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Global Biodiversity in a Changing Environment

Scenarios for the 21st Century

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9. Mediterranean-Climate Ecosystems

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In this chapter we will review the current status of biological diversity in the mediterranean-climate regions of the world, making comparisons among them, as well as examining the threats to biological systems now and in the future. Mediterranean-type climates, which are characterized by a predominantly winter rainfall regime, exist in five regions of the world: parts of California, South Africa, Chile, southern Australia, and the Mediterranean basin. Even though all of these regions share broad climatic conditions and contain ecosystems that have similar structures and dynamics (Hobbs et al. 1995), each region has a unique history of human habitation and use. There is a long history of comparative biotic studies among these regions upon which we draw; however, there are no comparisons of the social drivers of land-use change among these areas. Our analyses are therefore less complete than we would like.

There are many limitations to the development of plausible scenarios of biodiversity change in mediterranean-climate regions. At the most general level, all mediterranean regions are relatively narrow and predominantly along the coasts of continents. For this reason they fall within general circulation model (GCM) grid cells that are mostly water. Further, the metric of a GCM output, average temperature increase, is not too helpful for biogeographic predictions, particularly in this topographically diverse region. Most serious, though, is the lack of good resolution on predictions on the amount and seasonality of rainfall, one of the most important controllers of biotic patterns in this summer-drought region. A further complication is the lack

of information on what might happen to upwelling patterns of the coastal waters, an important controller of local climate. We probably have a better capability to predict what will happen to land use, with the ever-growing populations, than we have for climate.

In all mediterranean-climate regions, there are an extraordinary number of biomes: grasslands, shrublands, woodlands, and forests of varying types and hence numerous ecotones. To a large degree these ecotones are controlled by climate, both past and present, and by fire regimes and soil types. Land-use patterns have more recently changed boundaries either completely, or indirectly, by grazing, for example. Some of these boundaries are complex. For example, some boundaries between shrublands and grasslands are partly controlled by mammals (Bartholomew, 1970). Others (e.g., the boundaries between redwood forest and adjacent meadows) may be partly biotically controlled because the redwoods augment local precipitation by trapping fog (Ingraham and Matthews, 1995).

It is now well accepted that biomes will not shift en masse with climate change; rather, the distributions of species will be affected individually. Because we have so little information on the detailed ecology of most species in these regions we thus face an enormous challenge in predicting potential shifts in species abundances and distributions.

Mediterranean-climate regions have an unusual number of biomes and biome boundaries, and they are also generally rich in endemic and rare species, many with very localized distributions. It is these latter types for which the prognosis under global change is not easy. Many of these organisms are now localized in parks and preserves, or in fragments of relatively undisturbed habitat surrounded by degraded or altered landscapes, leaving little place for migration in response to climatic change, even if this were possible on biological grounds. Thus, predictions based solely on climate-controlled biogeography may not be realistic because of the importance of new land-surface alterations in determining migration potential.

Finally, the biota is changing rapidly in composition in all mediterranean-climate regions due to the increasing load of invasive species. We do not yet have a robust theory to tell us which new species will successfully invade in the coming years under present conditions, much less under conditions of climate change.

In the following sections we first view the richness and patterning of biodiversity in the various mediterranean-climate regions. We will then examine the potential consequences of global changes on these patterns. Our coverage is of necessity uneven because equal information is not available from all of these regions.

Biodiversity Patterns

Australia

Because of the broad range of precipitation, soils, and landforms, the mediterranean area of southwestern Australia encompasses a wide array of

ecosystem types, ranging from closed forests to open savanna woodlands and shrublands (Beard and Sprenger 1984ab; Beard 1990; Hobbs 1992; Hopper 1992). Forest vegetation is generally restricted to the higher rainfall areas (>750 mm); at lower rainfalls the distribution of woodland, mallee, shrubland, and heath vegetation types is determined mainly by substrate type. There are additional types that occupy a relatively small area but are important ecologically [e.g., permanent and ephemeral-lake systems (both salt and freshwater) and granite outcrops].

Southwestern Australia has a high level of plant species diversity, both within and among communities. The Southwest Botanical Province (0.3×10^6 km 2) is a recognized hotspot for floristic biodiversity and endemism (Groombridge 1992; Hopper et al. 1996). Three decades ago Beard (1965) recorded just 3611 named taxa for the Southwest Botanical Province. Now an estimate of 8000 species in this region seems reasonable, with about 75% endemism.

The flora of the southwest is dominated by genera of woody perennials in families such as the Myrtaceae, Proteaceae, Fabaceae, and Epacridaceae. The flora has radiated greatly at the species level, whereas diversity at the family and genus levels is relatively low (Lamont et al. 1984). In the southwest, *Acacia* has at least 400+ species, *Eucalyptus* 300+, *Grevillea* 200+, *Stylidium* and *Melaleuca* 150+, and *Hakea* and *Caladenia* 100+. Such speciation has been concentrated in the Transitional Rainfall Zone for the majority of woody perennial taxa (Hopper 1979; Lamont, et al. 1984).

The remarkable species richness is the end-product of long and complex evolutionary processes, stimulated by environmental perturbations in the late Tertiary and Quaternary (Hopper 1979, 1992; Hopper et al. 1996). The high floristic diversity of the region is attributed to this long evolutionary history in isolation from the rest of Australia, the lack of glaciation, and complex historical and current disturbance patterns. The evolution and persistence of so many rare locally endemic species, particularly in the Transitional Rainfall Zone flora, has been interpreted as being in response to dynamic environments subject to recurrent and unpredictable environmental change (Main 1982; Pate and Hopper 1993).

Although southwestern Australia retains elements of the mammal fauna that are now missing from the rest of the continent (e.g., Kennedy 1990), levels of faunal diversity and endemism do not, in general, match those of the flora. Many of the species in the region are representatives of either arid or more mesic zones, and the mediterranean-climate region represents the limits of their distributions. Such species are commonly confined to the periphery of the mediterranean-climate region. This pattern reflects the transitional nature of the mediterranean-climate zone between the drier inland areas and the more mesic environments to the east and southeast. The low level of mammalian endemism suggests that the distribution of many vertebrate species in the region may largely be a consequence of historical and biogeographic factors rather than a result of adaptations to local ecological conditions. Much of the vertebrate fauna has broad environmental tolerances that enable it to persist under a wide range of conditions,

including those presented by the marked seasonal climate of mediterranean regions.

Birds also show a low level of endemism. Only nine species are endemic to the mediterranean-climate zone (Schodde 1981), although more than 190 species have been recorded in the western Australian wheatbelt region alone (Saunders and Ingram 1995). Of more than 80 species of mammals recorded from the Western Australian mediterranean region, 16 (approximately 20%) are endemic to it, whereas approximately 28% of the mediterranean zone reptiles are endemic. In contrast, 64% of the 36 frog species found in the region are endemic (data from distribution maps of Strahan 1983; Cogger 1986). Many other invertebrate groups also show a high degree of endemism that reflects the dispersal characteristics of particular taxonomic groups. More vagile groups (e.g., butterflies and grasshoppers) have a higher proportion of species that extend beyond the region, whereas many terrestrial and epigaeic arthropods (e.g., scorpions and mites) have very restricted distributions (Mark Harvey, personal communication).

Mediterranean Basin

The Mediterranean flora encompasses a total of about 25,000 plant species within an area of $2.3 \times 10^6 \text{ km}^2$. Species richness averages from around 10–30 species per square meter to 30–50 per 100 m^2 and more than 100 species per ha (Westman 1988). In a comparison of 0.1 ha plots from all mediterranean climatic regions, the highest species richness was found in disturbed areas in Israel (Mooney 1988).

High diversity in the Mediterranean results from a number of factors. The Mediterranean region is located at the confluence of three important biogeographic regions: paleoarctic, North African, and Caucasian. It has acquired elements from all three regions (Quézel 1985). In addition, the physical geography is very diverse, with rugged topography (mountain ranges reaching above 4000 m located at short distances from the coast of the Mediterranean Sea) and a large number of islands and peninsulas. Related to this geographic diversity is a wide range of climatic conditions ranging from warm semi-desert conditions in North Africa to mild or even cold winters, including frequent frost, to the north. The general topographic and climatic complexity has been overlain by a long history of human occupation that has involved continuous disturbance for several millennia. The region has been logged, cultivated, grazed, and burned for a long enough time for evolutionary changes to have taken place in the flora in response to these disturbances.

In addition to high overall species diversity, the region is characterized by a high landscape-scale (β) diversity. This results from the complex physical geography and the long history of human occupation with a fine-grained distribution of land uses. Many Mediterranean landscapes are mosaics of communities at different successional stages that are the result of differing

disturbance regimes and histories. Examples of these highly diverse managed landscapes are the traditional intermixed patches of woodlands, shrublands, pastures, and croplands, with a high diversity of annual grasses capable of surviving multiple stresses (e.g., fire, drought, grazing, and cutting) (Naveh and Whittaker 1979; Blondel and Aronson 1995). These types of landscapes are commonly found in France, Spain (Dehesas), and Portugal (Montados) (Joffre et al. 1988; Ibañez et al. 1989).

High endemism is also a characteristic of the Mediterranean flora. Endemism is positively correlated with species richness, and it is highest in the Iberian Peninsula, Greece, Morocco, and Turkey. In general, calcareous areas tend to have higher species richness than areas on acid substrates. Of the 25,000 species, 37% are endemic to the region, representing about 10,800 taxa of the total Mediterranean vascular flora (Greuter 1995). Others have estimated the percentage of endemic species as high as 50% (Quézel 1985). This high level of endemism has been linked to the complex geography noted earlier, and the thousands of islands and islets particularly in the eastern Mediterranean Basin (Quézel 1985; Quézel and Médail 1995). Greece alone has as many as 2000 island and islets (Tzanoudakis and Panitsa 1995). The eight largest island territories of the Mediterranean have more than 1000 single-area endemics. The high level of endemism may also reflect the high number of annuals which, due to their short generation time, rapidly evolve and speciate (Quézel 1995).

Of the 3583 species endemic to individual Mediterranean countries nearly 2000 are rare or threatened (Léon et al. 1985; Cody 1986). In contrast, if nonendemic species are included, Greuter (1994) estimated that 4251 species are threatened, as a result of agriculture, over-grazing, deforestation, and urbanization. Somewhat different numbers are given by The World Conservation Monitoring Center (in Ramade 1990) that suggested that of 4777 species endemic to a single Mediterranean country (excluding Syria, Lebanon, and Turkey), 2758 are Rare, 180 Endangered, 344 Vulnerable, and 454 of Indeterminate Status.

The Mediterranean region has 70–80% of the Palearctic fauna of birds, mammals, reptiles, and amphibians (Oosterbroek 1994) and 75% of the insect orders (Balletto and Casale 1991) and a high degree of richness and endemism (Table 9.1).

Table 9.1. Estimated total number of species (and endemics, as a percentage of the total number of species) for vertebrates, and number species and subspecies for insect groups in the Mediterranean region

	Breeding birds	Mammals	Reptiles	Amphibians	Neuropteran	Rhopalocer	Tipulidae
Total spp	399	195	163	65	461	677	498
Endemics	45 (11%)	40 (21%)	77 (47%)	27 (42%)	230 (50%)	416 (61%)	361 (72%)

Data from Oosterbroek 1994.

The regions with highest floristic species richness are West Asia Minor (Greek islands along the Turkey coast, Cyprus, part of Turkey, Lebanon, and Israel), the Balkans (former Yugoslavia, Albania, Greece, European part of Turkey), followed by the Iberian Peninsula. If East Asia Minor is considered (Eastern Turkey, Armenia, northwest Iran, southern halves of Georgia and Azerbaydzhān), species richness is among the highest of all. Italy and the Iberian Peninsula show the highest higher taxa diversity of all areas of the Mediterranean (Oosterbroek and Arntzen 1992).

For vertebrate fauna, reptiles and amphibians are the groups with the highest percentage of endemic species, whereas insects have the highest endemic percentage of all in part because both species and subspecies are taken into account.

In the northern Mediterranean, open landscape mosaics are also the cause of high bird community richness, which decreases with an increasingly closed canopy of evergreen forests (Tellería et al. 1992). A great deal of bird diversity is due to the fact that the Mediterranean region is an important stopover place for the Afro-Palearctic migration, and croplands, meadows, and wetlands are critical to that migration route (Farina 1989). Coastal and inland wetlands are the biodiversity hot spots for waterbirds (Van der Hane and Van den Berk 1994).

Another group with special value for its contribution to the total biodiversity pool is the freshwater fish. There are 229 endemic fish taxa (132 species and 97 subspecies) in the northern Mediterranean that represent 13 families (Crivelli and Maitland 1995).

South Africa

The southwestern Cape region of South Africa has a diversity of ecosystem types related to the range of mean annual rainfall, soil type and topography. Under higher rainfall conditions (ca. 800–1600 mm pa) remnants of closed evergreen forests occur in sites that are well protected from fire. Under lower rainfall conditions remnants of related evergreen shrublands, but with many more spinescent and succulent species, survive along the coast and occasionally on inland lower mountain slopes. These shrublands are also fire sensitive and restricted to areas that seldom burn. Most of the mountains and coastal lowlands of the Cape, however, are dominated by fynbos, a fire-prone shrubland characterised by the presence of stiff, sclerophyllous, reed-like Restionaceae, ericoid shrubs and broad-leaved shrubby members of the Proteaceae. Fynbos occurs on nutrient-poor soils over a wide rainfall gradient from 250 mm to 3000 mm per annum. It is replaced by renosterveld shrublands, which are also fire-prone, and dominated by Asteraceae and a grassy herbaceous layer (often dominated by C4 grasses) on clay rich soils below 700 mm rainfall. At the drier ends of fynbos distribution (<250 mm rainfall pa), succulent shrublands are found. These are not fire-prone. Unlike Californian succulent shrublands, the dominant elements are leaf succulents.

The summer-dry climate region of South Africa thus supports a rich diversity of ecosystem types with evergreen forests and shrublands that do not burn, fire-prone heathlike shrublands, fire-prone asteraceous shrublands, and succulent shrublands. The region is strikingly different from the rest of South Africa and most other mediterranean regions, in having virtually no grasslands and savannas.

The flora of the Cape Region, which is characterized by substantial winter rainfall, is among the richest in the world for similar-sized areas. There are some 8600 plant species of which 68% are endemic (Bond and Goldblatt 1984). Seven families and 248 genera are endemic, or nearly so, to the region. In comparison to other mediterranean-type regions, the Cape has unusually large species-family ratios (i.e., very species-rich genera), but generic diversity is not unusual. Western Australia shows similar patterns of high levels of intrageneric diversity (Linder et al. 1992).

The succulent shrublands are extremely rich in species, particularly leaf-succulents in the Mesembryanthemaceae. The biome includes the Namaqua-land flora of the west coast, which is extremely rich in annuals and geophytes and provides a spring floral display that attracts thousands of visitors annually. The biome has more than 5000 species, of which more than 50% are endemic, making it the richest semi-arid vegetation anywhere (Milton et al. 1997).

Southern Africa has a rich vertebrate fauna in world terms, but most of it is concentrated in summer rainfall savannas (Siegfried 1989). The two winter rainfall biomes (fynbos and succulent Karoo) have conspicuously low densities, both of larger vertebrates and insects, but measures of species richness per unit area are relatively high for amphibians, reptiles, birds, and mammals in southern Africa (Siegfried 1989). The fauna does not match the flora in endemism, as was noted for Australia. Fynbos has only seven endemic mammals and six endemic bird species. Included among the mammals were the extinct blue antelope, the bontebok, the Cape mountain zebra, the Cape dune mole rat (a large fossorial species occurring on lowland sandy soils), and several species of rodents and shrews. There are higher levels of endemism in other groups. Nine of 30 frog species and nearly half of the 30 freshwater fish species are endemic. The lizard fauna is rich with at least 50 species, but is still being explored. There appears to be a number of closely related vicariant endemics in groups such as dwarf chameleons and geckoes. There is a high diversity of tortoises (12 species), especially in the succulent Karoo, and one endemic fynbos species.

Chile

The mediterranean-climate area of central Chile is an area of high vegetation diversity and species richness. Together with the winter rainfall deserts to the north, also of mediterranean tendency, it comprises one of the world's 24 globally recognized threatened hotspots (Mittermeier et al. 1988), and has

Table 9.2. Species richness and endemism in the native mediterranean-type climate flora of central Chile based on the area between 32°S and 40°S, all vegetation types included

Ecoregion	Area (km ² × 10 ³)	No. species	Species endemic to Flora of Chile	Percent species endemic to Flora of Chile	No. species endemic to area	Percent species endemic to area
Summer rainfall area	154	ca. 825				
Winter rainfall areas (desert + medit)	300	3429	1821	53.1	1602	46.7
Deserts	145	1893	1100	58.1	605	31.9
Mediterranean	155	2537	1176	46.3	593	23.4
Cool temperate area	303	ca. 1360				
Continental Chile*	737	5082	2630	51.8	2630	51.8

Data are for species and varieties; from Marticorena 1990.

From Arroyo and Cavieras 1997.

Data are also given for the winter rainfall deserts (area between 25°S and 32°S and the coastal deserts Regions to around Pisagua), the summer rainfall area (Regions north of 25°S, excluding the coastal deserts), the cool temperate area (area between 40°S to 56°S), and continental Chile.

been considered as a World Center of Plant Diversity (Davis et al. 1997). Local vegetation diversity has been enhanced by major vegetation reorganization in the Pleistocene and Holocene (Villagrán 1994). The highly dissected landscape, which results from Pleistocene uplifting the dominant Andean chain, has provided a theater for much local speciation, especially in the herbaceous flora. Because it is positioned at the crossroads of two major biogeographic regions, the Neotropics and the ancient Gondwanan province, it is not uncommon to find dominant woody taxa of widely different biogeographical origins existing side by side in the mediterranean vegetation of central Chile. Indeed, the mediterranean vegetation intergrades imperceptibly into southern temperate rainforest, which is a situation that would appear to be unique among the southern hemisphere mediterranean-type climate areas.

Central Chile (the mediterranean climate portions in a strict sense) has a rich and endemic flora (Table 9.2) with high life-form diversity (Montenegro and Ginocchi 1995; Arroyo and Cavieras 1997; Arroyo et al. 1997). Compared with the mediterranean flora of the California Floristic Province, which is its closest analog (Mooney 1977), central Chile stands out for its higher proportion of woody species and genera, and a significantly smaller annual flora (Arroyo et al. 1997). Whereas 30% of the native flora of the California

Floristic Province is annual, a mere 16% of Chilean mediterranean species are annual. Twenty-one percent of the mediterranean flora of Chile is woody, in comparison with 14% in the California Floristic Province. This difference in life-form composition in the two presently climatically similar areas has been related to an accumulated historical effect of a more equitable climate in southern South America (Arroyo et al. 1997).

For overall richness, Arroyo et al. (1997) cite a total of 2395 vascular plant species (i.e., angiosperms, gymnosperms, and ferns), in 591 genera, that occur between the northern limit of the Province of Choapa (31°S–31°30'S) to the southern limits of the Provinces of Concepción and Ñuble (ca. 37°15'S). There are 437 herbaceous genera in central Chile and 180 genera containing woody species (Arroyo et al. 1997). Thus, a very high proportion of the phylogenetic richness is found in the herbaceous flora. For the larger area between 32° and 40°S there are 2537 species (Arroyo and Cavieras 1997). Species accumulation curves for the central Chilean region approach an asymptote, which suggests that the total flora is relatively well known (Maldonado et al. 1995).

The hyperarid winter rainfall deserts, which is also a mediterranean-type climate in a wider sense, support 1893 species (Table 9.2). Together, the more typical mediterranean-type climate and the hyperarid winter rainfall deserts (i.e., winter rainfall area) support a flora of some 3429 species.

The richness of the mediterranean-climate area is best appreciated by comparing the number of species present with other major ecoregions of Chile, bearing in mind, size of land area (Table 9.2). Although only slightly larger than the drier winter-rainfall desert area, it has more than 600 more species. The cool temperate forest zone (including all vegetation types) south of 40°S, for an area a little under twice the size of central Chile (Table 9.2), has only around recorded 1360 species. Plant species-richness in central Chile is relatively low in comparison with other mediterranean-type climate areas (Cowling et al. 1996). In comparison with California, central Chile has fewer genera than are found in the California Floristic Province for a given area (Arroyo et al. 1997). Increasing isolation from potential sources of biota east of the Andean chain that ensued as of the rapid uplift of the Andes in the Pliocene and Pleistocene (Arroyo et al. 1997) appears to have resulted in fewer genera dispersing into the area of central Chile.

Endemism in the mediterranean-climate area, a relatively small geographical area (Table 9.2), is around 23%; however, an outstanding 47% of species in the larger winter rainfall area, which is the more natural biogeographic unit in Chile, are endemic. Endemism is also high in the winter rainfall deserts per se (32%). The high level of endemism considering the full winter rainfall area has been enhanced by continental Chile's islandlike nature. Bordered to the west by the Pacific Ocean, to the east by the high Andean crest and to the north by an area of extreme aridity, interchange with adjacent continental areas has been restricted over the course of evolution of Chile's mediterranean flora (Arroyo et al. 1996, 1998; Villagrán and Hinojosa 1997).

Table 9.3. Species richness (and percentage endemism where available) in some well-studied groups of animals in the mediterranean area of Chile

Group	Asilidae	Butterflies	Ants	Apoidea	Fresh water fish	Amphibians	Reptiles	Land birds	Mammals
Species	72	97	51	187	24	25	39	179	51
Endemic species (%)	—	—	—	—	7 (29%)	12 (48%)	13 (33%)	1 (1%)	3 (6%)

Data refer to the area between 32–40°S. Data for amphibians, reptiles, land birds, and mammals from Arroyo et al. 1998. Data for Asilidae compiled from Artigas 1970; butterflies: Peña and Ugarte 1997; ants: Snelling and Hunt 1975; Apoidea: Toro 1986; fresh water fish: Arratia 1981. See Table 9.2 for data on vascular plants.

The mediterranean-type climate area of Chile shows both high species-richness and high vegetation diversity. The main vegetation types are relict rainforest, evergreen *Nothofagus* forest, deciduous *Nothofagus* forest, sclerophyllous forest, matorral, northern coastal matorral, succulent and inland scrub, montane sclerophyllous forest, montane coniferous forest, and alpine (Arroyo et al. 1997).

Species richness data for Chilean mediterranean-climate region groups, in addition to plants, are shown in Table 9.3. Overall, species richness is higher in the mediterranean areas in comparison with other ecoregions of Chile (data not shown), particularly considering that the southern temperate region is almost twice the size of the mediterranean-climate region. Notable peaks in species richness in the mediterranean area are seen in butterflies, Asilidae, ants, reptiles, plants, and Apoidea.

California

As in other mediterranean-climate regions California has a diversity of ecosystem types. This is in part due to its complex history as well as to topographic diversity. California has relictual forests (e.g., the redwood forests) that are remnants of vegetation types that were much more widely distributed in the past, when summer rainfall was still present. These forests are now restricted to the coastal fog belt where they are able to supplement the rain with fog drip in the summer. California has extensive development of scrubland, chaparral (dominated by many species from the genera *Arctostaphylos*, *Ceanothus*, and *Adenostoma*). In moister sites forests occur dominated by evergreen *Quercus* species. At the drier ends of the chaparral distribution, coastal and succulent scrublands are found. The coastal hills and inland valleys, where not totally covered by agriculture, are dominated by deciduous *Quercus* species and alien annual grass savannas. At higher elevations species-rich montane coniferous forests occur. Thus, there are evergreen and deciduous forests, savannas, and scrublands of various types within the summer-dry climate of California.

The mediterranean climatic region covers an area of about 130,000 km² in Chile and 250,000 km² in California (Arroyo et al. 1995), with about 2500 and

4240 plant species, respectively. The Chilean flora has less within-genus diversity and a lower representation of annuals. A full one third of the California flora is endemic, whereas the Chilean mediterranean climatic flora is about 25% endemic, reflecting an apparently wider habitat distribution of many Chilean plants in contrast to their Californian counterparts (e.g., gamma diversity for birds is greater in California than it is in Chile) (Cody et al. 1977). The Chilean flora has only about 16% annuals, whereas California has 30%. This difference may relate to the more equitable climate of Chile.

Summary of Biodiversity Patterns in Mediterranean-Climate Regions

All of the mediterranean-climate regions of the world are species-rich with a high degree of endemism, particularly for plants, but less so for birds and mammals. These differences are due to the degree of natural dispersability of these latter organisms. Further, these areas have very high numbers of rare and threatened species, as well as have high biome diversity, including grasslands, shrublands, woodlands, and forests. Most of these regions are rich in species for certain key genera, although Chile seems to be an exception to this trend. There are also differences in the proportional species in various life forms (e.g., California has a larger fraction of annual herbs in the flora than does Chile).

As discussed later, the biota of Chile, California, and the Mediterranean Basin have more generalized pollinator and disperser relations than does the biota of South Africa and Australia. This has implications for community stability under global change.

In summary, these areas are similar in their high species and ecosystem richness but they differ in a number of important properties relating to life-form richness and biotic interactions that will be influenced by global change.

Climatic Patterns, Climate Change Scenarios, and Impacts on Biota

Australia

Under the current climatic regime, considerable variation in rainfall amount and distribution occurs across the mediterranean-climate zone of Western Australia (Hobbs 1992). Rainfall declines from about 1500 mm/year in the extreme southwest (Gentilli 1989) to about 250 mm at the eastern edge of the area, which could be classed as mediterranean, and the length of the summer drought increases correspondingly.

Australian and South African mediterranean climates differ from those of the other mediterranean regions (i.e., the Mediterranean Basin, California, and Chile) by having summer rainfall as a common, if unpredictable, occurrence (di Castri 1981). The current winter rainfall regime has been in effect

for only the last 2.5 million years. During that period there have been numerous warm wet/cold dry fluctuations (Churchill 1968; Bowler 1982; Lamont et al. 1984).

Annual variations in rainfall amounts and distributions, coupled with relatively short historical records, make the detection of any long-term trends in rainfall in the mediterranean region of Western Australia difficult (Saunders and Hobbs 1992). Pittock (1988) indicated a possible decline in winter rainfall of 2.9–4.8% per decade between 1913 and 1986 for southwestern Australia. It is uncertain whether these changes result directly from changes in regional climatic patterns, or from an interaction with changing land cover as a result of vegetation clearance for agriculture (Smith et al. 1992; Lyons et al. 1993; Whetton et al. 1994).

Scenarios of climate change, in response to CO_2 increases, suggest temperature increases of between 0.5 and 1.6°C by 2030 for southwestern Australia (Whetton et al. 1994). Five climate models used for this study all indicated an increase in summer rainfalls and small (not necessarily significant) decreases in winter rainfall. Increases in summer rainfall ranged from 9 to 33% and decreases in winter from 2 to 14%.

The impacts of any likely climate change on biodiversity in southwestern Australia are hard to predict because of a lack of basic information on environmental tolerances of species and because the altered and fragmented nature of many ecosystems is likely to inhibit or modify any possible biotic response to climate. Any changes in current rainfall patterns are, however, likely to have profound effects on land use in the wheatbelt region, with follow-on impacts on biodiversity. Reductions in winter rainfall are liable to render large areas increasingly marginal for agricultural production, potentially leading to their abandonment. Whether this will result in the reinstatement of native vegetation without management intervention is debatable (Yates and Hobbs 1997). Increased summer rainfall may lead to increasing erosion and runoff unless extensive revegetation has occurred. Increased summer rainfall may also favor the increased spread of the disease *Phytophthora cinnamomi*. Increased temperatures are likely to mean a higher incidence of extreme temperatures, with implications for the biota. For example, extreme summer temperatures have been observed to lead to tree deaths.

Mediterranean Basin

GCMs are predicting a warming of about 2°C in winter, and from 2 to 3°C in summer for the Mediterranean regions by 2100 (Palutikof and Wigley 1996). Changes in total rainfall and temporal distribution are more poorly understood, but current predictions suggest that there will be slightly increased precipitation during winter and a decrease of summer precipitation by 5–15%. There is already evidence of decreased cloudiness and precipitation in the central and western Mediterranean Basin (Maheras 1988) and increased temperatures over the last century (Piñol et al. 1998). The latter

study showed an average increase of mean annual temperature of 0.10°C per decade for the period 1910–1994, and an increase of 0.3°C per decade during the last 20 years.

The effects of climate change on biodiversity in the Mediterranean Basin, and for mediterranean-climate regions in general, are expected to occur based on the following grounds. First, increased evapotranspiration will lead to increased water stress that will bring changes in community composition as species assemblages are reorganized according to the new environmental conditions. Second, an increase in winter temperatures is expected to affect biodiversity in the following ways.

First decrease or loss of relict temperate species present only in marginal habitats (north-facing mountain or cliff slopes): These species are more likely to be affected mostly by a decrease in water availability than by increased temperature directly, so predictions need to be linked to rainfall scenarios. These species might also be affected by decrease in frosts because many of them require chilling for germination. Second decrease or loss of species with late season germination because of large risk of establishment failure brought on by lack of water, and because of space preemption by early germinating species that will establish larger biomass throughout winter. Third consequences for recruitment of woody seedlings are uncertain. Woody seedlings are sensitive to competition for water (e.g., recruitment is rare and limited to "good years") (Bacilieri et al. 1993).

Fourth, warmer climate will push closed canopy evergreen-oak forests northward (Piñol et al. 1995) and ultimately, will shift forest communities in the south toward low-cover desert shrublands with the associated consequences on the water and carbon fluxes.

Changes in human activity and global warming will overall reduce plant diversity in such sensitive areas as temperate/mediterranean and mediterranean/desert ecotones. The abundance of endemic species will decrease with increasing aridity and there will be an increase in the abundance of annual species (Holzapfel et al. 1992). Studies in the southwest of the Iberian Peninsula show that species living in the dry end of the mediterranean climate have a low dispersal capacity that will prevent them from a successful northward displacement as rapid warming takes place (Merino et al. 1995). Other species, however, such as some evergreen trees of the genus *Quercus* evidently have a much faster dispersion capacity as they were found from southern Spain to Sweden during the northward migration that took place in the first half of the Holocene (Birks 1990).

South Africa

GCM scenarios for the Cape region, with a doubling of CO_2 , predict a rise in average temperature of 1–2.5°C, with uncertainty on the direction of change in precipitation, in total or seasonally (Hewitson and Crane 1996, Hudson 1997).

The possible consequences of climate change for biome limits in southern Africa have been explored by correlative studies (Ellery et al. 1991), primarily in summer rainfall areas. Euston-Brown (1995) studied the causes of biome boundaries near the eastern limits of the fynbos biome using both correlative methods and translocation experiments across altitudinal and geological gradients. He showed that several functional groups, characteristic of fynbos, are at their climatic limits. Global warming or rainfall reduction would therefore lead to the retreat of fynbos elements to higher, cooler elevations. The steep mountainous terrain would provide a topographic refuge for sensitive groups on mesic pole-facing aspects but they would be eliminated from lower elevations and from north-facing slopes.

The most sensitive functional groups were members of the Restionaceae and Proteaceae. Ericoid shrubs were the least sensitive and survived and grew when transferred to lower, warmer elevations. Functional groups representative of adjacent grassland and closed thicket formations (broad-leaved, non-fire-prone shrublands) survived transfer to fynbos soils at higher altitudes, suggesting that disturbance, rather than direct climatic or edaphic controls, limit their current distribution. Euston-Brown's (1995) study therefore suggests that the fynbos biome will shrink if effective precipitation decreases due to global warming. Patches will survive at higher elevations and on mesic slopes. The vegetation-replacing fynbos would likely depend more on the interaction between disturbance regime and climate than on climate alone. If fires become more frequent, then grasslands are likely to spread from the east to occupy fynbos areas (Trollope 1973). If fires are less frequent, then fynbos will be replaced by non-fire-prone thicket vegetation (Manders et al. 1992). Correlative studies of succulent Karoo species richness and growth-form diversity with climatic parameters show that both are positively correlated with climatic heterogeneity and rainfall evenness (Cowling et al. 1994). The extent of succulent Karoo is therefore most sensitive to a change in the seasonality of rainfall. Both biomes are geographically isolated at the southwestern tip of Africa. There is no refuge lying at cooler southern latitudes comparable to, say, South America. If global warming causes significant temperature change, fynbos remnants can only retreat to higher elevations in the mountains or more mesic slopes or soils. This must place many fynbos species at risk of extinction. Succulent Karoo occupies a flatter landscape, especially along the west coast. In the absence of topographic refugia, the entire biome is severely threatened with extinction. Both biomes are intimately associated with winter rainfall climates. If global change leads to rapid change in rainfall seasonality, large-scale extinction could be expected.

In contrast to other mediterranean regions, the mediterranean shrublands of South Africa and Australia are characterized by many plant species with specialized insect or vertebrate pollinated flowers and hundreds of species dependent on ants for seed dispersal (Johnson 1992). Given the short life-span of many plant species, and therefore their high dependence on seeds,

these systems must rank as among the most vulnerable anywhere to cascading extinctions caused by loss of mutualist partners (Bond 1994). It is still poorly known whether climate or land-use change will result in the loss of such partners (Bond 1995).

California and Chile

The projections for climate change for Chile and California differ, due to differences in land-sea ratios (Trenberth 1993). The mediterranean-climate latitudes of California are expected to warm nearly twice as fast as these regions in Chile. Projections of temperature change with a CO_2 doubling will average 3°C warmer in the north and less than 2°C warmer in the south, at latitudes of around 40°C .

In an analysis of the climate change expected for California with a doubling of CO_2 , Knox (1991) predicted a rise in average temperature of $2\text{--}4^\circ\text{C}$, precipitation changing between plus to minus 20% of current values, snow level rising 100 m/degree increase in temperature, increased temperatures of shallow water bodies, and a poleward shift of storm tracks.

One of the distinctive features of coastal Californian and Chile is fog. Fog results from the condensation of moisture contained in the air moving in from the Pacific as it hits the cold water surfaces along the coast caused by upwelling. Subsiding air in these regions forms a cap and results in the fog layer being close to the ground. Bakun (1990) predicts that climate warming will cause a greater differential temperature between land and water and hence increase the winds that lead to upwelling, thus increasing fog amount. McBean (1996) cites work that predicts an opposite result due to effects on subsiding air; however, with either an increase or decrease there would be important effects on the fog-requiring vegetation of these regions. There has been a trend over the past decades for an increase in wind stress off of the Californian coasts (Hsieh and Boer 1992).

The fates of the biota of California and Chile, as with other mediterranean-climate regions, are uncertain because of the many interactions and feedbacks that will occur between climate changes per se and with other global changes. Botkin et al. (1991), however, make the following predictions for California based on a doubling of CO_2 concentrations, noting the difficulties of making predictions based on the topographic diversity of this region:

Increasing temperatures and decreasing soil moisture will lead to increased fire frequency in the short run with an acceleration of vegetation change. In the longer run there will be a decrease in forest biomass. Change in forest composition is due to such factors as the loss of the winter chill conditions necessary for germination and growth of Douglas fir, as one example. Other impacts may include a change in tempo of recycling due to increased temperature, and movement of forests upslope from present locations.

Knox (1991) concluded that 20–50% of the area currently occupied by a given vegetation type would be preempted by new ones. Other analyses for California are given in Keeley and Mooney (1993), Westman and Malanson (1992), and Malanson and O'Leary (1995).

Invasive species will likely be more pervasive and numerous with the community disruption that will accompany rapid climate change. If there is a shift in the seasonality of rainfall, we could see changes in abundance of C_4 weeds that need summer rain or irrigation.

The biogeographic model MAPPS (Neilson 1995) projects vegetation response to different climatic scenarios for doubled CO_2 , utilizing growth form responses to climate rather than responses of whole biomes or of individual species, as given in Malanson and O'Leary (1995). Figure 9.1A (see color insert) gives the current aggregated vegetation distribution in California according to the MAPPS model (derived from simulations explained in Neilson et al. (1998) for three different Global Circulation Models [OSU, GISS, and the Hadley Center Model (HADCM2SUL)]). The Hadley model, which incorporates sulphate aerosols into the simulations, has the greatest impact on a doubled CO_2 world, with current desert systems becoming grasslands and shrublands turning more into woodlands (i.e., an apparently more mesic California). The discrepancy in responses of a single vegetation model to different global climate-change scenarios highlights the fact that we are still in a very early stage of making predictions of what the future will bring.

Summary of Expected Climate Change and Impacts

All mediterranean-climate regions will show an increased temperature with a doubling of atmospheric CO_2 concentration. The amount of change will differ among these regions in relation to the prevailing water-to-land mass. The temperature changes will have a large impact on the hydrology, and hence biology, of these regions, including impacts on snow-melt periods, which are important biologically in these summer dry areas. Most regions will see an increased amount of precipitation; however, how these changes will play out seasonally is not agreed upon either for a given area or among areas. Understanding changes in seasonality of precipitation in these arid regions is crucial for making realistic predictions of climate impact on the biota. In addition, how coastal fog patterns will be affected is not agreed upon, yet it has large potential importance in controlling biotic patterns. Fire climates will be affected with increasing temperatures and evapotranspiration, as discussed later, with differing biotic consequences in each region.

Direct impacts of climate change on the biota of mediterranean-climate regions are predicted to be profound. Mediterranean-climate regions are particularly vulnerable because of their high degree of endemism and localized species distributions. Temperature effects alone will have a big impact

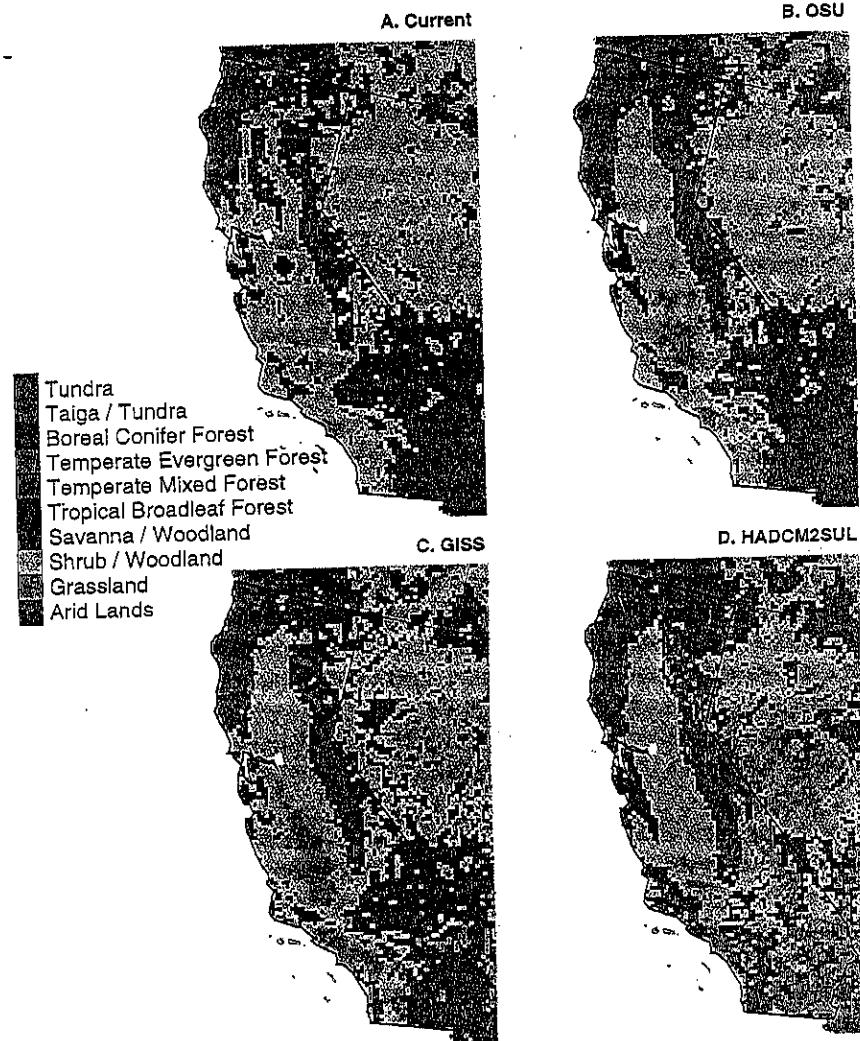


Figure 9.1. Modeled responses of California vegetation to different climate model projections for a doubled CO_2 world. (A) Present vegetation, (B) response to the OSU climate model, (C) to GISS model, and (D) to the Hadley Center model (HADCM2SUL) (see color insert).

on biotic distributions in mountainous regions, and along north-south gradients, as has already been observed for butterflies. Temperature-driven changes in evapotranspiration will have direct and indirect effects (changing fire climates) on the biota. The high numbers of narrowly distributed species in these regions will certainly be threatened by a rapidly changing climate. Shifts in the many ecotones between the diversity of biome types will be

expected. These general trends will be influenced by the other global changes discussed later.

Invasive Species

Australia

Introduced predators, particularly foxes and cats, are a major cause of the complete or near extinction of many Australian marsupials (Burbidge and McKenzie 1989; Friend 1990). Indeed, Western Australian forests have provided the last refuge for a number of marsupial species, presumably because fox numbers remained lower there than in other areas. Predator control is now practiced in many areas, with obvious success indicated by increases in abundances of native mammals (Kinnear et al. 1988; Friend 1990). Poisoning of introduced predators using 1080 (sodium monofluoroacetate) poison is possible because the resident mammal populations have developed a tolerance to the poison through coevolution with plants that contain it (Twigg and King 1991). A large-scale program of fox eradication, entitled "Western Shield," promises to allow recovery or reintroduction of endangered mammals in many forest and nonforest areas.

Invasive plants are another major threat to many mediterranean-climate ecosystems in Australia (Humphries et al. 1991; Humphries 1993). Individual invaders [e.g., bridal creeper (*Myrsiphyllum asparagoides*)] have the potential to crowd out native species and alter vegetation composition and structure. Herbaceous species, especially grasses, also have the potential to alter fire regimes by changing the structure and availability of fuel (D'Antonio and Vitousek 1992). About 1500 species are currently naturalized across all of Australia, with 848 species recorded from Western Australia (Keighery 1991). There are 220 species that are recognized as noxious weeds across Australia (Parsons and Cuthbertson 1992), and many are problems in native ecosystems. Additional species, such as invasive pine species (Richardson et al. 1994), may become problems in the future (Hobbs 1993a).

The relatively high levels of invasion by mammals, plants, and fish in Western Australia undoubtedly result mainly from the deliberate introduction of these organisms for agriculture, horticulture, or sport. New species of plants continue to be introduced (Rejmánek and Randall 1994; Keighery 1995), and some rapidly extend their range (Dodd and Moore 1993). Australia continues to import plant species without due consideration for the potential threats of invasiveness. For most animal groups, the rates of introduction are now probably slower, although the invasion of a southwestern Australian river system by *Perca fluviatilis* (Hutchison and Armstrong 1993) indicates that the problem continues.

The introduced fungus *Phytophthora cinammomi* is a major factor influencing forest and shrub ecosystems in Western Australia and in other parts of the country (Dell and Malajczuk 1989). Depending on the severity of attack,

Phytophthora causes the loss of overstorey and understorey plant species. A large number of plant species are susceptible to the fungus, and it is likely that others are impacted by the changes in microclimate and local moisture relations caused by loss of overstorey cover. This fungus and other diseases are also important in other nonforest communities, including the floristically rich kwongan heath (Wills 1993; Wills and Keighery 1994).

Mediterranean Basin

Most of the invasive species in the Mediterranean have been human-facilitated or intentionally introduced, either associated with human settlement or agricultural trade. Thus, invasions will probably continue in the future as barriers among the European Union countries disappear and human migration increases, particularly from the south to the north.

In southern France about 60 species belonging to 17 different families are presently naturalized (Guillelm and Maillet 1982). Four families are strongly represented: Asteraceae, Poaceae, Amaranthaceae, and Solanaceae. These species originate from temperate, mediterranean-climate, or subtropical regions of the Americas and Asia.

An interesting trend concerns the increase in subtropical and tropical species. This increase is strongly linked to irrigated land where these species can thrive because their lifecycle is offset relative to native agricultural weeds that are predominantly winter annuals. Indeed C₄ metabolism is a common feature among exotics.

It has been suggested that abandoned fields, which are disturbed and relatively fertile, are highly invasible because of their simple food webs and trophic interactions. As an example, *Opuntia ficus-indica* has been reported to invade abandoned fields in the northeast of the Iberian Peninsula (M. Vilà, personal communication). This species may be further favored by predicted increases of atmospheric CO₂ (García de Cota and Nobel 1990) and water stress (Luo and Nobel 1993). Abandoned fields in southern France are invaded by two alien woody species—tree of heaven (*Ailanthus elegantissima*) and wattle (*Acacia dealbata*) (Blondel and Aronson 1995)—although revegetation after field abandonment is largely controlled by the seed availability from the surrounding native woody vegetation.

In general, plant invasions seem to be more frequent and often successful, and follow more predictable patterns than do animal invasions (di Castri 1991). The introduction of freshwater fish species has been the most numerous among vertebrates, yet the effects on local populations and ecosystem functioning have been poorly studied (Crivelli 1995). To the present, 70 introduced exotic or translocated fish species and subspecies have been reported in the northern mediterranean region. All of them have been intentional human introductions (Crivelli 1995). Continuous species introductions, wetland depletion, and increased water pollution, by a more resource-demanding human population, will lead to an overall impov-

erishment of native populations of freshwater fish species in the next decades.

South Africa

Alien invasive plants, mostly trees or shrubs from other mediterranean regions, pose by far the greatest immediate threat to the Cape flora (MacDonald 1989, Richardson et al. 1996). Pines and Hakea species (Australian Proteaceae) have invaded 14% of the remaining areas of mountain fynbos, whereas Australian *Acacia* species have invaded up to 68% of the remaining area of lowland fynbos. The invasive species overtop native shrubland species, suppressing most of them and leading to local extinction and a marked reduction in biodiversity (Richardson et al. 1996). Among the most significant changes in ecosystem processes is the reduction in runoff from invaded catchments estimated to be between 30 and 70% lower than uninvaded fynbos (Le Maitre et al. 1996). Alien species also alter fuel conditions, causing more intense fires that in turn cause accelerated soil erosion after fire (Richardson et al. 1997). The invasive acacias accumulate nutrients in the surface soil layers to the point where it becomes very difficult to restore fynbos species adapted to nutrient-poor conditions in areas cleared of aliens (Stock and Allsopp 1992).

Alien invasion is much less significant in the succulent shrublands; however, *Prosopis* (mesquite) is a locally important invader along water courses with species of Chenopodiaceae and *Opuntia* spreading locally in dryland areas (Richardson et al. 1997).

In South Africa, the threat of invasive trees to water supply has led to extensive alien clearing using mechanical methods supplemented by release of biological control agents. About 60,000 ha of the 1.15 million ha of fynbos catchments are treated each year by felling dense stands of *Pinus* and *Hakea* species. Efforts at controlling the problem include the deployment of thousands of previously unemployed workers in an ambitious attempt at large-scale environmental restoration through alien removal. Economic analyses indicate that savings in terms of increased water run-off make the expense of alien clearing cost-effective (van Wilgen et al. 1996).

Chile

Alien invasive species are widely distributed altitudinally and latitudinally in the Chilean mediterranean-climate area today. Marticorena (1990) provides a figure of 657 introduced taxa (i.e., species, subspecies, and varieties) for all of continental Chile, but this figure is probably now closer to 700 (Marticorena, unpublished data). About two thirds of these species are in the mediterranean-climate area, with more than 400 in the metropolitan region (Santiago-Valparaiso district) where Chile's population is concentrated. As in other mediterranean-climate areas, an overwhelming number of the introduced species are of Old World origin. Most are herbaceous, with many

annuals. Important sources of invasive species in central Chile are cultivated plants in botanical gardens, escaped medicinal plants, and forage plants (Matthei 1995). Many of these intentionally introduced species today are now serious weeds of agricultural crops and common inhabitants of disturbed areas. In structurally undisturbed vegetation, the relatively low percentage of native annuals in the flora of central Chile (Arroyo et al. 1995) is a feature that could engender greater susceptibility to invasion by exotic species than in climatically similar California. A surprising number of weedy species in the far north of Chile are of subtropical origin (Matthei 1995) and could penetrate further south with global warming, especially where irrigation agriculture is practiced, as is the case in the central valley. Increased trade and traffic between the countries of the southern Pacific and the lowering of trade barriers among the countries of Mercosur are expected to increase the number of invasive species establishing in central Chile in the coming century. A number of the world's worst weeds occurring in New Zealand and Australia, Argentina, and Uruguay have not yet been reported in Chile (Holm 1997).

California

There are more than 1000 established alien plants in the Californian flora (Rejmanek and Randall, 1994) representing about 20% of the flora. The numbers of new plant invasives may be slowing in California, although this is certainly not the case for marine organisms (Cohen and Carlton 1998). There are many more invasive species than there are endangered and threatened ones in California (Hobbs and Mooney 1997), even though California has one of the highest numbers of endangered species in the United States. Many of these invasive species have had large ecosystem impacts in terrestrial, freshwater, and coastal marine ecosystems (Dukes and Mooney 1999).

Summary of Invasive Species

All of the mediterranean-climate regions are heavily impacted by invasive species with a prognosis of greater numbers of invasives becoming established in the future with land-use and climate change. These areas differ in that in some regions (i.e., South Africa) invasive shrubs and trees are doing the most damage, whereas the herbaceous plants are the greatest pests in Chile and California. Australia, has many invasive mammals also causing damage.

Land-Use and Cover Change

An overview of the impact of land use on the biodiversity of mediterranean-type ecosystems has appeared (Rundel et al. 1998). We will address potential land-use changes in each of these regions separately.

Australia

Producing future scenarios requires an understanding of the changes already underway because of trends in land use, particularly in relation to urban growth, forestry, and agricultural development. Urban development in the Perth metropolitan region is spreading rapidly as the population of the city grows. Particular threats to the remaining biodiversity come from altered fire regimes, weed invasion, and, in the case of wetlands, altered hydrology and eutrophication. Arson is a major cause of bushfires (Dixon et al. 1995; Pigott and Loneragan 1995).

Forest systems of Western Australia have been managed in a variety of ways for timber production over the past century (Dargavel 1995). The most important impacts on forest systems are forest management practices, in particular timber harvesting, fuel reduction burning, and the impacts of invasive species, including the introduced pathogen, *Phytophthora cinnamomi*. The jarrah (*Eucalyptus marginata*) forest is currently subjected to widespread short-rotation fuel reduction burning, which has evolved to reduce the risk of destructive wildfires. Controversy surrounds the questions of whether such a burning regime is effective and whether it has adverse impacts on the forest ecosystem (McGrath 1985; Tingay 1985; Underwood et al. 1985). It has been claimed that the current regime mimics the regime prevailing prior to European settlement (Hallam 1975; Burrows et al. 1995), although the evidence for this is not compelling, and basic knowledge on Aboriginal fire regimes is scant (Williams and Gill 1995). Among other factors future scenarios depend on the interaction between *Phytophthora* and changes in rainfall amounts and distributions, the long-term impacts of continued fuel reduction burning, and the success of current attempts to control feral predators.

In agricultural landscapes, profound changes in nutrient, energy, and water fluxes have occurred as a result of the replacement of perennial vegetation with predominantly annual crops and pastures (Hobbs and Saunders 1993). Changed energy fluxes and wind regimes result from the change from tall evergreen vegetation to the alternating short annual vegetation and bare soil associated with agriculture (Hobbs 1993b). In addition to influencing local microclimates, these changes may have regional scale implications. Rainfall patterns in southwestern Australia have changed over the past century, such that annual amounts have declined in the agricultural areas, but increased in the adjacent inland areas (Pittock 1988). Smith et al. (1992) have suggested that these changes could be associated with the effects of changing albedo on cloud formation. Evidence for this comes from a phenomenon frequently observed in satellite images for the area, whereby clouds are found only above the large areas of native vegetation remaining in the wheatbelt and to the east of the line between cleared and uncleared land.

The landscape has changed from one in which considerable internal nutrient redistribution occurs, but little net loss is evident, to one in which large

water erosion and harvesting (Hobbs 1993b). In the fragmented wheatbelt landscape, remnant native vegetation on low-nutrient soils are set in an agricultural matrix with elevated nutrient levels and increased mobility of topsoil. Loss of topsoil by wind and water erosion, especially during episodic storm events, is a major problem over much of the wheatbelt and can bring nutrient-rich soil into remnant areas and hence alter the nutrient regime. This has important implications for weed invasion, which is promoted by nutrient increase (Hobbs and Atkins 1988).

Rising water tables also threaten biodiversity. Within uncleared vegetation, plant architecture, soil structure, and soil biotic activity channel and redistribute rainfall, and most is utilized and transpired or evaporated, with little runoff or transfer to the water table (Nulsen et al. 1986; McFarlane et al. 1992; McFarlane et al. 1993). Removal of native vegetation and replacement with annual crops and pastures results in considerably less efficient use of rainfall, increased runoff, and greater inputs to the water table. This has led to rising water tables, with rises of 50 cm/year or more recorded in some areas (George et al. 1995). Beneath much of the wheatbelt are considerable quantities of salt stored at depth, resulting from a long history of input in ocean-derived rainfall coupled with poor drainage (Hingston and Galaitis 1976). As water tables rise, the stored salt is mobilized, and, wherever the water table reaches the surface, salinization occurs, posing a threat to a significant proportion of the wheatbelt (McFarlane et al. 1993; Nulsen 1993; George et al. 1995). Although native vegetation within remnants still uses water more efficiently than the surrounding crops and pastures, the overriding influence of the agricultural matrix means that water tables are rising even under large remnants (Salama et al. 1994). Many low-lying areas have already been affected, and most of the previously fresh water lakes have gone saline (Froend et al. 1987; Froend and McComb 1991; Hobbs et al. 1993). In some areas the water table is rising so quickly that remnant vegetation will be destroyed within the next 5–10 years, whereas the timescale is longer but the problem is no less insidious in lower rainfall areas.

The processes already established will in large part determine future trends in biodiversity. Extensive habitat removal and fragmentation over the past 50–100 years is likely to have created a situation where some species have been lost already, but others remain in populations that are not viable in the long term. The “extinction debt” is thus likely to result in continued loss of species from the region, unless restorative measures are undertaken. Future scenarios for the agricultural area thus depend in large part on the type and magnitude of human response to the changes discussed earlier. Maintenance of a “business as usual” farming system of mixed annual cropping and pastures will result in continued degradation of both agricultural and conservation lands through rising water tables, salinization, and erosion. On the other hand, extensive modification of farming practices to include considerably more perennial vegetation (e.g., alley farming, tree plantations, and perennial

Mediterranean Basin

The decrease of farming and agricultural practices in the northern Mediterranean Basin, as a result of more "efficient" production systems and growing urbanization, is leading to an abandonment of farmland and subsequent encroachment of woody vegetation (Moreno et al. 1998). This phenomenon started at the beginning of the century and is now being accelerated by the new Common Agriculture Policy of the European Community. During the period 1965–1985 rangelands and croplands receded by 7% and 9%, respectively (Le Houréou 1992). This is leading to an increase in homogenization of the landscape and loss of highly diverse and species-rich systems, although increasing urbanization will counteract the vegetation expansion. This differs from the situation in Australia, where fragmentation is the cause of loss of diversity—here, diversity loss results from the reduction in management input in systems with a long history of human management. Unique cases of loss of highly diverse landscapes are the loss of managed systems (e.g., the "dehesas" in Spain and "montados" in Portugal) (García et al. 1994), and the mosaic landscapes that intermix natural and managed patches in France and Italy. All of these systems have high species and landscape diversity.

In general, faunal diversity is also higher in regions where the landscape offers some patchiness with open areas, shrublands, and forests, and biodiversity decreases in landscapes dominated by closed-canopy forests (Tellería et al. 1992). With the continuous abandonment of cropland (e.g., the wheat fields in Spain that maintain large and diverse bird populations) (Díaz and Tellería 1994), the future avifauna diversity is predicted to decline.

Other types of activities are increasingly causing major anthropogenic disturbances (e.g., road construction, urban development, and forest clear cutting). Natural disturbances by wild mammals are increasing (e.g., the case of wild boar whose populations are building up in many forests of the western Mediterranean).

In general, changes in management strategies that alter landscape units and its structure will bring the largest changes in biodiversity (birds, Tellería et al. 1992). Increases in human population and tourism will have the strongest impact on the flora and fauna of islands with a predicted overall impoverishment (Balearic Islands, Mus 1995). Finally, increasing water demand for an expanding urban population and for use in more intensive agroindustrial farming is predicted to lower water tables in the more arid regions of the Mediterranean. This lowering of the water table affects the dynamics of temporary ponds and streams that are causing a decline of amphibian populations in the central Iberian Peninsula (Rodríguez-Jiménez 1988).

Trends in the European Mediterranean contrast with those of North Africa and Near East, where arid steppes and rangelands are being cleared for grain production. During the period 1965–1985 forest and shrublands receded by 3% and cropland expanded by 5% (Le Houréou 1992). In the next decades the Mediterranean coast of North Africa will also see a fast-

growing tourist industry moving on the coastal areas and replacing natural habitats and farmlands, with a consequent loss of habitat and hence of biodiversity.

Wetlands and coastal dunes are the notable exception to the stability in regional species diversity. Indeed, the Mediterranean coast is subjected to ever-increasing pressures from urban and tourism-oriented development. Wetlands and their species are under serious threats due to draining, spraying with pesticides, and repeated disturbance (e.g., by recreation vehicles) (Naveh and Liebermann 1994). As a result, numbers of declining or endangered species are higher for coastal regions (Barbéro 1989).

Many crucial habitats in the Mediterranean Basin, in relation to biodiversity, are very vulnerable to changing land-use patterns. River deltas and salt marshes in the Mediterranean Basin are focal breeding areas, and in many cases they are internationally important stopover points in the Afro-Paleoarctic migration system. This migration route goes from as far north as Sweden, over the Mediterranean region, to East Africa and the Middle East (Bairlein 1991). These areas are hotspots for animal biodiversity, especially waterbirds (Van der Hane and Van Den Berk 1994). They are particularly vulnerable because climate change will bring sea-level rise, salinity increase, and changes in the rates of sediment deposition (Sánchez-Arcilla et al. 1996). This will be in addition to the human impacts by upstream dams, catchment erosion, and organic pollution that are expected to increase as human population increases.

South Africa

About one third of the area occupied by fynbos and one quarter occupied by succulent Karoo has been transformed (Rebelo 1997). Fynbos covers both steep mountainous terrain and lowland areas. Only 7% of mountain fynbos has been transformed, largely by afforestation, but 50% of lowland fynbos and more than 90% of renosterveld have been converted to cropland or plantation forestry. Fifteen percent of the total fynbos area is conserved, largely in the steep mountainous areas. A little more than 2% of succulent Karoo falls into protected areas.

Many areas, especially along the coast, are undergoing rapid urban development. Farmlands outside protected areas have traditionally been used for extensive livestock farming. This form of farming has generally been considered relatively benign in terms of biodiversity impacts. Innovations in farming, however, can cause extremely rapid land-use change. For example, the introduction of fixed-point irrigation from aquifers caused proliferation of crop farming in sandy west coast areas previously of very low agricultural value. Ostrich farming in the succulent Karoo has also led to very rapid habitat transformation of marginal farming land rich in native plant species. These unpredictable changes to the rural status quo indicate the critical importance of protected areas for long-term conservation.

South Africa is a rapidly urbanizing society and is one of the few countries in Africa south of the Sahara with more than half its population living in cities. This may help reduce pressure for transformation of natural vegetation for agricultural purposes. The spread of cities, however, is already threatening many sensitive areas. Both biomes are sensitive to such localized development because of the many localized endemic species.

California and Chile

Habitat loss in California has been substantial, and the growing human population insures that it will increase. Virtually all of the wetland, riparian, annual grassland, coastal sage, and vernal pools have either been destroyed or substantially modified (Hobbs and Mooney, 1997). Rivers have been dammed and diverted, marshes have been filled, and the coastal plains have been extensively developed. There does seem to be a movement to reverse the trends of the past with efforts to restore riparian areas in particular and to protect and restore wetlands. A massive effort to restore the biotic systems of the San Francisco Bay is underway that involves a coalition of farmers, conservationists, and fisherman. There are similar innovative plans to develop the remaining coastal sage areas sustainably.

In Chile, habitat modification has been more modest, influencing primarily the central zone where the population is most concentrated. In the mediterranean area of Chile 24% of the land area is dedicated to intensive agriculture, 13% to plantation forestry, and 1% urbanization, such that close to 40% of the land area is subjected to intensive use (Arroyo et al. 1998). Perhaps as much as 50% of the remaining shrublands are subjected to grazing, although not necessarily of an intensive kind. Pine and eucalyptus plantations that now cover over 2 million hectares (CONAF 1997) are particularly important and are centered over the area of maximum tree species and woody plant endemism (Armesto et al. 1988). Unlike in all other mediterranean-type climate areas, natural lightning-ignited fires do not occur in central Chile, and fire is probably not a natural factor that has molded adaptive responses (Armesto et al. 1995). From the 1970s to the 1990s, around 15,000–49,000 ha/year of natural vegetation in Chile burned (INFOR 1997), with most of the fires occurring in the mediterranean area. Such unnatural fires will both affect local plant and animal biodiversity and provoke further spread of fast-growing invasive species in central Chile. The subarid regions to the north have been degraded considerably by overgrazing (Hajek et al. 1990). With economic growth and the development of the south, in particular, we can expect a much accelerated habitat modification.

The exploitation of forests in California and Chile has had a very different history. For example, in California, a long period of the utilization of coastal redwoods has left less than 5% of old growth, and this is principally in parks. Even the Sierra Nevada has been gradually logged of old growth in the National Forests. The Giant Sequoia was saved from exploitation principally

because it was not economically feasible to harvest. Plantation forestry has been practiced in the northern part of California, but principally with native species. Early plantations of *Eucalyptus* in southern California never became commercially viable.

Agriculture is much more extensively developed in California than it is in Chile. Agriculture is very resource intensive, utilizing 80% of all of the available fresh water of California. Large water projects subsidize agricultural activities, often to the detriment of the long-term system sustainability, as happened in the irrigation of the west side of the San Joaquin valley. These water projects have altered the total hydrology of the state in a major way. Further water-intensive crops (e.g., rice) are grown in a climate that could not sustain it without the water that has been diverted from aquatic ecosystems.

Summary of Land-Use Change

Overall, land use will be by far the most important factor for the future of biodiversity in the Mediterranean. Patterns of extinction, therefore, are likely to be linked with political and socioeconomic factors that will determine coastal development, agricultural policy, and forestry. Although the mediterranean-climate regions of the world share a common set of ecosystem types and, to a certain extent, future climatic regimes, they differ greatly in present and projected population sizes, growth rates, and densities, as well as GNPs, all of which will have a large impact on land use, biotic invasions, atmospheric composition, and, hence, biotic impacts (Hobbs et al. 1995). Further, these regions differ in the amount of local resource extraction, again having differential effects on biotic systems. Even if their future climates were common, therefore, the prospects for biotic systems will be quite different. In California, for example, population growth is pushing urbanization into areas that were formerly farmland; in turn, farming is utilizing more marginal lands. In other mediterranean-climate regions we are seeing abandonment of farmland and regression to natural systems. The attractiveness of mediterranean climates will continue to make these areas grow in population and economy disproportionately; hence, the social dimensions of change will exceed those of many other regions of the world.

Other Global Changes

Increased Atmospheric CO₂

Monoliths of Mediterranean grasslands exposed to elevated CO₂ show small NPP responses because low nutrient availability limits the extent of the production response (Navas et al. 1995). Elevated CO₂, however, is expected to change species composition because of the highly variable interspecific CO₂ response that has been observed in a variety of Mediterranean species

(Roumet et al. 1996). There were differential species responses in a calcareous grassland in Italy exposed to elevated CO₂ (F. Miglietta, personal communication).

There is still little evidence on the effects of elevated CO₂ on ecosystems of the Mediterranean region, but a moderate increase in productivity is expected largely due to improved water relations (Hättenschwiler et al. 1997). The study of 14 Mediterranean species collected over the past 240 years (Pefñuelas and Matamala 1990) and the study of *Olea europaea* over the last several thousand years (Beerling and Chaloner 1993) showed a consistent decrease in stomatal density. Potential water savings can favor late growing season species, and, hence, drive important changes in community composition, as has been reported for a California annual grassland exposed to elevated CO₂ (Field et al. 1996). The increase in water savings in grasslands may result in invasions by shrub species, as presently occurs in wet years (Williams et al. 1987). Likewise, in many cases elevated CO₂ favors N₂-fixing plants, as in the case of *Lotus* in assemblages of annual species dominated by *Bromus* and *Avena* (J. Canadell, unpublished). Thus, drought-tolerant N₂-fixers are good candidates to expand in a warmer Mediterranean with high CO₂.

Nitrogen Deposition

Nitrogen and acid deposition are important regional global change issues that affect most ecosystems. Alterations in productivity, nutrient flux, and trophic changes are documented for the western Mediterranean and are attributed to increased nitrogen supplies, to a large extent from atmospheric deposition (Paerl 1993, 1995). Nitrogen deposition impacts plant community composition by favoring fast-growing species and decreasing overall biodiversity, as seen experimentally elsewhere (Wedin and Tilman 1996). In addition, a large fraction of the endangered species grow in habitats that are N-deficient (Ellenberg 1993); therefore, increasing eutrophication from atmospheric deposition may bring further complications to biodiversity conservation (Mooney et al. 1998).

Acid rain has been detected in regions of the Mediterranean where there are no local sources of acid loading [e.g., the Pyrenees (Spain-France), Sardinia (Italy), and Patras (Greece)], which indicates the long-range transport of anthropogenic inputs, mostly from northern countries (Glavas 1988; Camerero and Catalán 1993; LeBoloch and Guerzoni 1995). Although acid rain does reach southern Europe, soil acidification is less likely to occur than it does in central and northern Europe because of episodic dust events from the Sahara. The dust produces red-rains with a high ion concentration that has the capacity to neutralize acid. In eastern Spain, red rains in rural sites may account for as much as 50% of the mean annual precipitation, with enough alkalinity strength to neutralize the input of free acidity of acid precipitation (Rodà et al. 1993).

Overall, the effects of both nitrogen deposition and soil acidification are more of a concern in the northern Mediterranean countries than they are in the southern Mediterranean.

Nitrogen deposition is probably less severe in areas of low population density in other mediterranean-climate regions because air masses move onshore from large fetches of ocean. In closed basins with vehicular traffic, however, there can be sufficient nitrogen deposition to impact vegetation and its diversity. Stewart Weiss (personal communication) describes a loss of biodiversity in grasslands along a nitrogen deposition gradient in the San Francisco Bay area. A rather large shift in composition has been noted in a relatively short time, indicating the great impact that increases in nitrogen can have in the Californian nitrogen-limited ecosystems. In general, in California, as elsewhere, species diversity decreases under increasing N deposition.

Tropospheric Ozone

Levels of ozone two- to threefold higher than those considered damaging for vegetation are measured in the western Mediterranean (Millán et al. 1996). These high levels of ozone of the highly populated Mediterranean coast are transported to 60–100 km inland with the sea breezes almost every day from spring to fall (Millán et al. 1996; see also Klasinc and Cvitas 1996).

One of the most common effects of ozone is a change in species composition because of the high interspecific sensitivity to damage by photochemical pollutants (e.g., ozone). In Israel, high levels of tropospheric ozone have been associated with the general decline of *Pinus halepensis* and the disappearance of the lichen *Xanthoria parietina* from maquis (Naveh et al. 1980). In California, Miller et al. (1982) note that in the mountains near Los Angeles, pines are similarly not competing as well as fir and oaks because of the former's greater sensitivity to ozone injury, particularly in wet years.

Ozone effects are especially damaging for Mediterranean vegetation because drought has been shown to increase species sensitivity to photoinhibition due to ozone exposure, for instance in *P. halepensis* (Wellburn et al. 1996). In fact, the general decline of *P. halepensis* forests in large areas of the Mediterranean has been attributed to the combined detrimental effects of ozone and drought (Klasinc and Cvitas 1996; Wellburn et al. 1996).

Thus, changes in species composition and probably species impoverishment make tropospheric ozone an important factor in altering and diminishing biodiversity. Because it decreases stomatal conductance, elevated CO₂ may ameliorate damage to ozone.

Both coastal California and Chile have ideal conditions for the buildup of tropospheric ozone. They are regions of high sunshine and they have steep coastal mountains that can trap the westward-moving air masses that travel over the ocean to the coastal cities. Tropospheric ozone concentrations have

climate change on top of these other stressors indicate even greater changes. The least predictable climatic change (i.e., the change in precipitation pattern) is the one that presumably would have the greatest impact on ecosystem distribution and function. Temperature change alone, however, will have a large impact on those mediterranean systems at high elevations where entire ecosystems may be at risk on the lower peaks. A changed fire frequency will also play a large role in shaping the biotic landscape of the future. It is probably safe to say that of all of the world's ecosystems those of mediterranean regions may see the greatest impact on biodiversity from global change because the diversity and endemism are so high in these regions, as is potential population growth and land-use change. The kinds of global changes anticipated are many and are interactive.

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COLOR PLATE I

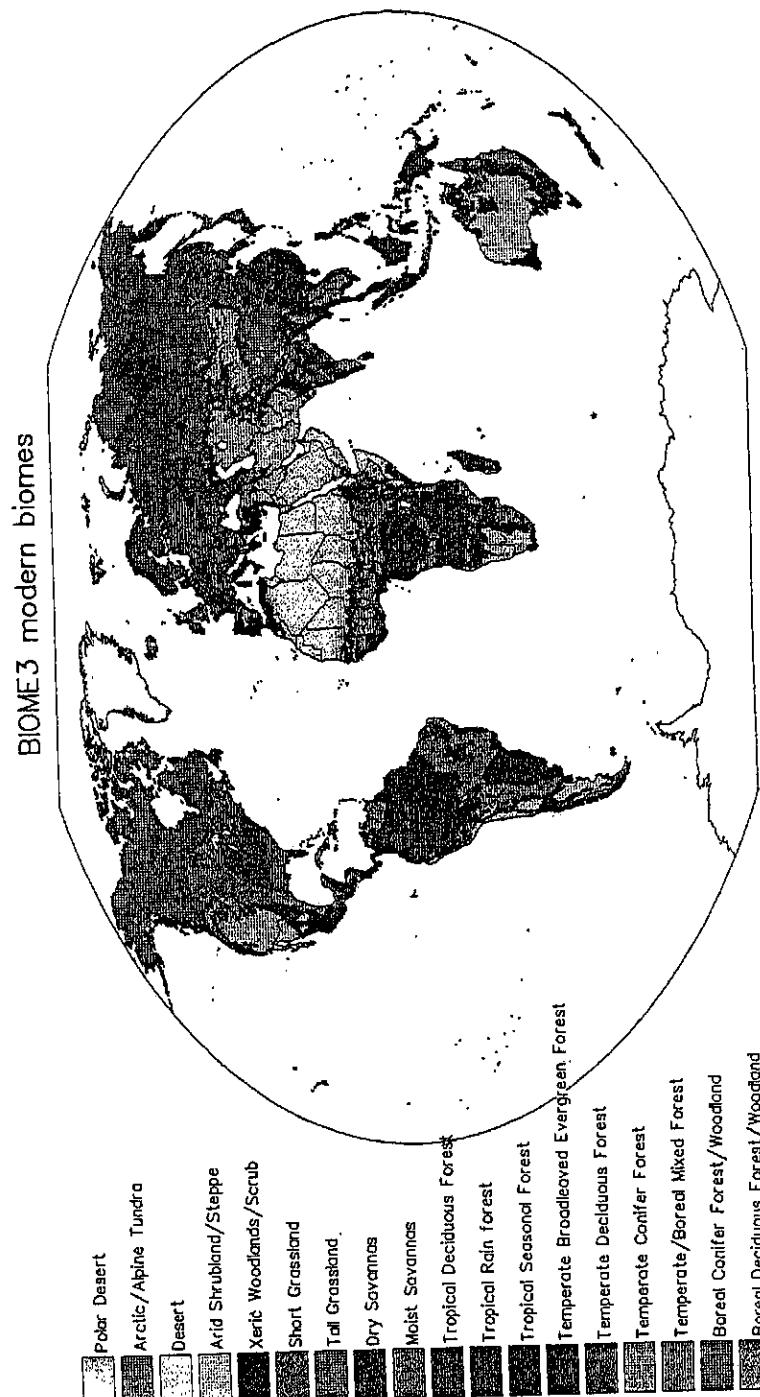
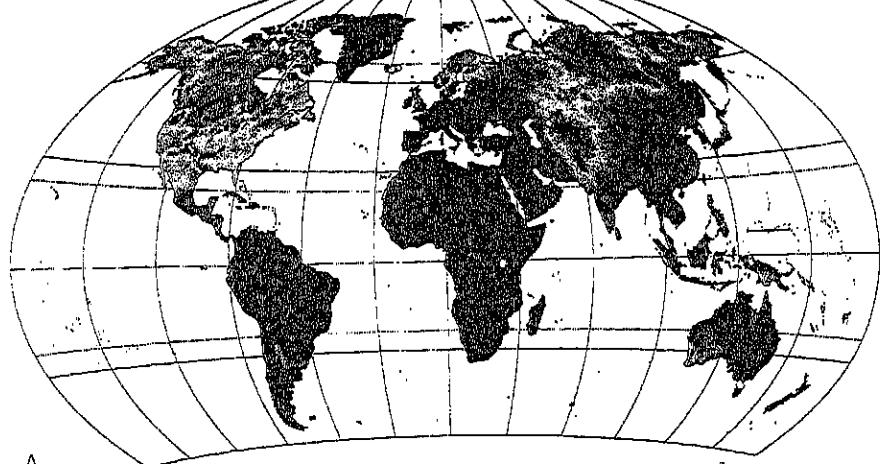


Figure 2.3. Global biome distribution under present day climate as simulated by BIOME3.

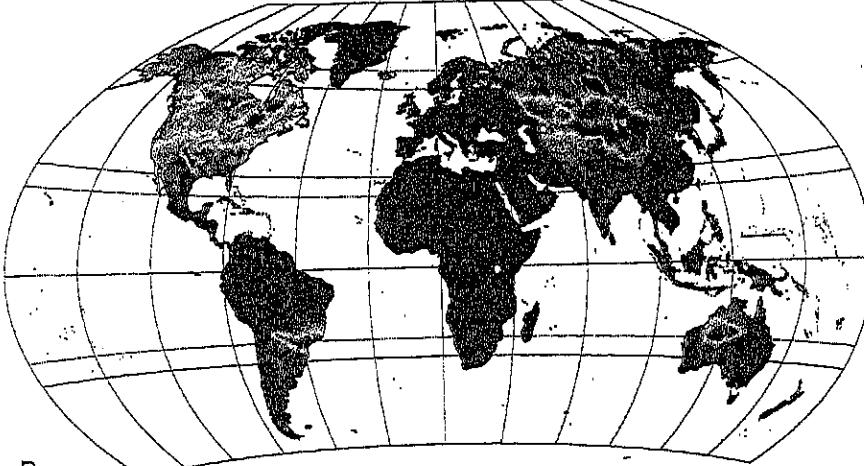
COLOR PLATE II

T-106 Temperature Anomaly (January)



A

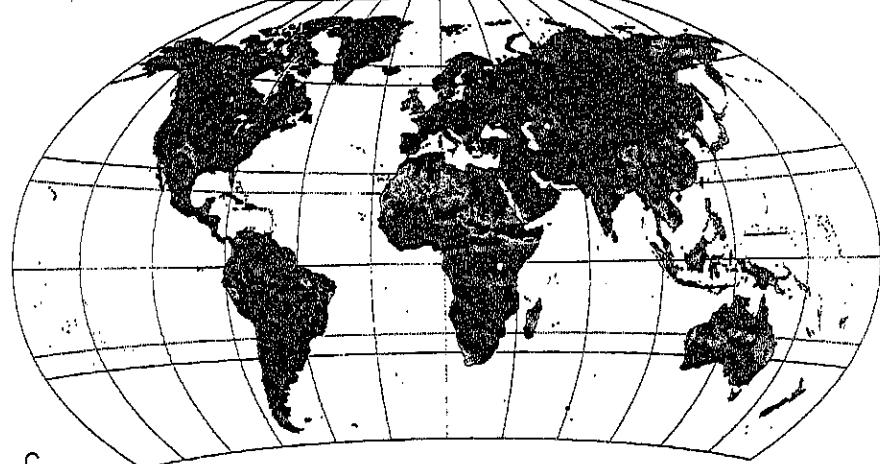
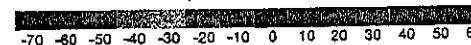
T-106 Temperature Anomaly (July)



B

COLOR PLATE III

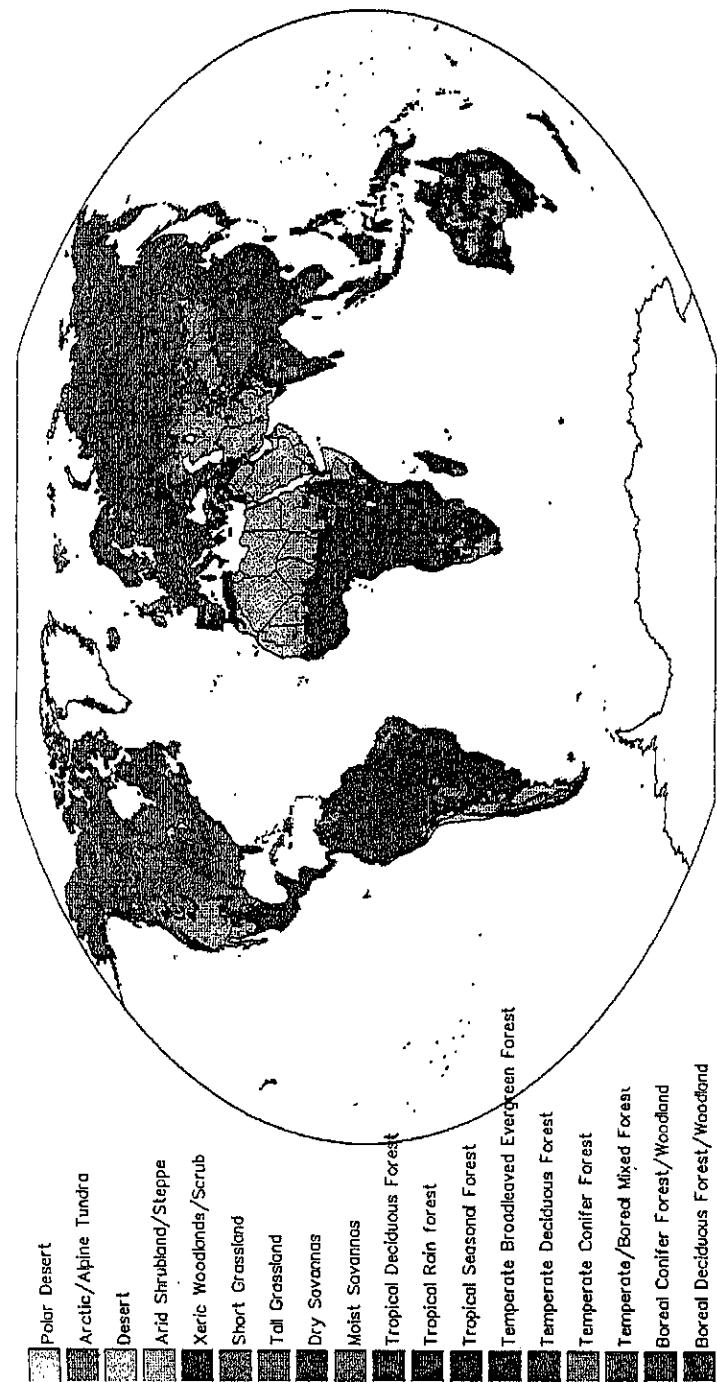
T-106 Precipitation Anomaly (cm/yr)



C

Figure 2.4. Global anomalies (differences between simulated current and 2XCO₂ climates) using the Hamburg ECHAM3 atmospheric general circulation model: (A) Temperature anomaly (January), (B) Temperature anomaly (July), (C) Precipitation anomaly (cm/yr).

BIOME3 T106 biomes

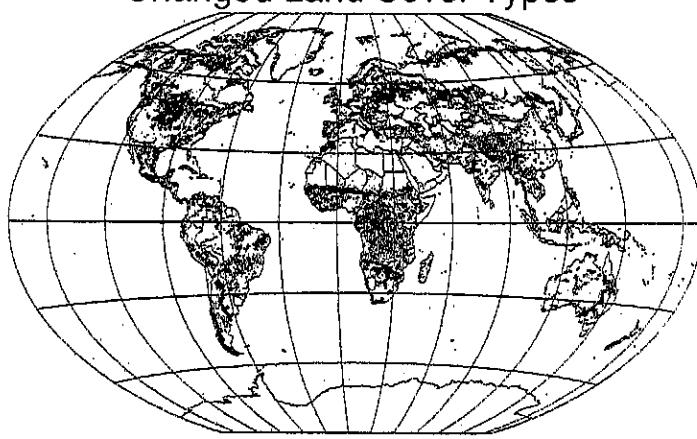
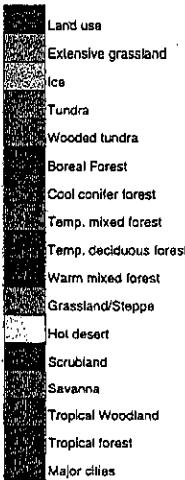


COLOR PLATE IV

Figure 2.5. Global biome distribution under a $2x\text{CO}_2$ climate (Hamburg ECHAM3 climate model) as simulated by BIOME3 including
the effects of CO_2 .

COLOR PLATE V

Changed Land Cover Types



New Land Cover Types



Figure 3.3. Change in actual land cover in 2100 for scenario A. The top panel presents the changes of the original vegetation. Red denotes agricultural land that is abandoned. The lower panel presents the future land cover. Red denotes the expansion of agricultural land, while orange depicts regrowth after clear-cut or abandonment.

COLOR PLATE VI

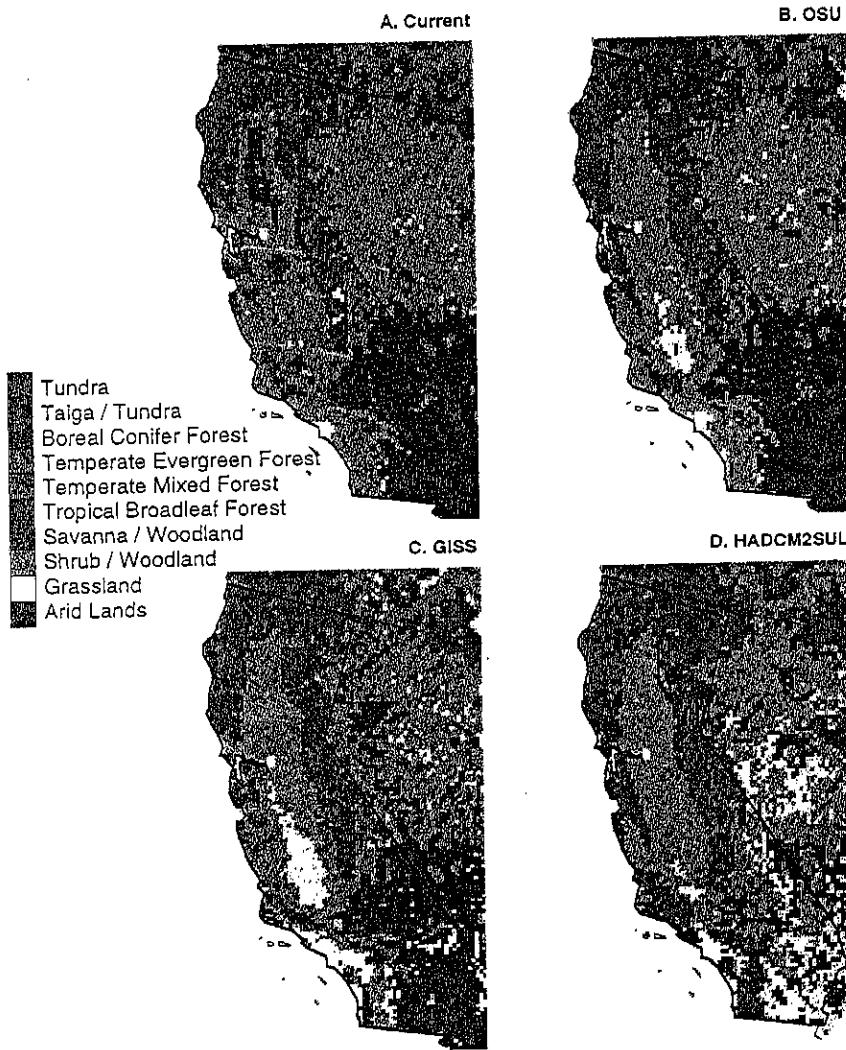


Figure 9.1. Modelled responses of California vegetation to different climate model projections for a doubled CO₂ world. (A) Present vegetation, (B) response to the OSU climate model, (C) to GISS model, and (D) to the Hadley Center model (HADCM2SUL).

COLOR PLATE VIII

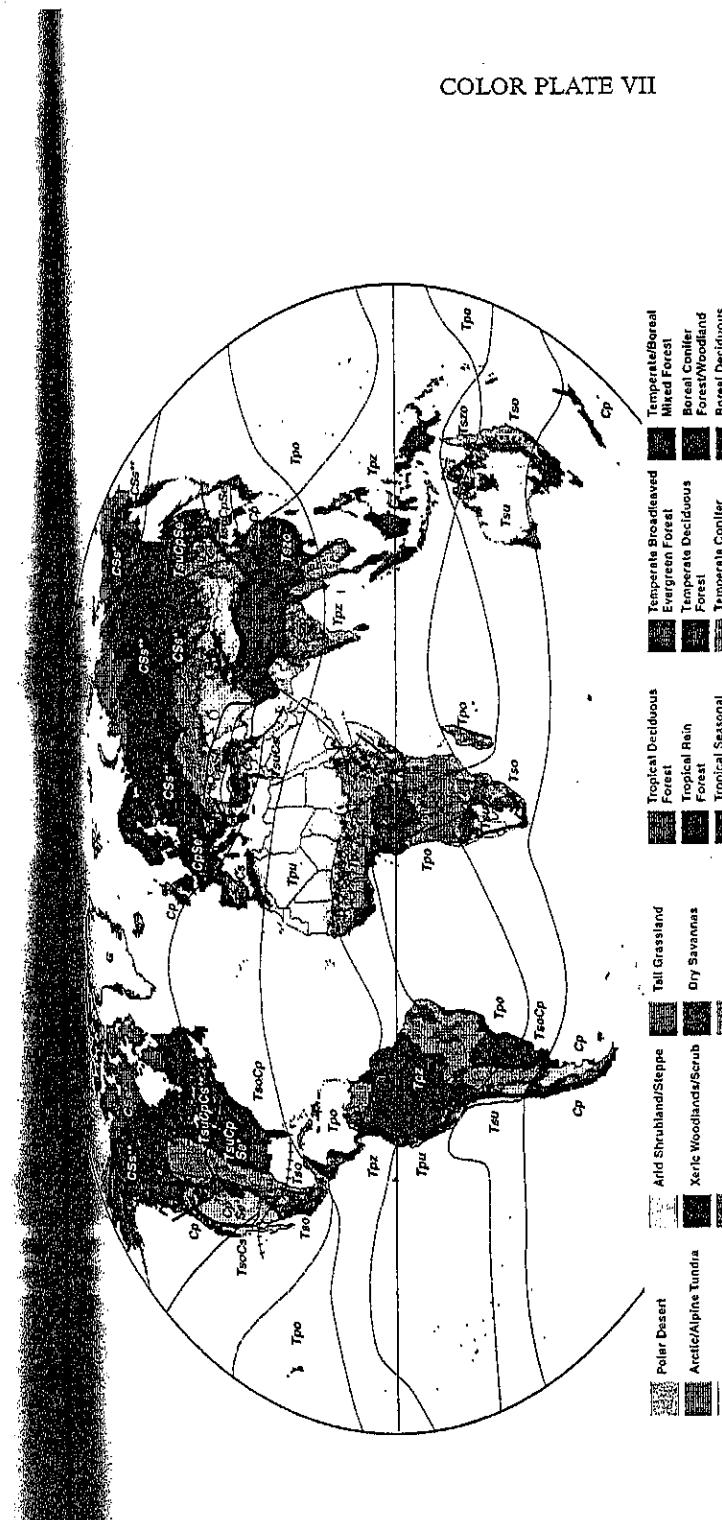
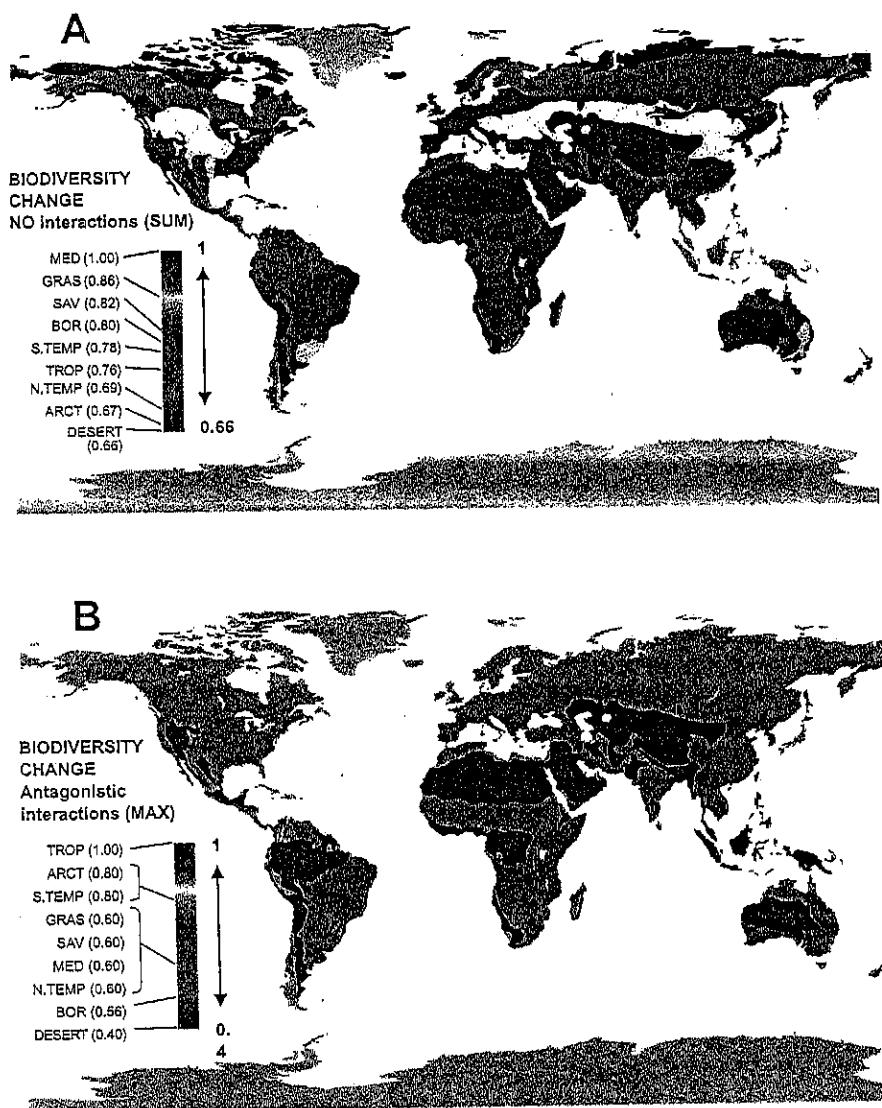


Figure 14.1. Hydroclimatology of floods (after Hayden, 1988, Figure 9, p. 23) combined with BIOME 3 map. After Hayden, the symbols for the flood zones include: T—barotropic; C—barocline; p—perennial; s—seasonal; z—Inter-Tropical Convergence Zone (ITCZ); o—organized convection; u—unorganized convection; S—snow cover; G—glacial; s—seasonal snow cover; e—ephemeral snow cover; *—snow cover 10 to 50 days; and **—snow cover 50 cm or more. The solid and dashed lines are the poleward limit of barotropic conditions in summer and winter, respectively. The average position of the ITCZ is shown by the dash-dot line for January and July. The cross-hatched line indicates for North America the equatorward limit of frontal cyclones. The double-dot-dash line indicates regions with the highest snow fall or duration of snow cover. The thick, solid line indicates the equatorward limit of snow cover for 50 days or more. Mountain regions are shown in solid gray shading. (Cartography kindly provided by D. I. Lawson.)

COLOR PLATE VIII

Biodiversity Scenarios



COLOR PLATE IX

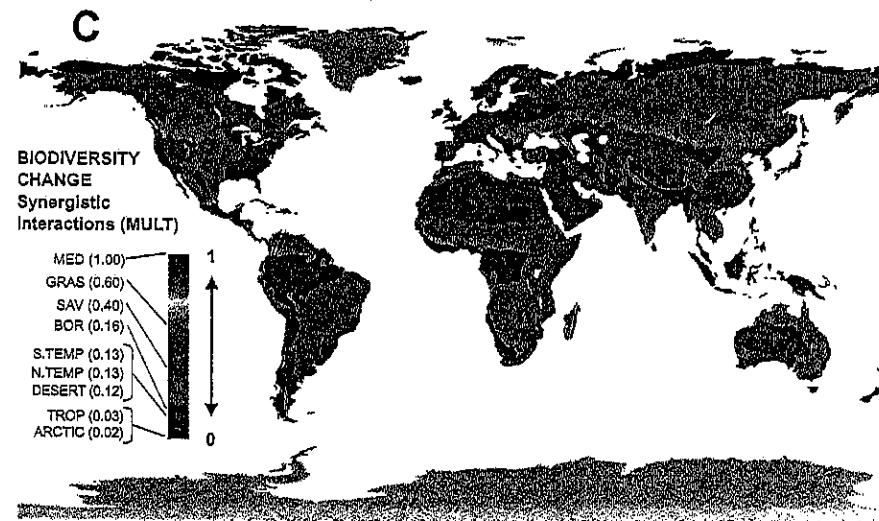


Figure 15.3. Maps of three scenarios of the expected change in biodiversity for the year 2100. Scenario A assumes that there are no interactions among drivers of biodiversity change, and consequently total change is calculated as the sum of the effects of each driver which in turn result from multiplying the expected change in the driver for a particular biome (Table 15.1a) times the effect of the driver which is also a biome specific characteristic (Table 15.1b). Scenario B assumes that total biodiversity change equals the change resulting from the driver that is expected to have the largest effect and is calculated as the maximum of the effects of all the drivers. Scenario C assumes synergistic interactions among the drivers, and consequently the total change is calculated as the product of the changes resulting from the action of each driver. The different colors represent the expected change in biodiversity from moderate to maximum for the different biomes of the world ranked according to the total expected change. The numbers in parentheses represent the total change in biodiversity relative to the maximum value projected for each scenario. The biomes are MED Mediterranean ecosystems, GRAS Grasslands, SAV Savannas, BOR Boreal forest, S. TEMP Southern temperate forest, TROP Tropical forest, N. TEMP Northern temperate forest, ARCT Arctic ecosystems, DESERT Desert. Values for alpine, stream, and lake ecosystems are not shown. (Redrawn with permission from Sala et al. 2000. Copyright 2000 American Association for the Advancement of Science.)

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