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The Mediterranean Environment of Central Chile

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The Mediterranean-type environment of South America, broadly defined as the continental area characterized by winter rainfall and summer drought, is confined to a narrow band about 1,000 km long on the western side of the Andes in north-central Chile (Arroyo et al., 1995, 1999). Although much has been written about the climate, vegetation, and landscapes of this part of Chile, and comparisons have been drawn with California and other Mediterranean-type regions of the world (Parsons, 1976; Mooney, 1977; Rundel, 1981; Arroyo et al., 1995), a modern synthesis of information on the physical setting, regional biota, and historical development of ecosystems in central Chile has not been attempted. This chapter is intended to provide such an integrated picture, emphasizing those aspects most peculiar to the region.

Since the earlier floristic work on the Chilean *matorral* (e.g. Mooney, 1977), the name given to the vegetation of central Chile, there is now a much greater appreciation of the geographic isolation and high levels of biological diversity and endemism in this region of South America (Arroyo and Cavieres, 1997; Villagrán, 1995; Arroyo et al., 1995, 1999). Because of the great richness and singularity of its terrestrial flora, this area of the continent is considered to be one of the world's 25 hotspots in which to conserve global biodiversity (Arroyo et al., 1999; Myers et al.,

2000). An analysis of the main features of the Mediterranean environment in South America should therefore address the causes of such high floristic richness, the nature of current threats to biodiversity, and the prospects for its conservation in the long-term. A discussion of conservation concerns closes the present chapter (but see also: Arroyo and Cavieres, 1997; and Arroyo et al., 1999). In view of the vast literature on the biota and physical setting of central Chile, this chapter adopts a selective approach, from a biogeographic perspective, of what we consider to be the most remarkable historical, physical, and ecological features of this environment, which in turn may explain its extraordinary richness in plants and animals.

11.1 The Physical Character of the Chilean Mediterranean-Type Ecosystems

Mediterranean-type ecosystems occupy a narrow band along the western margin of South America, from 30 to 36°S in central Chile (fig. 11.1). These ecosystems represent the transition between one of the driest deserts in the world, the southern Atacama Desert, north of 28°S, and the mixed deciduous-evergreen temperate forests, which occur south of
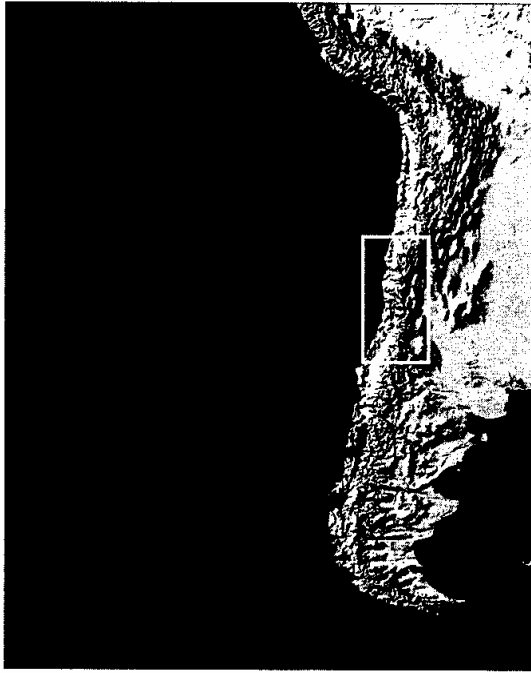
Figure 11.1 Topographic map of southwestern South America showing the approximate extent of the Mediterranean-climate region (box), 30–36°S, and the position of the massive Andean Cordillera, which intercepts winds flowing from both east and west, and locks the position of the anticyclone over the Pacific, thus configuring the "arid diagonal"

primarily from these sedimentary and volcanic materials. By contrast, soils in the Coastal Cordillera are developed on highly weathered metamorphic parent materials of Jurassic age. These soils have a high organic matter and clay content that makes them particularly susceptible to run-off erosion after the loss of plant cover.

Mountain chains with an east-west orientation (angosturas) interrupt the Central Depression both to the north and south of the Mediterranean-climate area, connecting the Andes with the Coastal Cordillera. The latter range reaches a maximum elevation of 2,200 m above sea level, thus allowing for the development of an alpine vegetation belt, above the sclerophyllous vegetation zone, in a way similar to the Andes. Several important river systems originating in the Andes cross the Central Depression in spacious and fertile valleys. From north to south these include the Limari, Aconcagua, Maipo, and Maule valleys. These river systems have been completely transformed by a long history of agricultural activity and presently sustain a major portion of the human population of Chile.

Climatic characterizations of the Chilean Mediterranean region have been provided by Miller et al. (1977), di Castri and Hajek (1975), and Arroyo et al. (1995), among others. A summary of salient features of this climatic regime is presented here, emphasizing those aspects that have received less attention in previous work. At the latitude of Santiago (33°S), rainstorms occur sporadically during the cooler months of the year (April to September), but drought may extend for as long as six months during the spring and summer (October to March). The single cool rainy season is a distinctive feature of north-central Chile, as it is of Mediterranean-type environments elsewhere. The monthly distribution and total amount of precipitation in a year, two of the most important variables affecting the local vegetation, vary greatly between years, although the former has received less emphasis.

This variable climatic regime can be explained by seasonal changes in the strength and latitudinal position of the South Pacific anticyclone, a high-pressure center located around 30°S off the Pacific coast of southern South America (see chapter 3; also Aceituno, 1988). During the austral summer, this high-pressure center occupies a broad latitudinal range off South America and blocks the westerly flow of humid air masses moving across the Pacific Ocean, thereby leaving central Chile completely dry. During the austral winter, however, the anticyclone weakens and may often be displaced equatorward, thus allowing for cyclonic storms and related frontal systems to progress toward central Chile. Because of the dominant role played by the South Pacific anticyclone in maintaining the seasonal rainfall pattern over central Chile, the atmospheric and oceanic conditions that affect the strength and latitudinal position of this high pressure system can greatly alter the amount and distribution of precipitation in the Chilean Mediterranean region. Large inter-annual variabil-

36°S (fig. 11.2). Mediterranean ecosystems in central Chile are therefore a highly heterogeneous vegetation mosaic. The major vegetation types are dry xerophytic thorn scrub dominated by deciduous shrubs and succulents; mesic communities dominated by evergreen sclerophyllous trees in the coastal and Andean foothills; and forests dominated by winter-deciduous trees in the south of the Mediterranean area. Within the latitudinal range of the Mediterranean-climate ecosystems, annual precipitation varies from less than 200 to 700 mm (Rundel, 1981).

Topographically, this ecologically complex region is characterized by the presence of two parallel mountain ranges oriented from north to south, the Coastal Cordillera and the Andes (fig. 11.1). These ranges are separated by a narrow tectonic basin, the 80–100-km wide Central Depression, which is filled with a large volume of rock waste derived mainly from the weathering and erosion of the Andes. Extensive accumulations of ignimbrites also occur, derived from the activity of Andean volcanoes during Pleistocene time. Soils in the Central Depression are derived
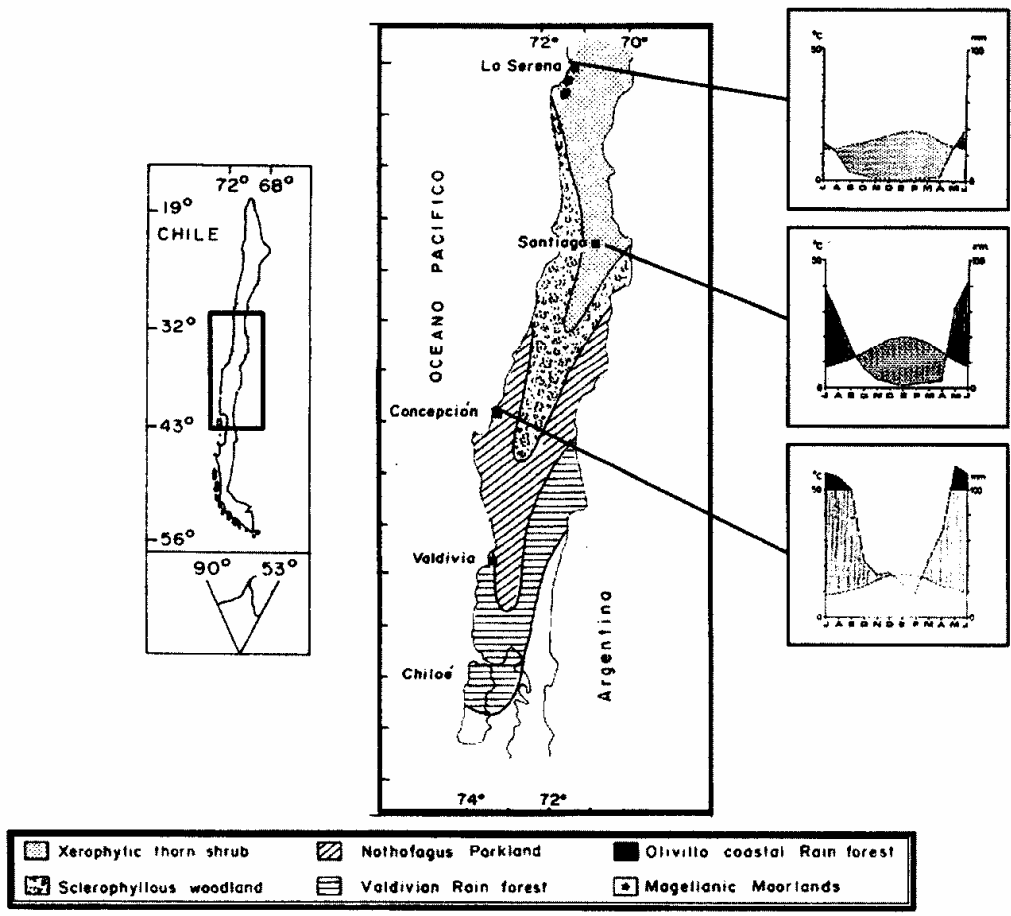
Figure 11.2 Central Chile showing the main vegetation zones for the late Holocene (modified from Villagrán, 1995). The Mediterranean-climate region includes xerophytic thorn scrub, Olivillo coastal rain forest, sclerophyllous woodland, and the northern zone of the *Nothofagus* parkland (Maulino forest). Climatic diagrams represent the latitudinal variation within the range of the Mediterranean environment.

ity in precipitation, associated with changes in anticyclone strength and position, is an intrinsic feature of the region.

In recent decades, a major component of the inter-annual variability in precipitation has been linked to El Niño–Southern Oscillation (ENSO) (Aceituno, 1988; Holmgren et al., 2001). During El Niño years, weakening of the anticyclone and decreased upwelling of ocean waters along the west coast of South America may cause large increases in total rainfall across the entire Mediterranean-climate region of Chile. In contrast, during longer La Niña episodes, due to the strengthening of the anticyclone, rainfall decreases well below the average, producing extremely dry conditions, particularly in the northern part of the Mediterranean region. These effects extend also to the wetter south-

ern limit of the region, causing long droughts with major ecological consequences (see chapter 19; also Holmgren et al., 2001). In recent years, the often dramatic environmental impacts of the long droughts associated with La Niña have been understood more thoroughly by the public because of marked reductions in irrigation water and potable water supplies, and the loss of generating capacity at hydroelectric power plants that depend on artificial dams placed across the main river systems of central Chile.

The climatic regime of central Chile differs in some important aspects from other Mediterranean ecosystems of the world because of the complete absence of summer rainfall and associated thunderstorm activity. This is a feature of great significance for understanding the disturbance regime

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that has historically affected Chilean Mediterranean ecosystems. It accounts for the negligible importance of natural fire as a shaper of vegetation structure and dynamics in central Chile. Summer rains, derived from an easterly source, are prevented from reaching Mediterranean Chile by the massive physical barrier of the Andes, where many peaks rise above 5,000 m, including the highest, Aconcagua (6,962 m; fig. 11.1). The rain-shadow effect of the Andes is responsible for maintaining the hyperarid conditions of the Atacama Desert in northern Chile (Arroyo et al., 1988), but it also isolates the Mediterranean region from the easterly flow of warm moist air that brings summer rainfall to the subtropical eastern side of the cordillera. Lightning storms that could start wildfires are rare in the Chilean Mediterranean region and when they do occur, occasionally in summer, they are generally confined to elevations above 3,000 m in the Andes (e.g., Arroyo et al., 1981), above the altitudinal limit of sclerophyllous vegetation.

Despite its narrowness, the Mediterranean region of Chile is characterized by pronounced environmental gradients from east to west. Particularly important, although often ignored, is the strong rain-shadow effect of the Coastal Cordillera. This range intercepts westerly wind flows of moist oceanic air, causing a substantial drop in precipitation in the Central Depression, an effect that has not been properly quantified but is evident from the comparison of rainfall records at climate stations both east and west of the range (e.g., Rundel, 1981). Consequently, habitats in the Central Depression are drier than the slopes of the Coastal Cordillera and the Andes. The drier vegetation zones in the north of the Mediterranean region are thus projected southward to higher latitudes along the Central Depression, giving each zone a V-shape on figure 11.2.

An additional moisture source for vegetation in the Coastal Cordillera derives from cloud-water condensation at altitudes above 600 m. A permanent fog-zone, triggered by a stable temperature inversion above the cold Humboldt Current (Rundel et al., 1991), forms at this altitude, supplementing rainfall, especially in the drier part of the Mediterranean-climate region where normal rainfall is insufficient to maintain vegetation (Kummerow, 1966; Rundel and Mahu, 1976). From 33 to 30°S, as annual rainfall declines to less than 200 mm, isolated patches of rainforest are maintained by fogs in the windward slopes of the coastal mountains (Rundel, 1981). Fog condensation in tree canopies may play a significant, but understudied, role in enhancing moisture and nutrient availability for sclerophyllous vegetation, especially through the long dry summers.

11.2 History of Semiarid Environments in Western South America

The history of the Mediterranean-type climate and vegetation of central Chile is connected with the development of the "arid diagonal" of South America (see chapter 2; also Hinojosa and Villagrán, 1997). The progress of aridity along the western margin of South America is coupled with the rise of the Andes, which interrupted the flow of moist air to southern Perú and northern Chile from tropical sources farther east, and with the beginning of the equatorward flow of cold Antarctic waters in the South Pacific. In this section, we summarize the current knowledge of the events that led to the onset of the Mediterranean-type climate in central Chile.

The Andean orogenesis has dominated the western margin of South America during the latter part of the Cenozoic Era. This massive geophysical transformation progressed through a series of tectonic uplifts that became more intense during the Neogene (Reynolds et al., 1990). Geologic dating of magmatism and exposed rocks across the Argentina-Chile border assigns the folding and shortening of the continental crust in central Chile to the last 15 Ma (million years before present), during which the Andes rose to elevations ranging from 3,000 m to more than 6,000 m (Reynolds et al., 1990). The final uplift of the Frontal Cordillera and Precordillera, dated to the Miocene between 15 and 8 Ma, progressively shut off the easterly flow of air masses originating in the tropics and subtropics farther east, leading to the establishment of the present Mediterranean climate in central Chile with its single rainy season. Prior to these events, tropical air masses flowed freely from east to west across South America, maintaining a wetter subtropical climate in central Chile, possibly with two rainy seasons (Hinojosa and Villagrán, 2005). The existence of a subtropical fossil flora of Miocene age, containing the ancestors of certain floristic components of the Chilean sclerophyllous vegetation (e.g., Lauraceae), has been documented in the Andean foothills near Santiago (Hinojosa and Villagrán, 1997). The character of this fossil assemblage supports the existence of a different climatic regime, with lower mountain ranges, in the middle Miocene, and suggests that the Mediterranean-type climate of central Chile did not become established until the late Neogene.

Another factor contributing to the desiccation of the climate along the western margin of South America was the establishment of the cold Humboldt Current, a major feature of the present oceanic circulation. The equatorward flow of cold polar waters began in earnest after the breakup of Gondwana. The separation of Antarctica, first from Africa, then from Australia, and later from southern South America, generated a massive westerly (zonal) circulation of water around Antarctica that reduced the poleward (meridional) flow of warm tropical waters (see chapter 2). The Antarctic Circumpolar Current did not fully form until the final opening of the Drake Passage after 35 Ma, but once it became established, Antarctic ice sheets expanded and the cooling of the proto-Humboldt Current was enhanced (Zachos et al., 2001). These events led to the de-

velopment of a steeper temperature gradient from tropical to high latitudes and probably to the present positioning and strength of the South Pacific anticyclone that determines the summer drought in central Chile.

The evolution of the morphological and physiological mechanisms that allowed the local flora, of tropical ancestry, to endure the long summer droughts characteristic of the Mediterranean-type climate must, therefore, have occurred during the Neogene. The ability to tolerate seasonal desiccation became the primary determinant of species survival during the Quaternary Period, as seasonal droughts in central Chile became more frequent and intense, especially during interglacial stages (Villagrán, 1995).

11.3 Mediterranean Vegetation Types

The mountainous topography of central Chile, with up to 6,000 m of relief, contrasting radiation and moisture regimes, strong rain-shadow effects, and a mosaic of soil types and nutrient supplies, generates pronounced environmental gradients that have stimulated the evolutionary differentiation of the biota (Armesto and Martínez, 1978; Rundel, 1981; Rozzi et al., 1989). High floristic richness and a diversity of plant communities are a consequence of this environmental heterogeneity (Arroyo et al., 1993, 1995). In addition, strong climatic variability resulting from varying frequencies of ENSO events during the Quaternary (Villagrán, 1995; Holmgren et al., 2001) must have promoted genetic variability among local populations. The Mediterranean region is also a depository of ancient tropical lineages that found refuge in coastal valleys from the drying trend initiated by Neogene uplift of the Andes (Troncoso et al., 1980; Villagrán and Armesto, 1980; Arroyo et al., 1995; Hinojosa et al., 2006). Also, as a consequence of the repeated cooling and warming cycles of the Quaternary, the regional vegetation has been exposed to wetter or drier periods relative to present conditions (Villagrán, 1995). In response to these cycles, xerophytic and cool-temperate forest taxa have successively expanded and contracted their ranges in central Chile at different times in the past, as documented from pollen studies (Heusser, 1983; Villagrán, 1995). These floral migrations must have contributed greatly to increased species richness and the heterogeneity of the vegetation mosaic within the Mediterranean zone (Villagrán, 1995, Arroyo et al., 1995). Andean uplift also provided opportunities for colonization and differentiation of local alpine floras, adding further to the floristic richness and diversity of vegetation types in the region.

In addition, the strong influence of insect and bird pollinators in the evolution of plant-reproductive strategies in Mediterranean-type ecosystems (Arroyo and Uslar, 1993; Arroyo et al., 1993, 1995) and the role of animals in the dispersal of seeds of sclerophyllous tree species (Hoffmann

and Armesto 1995) are important conditions favoring genetic variability and speciation in biotic communities within the region. High levels of self-incompatibility have been documented for the woody species in montane sclerophyllous vegetation (Arroyo and Uslar, 1993).

Arroyo et al. (1995) recognized a greater diversity of vegetation types in the Mediterranean-climate region of central Chile than previously described in the context of comparative studies of analogous ecosystems in Chile and California (e.g., Parsons, 1976; Mooney, 1977; Rundel, 1981). In the following account of the vegetation of central Chile, the general floristic scheme proposed by Arroyo et al. (1995) will be followed for describing the main vegetation types, although names given here to some vegetation units may differ. A few vegetation types not listed by Arroyo et al. are also included (table 11.1). We discuss each vegetation type in terms of its relative importance regarding floristic richness, endemism, distribution, and natural history. Gaps in knowledge are indicated. The conservation status of Mediterranean ecosystems in Chile will be considered later, although a brief mention of the history of these plant formations is made here. Finally we discuss succinctly the main floristic affinities of the vegetation of central Chile with other dry plant formations found in South America.

11.3.1 Relict Coastal Forests

Olivillo Forests A widely distributed vegetation type in central Chile is the coastal forest dominated by olivillo, *Aextoxicon punctatum*, a tree from the endemic monotypic family Aextoxicaceae (figs. 11.2, 11.3). These forests, described in detail by Muñoz and Pisano (1947), Villagrán and Armesto (1980), and Pérez and Villagrán (1985), have an important number of species of climbers and epiphytes, including narrow endemics such as *Peperomia coquimbensis* (Piperaceae). Olivillo forests are found as far north as the latitude of La Serena (30°S) in the semiarid region of Chile, immersed in a matrix of xerophytic vegetation. The northernmost extensions of Olivillo forests are known as the relict forests of Fray Jorge and Talinay (Troncoso et al., 1980), and occur as isolated forest fragments on the upper slopes of the coastal mountains, under the direct influence of maritime fogs. Eco-physiological studies have shown that fog condensation is the main source of water and nutrients for these isolated relict forests (Kummerow, 1966; P.E. Vidiella and T.E. Dawson, unpublished). Other isolated patches of Olivillo forest are scattered across coastal mountaintops between Fray Jorge and the coast, from where these forests extend more or less continuously southward at lower elevations, especially on slopes and valleys facing the ocean (Villagrán and Armesto; 1980, Pérez and Villagrán, 1985).

The fragmented distribution of the flora of Olivillo forests in Chile has intrigued biogeographers for many years (e.g., Skottsberg, 1948; Schmithüsen, 1956; Muñoz and

Table 11.1 Major plant formations in central Chile, modified from Arroyo et al. (1995) and Rundel (1981)

| Plant formation	Approximate latitudinal range (°S) in central Chile	Commonly associated woody taxa
Olivillo forests	Fragmented 30–33 Continuous 33–36	*Aextoxicon punctatum, Myrceugenia correifolia, Raphithamnus spinosus, Drimys winteri, Sarmienta repens, Mitraria coccinea*
Nothofagus montane forest	Fragmented 33–36	*N. obliqua, Ribes punctatum, Lomatia hirsuta*
Maulino forest	35–36	*N. alessandrii, N. glauca, N. dombeyi, Gomortega keule, Pitavia punctata, Cryptocarya alba*
Sclerophyllous matorral	32–36	*Cryptocarya alba, Quillaja saponaria, Lithrea caustica, Peumus boldus, Proustia pyrifolia, Kageneckia oblonga*
Summer-deciduous matorral with succulents	30–34	*Retanilla trinervia, Flourensia thurifera, Trichocereus, Eulychnia, Puya* spp.
Acacia caven savanna	30–36	*Prosopis chilensis, Cestrum parqui, Trevoa trinervis*
Swamp forests	Scattered patches	*Myrceugenia exsucca, R. spinosus, D. winteri, Boquila trifoliolata*
Palm forests	33–34	*Jubaea chilensis, Cryptocarya alba, Drimys winteri, Schinus latifolius*
Coastal matorral	30–36	*Lithrea caustica, Bahia ambrosioides, Schinus latifolius, Escallonia pulverulenta, Senna* spp.
Andean montane woodland	Discontinuous 32–36	*Kageneckia angustifolia, Schinus montanus, Austrocedrus chilensis*
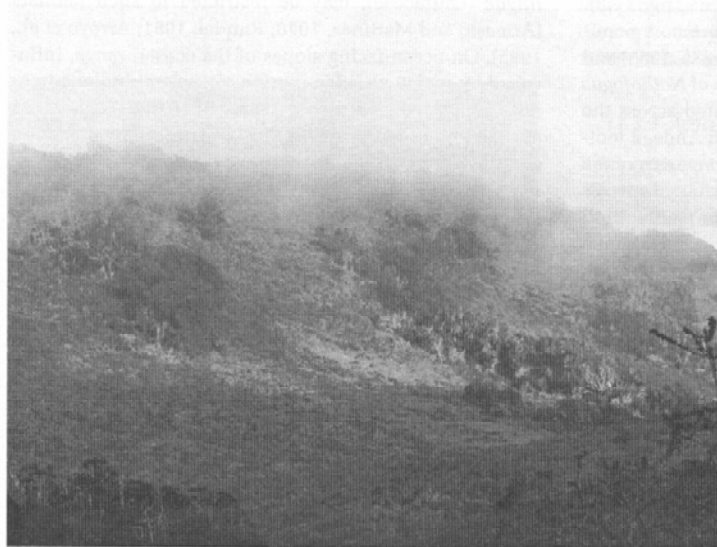
Figure 11.3 Olivillo forests in Fray Jorge National Park (30°S) (photo: J.J. Armesto)

Pisano, 1947; Villagrán and Armesto, 1980; Troncoso et al., 1980). Many plant species found in the northernmost relicts (e.g., *Sarmienta repens* and *Mitraria coccinea*, Gesneracieae, *Azara microphylla*, Celastraceae) also occur as components of the Valdivian evergreen rainforests, with a disjunction of nearly 900 km (Villagrán and Armesto, 1980). Current interpretations of the phylogenetic relations, South American distribution, and fossil record of the main relict taxa suggest that these floristic assemblages may be descendants of subtropical rainforests that occupied central Chile in the mid-Cenozoic, before the onset of events that shaped the Mediterranean-type climate (Troncoso et al., 1980; Villagrán, 1990; Hinojosa and Villagrán, 1997). They are consequently unrelated to equatorward advances of the southern temperate forests during colder and wetter intervals of the Pleistocene, as has sometimes been argued (e.g., Solbrig et al., 1977; Rundel, 1981). However, southern Chilean temperate forests are ancestrally related to these relict communities, thus explaining the considerable number of shared taxa. The future of these northern forest fragments, now designated as protected areas, remains uncertain in the face of past human disturbance by logging and fire, and present climatic desiccation. Understanding the ability of trees to capture moisture from cloud water, especially from the perspective of water supply to growing seedlings in the understory, and the climatic factors affecting the frequency of coastal fogs, are critical issues for the survival of these relicts.

Nothofagus Forests *Nothofagus* species (Nothofagaceae) occur in the Mediterranean region of central Chile at its southern boundary with the temperate rainforest region, and also as a chain of small fragmented populations above 1,000 m on the highest peaks of the Coastal Cordillera—El Roble, La Campana, and Altos de Cantillana (fig. 11.2). These forest fragments represent the northernmost populations of *Nothofagus* in South America (Casassa, 1985) and are isolated from the continuous distribution of *Nothofagus obliqua*, a deciduous tree broadly distributed across the Central Depression as well as on coastal and Andean foothills of south-central Chile . At the southern margin of the Mediterranean region, several narrowly distributed species of *Nothofagus* occur in mixed stands with both sclerophyllous species from central Chile and evergreen broad-leaved trees from the Valdivian temperate rainforest, a vegetation known locally as the *Maulino* forest (San Martin and Donoso, 1996). Two important narrow endemics of the *Maulino* forest are *Nothofagus glauca* and *N. alessandrii*, both deciduous. Sheltered ravines are dominated by the evergreen *N. dombeyi*, which is a characteristic tree species of the Valdivian rainforests farther south. Other narrow endemic tree species found in the coastal ranges near the southern limit of the Mediterranean region are *Gomortega keule* (Gomortegaceae) and *Pitavia punctata* (Rutaceae). The high local endemism probably reflects the

conservative character of coastal range habitats, compared to those of the Central Depression and Andean slopes (Hinojosa and Villagrán, 1997; Villagrán et al., 1998).

The disjunct northern populations of *Nothofagus obliqua* have been interpreted as remnants from a more continuous distribution that existed at lower elevations during colder stages of the Pleistocene (Villagrán, 1990). The cooler and wetter climate of the last cold stage would have facilitated the equatorward expansion of the *Nothofagus* woodlands in central Chile, an idea supported by fossil pollen assemblages from Laguna Tagua-Tagua, 100 km south of Santiago (Heusser, 1983).

11.3.2 Sclerophyllous Shrublands (Matorral) and Thorn Scrub

Evergreen sclerophyllous vegetation extends more or less continuously across both slopes of the Coastal Cordillera and into the foothills of the Andes, but it is more scattered in river valleys crossing the Central Depression (figs. 11.2, 11.4). It is the most common plant formation in central Chile, dominated by evergreen trees and shrubs, such as *Cryptocarya alba* (Lauraceae), *Lithrea caustica* (Anacardiaceae), *Quillaja saponaria* (Rosaceae), *Maytenus boaria* (Celastraceae), *Kageneckia oblonga* (Rosaceae), and *Peumus boldus* (Monimiaceae). The matorral commonly exhibits a patchy spatial structure with open spaces between shrub clumps, especially on the Andean foothills (Fuentes et al., 1986). However, in deep creeks and along permanent water courses, as well as on steep south-facing slopes in the coastal range, it may develop a continuous canopy, 8–12 m tall. Some tree species, such as *Beilschmiedia miersii* (Monimiaceae), *Drimys winteri* (Winteraceae), *Luma chequen* (Myrtaceae), *Citronella mucronata*, and *Persea lingue* (Lauraceae), may be restricted to such habitats (Armesto and Martínez, 1978; Rundel, 1981; Arroyo et al., 1995). On ocean-facing slopes of the coastal range, influenced by moisture-laden marine air, sclerophyllous trees such as *Cryptocarya alba* grow together with *Aextoxicon punctatum* (see above) and may be covered by a profuse growth of climbers, such as *Proustia pyrifolia* (Asteraceae), *Bomarea salsilla* (Amaryllidaceae), and *Lardizabala biternata*, (Lardizabalaceae) (fig. 11.5).

On dry north-facing slopes, or on frequently disturbed sites (Armesto and Martínez, 1978; Armesto and Gutiérrez, 1978), the sclerophyllous matorral is frequently replaced by a xerophytic thorn scrub, with a combination of deciduous shrubs, such as *Trevoa trinervis* (Rhamnaceae), *Flouresia thurifera* (Asteraceae), and *Colliguaja odorifera* (Euphorbiaceae), and often includes succulent species such as *Puya* spp. (Bromeliaceae) and columnar cacti, *Echinopsis* and *Eulychnia* spp., especially on steep rocky slopes (fig. 11.6).

There seems to be a fragile balance in the regional plant cover of central Chile between dry xerophytic vegetation

Figure 11.4 Coastal sclerophyllous shrubland (photo: J.J. Armesto)

and mesic sclerophyllous tree communities. This balance has historically depended on climatic cycles between conditions that are cool and wet, and those that are hot and dry, which in turn may be linked to varying frequencies of ENSO events in the South Pacific Ocean during the Holocene (Villagrán, 1995). Large-scale regeneration of sclerophyllous trees is normally limited by drought stress and the lack of seed banks (Fuentes et al., 1986; Jiménez and Armesto, 1992), except in unusually wet periods or along water courses. It is likely that the wet phases of ENSO

in central Chile are linked to significant regeneration of sclerophyllous tree species, especially in the drier habitats. Owing to recurrent anthropogenic disturbance through fire and permanent grazing pressure, however, vegetation cover may be presently shifting regionally toward dominance by dry xerophytic species (Armesto and Gutiérrez, 1978), despite a regional climatic trend towards increasing rainfall in the late Holocene (see below). Fossil pollen assemblages suggest that poleward expansions of the xerophytic thorn scrub and exclusion of sclerophyllous trees from large areas in the Central Depression occurred periodically during hot dry periods in the early Holocene (Heusser, 1983; Villa-Martínez and Villagrán, 1997; Villagrán, 1995).

11.3.3 Acacia caven Savanna

Xerophytic open woodlands, with the physiognomic aspect of a savanna (Fuentes et al., 1990), are widespread along the Central Depression in the Mediterranean-climate region, extending beyond the limit with the southern temperate forest region. These woodlands are dominated by leguminous trees, mainly *Acacia caven*, occasionally forming mixed stands with *Prosopis chilensis*, and have a dense herbaceous cover composed almost entirely of introduced European annual herbs (e.g., *Erodium* spp.) and grasses, which are typically associated with grazing pastures. Scattered patches of native perennials (*Loasa* spp.) and geophytes, such as *Pasithaea coerulea*, *Alstroemeria* spp., and *Leucocoryne* spp., and grazing-resistant *Cestrum parqui* (Solanaceae), can be found within the range of this dry plant formation. The same geophytes and perennials can be found

Figure 11.5 *Bomarea salisilla* (Amaryllidaceae), a vine endemic to coastal sclerophyllous mattoral (photo: J.J. Armesto)

Figure 11.6 Xerophytric thorn scrub (photo: J.J. Armesto)

of central Chile is the mixed sclerophyllous forest with numerically abundant populations of the tall endemic palm, *Jubaea chilensis* (fig. 11.7). These evergreen forests occur mainly on slopes and deep canyons of the Coastal Cordillera, and very likely profit from the moisture-laden marine air and the limited temperature oscillation in these habitats (Arroyo et al., 1995). The dominance by palms is another manifestation of the persistence of woody tropical lineages in maritime locations in central Chile. The physiognomic dominance of palms (up to 20 m tall) over the evergreen sclerophyllous canopy makes these local forests especially picturesque. Their distribution is presently limited to two small protected areas in central Chile, with scattered remnant populations in several coastal outposts around Valparaíso, and as far north as Illapel, suggesting that mixed palm forests may have been more widespread in the past. Palms have been intensely exploited for the production of syrup used for food and beverages since colonial times. Unfortunately, harvesting the syrup requires killing the palm trees that must be 30–40 years old to be of use (see later discussion on conservation). In addition, human-set fire probably contributed to the

in patches of sclerophyllous vegetation in coastal and Andean foothills. Some discussion has centered around the historical character of this dry formation (Arroyo et al., 1995). The high cover of introduced grasses under *Acacia* trees, and the resprouting ability of dominant shrubs, suggests that this vegetation type has been shaped by human impact, especially through cattle grazing and fire. In some cases, the invasion of the *Acacia caven* savanna by sclerophyllous species following the exclusion of fire and cattle has been postulated (Fuentes et al., 1986; Armesto and Pickett, 1985). However, it is also possible that this formation dominated the Central Depression before intense human impact, as a consequence of the rain-shadow effect of the Coastal Cordillera, and that at least part of its present distribution may have been associated with dry periods during the Holocene. This hypothesis remains to be tested. Whatever the case, this dry formation is expanding due to intense woodland clearing in the Central Depression and the dispersal of *Acacia caven* seeds by introduced cattle in recent times (Armesto and Gutiérrez, 1978).

11.3.4 Palm Forests

A narrowly distributed, and frequently overlooked, component of the mosaic of vegetation types in coastal areas

Figure 11.7 Palm forests in La Campana National Park, central Chile (photo: J.J. Armesto)

demise of the palm from many sites, as the palms lack the resprouting ability of other sclerophyllous shrubs. Adult palms often survive ground fires because of their size, but regenerating juveniles are most certainly killed by fire and are conspicuously absent from most remnant populations. Propagation in tree nurseries and fire protection programs in the wild can help to prevent further population decline.

11.3.5 Swamp Forests

Another often overlooked, but ecologically important component of the Chilean Mediterranean vegetation are the swamp forests (*bosques pantanosos*), which are scattered at various locations, generally in the narrow coastal plains between the Pacific Ocean and the Coastal Cordillera (fig. 11.8; Ramírez et al., 1996). Several woody species are characteristically or exclusively found in these swamp communities, particularly *Myrecugenia exsucca* (Myrtaceae), *Blepharocalyx cruckshanksii* (Myrtaceae), and vines such as *Boquila trifoliolata* (Lardizabalaceae). The origin of these coastal swamp forests has been studied recently by Villagrán and Varela (1990), Villa-Martínez and Villagrán (1997), and Maldonado (1999). Their results indicate that most swamp forests originated no earlier than the last 5,000 years, as a result of factors that contributed to raise the water table in small coastal basins, leading to sediment accumulation and later invasion by trees. These factors involved the blocking of local streams by littoral dune systems, a climatic trend toward wetter conditions in the late Holocene, and recent expansion of evergreen sclerophyllous species (Villa-Martínez and Villagrán, 1997). Swamps are thus living witnesses to recent climatic

fluctuations in central Chile, possibly associated with changes in the frequency of ENSO events (Villagrán 1995). They are unrelated to relict Olivillo forests mentioned earlier, except that they share some species with avian-dispersed fleshy fruits (e.g., *Drimys winteri*) that may be recent colonizers of these wetlands.

11.3.6 Coastal Matorral

The coastal plain is underdeveloped in most of central Chile. However, in some areas marine terraces formed by Pleistocene sea-level changes and tectonic events, often covered by fossil dunes, have provided open spaces for the development of coastal plant formations that include sclerophyllous shrubs (e.g., *Lithrea caustica*, *Schinus latifolius*, both Anacardiaceae), together with typical littoral plants (e.g., *Bahia ambrosioides*, Asteraceae; *Heliotropium chilensis*, Scrophulariaceae), and including some narrow endemics (e.g., *Lucuma valparidisiaca*, *Lobelia salicifolia*, Lobeliaceae, *Myrcianthes coquimbensis*, Myrtaceae). A number of geophytes that flower massively in wet years enrich the coastal matorral formation, including *Alstroemeria* spp., *Leucocoryne* spp., *Hippeastrum* spp., *Pasithea coerulea*, and some orchid species.

11.3.7 Andean Montane Woodland

Finally, above 1,500 m in the Andean mountains, an upland sclerophyllous woodland is found that differs in composition from the mesic communities in the foothills of the Andes (Hoffmann and Hoffmann, 1982; Arroyo et al., 1995) and from the upland *Nothofagus* communities of the

Figure 11.8 Swamp forest (Quintero, central Chile) (photo: J.J. Armesto)

Coastal Cordillera. This vegetation is dominated by *Kageneckia angustifolia* (Rosaceae), which is restricted to this altitudinal belt and constitutes a discontinuous treeline (Arroyo and Uslar, 1993). Above treeline, at 2300 m in central Chile, the montane woodland gives way to a low subalpine shrubland (Arroyo et al., 1981). Scattered patches of the conifer *Austrocedrus chilensis* (Cupressaceae) occur near the treeline at various locations between 32 and 36°S (Rundel, 1981). The distribution of *Austrocedrus* becomes more continuous on the eastern side of the Andes south of 36°S. The presence in central Chile of these relict stands of *Austrocedrus*, which rely strongly on their sprouting ability for reproduction and currently lack seedling regeneration, is another indication that the vegetation of central Chile is very sensitive to climatic variability over large temporal scales (C. Le-Quesne and J.C. Aravena, personal communication). These long-lived populations are probably remnants of stands that became established in wetter periods of the Holocene.

11.4 Floristic Affinities of Chilean Matorral with Other Dry Plant Formations

The Andean uplift fragmented the rich subtropical floras that prospered in the north-central regions of Chile and Argentina, extending to Bolivia and southern Brazil, during mid-Cenozoic time (Hinojosa and Villagrán, 1997). This process would have been gradual, producing the early segregation of more mesic taxa, followed by the development of a still continuous xerophytic flora. The present Mediterranean flora of central Chile must have originated from this transitional dry vegetation.

Based on physiognomic and floristic attributes, Sarmiento (1975) recognized 13 arid plant formations in South America, including the semiarid formations of north-central Chile. The area of Mediterranean vegetation analyzed by Sarmiento (1975) is equivalent to the summer-deciduous matorral, with succulents or *Acacia caven* savanna, as defined above (table 11.1), both subtypes of Mediterranean vegetation. The following genera are cited by Sarmiento as belonging to the semiarid formation of north-central Chile: *Geoffroea*, *Prosopis*, *Proustia*, *Puya*, and *Trichocereus*. Considering floristic similarities at the genus level (Sorensen's similarity coefficient) among these 13 arid plant formations, as reported by Sarmiento (1975), we constructed the dendrogram shown in figure 11.9. The Mediterranean vegetation of north-central Chile is weakly related to the driest vegetation types within South America, even those associated with the Pacific coastal desert and the occidental Andes, which are geographically contiguous. In contrast, it has stronger floristic affinities (43%) with two formations found on the eastern side of the Andes (the Monte and Andean Prepuna). These relationships suggest that these dry vegetation formations were connected in past geologic times (Cabrera and Willink, 1980; Hinojosa and Villagrán, 1997). The breakup of the dry trans-andean flora is probably related to the time of maximum Andean uplift. According to Gregory-Wodzicki (2000), the central Andes reached half of their present altitude by 10.7 Ma. This elevation was probably sufficient for the establishment of semiarid environments, but the floristic connection across the Andes could have been maintained for some time. The shift to much drier conditions in northern Chile and Argentina is indicated by the replacement of C3 by C4 grasses in northwest Argentina, recorded at 7 Ma (Latorre et al., 1997). This may be the
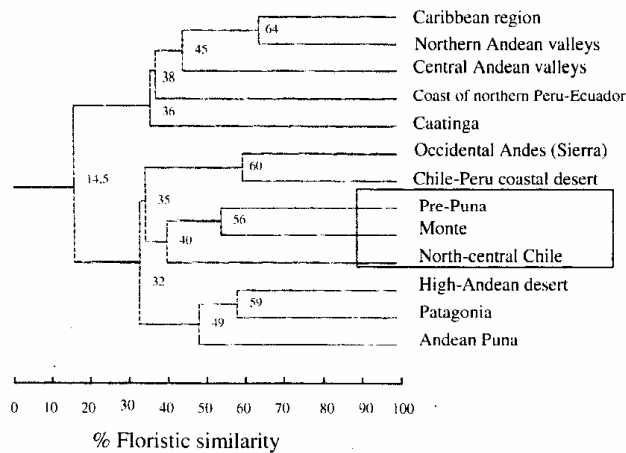

Figure 11.9 Dendrogram representing floristic affinities among dry plant formations within South America (data from Sarmiento 1975, based on woody species only). The closest affinities of the Mediterranean flora (north-central Chile) are with the Pre-Puna and Monte vegetation of the eastern side of the Andes (box).

minimum age for the initial separation of the dry plant formations on both sides of the Andes and the subsequent isolation of the Mediterranean vegetation in South America.

11.5 Human Impacts on the Chilean Mediterranean Ecosystem

Mediterranean-type ecosystems in South America, as elsewhere in the world, have long been modified by human activities. Because of the large population contained within its relatively small area, human impacts have been probably more pervasive in central Chile than in many other parts of South America (Arroyo et al., 1995). Greater human impact on the sclerophyllous vegetation of central Chile may be expected from the fact that humans frequently use uncontrolled fire to open areas for agriculture and settlement. The effects of fire on local ecosystems would have been greater in central Chile than in other Mediterranean-climate areas where wildfire has been a regular component of the disturbance regime at least through the Pleistocene. For example, the Mediterranean-type ecosystems of California exhibit a higher species richness of annuals (Arroyo et al., 1995) and larger seed banks of woody species (Jiménez and Armesto, 1992) than those of central Chile, thus providing indirect evidence that Californian ecosystems may be more resilient to fire disturbance. Presently, as discussed below, several factors associated with a long human presence influence vegetation dynamics and the distribution of plant communities in central Chile.

11.5.1 Succession and Disturbance

Successional recovery of sclerophyllous vegetation in many open areas of central Chile, including abandoned farmland, is a slow process (Fuentes et al., 1986; Armesto et al., 1995). Slow vegetation change may be a consequence of environmental conditions that are limiting for seedling recruitment. These include grazing by introduced herbivores, such as rabbits and goats, especially in open spaces between shrub patches, nd physiological stress related to the long summer droughts (Fuentes et al., 1986; Armesto et al., 1995). Although climatic trends may significantly influence the probability of successful establishment and expansion of shrublands into open, less favorable habitats (Arroyo et al., 1993), several conditions derived from human impact may prevent the regeneration of matorral shrubs and trees. The most important factor is the notable increase in the frequency and extent of human-set fire (Armesto et al., 1995), which is directly related to the growth of human settlements in central Chile. Fire-recurrence cycles of 20 years or less, as controlled by rates of fuel accumulation from resprouting species, are not uncommon in many areas of central Chile,

especially in the foothills of the two mountain ranges and in the Central Depression. Most likely, fires led to negative selection of species that are unable to resprout from rootstocks and must result in widespread mortality of young plants. Succession may also be impaired by limited seed dispersal from population sources (Jiménez and Armesto, 1992). Many sclerophyllous shrub species bear fleshy fruits dispersed by animals (Hoffmann and Armesto, 1995) and require the presence of perching trees to be recruited on open areas (Armesto and Pickett, 1985). Consequently, the loss of tree cover from large areas of central Chile may have a negative feedback on immigration via seed dispersal.

11.5.2 Invasion

A second relevant impact of humans on Mediterranean-climate regions is the introduction of exotic species of plants and animals (Sala et al., 2000). The original landscapes of central Chile have been greatly transformed by the deliberate introduction of vertebrate species such as goats and rabbits (whose range expanded from southern Chile). Rabbits and goats are major predators of shrub seedlings, thereby limiting population regeneration in open areas (Fuentes et al., 1983, Fuentes and Muñoz, 1995). It is likely that herbivore pressure in the Mediterranean region is presently much greater than before Europeans arrived in Chile. Natural herbivores, such as rodents, probably had a more limited impact on vegetation due to their control by native predators, although the latter are now much reduced in number (Jaksic, 1997). Little is known about the past effects of wild populations of guanacos (*Lama guanicoe*) on the vegetation of central Chile, from where these animals are long gone.

Furthermore, the large-scale planting of *Eucalyptus* spp. and *Pinus radiata* for forestry purposes has profoundly changed the landscape of central Chile, especially along the coast. In addition, many weedy species have accidentally spread through central Chile, along roadsides, making this region the richest in the country in terms of numbers of exotic species, with more than 400 recorded taxa (Arroyo and Cavieres, 1997). Ecosystems in the foothills of the two mountain ranges and the Central Depression, subjected to intense grazing pressure by cattle, have been heavily invaded by annuals, originally rare in central Chile (Arroyo et al., 1995). Among the most common introduced annuals are *Erodium* spp., *Bromus* spp., and *Avena* spp. The ecological impact of exotic weeds on sclerophyllous vegetation has been less studied than the effects of introduced herbivorous mammals, which are well documented (Fuentes and Muñoz, 1995). In the Coastal Cordillera, extensive areas of species-rich sclerophyllous vegetation, with a native herbaceous flora, have been replaced by a closed canopy of pines and eucalyptus, leading to considerable habitat loss. One of the most dramatic

cases is the near demise of the Maulino forest as the coastal mountains in the southern parts of the Mediterranean region have become almost completely covered by a blanket of forest plantations (Bustamante and Castor, 1998).

11.5.3 Hydrologic Problems

Two effects associated with recurrent fire and logging for firewood are significant in relation to the water supply to sclerophyllous vegetation. On the one hand, the loss of forest cover and the exposure of bare ground have increased the amount of surface runoff, leading to massive losses of organic soil and nutrients to downstream ecosystems. These losses can affect the ability of sclerophyllous vegetation to recover from disturbance, slowing down succession. Disturbance effects may be enhanced further by the extreme variability of precipitation in this climatic regime, leading to serious runoff and erosion problems when burning or logging of native vegetation, or plantations, coincide with wet years. On the other hand, frequent anthropogenic fire and logging appear to have changed the physiognomic structure of sclerophyllous vegetation everywhere, converting tall forests into low-stature shrublands, with many stems sprouting from the base of each shrub. The loss of stature of sclerophyllous vegetation may be critical, especially in upland areas of the Coastal Cordillera where interception of maritime fogs contributes importantly to the ecosystem's water supply. Consequently, a long history of chronic disturbance to coastal vegetation has disrupted the hydrologic cycle over many years, with a negative feedback on plant cover and tree regeneration, causing further desiccation and loss of forest habitat.

11.6 Prospects for Conservation and Restoration of Degraded Lands

The conservation of Mediterranean-type ecosystems in central Chile, as in other Mediterranean regions of the world, is a serious challenge because of the long history of human occupation and the present relevance of the areas for agriculture, industry, and human habitation (Armesto et al., 1998). The challenge is greater in Chile because less than 5% of the areas currently protected by the state are found within the Mediterranean-climate region, which in turn contains about 50% of the vascular plant species endemic to the Chilean flora (Arroyo et al., 1995). In addition, about two-thirds of the vegetation types in central Chile are poorly represented or absent from the national system of protected areas, which is also flawed by a serious lack of attention to the herbaceous flora (Arroyo et al., 1995). For the benefit of land managers, and as a reference for more quantitative assessments in the future, a qualitative ranking of the present conservation status of the major plant formations in central Chile is given in table 11.2. This assessment shows that most plant formations in central Chile are represented in only one or two conservation areas (national parks, or the less restrictive forest reserves), and that the majority of these originally narrowly distributed communities currently have a greatly restricted and/or fragmented range due to human exploitation or past disturbance. Consequently, we consider these ecosystems either threatened or endangered (table 11.2).

Considering the high demand on the land, there is little chance that the number of protected areas in central Chile could be greatly increased through direct government efforts. Nevertheless, public or private initiatives to increase

Table 11.2 Representation in protected areas and qualitative conservation status of major plant formations in central Chile

Plant formation	Representation in protected areas (number)*	Conservation status **
Olivillo forests	P (1) only in the north	Threatened
Nothofagus montane forest	P (1)	Endangered
Maulino forest	R (2)	Endangered
Sclerophyllous matorral	P (1), R (1)	Threatened
Summer-deciduous matorral with succulents	P (1), R (1)	No danger
Acacia caven savanna	R (1)	No danger
Swamp forests	(1) Municipal park	Endangered
Palm forests	P (1), R (1)	Threatened
Coastal matorral	P (1)	Threatened
Andean montane woodland	P (1)	Endangered

*P = national parks, R = national forest reserves, M = national monuments
**Endangered = greatly restricted in distribution due to human exploitation or disturbance, only few, small patches left. Threatened = restricted distribution due to human exploitation or disturbance, several large patches still persist. No danger = broadly distributed in central Chile.

the extent of protected land should be strongly encouraged, especially given the limited protection of critical remnant sites that help sustain the elevated species richness and endemism of this region. Even small areas, if set aside for preservation, may contain an unusually high number of species and should have a significant conservation value (Arroyo et al., 1995). A high priority in the agenda for the conservation of biodiversity in central Chile must be placed on the regulation of land use, particularly in restricting the use of fire. Restoration programs based on plantations of native shrubs and trees should be favored over the expansion of exotic tree plantations in coastal areas, especially considering the flammability of pine and eucalyptus plantations and the potential loss of some of the most valuable habitats for the native flora and fauna (Arroyo et al., 1999, Arroyo and Cavieres, 1997). Restoration efforts, although expensive, must consider the need to exclude exotic herbivores, such as cattle, goats, and rabbits, and keep in mind the large inter-annual variability in precipitation, which may limit the survival probability of young trees. Nevertheless, restoration programs should have added economic value because of their potential to reduce runoff and erosion rates, and the risk of destructive landslides that periodically affect rural and urban landscapes in central Chile, causing significant losses of human life and property.

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