Biological Invasions: a Global Perspective
Edited by J. A. Drake *et al.*

CHAPTER 8

The Characteristics of Invaded Mediterranean-climate Regions

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8.1 INTRODUCTION

Invasions by introduced organisms of the mediterranean regions of the world have held a special intrigue, because of the contrasts among the regions in the manifestation of the invasions, because the invasions seem to have been unusually severe for continental situations, and because mediterranean regions provide useful test cases.

This is a brief synthesis of the degrees and patterns of invasion, with emphasis on California, Chile, Australia, and South Africa. We explore possible explanations for any differences in the invasions between the various regions by reference to history, the physical environment, the patterns of disturbance, and factors associated with the biotic communities. Cases of invasive species are analysed to find reasons for differences in their behaviour on different continents. The Mediterranean Basin is not included in the analysis. Di Castri (this volume) summarizes historical information pertaining to that region.

For this review, we took mediterranean California to be equivalent to the Californian Floristic Province (Barbour and Major, 1977). The equivalent in Chile was taken to include the region of the matorral and espinal of the Coastal Ranges, the Central Valley, and the Andean foothills (Rundel, 1981). In Australia, the southern open-forests, southern sclerophyll communities, and mallee (Specht, 1981) were included, and in South Africa, the Fynbos Biome (Rutherford and Westfall, 1986).

8.2 PATTERNS OF INVASION IN DIFFERENT MEDITERRANEAN ECOSYSTEMS

8.2.1 Degrees and patterns of invasion in the different regions

Mediterranean ecosystems are often occupied by introduced plant species to the point that the native plant species are almost entirely displaced from their original habitat (Mooney, Hamburg, and Drake, 1986; Macdonald and Richardson, 1986). In California, Chile, and many Australian habitats, the displacement has been by many species of introduced herbs, mainly annuals. In California, this extreme invasion has occurred over an area of about nine million hectares of grassland and woodland (Heady, 1977). In the fynbos of the Cape Province of South Africa, about 800 000 hectares have been invaded by a total of around 20 species, mainly trees and shrubs (Macdonald and Richardson, 1986). A total of 674 introduced plant species have been recorded as naturalized in the state of California, with a native flora of about 5000 species (Mooney *et al.*, 1986), and 367 in the region of the Fynbos Biome of the southwestern Cape, with about 8500 native species. South Australia and Victoria have naturalized floras of 517 and 550 species, respectively (Specht, 1981).

Despite the extensive invasion of these natural landscapes, there are few data for a quantitative comparison between the mediterranean regions of the different continents, nor between regions within continents. Macdonald (1984) found that, with some exceptions, fynbos ecosystems were more extensively invaded by introduced plants than were other South African ecosystems. Fox and Fox (1986) concluded from a study of reserves in New South Wales that undisturbed heathlands were more severely invaded by introduced plants than were other ecosystems, though not where disturbed ecosystems were compared. Macdonald, Powrie and Siegfried (1986) analysed data on the sizes of invasive floras and faunas in different reserves in South Africa as well as data on the frequency of remains of the house mouse *Mus musculus* and black rat *Rattus rattus* in owl pellets. They found little evidence that the plant invasions of the fynbos were greater than those in other biomes. However the number of species of introduced birds and mammals was higher in fynbos nature reserves. The grasslands of the American Midwest are as much invaded as those of the chaparral region (Mack, this volume, cf. Heady, 1977 and Mooney *et al.*, 1986), but the mediterranean region in California tends to have a larger invasive flora than adjacent biomes (Figure 8.1). It seems that mediterranean habitats are often distinguished by a higher degree of invasion than are the habitats of other continental regions, but that this is not always so.

The relationship between the numbers of introduced plant species and natives in the floras of California is compared with that of the Cape fynbos in Figure 8.1. The Cape data set is biased, being from reserves, but includes several observations for areas which were previously disturbed and only recently reserved. Equivalent areas contain much smaller total floras in California than in the fynbos (Kruger and Taylor, 1979), so that areal extent should be considered when making this comparison, but the ratio of introduced species to natives tends to be consistently higher in California than in the Cape, with a few exceptions. The heavily disturbed Tygerberg Nature Reserve, with relatively fertile soils, has as high a proportion of introduced species (Table 8.4) as do many Californian areas, and in California the San Dimas Experimental Forest, which includes areas sown

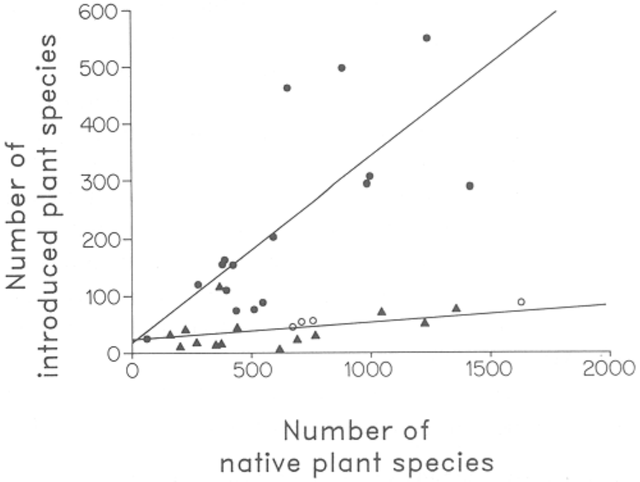

Figure 8.1. Relationships between numbers of naturalized introduced species and numbers of native species within defined land areas in California and the Cape. Dots represent data for mediterranean sites in California (r^2 for the linear regression $= 0,54$), circles are for non-mediterranean sites in California, and triangles are for mediterranean sites in the Cape ($r^2 = 0.14$) (See text for further explanation.)

to pasture grasses but which is mostly well protected, has a relatively low proportion of introduced to native species (77 to 442; Mooney and Parsons, 1973). Nevertheless, even small fynbos reserves that have had a history of disturbance, such as the Cape Flats Nature Reserve and Goukamma, have relatively fewer invasive plant species that do California areas. And in California, areas such as the Santa Monica Mountains, most of which are incorporated in National Forests, have high proportions of introduced species in their floras. The higher ratio of invasive plant species to native plant species in the relatively poorer floras of California is striking.

In the case of animals, even less comparative data are available. Several species of reptiles, birds, and mammals have naturalized within all the mediterranean regions but most are commensal with humans. Among birds, such cosmopolitan commensals as the feral pigeon *Columba livia* and the house sparrow *Passer domesticus* have succeeded in all the regions. The European starling *Sturnus vulgaris* is now abundant in the Cape, California, and the southern and eastern portions of Australia. It is being actively prevented from spreading into southwestern Australia and has not yet been introduced to Chile (Long, 1981). Birds which are not commensals have succeeded on some continents but not on others. No gamebird species from other continents have successfully established in the Cape (Brooke, Lloyd, and de Villiers 1986). By contrast, both the chukar partridge *Alectoris chukar* and the ring-necked pheasant *Phasianus colchicus* have become invaders in California. In Chile the California quail *Lophortyx californicus* has established and spread but the ring-necked pheasant has failed there as in Australia, despite repeated introductions. The mediterranean regions of Australia have been invaded by at least two doves (in addition to the feral pigeon) and nine passerines. This is considerably more than have established in any of the mediterranean regions of other continents (Long, 1981).

One or more species of mammal has invaded natural habitats on each continent and caused noticeable modification to the native communities (Table 8.1). More species of mammal invade Australian mediterranean regions, and each mostly in greater abundance, than in the others (see below), though, once more, the indications are that mediterranean ecosystems are not singular in this respect (e.g. Myers, 1986).

Invertebrate invaders of mediterranean ecosystems outside transformed habitats have seldom been documented (Groves and Burdon, 1986; Macdonald

Table 8.1. List of invasive mammals in the four mediterranean-type regions. I: invasive, widespread; i: invasive, local; S: introduced, widely established but not invasive in untransformed habitats; s: as for S, but local; F: introduced, but failed to establish (including domestic animals that have not become feral). Collated from information in Brooke *et al.* (1986), Mooney *et al.* (1986), Myers (1986), and Fuentes *et al.* (1984) and references therein

Common name	Scientific name	Region			
		California	Chile	Cape	Australia
Virginia opossum	*Didelphis virginiana*	I			
European rabbit	*Oryctolagus cuniculus*	F	I	F	I
European hare	*Lepus europeus*		I		I
Grey squirrel	*Sciurus carolinensis*	S		S	F
Fox squirrel	*Sciurus niger*	s			
Brown rat	*Rattus norvegicus*	S	S	s	S
Black rat	*Rattus rattus*	S	S/I	S	I
House mouse	*Mus musculus*	S	S/I	S	I
Feral dog	*Canis familiaris*	S	?	s	I
Red fox	*Vulpes vulpes*				I
Domestic cat	*Felis catus*	F	F	F	I
Donkey	*Equus asinus*	i		i	i
Feral horse	*Equus caballo*	I		i	I
Feral pig	*Sus scrofa*	I	F	s	I
Feral cattle	*Bos taurus*	i	F	i	i
Fallow deer	*Dama dama*			s	I
Red deer	*Cervus elaphus*			F	I
Sambar	*Cervus unicolor*				I
Hog deer	*Axis porcinus*				i
Feral sheep	*Ovis ammon musimon*	F	F	F	I
Feral goat	*Capra hircus*	F	F	F	I
Barbary sheep	*Ammotragus lervia*	I			
Himalayan tahr	*Hemitragus jemlahicus*	I		i	

and Richardson, 1986; Mooney *et al.*, 1986). The unaided spread of the Argentine ant *Iridomyrmex humilis* into relatively undisturbed fynbos communities from foci associated with human occupation or traffic (De Kock, unpublished; Donelly and Gilliomee, 1985; Macdonald and Richardson, 1986) has disrupted both the native ant communities and the patterns of recruitment in native species of myrmecochorous plants (Bond and Slingsby, 1984). This has apparently not occurred elsewhere (e.g. Majer, 1978). The means by which this species, which has a low capacity for dispersal, spreads from infected foci into communities rich in ant species is not known, but the potential exists for extensive and severe impacts on natural ecosystems.

Overall, therefore, there are substantial differences among the regions with regard to the invasions that have occurred, as well as some general similarities.

8.2.2 Invasive floras: correspondences and divergences in different regions

In all the regions discussed here, though to a lesser extent in Chile, the major vegetation patterns are strongly determined by edaphic factors (e.g. Raven 1977; Specht and Moll, 1983). There are marked disparities in the kind and degree of invasion of the different vegetation formations.

The forests of California are not much invaded by introduced plants, despite extensive and regular disturbance by forest operations including clearfelling (Mooney *et al.*, 1986). Coastal dune vegetation, salt marshes, valley grasslands, and oak woodlands are often heavily invaded. In the coastal dunes, up to 43% of the species in a community may be introduced, and the spread of the marram grass *Ammophila arenaria* has caused marked change to coastal dune landscapes in northern California (Barbour *et al.*, 1981). Introduced grasses and forbs, principally annuals, dominate the communities in the valley grasslands (McNaughton, 1968; Gulmon, 1977) and similarly occupy the understorey in oak woodlands (Heady, 1977). The composition of these communities varies along environmental gradients (Janes in Heady, 1977), with succession after fire and with variable grazing pressure (Heady, 1977), and from year to year (Gulmon, 1977, 1979), but the composition at a site shows no net change over time (Gulmon, 1977, 1979) and little or no recovery of the original native composition occurs if the grassland is protected against grazing and other factors of disturbance (Heady, 1977; Mack, this volume).

Mature California chaparral has few or no invaders other than those found in mechanically disturbed sites, although many introduced annuals and a few perennials may be found among the post-fire herbaceous flora. In post-fire chaparral in San Diego County, Keeley *et al.*, (1981) recorded 11 introduced species among 99 herbaceous species present after fire. Grasses such as *Bromus mollis* and *Bromus rubens* and forbs such as *Centaurea cyanus* were sometimes prominent, though most species had less than 0.1% cover and all disappeared within a few years after fire. *Lolium multiflorum* dominated in some cases, but this was where it had been sown as a soil conservation measure. Naturalized shrubs from the Mediterranean Basin, such as *Cistus* spp., have not invaded chaparral (Montgomery and Strid, 1976). The mature chaparral, which is relatively poor in plant species, is thus singularly free of introduced species.

The pattern of invasion of California grasslands is repeated in Chile, with most of the introduced species being shared between the regions (Gulmon, 1977; see later). However, unlike California chaparral, the Chilean matorral is extensively occupied in its mature state by elements of the same exotic flora, evidently because the prevalent grazing and burning of the matorral and the extensive wood-cutting maintains open canopies (Keeley and Johnson, 1977). But the richest representation of exotic herbs is found soon after fire and the abundance and diversity of introduced species declines thereafter (Keeley and Johnson, 1977).

Few data are available for the whole mediterranean region of Australia. In South Australia, pronounced differences are found in the relative degree of invasion of the different major ecosystems there. Relative to the native flora, the most invasive species are found in the coastal and the savanna land systems, and the least in the sclerophyll and the mallee land systems—the arid land system being not strictly mediterranean in climate (Table 8.2; Specht, 1972). This pattern correlates broadly with the abundance of the invasive plants. Specht (1972) argued that the plant species introduced South Australia were not pre-adapted to low soil fertility and hence were excluded from the infertile sclerophyll and mallee land systems, except where they were admitted along roadsides and similar disturbed sites. Soil fertility as a determinant of the form of plant invaders is discussed later.

Table 8.2. Numbers of naturalized introduced plant species in the different major land systems of South Australia, relative to the sizes of the native floras (after Specht, 1972)

Land system	Number of plant species	
	Native	Introduced
Mediterranean		
Coastal	56	22
Sclerophyll	344	18
Savanna	304	127
Mallee	424	40
Not Mediterranean		
Arid	231	5

Data from various sources have been used to derive the illustrative cases summarized in Table 8.3. The invasive populations in California and Chile are dominated by annual and biennial herbs, especially grasses of the genera *Avena*, *Bromus*, *Festuca*, and *Hordeum*, and forbs in the Geraniaceae and Asteraceae. In Australia and the Cape, these forms invade only on moderately fertile substrates, i.e. moderately leached soils in the terminology of Specht and Moll (1983). These patterns have been well documented for South Australia by Specht (1972). Grasslands and *Eucalyptus* woodlands on more fertile soils are widely invaded by

Table 8.3. List of prominent invasive plant species of the four mediterranean-type regions, with indications of their distributions. Information is derived from McNaughton (1968), Specht (1972), Gulmon (1977), Bridgewater and Backshall (1981), Macdonald and Jarman (1984), J. A. Vlok (unpublished), and Wells *et al.* (1986). The symbol I indicates that the species has been recorded as introduced in the region but has not been observed to spread, + that the species has naturalized but does not spread except in markedly disturbed habitats (road cuts and similar), and + + that the species has been observed to spread widely in natural vegetation. The columns headed 'low' and 'mod' for Australia and the Cape refer to substrates with low and moderate nutrient supplies, respectively, corresponding with the highly leached and moderately leached categories of Specht and Moll (1983)

Species	Region					
	California	Chile	Australia		Cape	
			low	mod	low	mod
Shrubs and trees						
Acacia cyclops and congeners	I	I	—	—	+ +	+
Pinus halepensis	I	—	?	?	+	+ +
Pinus pinaster	?	—	I	?	+ +	I
Pinus radiata	—	I	+	+ +	+ +	+
Hakea sericea and congeners	I	—	—	—	+ +	I
Cytisus scoparius	+	?	I	+	I	I
Annual and biennial herbs						
Aira caryophyllea	+ +	+ +	I	+	I	+ +
Anagallis arvensis	+	+	I	+ +	I	+ +
Arctotheca calendula	I	I	I	+ +	—	—
Avena barbata and congeners	+ +	+ +	I	+ +	I	+ +
Brachypodion distachyon	+ +	?	I	+	?	?
Briza maxima and *B minor*	+ +	+ +	I	+ +	I	+ +
Bromus mollis and congeners	+ +	+ +	I	+ +	I	+ +
Echium lycopsis	I	I	I	+ +	I	+ +
Erodium cicutarium, *E. moschatum*, and congeners	+ +	+ +	I	+ +	I	+ +
Hypochoeris glabra	+ +	+ +	I	+ +	I	+ +
Lolium multiflorum and congeners	+ +	+ +	I	+ +	I	+ +
Vicia bengalensis	?	?	I	+ +	I	+ +

herbaceous species from the Mediterranean Basin and South Africa, and some trees and shrubs such as *Olea europaea, Lavandula stoechas*, and *Lycium ferocissimum* (lately, also *Pinus radiata*—Van der Sommen, 1986). Mallee vegetation has been little invaded, as also the heaths and the *Eucalyptus* woodland with sclerophyllous understories. The sclerophyll land system is now being invaded by *Pinus radiata* but principally on more fertile sites (Van der Sommen, 1986), and most invasions are by herbaceous species from Europe and South Africa. One feature of the exotic herbaceous flora of Australia is the abundance of geophytes from South Africa. This life form has also invaded elsewhere (e.g. *Iris pseudacorus* in California—Raven and Thomas, 1970) but then few species have been involved.

Where the habitats in the four different regions are similar in climate and substrate, the same species of plant invaders tend to be found. Gulmon (1977) has analysed the composition of grasslands in Chile and California. Twenty-seven of the 48 introduced species recorded in her samples for both continents have been recorded as established in natural or nearly natural ecosystems in South Africa by Wells *et al.* (1986) and by Macdonald (personal communication) and Vlok (unpublished), and of these 24 were recorded for lowland habitats, with more fertile soils, in the fynbos biome. Thirty-four species were shared between California and Chile, and 16 are common to all three regions. Some of the dominant species in her samples have been recorded by Vlok (unpublished) in a recent survey of reserves in Coastal Renosterveld and other coastal vegetation. There included *Avena barbata, A. fatua, Erodium moschatum, Lolium multiflorum*, and *Vulpia* (*Festuca*) *myuros*. The level of invasion correlated with degree of disturbance, i.e. cultivation history in this case.

There are similar correspondences between the Cape and California in the identity of dominant invasive plants reported for California grasslands by McNaughton (1968). However, among the dominants in Gulmon's samples are some species such as *Aira caryophyllea* and *Festuca dertonensis* (annuals in the Poaceae), and *Brassica nigra* (Brassicaceae) which are recorded for South Africa but not as dominants. Many of the dominant invaders sampled by McNaughton (1968) and Gulmon (1977) are not recorded as naturalized in South Africa (Wells *et al.*, 1986). Gulmon (1977) also emphasized the differences between Chile and California that were evident in the identity and abundances of the plants sampled, despite overall convergence. For example, *Festuca dertonensis* was dominant in Chile, but rare or absent in California. *Avena fatua* was among the dominants in California, but not recorded in her sample from Chile (though present elsewhere E. R. Fuentes, personal communication). Thus, there are as many substantial differences in the patterns of plant invasions of like habitats on the different continents as there are similarities, which may be owing to the detailed differences between continents in history, climate, substrate fertility, and disturbance regime (e.g. Gulmon, 1977).

In the fynbos region, the most prominent plant invaders are trees and shrubs

(Macdonald and Richardson, 1986). By their nature these species persist through the course of succession after fire. None except for *Pinus radiata* is found to be invasive on the other three continents, even though some, such as species of *Acacia* and *Pinus*, have been introduced to California (Mathias and McClintock, 1963) and to a lesser extent, Chile (F. J. Kruger, personal observation). *Acacia cyclops, A. dealbata, A. longifolia, A. saligna, Eucalyptus lehmannii, Leptospermum laevigatum*, and *Pinus halepensis* are widely used as ornamentals in southern California, in various climatic conditions and in situations adjoining a diversity of natural habitats. The cultivated trees flower and fruit in abundance, yet nowhere do they invade the adjoining natural vegetation. Even on mechanically disturbed sites, only *A. saligna* was noted to recruit young plants (F. J. Kruger, personal observation). In the Cape these invaders are confined entirely, or virtually so, to areas with severely nutrient-deficient soils (Macdonald and Richardson, 1986), habitats which are not found in Chile or California (see also later).

Therefore, there is a tendency for similar plant invasions to occur in relatively fertile habitats on the different continents and the differences in abundance may reflect different disturbance histories (see later) or differences in the details of environmental regimes, such as the length of summer drought or the quantity of winter rainfall (Jackson, 1985). Only Australia and South Africa share extensive infertile habitats in the mediterranean-climate zones, and there are as yet few correspondences between the invasive floras in these habitats on the two continents. Major discrepancies between regions may be due to historical accident. An example is *Arctotheca* (*Cryptostemma*) *calendula*, the Cape weed, which is abundant in mediterranean Australia but absent from California where it apparently has the potential to invade (Heady, 1977).

8.3 HISTORICAL AND CULTURAL FACTORS

The human history of the Cape region differs substantially from that of the other regions (Deacon, 1986). Sparse populations of Early Stone Age people occupied the area from about 1.0–1.5 million years before the present (BP). Changes in technology at about 150 000 year BP, at the start of the Middle Stone Age, included the control of fire. These hunter-gatherers probably had relatively little influence on the biota. For example, the extinctions of plant and animal species that occurred during this time were due to climate change rather than human activity (Deacon, 1986). Khoi pastoralists arrived on the scene at about 2 000 years BP, bringing sheep, cattle, goats, and dogs to the area for the first time. Although the extinction of at least one species of antelope, the bluebuck *Hippotragus leucophaeus*, has been ascribed to the competition with the new grazers (Deacon, 1986), the paleoecological record does not reflect major changes in the flora which correlate with the arrival of pastoralism (e.g. Scholtz, 1986).

In addition to the domesticated animals of the pastoralists, these early people introduced at least some species of plants, such as *Ricinus communis*, dated to at least 3 000 years BP, and *Medicago polymorpha* (about 1 200 years BP). Cape ecosystems have had a long history of gradual evolution with humankind so that any ecological study must account for the effects of people on the habitat, but the per-European settlements evidently did not have the marked and abrupt ecological consequences as did similar settlements on other continents.

The next human colonists in the Cape were the Europeans who settled in 1652. Their population reached about 1300 after 50 years and 150 years passed before the whole of the fynbos region as settled. Agricultural development was slow until the diamond and gold mines in the interior created a demand for agricultural produce from around 1870 onward. The impact of the changes wrought to vegetation by new grazing patterns was apparent from within about a century of settlement, although this involved the replacement of native perennial grasslands by native shrubs in genera such as *Elytropappus* and *Relhania* rather than invasions of introduced herbs (Cowling, 1983; Scholtz, 1986).

In Australia the arrival of the Aborigines at about 40000 years BP resulted in marked changes to the ecosystems, principally because of the customary use of fire to regulate the condition of vegetation and animal populations (Kershaw, 1986). Aborigines introduced no plants (Groves, 1986a), but brought the dingo *Canis familiaris dingo* about 3500 years BP and this evidently contributed to the extinction of native predators such as the thylacine (Myers, 1986). European settlement was relatively late, from about 1830 onward. Population densities have remained low to the present day. Western Australia, for example, has a population density of less than 0.6 per square kilometre with 70% of the people living in the Perth region. However, this settlement had profound effects on ecosystems. The grazers they introduced differed markedly from native herbivores in their foraging patterns (Specht, 1972; Myers, 1986). Native animal communities were disrupted through the persecution of both predators and grazing animals (Myers, 1986). There was extensive deforestation to develop pasture land, and widespread propagation of introduced pasture species, mainly of Mediterranean origin but also from southern Africa and elsewhere, as well as fertilization of pastures (Specht, 1972, 1981; Moore, 1975).

Chile and California were settled only from about 12 000 years BP, perhaps earlier (Bray, 1986), by small populations of Indians who later developed forms of shifting cultivation for the production of several different crop species. Burning of the shrublands was evidently general practice. In Chile, Indians introduced domesticated camelids shortly before European settlement. There the Indian economy was evidently little affected by the Incan conquest in the late 15th century, except near irrigation settlements (Aschmann, 1977). Spanish colonists arrived in Chile in the first half of the 16th century (Mooney *et al.*, 1972; Aschmann and Bahre, 1977). Cattle ranching developed rapidly and complaints of over-grazing were noted from an early stage (Bahre, 1979). European settlement was accompanied by local deforestation stimulated by the needs of mining, construction, and fuel (Mooney *et al*., 1972; Bahre, 1979). Extensive agriculture in the Chilean Central Valley with sheep herding and wood-gathering on the matorral-covered slopes are patterns which have persisted to the present day (Cañas *et al*., 1982), and the structure of the natural vegetation has been severely modified almost everywhere (Aschmann and Bahre, 1977; Bahre 1979).

California was effectively settled by the Spaniards only in 1769, and European populations did not grow until toward the end of the century. Replacement of the herbaceous layers in lowland vegetation by Mediterranean herbs occurred rapidly from the middle of the 19th century, in association with the growth and intensification of stock ranching (Aschmann and Bahre, 1977; Jackson, 1985).

Thus, all these regions were occupied by aboriginal populations who managed fire but husbanded relatively few domesticated plants or animals. European settlers effectively displaced these economies and, besides bringing a diversity of domesticated and other organisms, introduced new regimes of disturbance to the natural ecosystems. The similarities of climate with that of the Mediterranean Basin and the traffic between Europe and the colonies, together with the availability of a weed flora pre-adapted to the new environments through the selective influence of millennia of human activity (Naveh, 1967, 1975; Raven, 1977; Jackson, 1985), led naturally to the spread of herbaceous plants from this source in the new regions. However, there were important differences among the regions in the patterns of introduction, owing partly to differences in the natural resources of the newly settled areas, and partly to cultural differences between the settler societies. The colonial links through Britain between Australia and South Africa, for example, may have ensured earlier exchange of many species of trees and shrubs than would have been the case for other continents (e.g. Shaughnessy, 1986). The direct traffic between Spain and California and Chile would also have biased the introduction of Mediterranean plants to these regions, relative to the Cape and Australia (Groves, 1986b).

In the Cape, little forest was available as a source of timber and fuel and there were few trees for shelter. Trees were immediately introduced from Europe. These included *Pinus pinaster*, now a major weed (Shaughnessy, 1986). Many other trees and shrubs were introduced in the first half of the 19th century and subsequently. There is at least tentative evidence of a progressive degree of naturalization among the introduced flora, so that the time-course of introduction in itself must be factored into any analysis of the causes of invasion (Baker, 1986; Kruger, Richardson, and Van Wilgen, 1986), together with patterns of cultivation (Shaughnessy 1986). On the other continents the settlers had less need to plant trees and shrubs, so that fewer species were introduced, and these later, than was the case in the Cape. This must explain part of the differences between regions in their invasive floras.

Australian environments are marked by the diversity and abundance of introduced vertebrate animals as well as by their extensive alien flora (Myers, 1986). These animals were actively encouraged by acclimatization societies in the second half of the 19th century. Similar societies never occurred in South Africa, where introduced vertebrates are rare outside sites of human occupancy and the aquatic habitats (Brooke *et al.*, 1986), so that differences between these two regions in the extent of invasion by exotic vertebrates may in part be owing to cultural and historical factors. Among the mammals listed by Myers (1986) as being invasive in Australia, only feral cattle, horses and donkeys have succeeded in invading natural habitats in the other regions and then on a small scale (Table 8.1), though the rabbit and the European hare are widespread in Chile. Species such as the pig, rabbit, and fallow deer, which are widely established in Australia and elsewhere in natural habitats, have failed to establish feral populations in the Cape in spite of repeated introduction (Brooke *et al.*, 1986). There is thus a greater rate of success in establishment of feral populations of introduced mammals in Australia than in South Africa, in mediterranean environments as well as others.

The profound transformation of ecosystems in these regions from the conditions of 500 years ago has been strongly patterned by topography in all cases except Australia. In the Cape, up to 85% of the lowland vegetation on fertile soils, the Coastal Renosterveld, has been converted to agricultural fields (Moll and Bossi, 1984). By contrast, as little as 10–20% of the Mountain Fynbos, on rugged terrain with highly leached soils, has been transformed (Cook in Kruger, 1982; Moll and Bossi, 1984). About 20% of the area of Mountain Fynbos has legal conservation status but for the lowlands this fraction is barely more than 1% (Greyling and Huntley, 1984).

Like the Cape, California and Chile have been markedly transformed in the lowlands (Aschmann and Bahre, 1977; Canas *et al.*, 1982; Mooney *et al.*, 1986). The uplands are well conserved in California, with around 50% of the state in public ownership (Mooney *et al.*, 1986), whereas little of Chile is formally conserved and the uplands are still used in a system of transhumance (Bahre 1979; Cañas *et al.*, 1982) as well as being used through the year for grazing, small-scale agriculture, and for wood-gathering (E. R. Fuentes, personal communication). In Australia, land within the 500 mm rainfall isohyet in the mediterranean regions is now mainly under pastures for cattle and sheep if not under crops (Moore, 1975). Beard (1984) estimated that up to 54% of the approximately 120 000 square kilometers the sclerophyllous shrublands of western Australia have been transformed. There are nevertheless large tracts of natural vegetation in national parks and forestry reserves (e.g. Hopper and Muir, 1984).

The uplands in California and South Africa are managed principally as watersheds and for nature conservation. Management is relatively intensive and, in the latter case at least, the practices specifically provide for the exclusion or control of invasive species (Macdonald and Richardson, 1986). Fire exclusion policies have given way to the managed use of fire to serve conservation objectives. Much effort has gone into afforestation with introduced species in the Cape, some of this having been fairly haphazard (e.g. Shaughnessy, 1986). There has been little or no afforestation in California, where instead there have been attempts to convert chaparral to relatively non-flammable herbaceous sward or to pastures, and introduced plants have been sown extensively for this purpose as well as for soil conservation (Hanes, 1977). The intensive exploitation of the matorral in Chile has been accompanied by little management for conservation. It is difficult to generalize for the complex picture in Australia, beyond to say that in such a sparsely populated region, distance is important so that natural areas remote from centres of development show less invasions than do those closer by (e.g. Bridgewater and Backshall, 1981; Muir, 1983).

These patterns are summarized schematically in Table 8.4. Each region is distinguished by patterns of land use that must in some degree have a differential effect on the establishment and spread of introduced species. The effect of people on remaining natural vegetation is apparently strongest in Chile. In California, the active propagation and spread of introduced species is presently perhaps confined to those for amenity in urban areas, though until recently a significant fraction of the wild landscape was subject to the introduction and spread of exotic plants for pasturage and watershed management (Hanes, 1977; Mooney *et al.*, 1986). The situation in Australia is dominated by the past energetic efforts to manipulate the pastures, and competing grazers and predators as described previously, as well as legacies of animal introductions. In places, plantation forests provide a permanent source of plant invasion. In South Africa, although afforestation with introduced trees provides a permanent source of propagules for invading species of *Pinus* and *Eucalyptus*, most of the extensive invasions are by plants introduced over the past century or more, but which are now little used.

In every case where the evidence is available, the degree of invasion of any given habitat is in some degree a function of distance from urban centres or centres of occupation (Frenkel, 1977; Muir, 1983; Macdonald *et al.*, 1988).

These differences in the histories of introductions affect our ability to provide ecological explanations for differences between the regions in the degree and nature of invasions found there. Because no adequate historical analyses are available, with exceptions in detailed cases such as that of Shaughnessy (1986) for trees and shrubs in the Cape Peninsula and for the rabbit in Australia (Myers, 1986), it is necessary to consider history separately for each species examined. It is equally important to consider the differences that may exist in the pattern and trend in human disturbance to the environment.

8.4 ENVIRONMENTAL CORRELATES WITH PATTERNS OF INVASION

8.4.1 Climate

Homoclimatic analysis reveals the geographical patterns of similarities in climates (e.g. Russel and Moore, 1976) and such similarity permits probabilistic

Table 8.4. A summary of historical factors likely to have influenced invasions of introduced plants in the four recently colonized mediterranean climate regions, collated from sources quoted in the text. The symbols '+' indicates an increase in the given factors, by up to three levels, and '–' a decrease

	REGION			
FACTOR	CAPE	AUSTRALIA	CALIFORNIA	CHILE
Length of human occupancy, years	1, 0–1, 5 million	40 000	12 000 (30 000?)	12 000 (30 000?)
Length of time since European settlement, years	330	150	215	450
Fire Regime				
Changes to natural regime due to early humans				
—Frequency	+ +	+ + +	+	+
—Size	– –	– – –	?	– – –
—Season	?	?	?	?
Period of exposure to altered fire regime, years	150 000	40 000	12 000	12 000
Changing due to Europeans, from early human regime				
—Frequency	0/–	—	+/–	–
—Size	+/–	+ + +	+ ?	–
—Season	+ +	?	+ + +	?
Grazing Regime				
Change due to humans				
—Intensity	+ + (lowlands)	+ + +	+ + + (lowlands)	+ + +
Type of introduced herbivores				
—Domestic	0	+ + +	+ + +	+ + +
—Invasive	nil	+ + +	nil	nil
Period of exposure to altered regime prior to European settlement, years	1700	nil	nil	nil
Elimination of native large herbivores	+ + + (post settlement)	+ + (post settlement)	+ (lowlands)	+ (uplands)

Deforestation				
Historical	0/+	+ + +	+ + (lowlands)	+
Current	0	0	0	+ + +
Afforestation				
Extent	+ + +	+	0	+ +
Number of species	+ + +	+	0	+
Time since initation (years)	330	20–40	—	50
Sanddune stabilization	+ + +	+	+	0
Introduction of pasture forage plants	0	+ + +	+ + +	0
Cultivation				
Extent	+ + +	+	+ +	?
Period of time before European settlement, years	nil	nil	?	1000
Proportion of area now transformed	lowlands–68% montane–10%	mesic–c90% xeric–c10%	lowlands–c90% montane–c5%	?50%
Urban areas	+ +	+	+ + +	+

predictions of invasive success, i.e. species which are not pre-adapted to the new environment by evolution in similar climates in their source regions are unlikely to invade in the new environment (Specht, 1981; Groves, 1986b; Nix and Wapshere, 1986). Groves (1986b) has analysed the nature of mediterranean-type climates in relation to the establishment and spread of plants in new regions, emphasising the phenology of reproduction. In *Chrysanthemoides monilifera* invading Australia the subspecies are evidently confined to their appropriate homoclimes (Weiss, 1986). With a few exceptions, the Australian species of *Acacia* have remained within the Cape equivalent of their climatic and edaphic range in Australia (Milton 1981). For example, *Acacia pycnantha*, which is native to inland areas in southern Australia, has disappeared from the coastal Cape Flats while *A. cyclops* and *A. saligna* dominate the area: these three species were introduced at the same time (Shaughnessy, 1986). An obvious exception to this is *A. longifolia* which invades riparian habitats in both mediterranean and savanna habitats in South Africa (Macdonald, Jarman and Beeston, 1985) and spreads independently of climate.

But species often invade regions with climates differing in a greater of lesser degree from that of the source region. *Pinus radiata*, for example, thrives in mediterranean climates on various continents but also in climates different from that of its native habitats. It often regenerates and spreads unaided under such circumstances (Chilvers and Burdon, 1983; Hunter and Douglas, 1984; Richardson and Brown, 1986). The California poppy, *Escholtzia californica*, has naturalized and spread widely in Chile, extending into climatic regions that are markedly different from those at its source (Gulmon, 1977; Bahre, 1979; F. di Castri, personal communication). Mediterranean weeds spread in climates in Australia and California which often differ substantially from their native climates (Wapshere, 1984; Jackson, 1985). Similarly, *Hakea sericea*, introduced to South Africa from narrow provenances in south-eastern Australia (Neser, 1968; Kluge, 1983), spreads in habitats with diverse climates in the Cape (Fugler, 1982; see Russel and Moore, 1976 for climate similarities and contrasts). Competition from existing plants or predation by natural enemies is often important in confining the ranges of species in their source regions. For example, *Pinus halepensis* is limited in its distribution within its habitats in the Mediterranean Basin by competition from native grasses (Acherar, Lepart, and Debussche, 1984). Once released from these pressures, introduced species can sometimes invade areas with different climatic conditions to those in their native ranges. *P. halepensis* spreads wherever planted on more fertile soils in the Cape. Wapshere (1984) has emphasized this phenomenon for several herbaceous species in Australia. *Hypericum perforatum* invaded a wide range of habitats after its introduction to California. However, when insect herbivores from its natural range were introduced, *H. perforatum* became restricted to a limited subset of these habitats (Harper, 1977; see also Groves, this volume).

Nevertheless, climate, or at least site water balance, may explain the failure of certain species originating from regions with mediterranean climates to spread in some mediterranean region, when they are weeds in analogous regions elsewhere. *Acacia cyclops* and *A. longifolia*, which are important weeds in the Cape, are widely used in horticulture in California (Mathias and McLintock, 1963) yet have not naturalized and spread (Mooney *et al*., 1986). Shrubs in the California chaparral and the Chilean matorral are subject to pronounced water stress in summer, even when well established (Poole, Roberts and Miller 1981), much more so than their analogues in the Cape fynbos (Miller, Miller and Miller, 1983). *Acacia* spp. that are invasive in the Cape fynbos have relatively weak root systems which are slow to penetrate deeper layers of soil (Milton, 1981), and though they succeed in the Cape they are very likely to be excluded from chaparral habitats by summer drought.

8.4.2 Nutritional status of soils

The distribution of seasonal herbaceous species and of the various forms of evergreen sclerophylls in mediterranean climate regions is limited in the first instance by climate, principally the duration of the summer drought, and the availability of mineral nutrients (Miller, 1981; Specht and Moll, 1983).

There are pronounced differences between and within continents in the levels of mineral nutrients in soils of mediterranean regions, and this is reflected in patterns of vegetation (Specht and Moll, 1983). Difference in the success of invasion of contrasting habitats within the fynbos biome of the Cape by the various forms of introduced plants are correlated with the nutrient status of the soils. Trees and shrubs succeed on the highly leached soils of the Mountain Fynbos, whereas herbaceous forms tend to be the prevalent invaders on the more fertile sites of lowland habitats. In a sample of 14 reserves, the proportion of herbaceous species in the lowland habitats was significantly greater than in the montane habitats (Table 8.5; $F = 8.54$, $P > 0.05$, in a one-way analysis of variance). This trend is consistent with the observation that the introduced invasive flora of California, with uniformly richer soils than fynbos (di Castri, 1981), is nearly entirely dominated by herbaceous taxa (Mooney *et al*., 1986).

Specht (1963) and Heddle and Specht (1975) have demonstrated the limitations imposed by nutrient supply on invasions of heathland habitats by Mediterranean herbs. Fertilization allowed such species as *Aira caryophyllea* and *Vulpia myuros* to establish in communities from which they were otherwise absent. Annuals and many other seasonal herbs are unable to complete their lifecycles where rates of nutrient supply are low. Conversely, the evergreen shrubs of the nutrient-deficient ecosystems of the heathland and fynbos could be excluded from more fertile habitats by the toxic effects of high concentrations of nutrients in the soils or inherent limitations to nutrient uptake and use (Heddle and Specht 1975; Ozanne and Specht, 1981).

Although California grasslands in general are dominated by introduced

Table 8.5. Sizes of native and introduced floras in reserves in the fynbos regions with an analysis of the composition of the introduced floras in terms of life forms. Data collated by I. A. W. Macdonald and D. M. Richardson from lists supplied by the Forestry Branch of the Department of Environment Affairs and other sources

Vegetation type and reserve	Size of flora		Percentage of introduced species in given category		
	Native	Introduced	Trees and shrubs	Herbs	Other
Mountain fynbos					
Cape of Good Hope	1050	71	42	56	1
Fernkloof	773	31	48	48	3
Jonkershoek	1231	53	43	49	8
Table Mountain	1362	78	50	45	5
Vogegat	697	25	32	64	4
Zachariashoek	623	8	38	63	0
Lowland fynbos					
Cape Flats	165	34	6	91	3
Goukamma	356	15	27	67	7
Pella	379	18	28	72	0
Rondevlei	229	42	24	62	4
Coastal Renosterveld					
Bontebok National Park	446	46	46	50	4
Tygerberg	373	116	20	74	6
Strandveld					
Rocherpan	207	12	8	83	9
Fynbos–karoo transition					
Nieuwoudtville	276	19	5	84	11

species, those on serpentine soils are not (Mooney *et al*., 1986). This is evidently because the introduced flora includes few species able to compete with the natives under the nutrient limitations which characterize these habitats. When nutrient supply is improved, as on the mounds formed by gophers *Thomomys bottae* some introduced species such as *Bromus mollis* are able to establish and reproduce successfully (Hobbs and Mooney, 1985).

8.5 BIOTIC CORRELATES

8.5.1 Biotic interactions in plant invasions

Diverse interactions between the introduced and the native species, or between introduced species themselves, are involved in the invasion by alien plants, but these interactions have seldom been analysed to the extent needed to explain the similarities and differences among regions in the invasions observed.

Dispersal of alien plants is mainly by wind, but animals may often be important. The dispersal of many species of herbs is epizoochorous (Baker, 1965). Thirty-two per cent of invasive woody species in South Africa have fruit dispersed by vertebrates, or with the potential for this dispersal (Knight, 1986). In the fynbos biome, disproportionately few species of aliens are dispersed by animals but native animals are implicated in the dispersal of some of the more important invasive trees (Kruger, Richardson and Van Wilgen, 1986). It is likely that potential invaders in some regions have failed for lack of suitable dispersal agents.

The role of herbivores other than domesticated grazers in governing the spread of introduced plants has been identified in several cases. Introduced herbs, together with the native plants, are eliminated from the understory of mature chaparral by rodents acting alone or in concert with the suppressing effect of the shrub canopies (Westman, 1983). This is evidently also the case in the matorral of Chile, at least where the community of shrubs is relatively undisturbed (Fuentes and Etchegaray, 1983; Fuentes *et al.*, 1984). On a smaller scale Bartholomew (1970) found that the distinctive flora in the bare zones around shrubs in the coastal shrublands of California, which included unpalatable aliens such as species of *Anagallis* and *Centaurea*, was maintained by preferential grazing by small mammals. The animals sheltered in the shrub habitats but avoided the open grassland, and so foraged in the transition zone. In the matorral of Chile, open patches between native shrubs are maintained as habitats for introduced herbs by rabbits *Oryctolagus cuniculus* which venture from the shelter of the shrubs, unlike the native herbivores which are inhibited by their predator avoidance behaviour (Fuentes and Simonetti, 1982; Fuentes and Etchegaray, 1983). The native predators, in turn, have not yet adapted to preying upon the introduced rabbit (Fuentes and Simonetti, 1982).

Small herbivores has been noted to prevent the establishment of transplants of *Pinus radiata* in Chile (Fuentes and Etchegary, 1983) and this may be the reason why the pine is unable to spread naturally in Chile (personal communication from F. di Castri; E. R. Fuentes; C. Gonzalez; and P. D. Valenzuela), though it does in South Africa and Australia (see earlier).

The otherwise analogous plant communities in each of the mediterranean climate regions differ from each other in important aspects of community structure. For example, the strand communities of California have a low proportion of annuals by comparison with those in Israel (Barbour *et al.*, 1981).

Overall, shrublands of the fynbos lack trees in habitats where they would normaly be encountered elsewhere. Such differences have been cited as evidence for vacant niches, which in turn correlate with marked invasion by species of the missing growth form (e.g. Campbell, Mackenzie, and Moll, 1979). In the Cape, a rich local flora of the "missing" form is available locally, for example in the riverine and montane forests of the Cape. The question as to what it is that excludes the native trees from the communities concerned but admits the introduced trees is pertinent. The native forest trees lack ectomycorrhizae, in contrast with invading pines and eucalypts (Lamont, 1983). Whatever prevented the evolution of such mutualisms in the natives does not appear to operate on the aliens, and this together with the absence of a drain on internal reserves by herbivores and pathogens on the latter, may explain their advantage.

8.5.2 Biotic interactions in the invasion by introduced mammals

The house mouse *Mus musculus* and the brown rat *Rattus rattus*, ubiquitously commensal with humans, sometimes invade undisturbed habitats in mediterranean climate regions. In the Cape fynbos the house mouse has been recorded in nature reserves close to or surrounded by urban areas, or on sites otherwise influenced by human occupation (Macdonald, Powrie and Siegfried, 1986). There is no evidence of extensive penetration of fynbos habitats by introduced species of small mammals. Intensive studies of small mammal communities in several vegetation formations, variously disturbed by grazing and fire, have revealed no introduced species (e.g. Bond, Ferguson and Forsyth, 1980; Rautenbach and Nel, 1980; Nel, Rautenbach, and Breytenbach, 1980; Willan and Bigalke, 1982, David and Jarvis, 1983). The same seems to hold in Chilean and California systems (e.g. Jaksic, Janez and Fuentes, 1981; Wirtz, 1982; Quinn, 1983). The exception is the presence of *Mus musculus* in disturbed coastal sage of California, where introduced herbs have invaded (Blaustein, 1981), and its general occurrence in Australian heathland and sclerophyll forest, where the brown rat is also often present (Fox, Quinn, and Breytenbach, 1985; Catling, 1986; Fox and Fox, 1986). It was recorded in seven of eight samples in Australian reserves, but was recorded in none of six similar samples in the Cape fynbos; in California it was found in each of four samples from coastal sage, but in none of six in chaparral (Barnett, How and Humphrey, 1978; Glanz and Meserve, 1982; Kruger and Bigalke, 1984; and references quoted above). In all these systems there is a marked faunal succession after fire, but it is only in the Australian communities that the mouse appears in the succession, and there it is present in equal or greater numbers than other species, almost throughout the succession (Fox *et al.*, 1985).

Fox and Fox (1986) maintained that it is the reduction in the numbers of native mammal species caused by disturbance, i.e. presumed alteration of the fire regime, that admits the house mouse to the heathland communities, but this argument would not seem to be valid for California and the Cape. The reason may lie in the structure of the small-mammal communities, and their relative proneness to disturbance. In Australia, the mouse has been recorded in small mammal communities with between one and eight indigenous species present (e.g. Fox *et al.*, 1985). There is no consistent association between richness and the presence of aliens in the 26 samples from the literature cited above. A more complete explanation of the different invasions by the house mouse is necessary, which must take account of the particular characteristics of the mouse and of the native animals it encounters (cf. Myers, 1986; Pimm, this volume).

Brown (1975) has argued that small mammals of like size, i.e. where the larger is no more than 1.3 times heavier than the smaller, are excluded from coexistence by competition. In chaparral, the house mouse is likely to encounter one or more of five other rodents of nearly identical size. In fynbos, there are two natives of about the same size. In Australian heathland, one mammal of like size, *Sminthopsis murina*, is largely scansorial and unlikely to interact with the house mouse. The other, *Pseudomys novaehollandiae*, tends to be successionally segregated from the mouse. Fox and Pople (1984) have manipulated small-mammal communities in the heathland by removing and adding *P. novaehollandiae* and demonstrated significant increases in the house mouse population where the native had been removed, and decreases where it had been introduced. They suggested that the house mouse tended to avoid *P. novaehollandiae*, rather than that there was direct competition for resources. The house mouse is evidently prevented from invading undisturbed California coastal sage in a similar way by interaction with *Microtus californicus* (Blaustein, 1980).

It is possible that small disruptions to the relatively simple small-mammal communities of the Australian heathland (see Fox *et al.*, 1985) would suffice to admit the house mouse, whereas the native communities in California and the Cape, where fire regimes have also been modified in various directions, are more robust in this respect. Therefore, the susceptibility to disturbance may vary with the structure and dynamics of the small-mammal communities, in terms of the array of size classes and the behaviour of members of the relevant size classes, and this, rather than disturbance as such, may determine whether or not the mouse invades (e.g. Fox and Fox, 1986). However, the direct or indirect effects of predators, much depleted in Australian ecosystems (Myers, 1986) but not in others, may also govern the success of the mouse. For example in South African ecosystems in general, Macdonald, Powrie and Siegfried (1986) found that the incidence of remains of introduced rodents in owl pellets was negatively associated with the size of the pool of avian predators, and not at all with native small-mammal diversity. However, in Chile, pedators occur in sufficient abundance without controlling the invasion of European rabbit (Fuentes and Simonetti, 1982).

There are many substantial differences between and within continents in the structure and organization of small-mammal communities and the food habits and patterns of habitat use by different species in mediterranean-type regions (e.g.

Glanz and Meserve 1982). These are likely to differentially affect interactions with introduced species and hence the invasion of the latter.

8.5.3 Linked invasions

Successive invasions by introduced species may be expected and is sometimes evident. For example, the cat and the fox have followed and to some extent depended on the spread of the rabbit in Australia. In large areas the rabbit forms the main prey item of both these predators (Myers, 1986). The new arboreal habitats arising from the spread of introduced trees and shrubs in the Cape have favoured the extension of the range of the European starling (Winterbottom and Liversidge, 1954), as well as the immigration of native birds previously absent from the fynbos region (Macdonald 1986; Macdonald, Richardson and Powrie, 1986). In this way, the trend is set for the progressive change of natural communities.

8.5.4 Disturbance regimes

The natural or endogenous (Westman, 1986) disturbance regimes differ markedly among the regions discussed here. Chaparral ecosystems, especially those in the Transverse Ranges, have high rates of erosion because of rapid crustal uplift. Extensive mass-wastage of soils on the chaparral slopes occurs at San Dimas in California; up to 6% of the surface area on sites under burnt chaparral can consist of soil slips (Rice and Foggin, 1971; Rice, Ziemer and Hankin, 1982). Average annual yield of sediments and bed-load at San Dimas amounts to about 20 to 300 tonnes per ha per year, which may increase five-fold to 35-fold after fire (Rice, 1974). By contrast, the rates of erosion from the equally steep catchments of the Cape fynbos are negligible (Van Wyk, 1982). Fire regimes also differ markedly among the regions. Chaparral ecosystems tend to have large fires at long intervals (40 years and more), fynbos ecosystems have smaller fires more frequently (6–40 years), and matorral has even smaller fires (Aschmann and Bahre, 1977; Kruger, 1983). Heathlands in Australia experience fires once in about 5 to 15 or 20 years (Walker, 1981), perhaps more frequently elsewhere (Kruger, 1983), and the fires may be very large where natural vegetation is extensive (e.g. Coaldrake, 1951).

The role of natural disturbance regimes in determining the patterns of invasion has seldom been addressed directly. Chaparral, subject to the highest rates of erosion, has been little invaded. When chaparral is burnt, introduced herbs temporarily invade the community, but in low numbers, whereas they are abundant after fire in matorral, as discussed earlier. If, however, the chaparral is disturbed mechanically, for example by road cuts, then it is readily invaded by such plant species as *Brassica nigra* and *Cytisus scoparius* (e.g. Horton and Kraebel, 1955). Endogenous disturbance appears therefore to play a minor role in admitting invaders to chaparral relative to that of human disturbance.

Many invasive plant species are tolerant of or pre-adapted to the current fire regimes of their new habitats. Species such as *Hakea sericea, Pinus pinaster*, and *P. radiata* are well adapted to the fire regimes prevailing in Cape fynbos and their population growth is controlled by the incidence of fire (Kruger, 1977; Richardson and Brown, 1986; Richardson, Van Wilgen and Mitchell, 1987). In some cases an introduced species may invade when the disturbance regime differs substantially from that prevailing in its natural range. An example is *Pinus halepensis* which has invaded an area of Cape fynbos where the mean intervals between fires has been 11.6 years (Richardson, 1988), whereas in its natural range in the Mediterranean Basin fires occur at average intervals of 25 years (LeHouerou, 1981). On the other hand, some species which do not invade may be excluded from the natural habitat by the fire regime. A study of four species of Hakea in the Cape indicated that the limited invasion by one, *H. suaveolens*, was because its life cycle was marked by long juvenile periods and low fecundity at ages when fires are likely to recur (Richardson *et al.*, 1987). *H. salicifolia*, equally precocious and fecund as *H. sericea*, one of the successful invaders, has failed to invade natural vegetation, possibly because the follicles of its fruit has walls too thin to shield the seed against fires in the fynbos. Nevertheless, successful invaders such as *P. pinaster* and *P. radiata* do not necessarily depend on fire for their entry into the vegetation (Richardson and Brown, 1986), nor would they be excluded from any of the mediterranean regions by the fire regimes prevailing there.

Modification of the fire regime has led to successful invasion in at least some plants. Baird (1977) has monitored the invasion of the understorey of sclerophyll woodland in King's Park, Western Australia by veld grass *Ehrharta calycina* and has shown how this alien grass increased in abundance with fires recurring at intervals of about six years, a frequency shorter than the natural regime, and then declined when fire was excluded (see also Groves, this volume). Invasion of woody communities by herbaceous plants may in itself modify the fire regime to the advantage of the invader. Zedler *et al.* (1983) have documented such feedback. They recorded how the artificial establishment of *Lolium multiflorum* in chaparral after a wildfire, followed by favourable rainfall resulted in another fire after two years. This caused a reduction in populations of native shrub species and a shift in species composition, together probably with greater persistence of introduced herbs of several species.

Disturbance to vegetation by grazing is often cited as a key factor in invasions of exotic plants. Specht (1972) argued that grazing by the native Australian fauna, such as the kangaroo and the wallaby, had minimal effects on Australian plant communities. Sheep, cattle and horses introduced during the 19th century rapidly altered the herbaceous stratum in regions with relatively fertile soils so that native perennial grasses tended to disappear, to be replaced by introduced annuals from the typical Mediterranean genera as well as Mediterranean and Cape geophytes (see also Mack, this volume). Moore (1975, and references therein) has demonstrated this direct effect of grazing by means of field experiments. Grazing effects on this scale have occurred in California and Chile but not in fynbos, as mentioned earlier. It has been speculated that, if anything, the relaxation of native herbivore pressure through overhunting has facilitated invasion by certain palatable plant species (Macdonald, 1984).

Introduced domestic goats and feral European rabbits in Chile have disrupted recruitment of native trees and shrubs, while simultaneously reducing their cover. Rabbits forage more widely for seedlings of woody plants as well as for native herbaceous species than do the native small mammals, while allowing introduced herbaceous species to persist in openings (see earlier). These subtle disturbances to native patterns of herbivory and seedling predation evidently reinforce strongly the simple effects of direct disturbance by alien browsers, and thus the spread of introduced herbaceous vegetation (Fuentes and Simmonetti, 1982; Fuentes and Etchegaray, 1983).

Mack (this volume) contends that the native tussock grasses lacked the morphological and tillering characteristics necessary to survive the new patterns of defoliation and trampling to which they were subject to with the arrival of domestic stock. Experimental work to evaluate the effects of grazing on the native tussocks in California has not been done and, since the tussocks have virtually disappeared, the reasons for the invasion must remain conjectural (Heady, 1977).

Disturbance of the habitat in a way that permits the entry of exotics may involve synergisms. In sclerophyll vegetation of low-nutrient habitats in Western Australia, Bridgewater and Backshall (1981) detected significant differences between the ratios of introduced to native plant species in two sets of samples, one close to and the other relatively remote from urban areas, in environments which were otherwise matched. They ascribed this to the combined effects of nutrient enrichment and the increased frequency of fire in the former case. They argued for a positive feedback between the incidence of nutrient-demanding herbs such as *Hypochoeris glabra* and *Anagallis arvensis*, patches of fertile soil, and the incidence of fire as a mechanism governing the patterns of invasions observed (see earlier). Lambert and Turner (1987) have found similar correlations in the vicinity of Sydney. Irrespective of the kind of disturbance, it may be the effects on nutrient supply patterns that are crucial in the invasions of such highly leached mediterranean ecosystems (see Hobbs, this volume).

8.6 CONCLUSIONS

The problem of invasive biotas is a pervasive element of land management in regions of mediterranean climates settled by Europeans during the last 400 years, and is likely to continue to grow. There are overall similarities in the invasions of similar environments in the four regions of mediterranean climate compared here, but there are many anomalies. The fact that introduced species vary in their invasive behaviour in different regions provides a series of on-going natural experiments in biological invasion. These offer opportunities to advance our understanding of the processes in general, as well a means to better management of mediterranean ecosystems.

Certain general problems could be usefully addressed at this stage. Attention to homoclime analysis would contribute rapidly to a basis of broad prediction. More important in the long run is the need to grasp fully the role of disturbance in governing invasions. Two aspects seem to be relevant. First, the consequences of a given disturbance depends on the properties of the ecosystem or community, as we have seen in the contrasting results of grazing in the Cape, compared with the other regions, and in the behaviour of the house mouse in Australia, compared with California and the Cape. The relative susceptibility of ecosystems to disturbance needs to be better understood. Second is the need to evaluate disturbance, not in terms of the elements of a given regime, such as the intensity, frequency, and timing of fire, but rather in terms of ecological effects. A uniform basis of comparison among the different kinds and degrees of disturbance is needed, and this is likely to be found in measuring changes in the availability of resources, and in the intensities of interactions among the members of a community (see, for example, Hobbs, this volume).

Patterns of invasion are obviously confounded by the different histories of each region, which have differentially affected the disturbance regimes as well as the availability of introduced organisms for invasion. The patterns of success or failure among the alien species on the different continents are broadly associated with differences in land use, as well as with the physical environmental factors and the nature of the communities encountered by the introduced species. Sometimes, selective introduction may have played a role. The reasons for success and failure have seldom been addressed directly.

With time, more introduced species will invade in each of the mediterranean regions considered here. Studies of the processes of invasion where this is occurring, and of the factors preventing it where invasion does not occur, would contribute substantially to our ability to manage these invasions.

ACKNOWLEDGEMENTS

This work was conducted as part of the conservation research programme of the Forestry Branch, and was partly supported by the South African National Programme for Environmental Sciences. We thank Eduardo Fuentes for comments on the manuscript.

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