resulted in substantial differences in the floras of deciduous forests. In North America and eastern Asia migrations were relatively unaffected by the large north–south mountain ranges (e.g., the Rocky Mountains and Appalachians), whereas the east–west ranges in Europe reduced the opportunities for plants to retreat to warmer regions and recolonize during interglacial periods. As a result, there are far fewer genera and species in Europe compared with eastern Asia and North America and, because of this, the relatively few European species tend to be more dominant due to the lack of competitors.

Although they naturally intergrade, as well as vary in detail, a number of main types of deciduous temperate forests are usually recognized:

- Western and central European oakwoods tend to be relatively open and light. The dominant species are the pedunculate and sessile oaks (*Quercus robur* and *Q. petraea*). Associated trees that are more or less common according to the nature of the soil include ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*), birch (*Betula pendula* and *B. pubescens*), elm (*Ulmus glabra, U. procera, U. carpinifolia*), lime (*Tilia cordata, T. platyphyllos*), cherry (*Prunus avium*), alder (*Alnus glutinosa*), and aspen (*Populus tremula*). Small trees and large shrubs include hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), field maple (*Acer campestre*), crab apple (*Malus sylvestris*), and three species of *Sorbus* (rowan, wild service tree, and whitebeam). There are also two evergreens, yew (*Taxus baccata*) and holly (*Ilex aquifolium*).
- The more luxuriant forests of eastern North America, eastern Asia, and southeastern Europe/Asia minor differ in species composition but are similar in appearance. The principal species usually include various oaks (*Quercus* spp.), beeches (*Fagus* spp.), birches (*Betula* spp.), hickories (*Carya* spp.), walnuts (*Juglans* spp.), maples (*Acer* spp.), limes (*Tilia* spp.), elms (*Ulmus* spp.), ash (*Fraxinus* spp.), tulip trees (*Liriodendron* spp.), sweet chestnuts (*Castanea* spp.), and hornbeams (*Carpinus* spp.). The lower stories are normally more luxuriant and varied than in the western and central European forests. In the colder eastern and more northern parts of North America, conifers such as *Pinus strobus* begin to appear with the deciduous trees.
- Beech forests which, especially in Europe, with the very shade-tolerant *Fagus sylvatica* form almost uniform, closed canopies and cast such dense shade that few shrubs or herbs can grow. Similar types, though on a smaller scale, are found with *F. orientalis* in Turkey and other parts of its range, and with *F. crenata* in Japan. In the higher mountains of central and southern Europe, the conifers *Abies alba* and *Picea abies* become admixed.
- Southern beech, especially *Nothofagus nervosa* (syn. *N. procera*) and *N. obliqua*, usually with associated evergreens such as *Laureliopsis philippiana, Laurelia sempervirens*, and *Persea lingua*. Numerous ferns and bryophytes are features of these forests.
- The damper deciduous woodlands, especially those on marshy ground, are dominated by alders (*Alnus* spp.), willows (*Salix* spp.), poplars (*Populus* spp.) and birches (*Betula* spp.). The understories may be dense, and climbers and epiphytes numerous.

See also: **Forest Ecosystems**: Fagaceae (Oaks, Beeches, Hickories and Nothofagus); Juglandaceae (The Walnut Family: Walnuts, Hickories, Pecans). **Plant Diversity in Forests**. **Genetics of Oaks**.

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Mediterranean Forest Ecosystems

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Introduction

Occupying only 2% of the world's surface area, the Mediterranean biome contains nearly 20% of the earth's total plant diversity, making the five regions of the world under a Mediterranean climate (the Mediterranean Basin, California, the South African Cape Province, south and southwestern Australia, and parts of central Chile) a very significant biodiversity hot spot, second only to tropical regions (**Figure 1**). Strong biogeographical, environmental and human-made constraints have shaped this structural and functional diversity. The most typical characteristics of Mediterranean forests, compared to temperate or boreal forests, are their spatial and temporal complexity and heterogeneity, not only in terms of the physical factors (geography, geology, geomorphology, pedology, and bioclimate) that prevail where they grow, but also in terms of their biological components and attributes: functional dynamics at local and landscape levels, floristic and faunistic composition, richness and biogeographic origins.

Mediterranean forests represent 1.8% of world forest area. In this article, we will focus our attention on forests of the largest Mediterranean region of the world, the Mediterranean basin, where historical and paleogeographical episodes, long-term human influence, and current geographical and climatic contrasts have created both high species and ecosystemic diversity and heterogeneity. A short comparative overview of all world Mediterranean forests will also be presented.

Definition of Mediterranean Forests

The Mediterranean Climate: A Strong Driver for Forest Type Diversity

The Mediterranean region *sensu stricto* is usually defined by its climate, which in turn is responsible for its flora. It stretches between the northern latitudes of

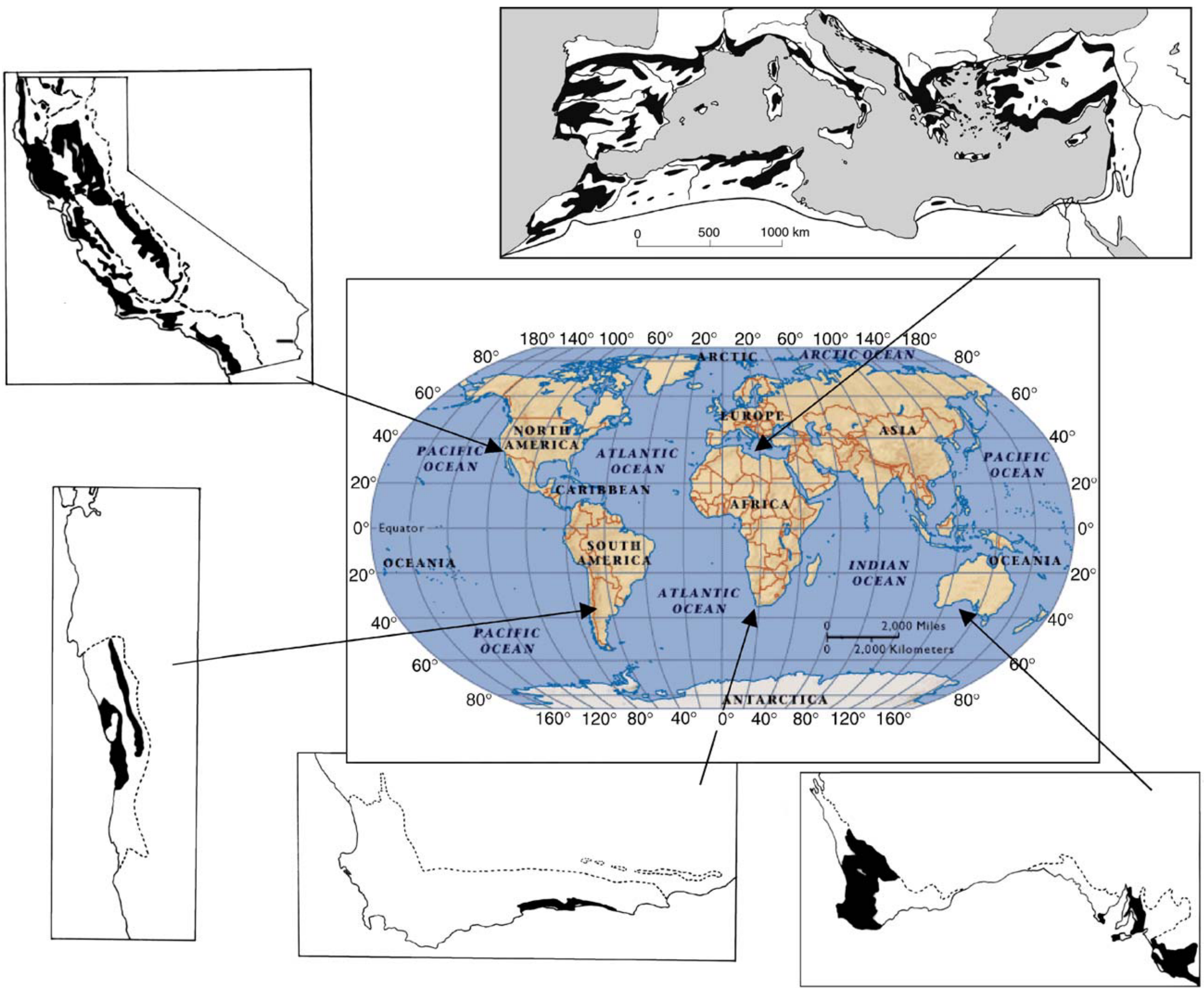

Figure 1 The world's Mediterranean regions. Plain or dotted lines indicate the limits of Mediterranean type ecosystems. Dark areas represent the extent of forest ecosystems. Modified from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier and Dalmann PR (1998) *Plant Life in the World Mediterranean Climates*. Oxford, UK: Oxford University Press.

25° and 45° over approximately 2 300 000 km^2. The originality of the Mediterranean climate, which is transitional between temperate and dry tropical climates, lies in the existence of a combined dry and hot summer period of variable length, which imposes a strong water stress on the vegetation during its growing season.

Mean minimum temperatures of the coldest month (*m*) are often used to define climatic subdivisions (**Table 1**). These values are correlated with elevation and to a lesser extent with increased latitude and continentality. In most places, *m* is between 0 and +3°C although extremes can reach +8 to +9°C in desert margins and –8 to –10°C on the highest mountains. This large-scale potential gradient is often locally modified by rainfall, soil type, and millennia-long human impact which has durably affected ecological equilibrium. The distribution of Mediterranean forest species is also shaped by irregular events such as late spring below freezing temperatures and absolute minimum temperatures. For example, the extremely cold winters of 1956 and 1985 contributed to determine the distribution of the olive tree (*Olea europaea*), Aleppo pine (*Pinus halepensis*), and holm oak (*Quercus ilex*) in the northern Mediterranean.

Rainfall is extremely variable among the Mediterranean regions, with mean annual values ranging from 100 to 2000 mm. The lowest values are found at desert margins especially in North Africa and the Near East. Below 100 mm per year is the borderline between the Mediterranean and the desert climates. Rainfalls higher than 1500 mm are mostly found on coastal mountain ranges. Rainfall plays an essential role in the organization of Mediterranean forests and can be used to define six different bioclimatic types (**Table 2**). Rainfall can also be extremely variable from year to year, which increases vegetation water stress, especially south of the Mediterranean.

Main Characteristics and Functional Definition

In the Mediterranean region, both open and closed canopy tree populations are considered to be forests. Closed canopy forests are similar in structure to temperate forests, such as those most common in Europe, where the undergrowth is limited and contains mostly shade-tolerant herbaceous species. Open canopy forests have few trees and their undergrowth is limited to a few or no forest-type herbaceous species. For ecological and functional reasons (see 'Current vegetation types' below), all Mediterranean ecosystems of more than 0.5 ha, where tree density is over 10% and tree height can reach over 5 m, are considered to be forests by the Food and Agriculture Organization (FAO) of the United Nations.

Mediterranean forests are less productive than the average world forests. The most productive ones are located in southern Europe, which contains more than 80% of total Mediterranean tree standing volume (**Table 3**).

Most comparative ecological and ecophysiological studies have shown that plant communities in the five Mediterranean regions of the world demonstrate similar strategies to resist climatic and edaphic stress as well as natural and human disturbances, such as wild fires. Sclerophylly (evergreen leaves coated with a thick cuticule) is one such common and widespread strategy. Other strategies include resprouting after disturbance, disturbance-dependent seed production and germination, complex root systems, cellular tolerance to low water potentials or high secondary compound production (e.g., terpenes).

Table 1 Vegetation levels showing the correspondence between temperature variants and dominant (and frequent) woody types of the Mediterranean basin

Vegetation level	*Temperature variant*	m *(°C)*	*T (°C)*	*Dominant woody species*
Infra-Mediterranean	Very hot	> +7°C	> +17°C	*Argania*, *Acacia gummifera*
Thermo-Mediterranean	Hot	+3 to +7°C	> +17°C	*Olea*, *Ceratonia*, *Pinus halepensis* and *P. brutia*, *Tetraclinis* (*Quercus*)
Meso-Mediterranean	Temperate	0 to +3°C	+13 to +17°C	Sclerophyll *Quercus*, *Pinus halepensis* and *P. brutia*
Supra-Mediterranean	Cool	−3 to 0°C	+8 to +13°C	Deciduous *Quercus*, *Ostrya*, *Carpinus orientalis* (*Pinus brutia*)
Mountain-Mediterranean	Cold	−7 to −3°C	+4 to +8°C	*Pinus nigra*, *Cedrus*, *Abies*, *Fagus*, *Juniperus*
Oro-Mediterranean	Very cold	< −7°C	< +4°C	*Juniperus*, prostrate spiny xerophytes

m, mean minimum temperatures of the coldest month; T, mean annual temperature.
Data from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen.* Paris: Elsevier.

Table 2 Types of bioclimates and their theoretical correspondence with the main vegetation types of the Mediterranean basin

Bioclimate	*Mean annual rainfall (for m = 0°C)*	*Number of months without rainfall*	*Main vegetation type*
Per-arid	<100 mm	11 to 12	Saharan
Arid	100 to 400 mm	7 to 10	Steppe and pre-steppe *(Juniperus turbinata*, *Pinus halepensis*, *Pistacia atlantica)*
Semi-arid	400 to 600 mm	5 to 7	Pre-forest *(Pinus halepensis*, *P. brutia*, *Juniperus* spp., *Quercus)*
Subhumid	600 to 800 mm	3 to 5	Forest (mostly sclerophyll *Quercus*, *Pinus halepensis*, *P. brutia*, *P. pinaster*, *P. pinea*, *P. nigra*, *Cedrus)*
Humid	800 to 1000 mm	1 to 3	Forest (mostly deciduous *Quercus*, *Pinus brutia*, *P. pinaster*, *P. nigra*, *Cedrus*, *Abies*, *Fagus)*
Perhumid	>1000 mm	less than 1	Forest (deciduous *Quercus*, *Cedrus, Abies, Fagus)*

m, mean minimum temperatures of the coldest month.
Data from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier.

Table 3 Distribution of forest volume and surface area among the three ecoregions of the Mediterranean basin

Region	*Mean biomass volume ($m^3\,ha^{-1}$)*	*Surface area, in 2000 ($ha \times 10^6$)*	*Forest area in the major forested countries of each region (%)*
Middle East	66	11	Turkey (90%)
North Africa	35	6.1	Morocco (50%) Algeria (35%)
Southern Europe	100	30	Spain (30%) Italy (25%) Greece (10%)

Data from Food and Agriculture Organization.

Forest Paleoecology: Current Biodiversity Explained by History

Pre-Pleistocene History: The Mixing of Floras of Different Origins

The current flora of the Mediterranean region arises from several biogeographic origins. Its coniferous flora diversified during the Cretaceous. Its angiosperm flora diversified during the early Tertiary, when the Mediterranean region was situated at the crossroads between Laurasia and the remains of Gondwana. Thus it includes tropical elements, mostly of African and Asian lineages, as well as extratropical elements, of autochthonous and northern lineages. This complex geological-scale paleogeography is one of the reasons that the Mediterranean has such a high plant biodiversity and woody species endemism. Two different lineage groups can be described for angiosperms:

1. A **pre-Pliocene group**, consisting of mostly sclerophyll taxa which resprout from stumps after disturbance (fire, clearance) and are often found in the most complex stages of ecosystem dynamics (e.g., *Arbutus unedo, Olea* spp., *Quercus* spp.).
2. A **post-Pliocene group**, including nonsclerophyll taxa which are obligate seeders after disturbance and are mostly found in the less advanced stages of ecosystem dynamics (e.g., *Cistus* spp., *Lavandula* spp.). These taxa successfully diversified and competed with taxa of the pre-Pliocene group due to their short life cycle, high seed production, and ecological plasticity towards the highly fluctuating Mediterranean bioclimatic cycles.

Strategies considered as typically Mediterranean could thus have emerged at the end of the Tertiary under a tropical climatic regime well before the advent of the Mediterranean climate, at the beginning of the Quaternary. Similarity between Mediterranean woody plants could be due more to phylogenetic inertia than to common adaptive strategies. The ability of Mediterranean woody species to resprout after fire, for example, does not originate from an adaptation to recurrent fires, but rather from an older adaptation to herbivory.

From Glacial Refugia to Current Distribution: Holocene Recolonization Pathways around the Mediterranean

In the more recent past, Mediterranean glacial refugia have played a key role in shaping the current genetic diversity of woody species and the spatial distribution of the main forest ecosystems around the Mediterranean and in Europe. Refugia are territories somewhat sheltered from the climatic disturbance of the most recent ice age (Würm) where plants survived the effects of the last glacial maximum (about 20 000 years ago). They contributed to the forest recolonization process that started approximately 13 000 years ago and lasted throughout the Holocene. They are responsible for the high floristic diversity of Mediterranean forests (compared to that of temperate European forests). Glacial refugium distribution estimated using paleoecological and phylogeographical data matches that of current high floristic richness and high endemism and rare woody species hot spots around the Mediterranean.

The main regions where temperate and thermophilous forest species survived around the Mediterranean are the Iberian, Italian, and Balkan peninsulas, the Black Sea region, some areas in North Africa, and the largest Mediterranean islands. Territories that link these primary refugia, such as the south of France and the borders of the Adriatic Sea (Slovenia and Croatia), possibly acted as secondary refugia. These refugia were characterized by high species richness. Once climatic conditions became truly favorable, the expansion of a highly diversified deciduous forest could happen rapidly over large territories, such as in the Pindos mountains in northwestern Greece where over 20 deciduous woody species could already be found in the early Preboreal (about 10 000 years ago). Some tree genera such as *Pinus*, *Quercus*, and *Corylus* seem to have been present in all southern European refugia, although others had a clear geographic distribution, e.g., *Abies alba, Fagus sylvatica* and *Carpinus* in the Italian and Balkan refugia (possibly in Spain as well), and *Tilia* and *Ulmus* in the eastern Mediterranean (**Figure 2**).

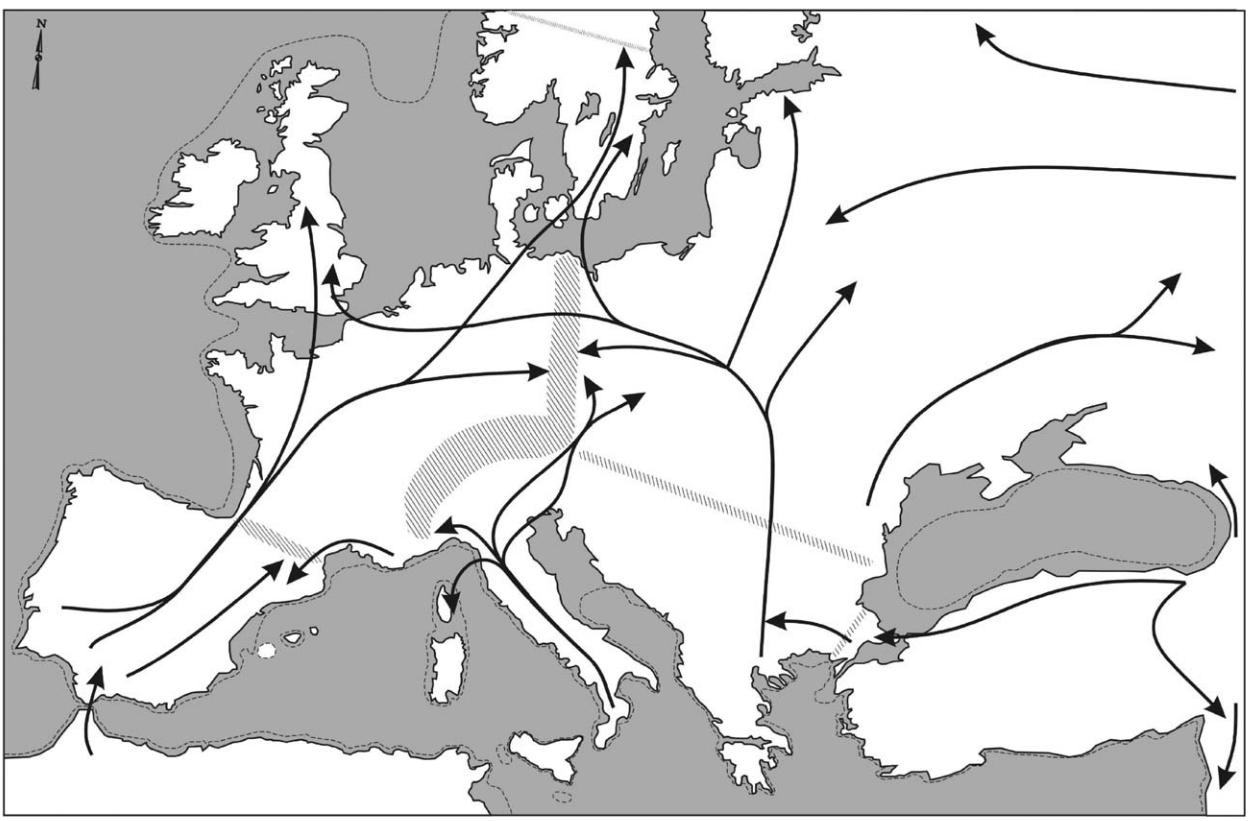

Figure 2 Main Holocene recolonization routes from glacial refugia in Europe. Dotted lines indicate the extent of land masses during Late Glacial maximum. Large shaded areas represent main hybrid zones and smaller ones represent secondary hybrid zones. Reproduced with permission from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier.

Current Vegetation Types

Structural and Regional Typology

The current diversity of Mediterranean forest structures can be organized into three major structural types based on bioclimatic and/or human impact criteria.

True forest vegetation types These are made of metastable equilibrium vegetation structures. Shade-tolerant plant species growing on evolved soils are dominant (**Figure 3**). These true forests constitute what were previously considered to be 'climax' forests; they are in fact the potential structures at the end of a dynamic ecological cycle that can be achieved where soil and climate conditions are favorable and where the impact of humans is not too strong.

Preforest types These can be divided into two categories. Under perhumid, humid, and subhumid bioclimates, they consist of vegetation structures that have undergone severe human impact, although their soil is still relatively well preserved (**Figure 4**). They are transitory structures from true forests to more open systems. Under semi-arid bioclimatic conditions, or under particularly stressful conditions (e.g., ultramafic substrates) in any bioclimate, preforests are composed of shrub-dominated vegetation structures with scattered trees (matorrals) under equilibrium (or close to equilibrium) at the human timescale. Conifer species play an important role in these structures.

Presteppic forest types Very frequent in southern and eastern Mediterranean, these consist of open-vegetation structures dominated by nonforest plant species under scattered trees. Nonforest species are steppe-type perennial species that can eventually be replaced by ruderal annual species when grazing occurs. Soils are usually poor and topsoil is frequently missing. Presteppes are most frequent under warm and hot temperature variants of arid (and sometimes semi-arid) bioclimates. They gradually merge into steppes under hotter and drier conditions. On mountains, presteppes are a transitional vegetation structure from forests (or preforests) to high elevation steppes dominated by low and scattered cushionlike spiny xerophytes.

These three main structural forest types are found in the four major geographical subdivisions of the Mediterranean basin (**Table 4**).

Current Evolution: Sclerophyllous Trees Replaced by Deciduous Trees

Traditional agriculture and grazing have been decreasing since the mid-twentieth century on low to medium elevation mountain ranges in the northern Mediterranean. This has led to a dramatic increase in forest cover and a change in forest composition. Concurrently, atmospheric CO_2 has been increasing because of industrial activity, thus increasing the productivity of many Mediterranean trees such as *Quercus ilex* and *Q. pubescens*.

One of the results of these changes is the physiognomical convergence of Mediterranean and non-Mediterranean forests when dominated by the same deciduous tree species (*Quercus*, *Fagus*, *Acer*, *Sorbus*). Areas where woody sclerophyll plants and heliophyllous conifers (*Pinus halepensis*, *P. sylvestris*) used to be the dominant species are now colonized by these deciduous trees, along with some mesophilic conifers (*Abies*, *Taxus*) and laurophyllous trees (*Ilex aquifolium*, *Laurus nobilis*). Deciduous *Quercus* around the Mediterranean and in California, and *Nothofagus* in Chile, currently play an extremely

Figure 3 Example of a true forest vegetation type: the Mediterranean *Fagus–Abies* mixed forest of Mont Ventoux, southeastern France.

Figure 4 Example of a true preforest vegetation type: cattle grazing in the Algerian Aures *Cedrus atlantica* forest.

Table 4 Main forest types of the four major geographical subdivisions of the Mediterranean basin, arranged according to vegetation level (see Table 1). Species names for each community refer to the dominant woody species

Vegetation level	*Northwestern Mediterranean communities*	*Southwestern Mediterranean communities*	*Northeastern Mediterranean communities*	*Southeastern Mediterranean communities*
Infra-Mediterranean		*Argania spinosa* and *Acacia gummifera*		
		Acacia raddiana		
Thermo-Mediterranean	*Olea europaea*, *Ceratonia* and *Chamaerops*	*Olea europaea*, *Ceratonia* and *Chamaerops*	*Olea europaea* and *Ceratonia*	*Olea europaea* and *Ceratonia*
	Quercus ilex and *Q. suber*	*Q. ilex* subsp. *rotundifolia*, *Q. suber*	*Quercus ilex*	*Quercus ilex*
	Pinus halepensis, *P. pinaster*, *P. pinea*	*Pinus halepensis* and *P. pinaster*	*Pinus halepensis*, *P. brutia*, *P. pinea*	*Pinus halepensis or P. brutia*
	Juniperus turbinata, *J. phoenicea*	*Juniperus turbinata, J. phoenicea*	*Cupressus sempervirens*	*Cupressus sempervirens*
	Quercus coccifera	*Quercus fruticosa*	*Quercus coccifera* subsp. *calliprinos*	*Quercus infectoria* and *Q. coccifera* subsp. *calliprinos*
		Pistacia atlantica	*Formations with Quercus ithaburensis* and *Q. pubescens*	*Quercus pubescens*, *Q. ithaburensis*
		Tetraclinis articulata, *Cupressus atlantica*		
Meso-Mediterranean	*Quercus ilex*, *Q. suber*	*Olea europaea*, *Ceratonia* and *Chamaerops*	*Quercus ilex*	*Quercus ilex*
	Quercus pubescens	*Quercus ilex* subsp. *Rotundifolia*, *Q. suber*	*Quercus coccifera* subsp. *calliprinos*	*Quercus coccifera* subsp. *calliprinos*
	Quercus coccifera	*Quercus canariensis*	*Quercus ithaburensis*	*Quercus ithaburensis*
	Quercus petraea subsp*. broteroi*	*Pistacia atlantica*	*Q. brachyphylla*, *Q. pubescens*	*Quercus infectoria*, *Q. cerris* subsp. *pseudocerris*
	Pinus halepensis	*Tetraclinis articulata*	*Pinus halepensis, P. brutia*	*Pinus brutia*, *P. halepensis, P. pinea*
	Quercus canariensis, *Q. pyrenaica*		*Cupressus sempervirens*	*Cupressus sempervirens*
				Cedrus brevifolia and *Quercus alnifolia* (Cyprus)
Supra-Mediterranean	*Quercus pubescens*, *Q. cerris*, *Q.petraea*	*Quercus canariensis*, *Q. faginea*, *Q. afares*	*Quercus frainetto* and *Q. cerris*	*Quercus frainetto* and *Q. cerris*
	Quercus faginea	*Quercus ilex* subsp. *rotundifolia*, *Q. suber*	*Quercus pubescens*, *Q. ithaburensis*	*Quercus infectoria*
	Abies alba, A. pinsapo	*Cedrus atlantica* and *Abies marocana*	*Abies cephalonica*	*Pinus brutia*
	Quercus robur, Q. petraea and *Q. pyrenaica*		*Cupressus sempervirens*	*Pinus nigra* subsp. *pallasiana*
	Ostrya carpinifolia and *Carpinus betulus*		*Ostrya carpinifolia* and *Carpinus orientalis*	*Carpinus orientalis* and *Ostrya carpinifolia*
	Pinus sylvestris		*Quercus petraea* and *Castanea sativa*	*Cupressus sempervirens*
	Castanea sativa		*Quercus pubescens* subsp. *anatolica*	*Quercus macranthera* subsp. *syspirensis*
Mountain-Mediterranean	*Pinus sylvestris*	*Pinus nigra* subsp. *mauretanica*	*Pinus nigra* subsp. *pallasiana*	*Pinus nigra* subsp. *pallasiana*
	*Pinus nigra (*subsp. *salzmannii* or *laricio)*	*Cedrus atlantica*	*Pinus heldreichii*	*Cedrus libani*
	Abies alba or A. pinsapo	*Abies marocana or A. numidica*	*Abies cephalonica, A. borisii-regis*	*Abies cilicica*
	Juniperus thurifera subsp*. thurifera*	*Juniperus thurifera* subsp. *africana*	*Abies nordamanniana, Abies bornmuelleriana* and *Juniperus excelsa*	*Juniperus foetidissima* and *J. excelsa*
	Fagus sylvatica subsp*. sylvatica*	*Quercus ilex* subsp. *rotundifolia*	*Fagus sylvatica sensu lato*	*Fagus sylvatica* subsp. *orientalis*
	Pinus uncinata and *P. mugo*		*Quercus petraea*	*Quercus petraea*
				Quercus brantii, *Q. ithaburensis* subsp. *look*
Oro-Mediterranean	*Juniperus thurifera* subsp. *Thurifera*	*Juniperus thurifera* subsp. *africana*	*Juniperus excelsa*	*Juniperus excelsa*
		Quercus ilex subsp. *rotundifolia*		

important role in the forest recruitment dynamics of previously traditionally cultivated or grazed lands. In forests least affected by humans, structures are shifting towards old-growth forest types where vertebrate seed dispersal plays a crucial role, and floristic and faunistic compositions are shifting towards medio-European or Euro-Asian dominated assemblages. Using sclerophylly to define Mediterranean forests is thus now an oversimplification.

Human Impact

Although human impact may have been already significant when people lived as hunter–gatherers, for example in increasing seed dispersal though seasonal migrations, it became truly significant for Mediterranean forests with the advent of domestication, about 10 000 years ago in the Near East. Because of an ever-increasing need for arable land for crop cultivation and grazing, the area of forest declined over the centuries, first sporadically around the main human settlements during the Atlantic period (about 4700 to 4500 years ago), then systematically during the Bronze Age and throughout Antiquity. Wood was then also used on a large scale for shipbuilding, carpentry, and many areas of human social life. Although it often slowed down during the Middle Ages as demographic pressure lessened, deforestation re-increased during the Renaissance. By the end of the nineteenth century, after the Industrial Revolution, the Mediterranean forest had lost three-fourths of its initial postglacial area. The consequences of this millennia-long impact have affected both vegetation structures and biodiversity.

Vegetation Structures

In areas where agricultural and grazing effects are the strongest, i.e., North Africa and most semi-arid and arid Eastern Mediterranean zones, forest ecosystems are no longer resilient, and a degradation cycle (often irreversible) starts as soil structure and water, nutrient, and carbon cycles are also affected, with often spectacular and dramatic effects (e.g. floods, landslides).

Four levels of increasing severity on forest structures can be described:

1. Transformation of forests and preforests into matorrals with scattered trees ('matorralization').
2. Transformation of woody matorrals dominated by resprouters into secondary, lower, matorrals mainly composed by seeders ('dematorralization').
3. In semi-arid bioclimates, replacement of matorrals by steppes dominated by non-woody perrenial species or low chamaephytes ('steppization').
4. Invasion of forest ecosystems by annual, often ruderal, or low-palatability species ('therophytization').

Biodiversity

Human impact on forest ecosystems can significantly modify all natural processes that regulate biodiversity at population, species, and ecosystem levels. Three categories of human impacts can be recognized, from strongest to probably least consequential.

Habitat destruction and fragmentation Traditionally the longest standing impact on forests over time, in relation to human settlements, habitat destruction has been driven by agriculture and grazing, wars and industrial activities, and carried out with tools such as wildfires and clear-cutting. It has led to the disappearance of ecosystems and species, as well as isolation of those that have remained. The main impacts on genetic processes for isolated populations are (1) reduction of long-distance gene flow, (2) increase of genetic drift and of consanguineous mating, leading to (3) loss of adaptive potential and eventually, (4) disappearance when the number of reproducing individuals is too small or when deleterious genes have accumulated.

Species introduction Exotic forest genetic resources have often been transported by humans throughout historical times because they were a potential food supply (e.g., *Pinus pinea, Olea europaea*), had landscape or religious value (*Cupressus sempervirens*), or were able to stop degradation processes and yield more wood than the local resource (e.g., in France, *Pinus nigra* subsp. *nigra* and *Cedrus atlantica* during the nineteeth century). More recently, with the advent of tree breeding, selected varieties have been planted extensively. Introduction of new taxa has led to the creation of completely new ecosystems, thus increasing biodiversity locally. However, phytosanitary risks are high in these artificial forests as they usually lack a complete biologically functional structure. Risks of hybridization are high when the exotic resource is genetically close to the local resource (e.g., subspecies of *Pinus nigra*), with potential reduction of fitness for the local resource.

Forestry practice Forests have been managed since the Middle Ages in Europe. Loss of biodiversity cannot be positively linked to forestry practice, except in the case of seed transfer over regions with very different ecological requirements (e.g., in southern France, Aleppo pines imported from Sicily died from frost during the winters of 1984 and 1985). However, recent studies indicate that reforestation reduces genetic diversity because of plant material selection in the nursery. When a stand is prepared for natural regeneration, a significant part of the sexually mature trees is removed, and thus part of the genetic diversity is eliminated from the original population, which may disturb mating systems, increase consanguineous mating and genetic drift, and impact the selective value of the future stand. Due to their long life cycle (long juvenile and long sexual maturity phases) and overlapping generations, trees may be able to compensate efficiently for these genetic impacts in their long-term adaptation.

Different Recent Human Impacts around the Mediterranean Basin

Although human impact was broadly similar during the Holocene, it diverged sharply among the different Mediterranean ecogeographic regions during the twentieth century.

In the northern Mediterranean, after the Industrial Revolution, the least productive agricultural and grazed lands were abandoned and became progressively colonized by expansionist (mostly conifer) species. Open lands have progressively changed into non human-impacted (except for some large-scale wildfires) preforest and forest structures. The FAO reported an annual increase of 0.3–0.9% in forest cover in the 1990s. There is a growing concern over loss of human-made biodiversity because of the disappearance of open grass and shrub ecosystems. Although habitat destruction remains a concern, especially along the coast because of urban extension, the main risks for forest genetic resources come from forest management, with the introduction of species and improved varieties and seed transfer, and their corollaries, hybridization and gene flow from cultivated to wild compartments.

In the southern Mediterranean, the use of forest resources is generally not sustained, although the FAO reported positive forest cover increase (from 0.2% to 1.4%) in the 1990s. Habitat destruction for agriculture, grazing, fuel wood, construction, etc. remains the major type of human impact. In North Africa, forest area per capita is less than 0.1 ha although it is 0.2–0.4 ha in the northern Mediterranean. In the past 30 years, forest product use has dramatically increased due to human demography. Illegal cuttings, forest clearing, overgrazing, and fuelwood exploitation are rapidly destroying forests and their associated biological resources. Low socioeconomic standards of rural populations are thus also a significant cause of habitat destruction.

In the eastern Mediterranean, the trend is somewhat similar to that of North Africa. Habitat destruction remains a high risk in countries where forest cover is already very limited and forest resources not sustained (e.g., Syria, Lebanon). In other countries, forest cover has grown tremendously (+4.9% in Israel) or steadily (+0.2% in Turkey) in the 1990s because of active reforestation and conservation programs.

Conservation of Mediterranean Forest Biodiversity: An International Effort

The need to conserve forests and their biodiversity has been internationally recognized since the United Nations Conference on Environment and Development (UNCED) in Rio during 1992. Conservation of biodiversity needs to be undertaken at three complementary levels:

- genes, where evolution can occur
- species and populations, where reproduction and gene flow can occur
- ecosystems (habitats), where organisms are sustained.

Ecosystems are usually preserved separately from genes. Species and populations can be a means to sustain gene diversity and future adaptation (forestry approach to conservation) or the primary target to protect through diversified and functional habitats (ecological approach to conservation).

Forest genes and populations Many forest conservation and sustainable management strategies designed globally can apply to the Mediterranean. Such is the case of the *in situ* and *ex situ* conservation networks advocated by the European Forest Genetic Resource Conservation Program (EUFORGEN), although they are still rare around the Mediterranean. *In situ* networks concern species of high ecological, patrimonial, and/or economic value that are not threatened with short-term extinction in their natural environment (e.g., *Pinus brutia* in Turkey, *Abies alba* in France). They are designed to make genetic evolution possible under current ecological constraints. *Ex situ* networks generally concern rare and endangered forest species. They are made of collections of selected or remaining genotypes conserved outside their normal ecological conditions. One current sustainable management strategy is the control of the origin and commerce of forest reproductive material (in Europe, see European Union directives 66/404/CEE and 71/161/CEE), which must come from certified seed stands and seed orchards and whose transfer from one ecological zone to another is under strict control. Other initiatives, sponsored by the FAO and the UN Environmental Program, have produced sets of indicators and guidelines for replacing yield-oriented forest management practice by the sustainable management of forest resources in Mediterranean countries.

Forest species and ecosystems (habitats) Species and ecological diversity are typically conserved and managed in natural parks and reserves. Many of such structures exist around the Mediterranean. However, out of 425 Man and Biosphere Reserves worldwide, only 32 shelter significant Mediterranean forest areas. Eastern Mediterranean forests are notably underprotected. Particularly, conservation of potential and old-growth sclerophyll and deciduous Mediterranean forests remains extremely limited as less than 2% have been included in natural parks or reserves. Old-growth Mediterranean forests contain many typical species that are rare because linked to large, nonfragmented, and undisturbed forest areas. Some of these species are functionally primordial, e.g., those related to organic matter decomposition. Because Mediterranean biodiversity arises from a high spatial and temporal heterogeneity, natural parks and reserves designed for Mediterranean forests must be large enough to include disturbance cycles (open and closed canopy structures, large vertebrate populations, fires, etc.) which can guarantee the maintenance of this typical biodiversity. They must also be large enough to include a complex mosaic of functionally diversified ecological structures, at equilibrium. Such requirements have guided the European Natura 2000 (European Union habitats directive 92/43/CEE) initiative for habitat conservation and the international efforts of the World Parks Congresses sponsored by the World Conservation Union (IUCN). Ideally, these guidelines should be included into forest practice, thus linking gene and ecosystem-oriented approaches to sustainable resource management.

A Global Comparative Assessment of the World Mediterranean-Type Forests

Species richness and diversity, which are the most frequently used parameters to describe and assess biodiversity, are scale-dependent. Three main types of spatial scales are generally recognized (**Table 5**). This partitioning of biodiversity makes it possible to compare ecosystem types. At the local scale (less than 0.1 ha), Mediterranean biodiversity is two times lower than that of tropical regions. Mean local (alpha) floristic diversity of the world Mediterranean forests is between 10 species m^{-2} and 25 to 110 species 1000 m^{-2}. At this spatial scale, woody plant communities of the Mediterranean basin are both very heterogeneous and also among the richest types, ahead of the alpha diversity found in the western Cape Province. However, habitat (beta) and regional (epsilon) scale diversities are much higher in the western Cape Province than around the Mediterranean, although they concern mainly matorral type (fynbos) vegetation.

From a biogeographic and ecological point of view, several forest types of the Mediterranean basin are relatively similar to those of the California Floristic Province, due to a pre-Atlantic ocean land connection which lasted until the Eocene (Madro-Tethysian flora) and explain the existence of some common tree genera (*Pinus*, *Quercus*, *Arbutus*, *Cupressus*, *Juniperus*). At low and medium altitudes, physiognomical similarities exist for sclerophyll oak forests. The existence of thermophilous coniferous at the thermo- and meso-Mediterranean (*Pinus halepensis*, *P. brutia*, *P. pinaster*) and thermo- and meso-Californian (*Pinus attenuata*, *P. sabiniana*, *Cupressus macrocarpa*) levels, but also of several mesophilous coniferous (*Abies*, *Pinus*) at higher altitude constitutes another key feature. A recent survey indicates that the Mediterranean region harbors a higher tree richness (290 indigenous trees with 201 endemics) than the California Floristic Province (173 trees with 77 endemics), although its area is seven times larger.

Northern hemisphere Mediterranean forests show a higher structural and species diversity than those of the southern hemisphere, because the latter cover less extensive areas and, as in South Africa, may be completely outside the range of Mediterranean bioclimate. The Southern Cape forests are very patchy and scarce, mainly made up of plants of a cool and humid Afromontane origin, with warm subtropical elements; sclerophyll trees and conifers (*Afrocarpus*, *Podocarpus*) predominate. Forests of Mediterranean Chile are more diverse due to the strong latitudinal gradient and the increase in rainfall from north to south; semi-arid *Acacia caven* and *Prosopis chilensis* forests in the north are succeeded by subtropical broadleaved and sclerophyll forests in the central region, and by deciduous *Nothofagus* forests farther south. Together with species-rich sclerophyll matorrals (kwongan and mallee), the woodlands of Mediterranean Australia are dominated by *Eucalyptus*, *Acacia*, and *Casuarina* on relatively fertile soils where mean annual rainfall exceeds 400 mm.

Outlook for the Future

The originality of the Mediterranean biome is dependent upon the interaction of complex ecological factors. However these ecosystems are fragile and global warming will undoubtedly soon be a major source of disturbance. Research and long-term monitoring of biodiversity and ecosystem functioning

Table 5 Main patterns of forest biodiversity in the five Mediterranean regions of the world in relation to spatial scale, species composition and level of disturbance

Major biodiversity drivers	*Mediterranean Basin (2 300 000 km²)*	*California Floristic Province (324 000 km²)*	*Mediterranean Chile (140 000 km²)*	*South and southwestern Australia (112 000 km²)*	*Western Cape Region (90 000 km²)*
Patterns of plant diversity					
Local within habitat (alpha diversity)	Medium to very high	Low to medium	Medium	Low to high	Medium to high
Differentiation among habitats (beta diversity)	Medium	Medium	Low to medium ?	High	Medium to high
Regional (epsilon diversity)	Medium	Medium	Low	High	High
Total plant species richness	~30 000	~4450	~2540	~8000	~9000
Major forest trees					
Sclerophyll	*Arbutus unedo*, *A. andrachne*, *Olea europaea*, *Ceratonia siliqua*, *Erica arborea*, *Phillyrea latifolia*, *Quercus ilex*, *Q. suber, Q. coccifera*	*Arbutus menziesii*, *Heteromeles arbutifolia*, *Lithocarpus densiflora*, *Quercus agrifolia*, *Q. chrysolepis*, *Q. wislizenii*, *Umbellularia californica*	*Colliguaja odorifera*, *Cryptocarya alba*, *Drimys winteri*, *Jubaea chilensis*, *Kageneckia angustifolia*, *Lithraea caustica*, *Peumus boldus*, *Maytenus boaria*, *Nothofagus dombeyii*, *Quillaja saponaria*	*Eucalyptus* spp. (*E. marginata*, *E. diversi-sicolor*, *E. incrassata*, *E. oleosa*, *E. wandoo*, *E. camaldulensis*, *E. calophylla*, *E. baxteri*), *Melaleuca* spp., *Acacia* spp., *Leptospermum* spp., *Banksia* spp.	*Maytenus* spp., *Olea capensis*, *Ocotea bullata*, *Virgilia divaricata*, *V. oroboides*, *Ilex mitis*, *Cunonia capensis*, *Pittosporum viridiflorum*, *Platylophus trifoliatus*, *Pterocelastrus rostratus*, *Schefflera jumbellifera*, *Sideroxylon inerme*
Broadleaved and semibroadleaved	*Castanea sativa*, *Fagus sylvatica*, *Carpinus orientalis*, *Fraxinus ornus*, *Ostrya carpinifolia*, *Platanus orientalis*, *Quercus pubescens*, *Q. canariensis*, *Q. afares*, *Q. ithaburensis*, *Q. pyrenaica*, *Q. frainetto*	*Aesculus californica*, *Quercus lobata*, *Q. douglasii*, *Q. engelmannii*, *Q. kelloggii*, *Q. garryana*	*Acacia caven*, *Nothofagus obliqua*		*Celtis africana*, *Ficus sur*, *Calodendron capense*
Coniferous and Casuarina (coniferous-like leaves)[a]	*Abies alba*, *A. borisii-regis*, *A. cephalonica*, *A. cilicica*, *Cedrus atlantica*, *C. libani*, *Cupressus sempervirens*, *Juniperus excelsa*, *J. thurifera*, *J. turbinata*, *Pinus brutia*, *P. halepensis*, *P. nigra*, *P. pinaster*, *P. pinea*, *P. sylvestris*, *Tetraclinis articulata*	*Abies bracteata*, *A. concolor*, *A. magnifica*, *Calocedrus decurrens*, *Cupressus macrocarpa*, *Pinus attenuata*, *P. contorta*, *P. coulteri*, *P. edulis*, *P. juarezensis*, *P. jeffreyi*, *P. lambertiana*, *P. monophylla*, *P. torreyana*, *Pseudotsuga menziesii*, *P. macrocarpa*, *Sequoia sempervirens*, *Sequoiadendron giganteum*	*Araucaria araucana*, *Austrocedrus chilensis*, *Fitzroya cupressoides*	*Casuarina* spp. (e.g., *C. pusilla*, *C. muellerana*)	*Afrocarpus falcatus*, *Podocarpus latifolius*, *P. elongatus*, *Widdringtonia cedarbergensis*
Impact of forest fires	Strong impact of anthropogenic fires; natural fires very rare	Predominance and high frequency of natural fires	Rarity of natural fires; anthropogenic fires uncommon	Frequent natural and anthropogenic fires	Frequent natural and anthropogenic fires
Other disturbances	Destruction and fragmentation, overgrazing, clear-cutting	Destruction and fragmentation, biological invasions	Destruction and fragmentation, overgrazing	Destruction and fragmentation, biological invasions	Destruction and fragmentation, afforestation, biological invasions

[a] Total plant richness refers to angiosperms, gymnosperms, and pteridophytes.

at a cross-continental Mediterranean scale must be combined with public awareness strategies and international policy-making, not only to understand but also to protect Mediterranean ecosystems effectively and use them efficiently, now and in the future.

See also: **Biodiversity**: Biodiversity in Forests; Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Forest Management for Conservation; Population, Conservation and Ecological Genetics. **Landscape and Planning**: Landscape Ecology, the Concepts. **Silviculture**: Forest Dynamics. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Temperate and Mediterranean Forests**: Southern Coniferous Forests. **Temperate Ecosystems**: Fagaceae; Pines; Spruces, Firs and Larches. **Tropical Ecosystems**: Acacias; Eucalypts.

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TEMPERATE ECOSYSTEMS

Contents

Alders, Birches and Willows

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Early botanists considered the alders (*Alnus*), birches (*Betula*), and willows (*Salix*) part of a large, closely related group of catkin-producing, woody species, known as the Amentiferae. This group was presumed to have a single origin, and also included the walnuts, oaks, figs, and elms. We now know, based on detailed morphological and molecular analyses, that many of these families are not closely related and that superficial resemblance based on catkins is due to convergence. In addition to sharing catkins, alders, birches, and willows are ecologically similar since they are important pioneer species of the northern temperate region. Furthermore, they have a diverse array of similar uses, especially gunpowder production.

Alnus and *Betula* comprise the monophyletic subfamily Betuloideae of the family Betulaceae, whilst the other four members (*Carpinus*, *Corylus*, *Ostrya*, and *Ostryopsis*) comprise subfamily Coryloideae. Traditionally, *Salix* and the genus *Populus* have comprised the family Salicaceae. However, using molecular data it has been proposed that the family Salicaceae should also encompass other genera, most notably the acyanogenic genera of the Flacourtiaceae.

The biology and ecology of alders, birches, and willows are briefly described and then the