by temperate biomes are uncertain. However, it may be related to the reforestation that has occurred during the past century, especially in North America. CO_2 fertilization, anthropogenic N deposition, and global warming may contribute as well.

At local to landscape levels there are tight links among forest structure, composition, and species richness; soil attributes; mineral and hydrological cycles; and human disturbances. In the moist temperate zone species richness tends to be higher on soils that are

better drained, warmer, and finer textured, with greater NO_3–N and P availability and higher cation saturation and lower Al^+ (toxic) levels, all associated with higher pH. These attributes are associated with many calcareous soils. Thinner calcareous soils, which apparently create greater spatial heterogeneity in forest canopies, are also associated with higher local richness. Hence, soil attributes are intimately related to pattern in species diversity. The extent to which these features are altered will directly affect biodiversity; the extent to which the community structure and composition are changed will feed back on these variables.

The strongest correlates of productivity tend to be soil texture and N cycling, which in turn are correlated with moisture retention, cation exchange, and maximum levels of humus accumulation. These correlations are strongest in undisturbed forests. Also, ecosystem control by soil texture extends over long time frames. Human disturbances can profoundly affect these links. Soil compaction with intensive forest management will have a cascading and long-term effect on nutrient and hydrological cycles. As the studies at Hubbard Brook Experimental Forest have demonstrated, forest clearing will dramatically alter watershed hydrology (increased water loss and sediment loss), nutrient cycling (with elevated nutrient loss), microclimate, and species composition for years or decades. Changes in forest species composition such as with conifer plantations will have an equally large effect. Substituting homogeneous conifers stands for mixed broad-leafed forests will increase C/N and lignin/C ratios, which in turn reduces decomposition rates, N mineralization rates, and pH, with cascading effects on cation exchange capacity and diversity in the soil flora and fauna. For example, in German *Picea* plantations, N cycling between canopy and forest soils is reduced by 75% from that observed in native beech forests. Moreover, with greater stem interception of precipitation, the conifer forest soils also become drier. In consequence, it may not be possible to successively reintroduce beech forests on these sites without large-scale soil amendments.

Even small changes in the broadleaf forest composition can alter decomposition rates and nutrient status. For example, sugar maple (*Acer saccharum*) and ash (*Fraxinus*) promote higher N mineralization, and sugar maple accumulates calcium. In contrast, oak-dominated forests have lower N mineralization. Substituting exotic species in plantations can dramatically alter ecosystem processes. *Eucalyptus* and *Melaleuca* tend to significantly lower water tables where they have been introduced. In the northeastern United States, Japanese bar-berry (*Berberis thunbergii*) has become a seriously invasive exotic, forming a continuous shrub layer. Under barberry canopies soil ammonium N levels are elevated, the soil flora and fauna are altered, and native species richness is depressed.

VIII. CONSERVATION STATUS

Table I shows the approximate extent of protected forests in each of the regional biomes based on WCMC global data for International Union for the Conservation of Nature (IUCN) conservation protection categories I–VI. Globally for temperate forests, 6 or 7% of the remaining forests receive some level of protection. This represents about 1 or 2% of the total temperate forest biome extent. Compared to other forest systems, temperate forests are slightly better protected than boreal forests (6 or 7% versus 5 or 6%) but apparently less well protected than tropical forests as a whole (10–12%).

There is considerable variation both within and among regions in the level of forest protection as well as among forest types. For example, temperate freshwater swamp forests are afforded the least protection (2.7% globally), whereas Southern Hemisphere evergreen broadleaf forests receive the highest level of protection (22.6% globally). Overall, Southern Hemisphere forests are afforded significantly better protection as a group than are northern forests.

The level of protection varies considerably among regions and countries within the temperate zone: Less than 3% of east Asian temperate forests are protected, but this varies with forest type from about 5% for cool to cold temperate and subtropical forests to 1% or less for most warm to hot temperate forests types (except for warm temperate rainforests, which only cover a tiny area and are about 15% protected). There is considerable variation among the countries of east Asia in the amount of forest afforded protection: almost 10% for Japan to less than 5% of China and less than 1% of North Korea. For Europe (excluding Russia) about 8% for the various forest types are given some protection. This also varies considerably among countries: As much as 25% of the broad-leafed deciduous forests in Germany are protected, whereas <1% in Bosnia and 2% in Russia are protected. For North America, the extent of forest protection varies from about 15% for conifer-dominated temperate rainforests to 7% for the northern cool or cold temperate forests and about 2% for the warm to hot temperate and subtropical forests versus more than 9% for North American boreal forests. The

forests of the Middle East, which are the most reduced in extent, are afforded the least protection over all. Less than 3% of the forests are protected in this zone. This varies from <1% in Georgia and Azerbaijan to 1% in Turkey and perhaps as much as 12% in Iran. About 8% of India's temperate forests have some level of conservation protection. For temperate Australia about 9% of the forests are protected; for New Zealand the figure is about 43%. For South Africa, about 24% of its southernmost temperate forests are protected. For South America, about 23% of the temperate forests are afforded some protection, but the vast majority (more than 90%) of these are the wet evergreen forests of the south, mostly located in Chile. Less than 2% of the sclerophyllous and dry temperate forest are protected. An estimated 8% of Brazil's temperate mixed conifer forests are protected.

Overall, the most well protected forests, on a relative scale, are the Southern Hemisphere temperate rainforests, the Pacific wet forests of western North America and east Asia, the northernmost temperate forest (mixed with boreal elements), and mixed temperate forests in mountainous areas. The most poorly protected are dry and sclerophyll leafed forests of the Northern Hemisphere, wet and rainforest broadleaf deciduous and evergreen forests in the Northern Hemisphere (very limited in extent), and moist temperate deciduous and evergreen broad-leafed forests of the Southern Hemisphere. East Asia has the highest percentage of temperate forest types receiving no protection, followed by the Middle East and South America.

In some ways these data are misleading. Many of the forests classified as receiving protection are plantation or otherwise highly managed forests. These are largely native species forests in Europe, North America, and Asia, but they tend to be managed as homogeneous, even-aged, monocultures with consequent reduced diversity and ecosystem services. Natural, undisturbed, or old-growth forests comprise only a small fraction of the remaining forests: western Europe, 1%; eastern North America, 1%; eastern Asia, 1%; Australia, about 5% (but probably <1% is unlogged); South Africa, <1%. Somewhat better off are New Zealand with about 25%, northwest (Pacific) North America with about 13%, and southern Chile with about 45%.

Some temperate forests are unique in that significant reforestation has occurred during the past century (about 1 or 2% increase on average per annum), primarily in Europe and eastern North America. However, most of these net gains in forest cover are intensively managed (in Europe and the southeastern United States). In northeastern North America, during the past century the landscape has reverted naturally from 50–90% agricultural to mostly forested, following the extensive abandonment of agriculture. Most of this forest is highly fragmented and fairly homogeneous, being of similar age. Consequently, the ecological functionality of these forests is limited. Elsewhere, temperate forest cover continues to decline at rates that vary from 1 to 10% pa.

IX. CONSERVATION AND PROTECTION STRATEGIES

How does one develop a strategy for conserving or protecting the remaining temperate forests of the world? Some authors focus on "hot spots" of diversity or endemism. Globally, most attention has been focused on tropical systems and recently Mediterranean systems. Temperate forest-dominated systems have received less attention. For example, of Conservation International's (CI's) 24 hot spots, only New Zealand is a temperate zone forest-dominated locality. However, in his most recent iteration of "megadiversity countries," Mittermeyer highlights 4 of 17 countries that contain important temperate forest biomes: China, the United States, Australia, and South Africa. Three of these (Australia, China, and South Africa) rank among the top 12 countries worldwide in species richness across phyla and species endemism. The four largely temperate countries also rank among the top globally in the number of IUCN Red Data Book (RDB) "threatened" plant species. Although these predominantly temperate floras are better known, as a group they have more RDB species than all of the tropical countries together. The WWF and the IUCN have also identified approximately 240 centers of plant diversity globally. Of these, about 15% represent temperate forest-dominated systems and another 10% represent other temperate biomes (e.g., shrublands, grasslands, and arid lands). Only 1 or 2% are boreal or polar, and the balance (~74%) are tropical.

There have been similar attempts to identify hot spots regionally. For example, WWF identified more than 100 forest hot spots across Europe, the Mediterranean Basin, and the Middle East. Regional centers of diversity can also be detected from taxon turnover. Data from the Atlas Florae Europaeae project, which compared the joint diversity of Pinaceae and Fagaceae across Europe at a 50-km grid scale, show highest joint species diversity in these two families in the Balkans, the southern Alps, the Carpathians, and the southern Pyrenees. This obviously reflects the high spatial heterogeneity in these localities.

Alternatively, conservation assessments may include such factors as taxon or clade irreplaceability, minimum area sets, minimum viable niche space, or ecosystem integrity. A study was done by the British NHM to select conservation priority areas for selected plant groups. This exercise was done on a 10° grid globally and regionally for all of Europe on a 50-km grid. The global analysis revealed top-priority sites in eastern China, southeastern Australia, and central Chile along with six tropical areas, plus secondary centers in southern Chile, the southeastern and western United States, central and southern China, northern Japan, southwestern Europe, eastern and southwestern Australia, and southern Africa along with nine secondary centers in the tropics. Within Europe, many priority sites were identified in the Balkan Peninsula and margins of the Mediterranean (which include forested lands). However, there are prioritized areas elsewhere throughout Europe at lower densities.

World Resources Institute (WRI) provides another perspective on priority sites for forest conservation. They recognize "frontier forests"—large tracts of intact forested ecosystems sufficient to maintain viable populations of all indigenous species. This perspective includes large, wide-ranging predators and migratory species and takes into account the prevailing natural disturbance patterns. These are thus considered intact, fully functional forested ecosystems or landscapes. Very few of these are in the temperate zone, and most are under medium or high threat. This contrasts with the tropical and boreal zones, in which there are many more large tracts identified as frontier forest, even if there are substantial areas at risk. No intact forested landscapes are found in temperate Europe or Africa. In North America only one small patch of transitional boreal forest in central Ontario and discontinuous tracts of conifer forests in coastal British Columbia and Alaska (all under threat) can be considered intact landscapes. In Asia, only a few small forest patches in the inaccessible mountains of central and south-central China, boreal transition forest patches along the border between China and Russia, and the Primorski Krai region of Pacific Russia are considered intact temperate forest landscapes. All but one small patch are under threat. In South America the only frontier temperate forest is in southern Chile and adjacent Argentina. Most of this region is considered to be at risk. In Australia, only a small rainforest patch in Tasmania is classified as intact. Small patches of frontier forest occur on the west coast of the south island of New Zealand and one patch in the central north island. All are at risk except for the Tasmania rainforest.

X. MAJOR THREATS TO CONSERVATION

Many major threats exist for conserving the biodiversity and ecosystems services provided by temperate forests locally, regionally, and globally. Certainly a major threat is homogenization of the landscape. This is a result of intensively managing forests as near monocultures of either native or exotic species, managing landscape for similar forest age and size classes, introducing invasive exotic species, and relying globally on only a few taxa for forest plantations (e.g., *P. radiata* or *Eucalyptus*). The consequences of these landscape management strategies are reductions in local or regional diversity and alternation of many ecosystem processes (e.g., nutrient and hydrological cycles) and soil attributes. Large-scale increases in timber harvesting may well have a negative impact on carbon source–sink relationships and atmospheric CO_2 levels.

Increasing urbanization of the landscape and continued harvesting of ever more remote forests will lead to a more fragmented landscape. The likelihood of these fragments maintaining ecosystem functionality is ever diminished. Within the next few decades, it is likely that no fully intact, functional forested landscapes will remain in the temperate zone, given current trends.

Atmospheric pollution from acid precipitation, and the associated ecosystem N and S loadings, remain prevalent in the north temperate zone and will have long-term effects. There is evidence that calcium is being rapidly depleted in acidic soils as a consequence of long-term acid precipitation. This will have cascading effects on forest soils and on major tree species performance, particularly those most sensitive to calcium levels such as sugar maple.

Projected global warming will have a major effect on northern temperate forests. The main direct effect of global warming will likely be seen in the boreal forest zone, with decreased periods of snow cover and hence changes in surface albedo. This will likely favor the expansion of temperate forests well north into the boreal zone. The community response patterns will be determined by dispersal characteristics of the biota and the availability of propagules in source populations. This in turn will be dictated by the configuration of forest fragments in the landscape.

In the Southern Hemisphere, the effects of global warming will be much smaller due to the moderating maritime influences. Atmospheric pollution effects are very negligible or very localized. The major threats to temperate forests here are deforestation, especially in

South America, and the pervasive effects of introduced exotic species in plantation or as escapes. *Eucalyptus* and northern pines (especially *P. radiata*) are planted in monocultures across the Southern Hemisphere, with negative effects on biodiversity, soil attributes, and hydrology.

XI. CONSERVATION OBJECTIVES AND RESEARCH NEEDS

Where do we need to focus attention to improve our understanding of temperate forests and develop a more effective conservation plan? Clearly we need better and more accurate means of mapping temperate forests and assessing their conservation status. There are large discrepancies and errors in assessing the current and potential forest cover for all forest types. We need more information on patterns of species occurrences (simply the presence/absence is sufficient) at a variety of scales throughout the temperate zone. Because distribution (and hence richness) patterns vary across spatial scales, one cannot simply rely on particular, arbitrary sample sizes (e.g., 0.04-, 0.1-, 1-, or 50-ha plots). Effort should be placed on inventorying poorly known areas, such as the Middle East. We need to have a better, predictive understanding of the links between forest structure and composition, ecosystem functions, and the effects of human disturbances.

There needs to be a concerted, manifold effort at developing a variety of different conservation strategies for temperate forests. These include targeting more protection for forested biomes with high ratios of people to forest area and forest biomes or forest types that are poorly protected. Examples include east Asian forests in general, north temperate broad-leafed rainforests, and subtropical dry forests. Moreover, concerted effort should be placed on protecting the few remaining intact frontier forests, especially those at high risk, and old-aged forest stands particularly where these comprise miniscule components of the landscape. However, the strategy needs to be inclusive, focusing on conserving the complete spatial and temporal heterogeneity of the landscape, even if this necessitates some human husbandry of the landscape.

Strategies for identifying priority conservation sites should not simply target sites with high species diversity and/or endemism. Alternative means of evaluation need to be incorporated as well, such as phylogenetic richness and irreplaceability, range rarity, ecosystem or landscape integrity, landscape heterogeneity that incorporates migration in the face of natural and human-made disturbances, and minimum niche space for all biotic components of the landscape. Only with a manifold creative approach can we hope to come to grips with the conservation of this critical suite of temperate forest biomes.

See Also the Following Articles

BOREAL FOREST ECOSYSTEMS • DEFORESTATION AND LAND CLEARING • ENDEMISM • FOREST ECOLOGY • HOTSPOTS • TEMPERATE GRASSLAND AND SHRUBLAND ECOSYSTEMS • TROPICAL FOREST ECOSYSTEMS

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