7 Mediterranean-Type Ecosystems: The Influence of Biodiversity on their Functioning

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7.1 INTRODUCTION

Ecosystems in the Mediterranean-climate regions of the world have served as a unit for comparative ecological studies for over two decades. The cohesiveness of research in this set of widely distributed regions rests on the similarity of the climates where they occur, and the identifiable convergence in elements of their vegetation structure (Di Castri and Mooney 1973). In this chapter we review functional aspects of what have come to be known as *Mediterranean-type ecosystems* (MTEs) in the context of a concerned global interest in the sustainability of the human environment and its dependence on biological diversity. The approach we adopt here is to look for evidence that this biodiversity, for which some MTEs are renowned (Cowling, 1992; Hobbs, 1992), has an influence on processes which are important both for the maintenance of natural systems, and for providing "ecosystem services" with human utility.

Almost a century ago, Schimper (1903) recognized the biological similarities between five widely separated regions characterized by Mediterranean-type climates, and much comparative work has been done on that basis since. These regions comprise the Mediterranean basin itself, a major portion of California, central Chile, the southwestern and southern extremities of South Africa, and parts of southwestern and southern Australia (Figure 7.1). The first attention paid to MTEs in terms of quantitative ecological research arose out of the International Biological Programme (IBP) of the 1960s and 1970s. Those efforts focused on comparisons between the Chilean and Californian systems (Mooney 1977), and dealt with parallel models of ecosystem processes, especially water flux (Fuentes *et al* 1995). Because of the already perceived similarities between vegetation in these and
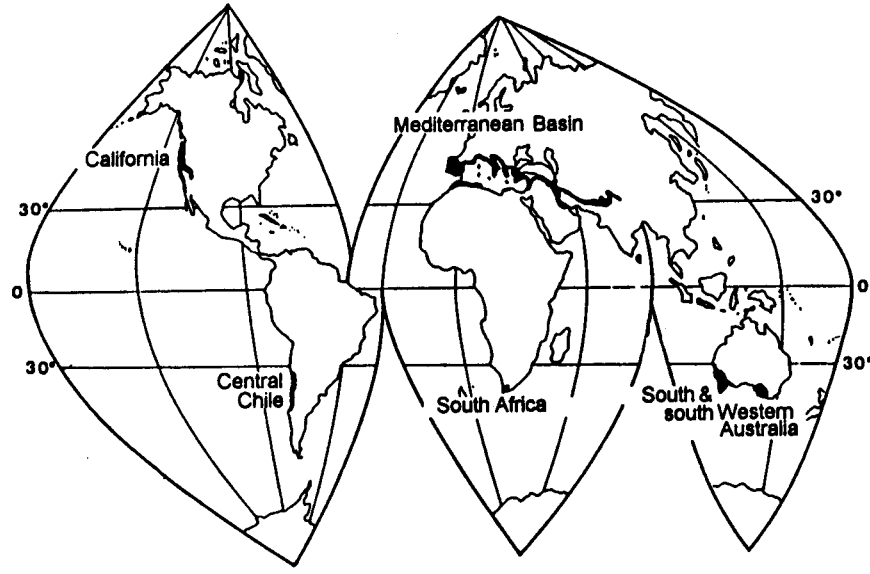
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Figure 7.1 Location of the five Mediterranean-climate regions around the world

the other three regions, the project was soon extended to include all five regions. The first broad comparative overview was published as an anthology which considered the origins and the convergent evolution of MTE components (Di Castri and Mooney 1973). Although the currently accepted classifications of MTEs is to some extent artificial, it does provide a basis for comparative work, as well as placing mild, temperate winter rainfall regions in perspective with other system types, such as forests, arid lands and even savannas.

It is against this backdrop that the MTE research collegium has grown, giving rise to an organizational structure known as ISOMED (the International Society of Mediterranean Ecologists), which has convened regular conferences under the label MEDECOS, plus a number of extra meetings on specific topics (Table 7.1). One of the more recent in this series of MTE meetings was convened under the auspices of ICSU's Scientific Committee on Problems of the Environment (SCOPE) (see Table 7.1), and dealt with the questions about the functional value of biodiversity. This chapter is based on that meeting and its proceedings (Richardson and Cowling 1993; Davis and Richardson 1995), and is a distillation of input by teams of ecologists from each of the five regions.

Table 7.1 Development of comparative and cooperative ecological work in MTEs as reflected by the convening of symposia and workshops and the publication of books

Date	Forum	Topic	Proceeding/reviews	Synthesis book
1971	MI, (Valdivia, Chile)	Comparisons of evolution and structure	—	Origin and structure of MTEs (Di Castri and Mooney 1973)
1977	M II, (Stanford, California)	Fire and management of ecosystems	Mooney and Conrad (1977)	
1980	M III (Stellenbosch, South Africa)	Role of nutrients in species and system convergence	Day (1983)	Kruger et al. (1983)
1981	Symposium (San Diego, California)	Dynamics and management of natural systems	Conrad and Oechel (1982)	
1984	M IV, (Perth, Australia)	Ecosystem resilience	Dell (1984)	Dell et al. (1986)
1987	M V, (Montpellier, France)	Time scales and water stress	Di Castri et al. (1988)	Roy et al. (1995)
1991	M VI, (Maleme, Crete)	Plant-animal interactions	Thanos (1992)	Arianoutsou and Groves (1993)
1992	Symposium and workshop (Cape Town, South Africa)	Biodiversity and ecosystem function	Richardson and Cowling (1993)	Davis and Richardson (1995)
1994	Vina del Mar, Chile	Land-use and ecosystem degradation		

Stand-alone publications
Plant response to stress (Tenhunen et al. 1987); data source book (Specht 1988)

[1]Meetings marked M are those held under the name of MEDECOS (=Mediterranean-type ecosystems as organized by the steering body ISOMED)

7.2 MTEs AS A CLASS OF SYSTEMS FOR TESTING THE HYPOTHESES GENERATED BY THE ASSERTION THAT BIODIVERSITY AFFECTS SYSTEM FUNCTION

Basic ecological research cannot be mobilized to provide complete and direct solutions to practical problems because of the constraints of time and repeatability in the empirical research process (Hilborn and Ludwig 1993). Application of ecological knowledge therefore relies on insights into underlying cause-and-effect relationships provided by cumulative experience and judicious experimental design. The patchiness of ecological knowledge, and the remoteness of the time when it will be sufficiently enlarged and integrated to be directly useful to managers of ecosystems, prompted Ehrlich (1993) to ask: "Need we know more?", with regard to a motivation for conserving biodiversity for the preservation of ecosystem function. If new ecological insights are so difficult to obtain, it is clear that current knowledge needs to be exploited to the full extent of its scientific basis if immediate and rational action is to be taken to maintain the human environment. The purpose of this chapter is therefore to contribute MTE knowledge to a potentially useful and important information base by:

- briefly reviewing the common base for MTE research;
- selecting appropriate examples of MTE work which shed some light on the probable links between biodiversity and system function;
- identifying and exploring departure points for further relevant research.

7.3 FEATURES OF MTEs

7.3.1 Climate

A Mediterranean-type climate is one with bi-seasonality in temperature and precipitation; winters are cool and wet, while summers are hot and dry (Köppen 1931). Aschmann (1973) provided a more quantitative definition using specific measures of rainfall and temperature. However, the distribution of land masses in the northern and southern hemispheres is not the same, and the gross energy budgets and atmospheric circulation patterns of Chile, South Africa and Australia are intrinsically different from those of the northern hemisphere. A global change model by Stouffer et al (1990), for instance, suggests that the latitudes containing the southern hemisphere MTEs will be subject to a much slower and more moderate warming than their northern hemisphere counterparts. On the basis of the model of Stouffer et al (1990) and already observable shifts, Fuentes et al. (1995) predicted that temperature increases associated with the doubling of atmospheric CO_2 will only be 1°C in central Chile, as opposed to 3°C in the northern hemisphere. This suggests

that if a future scenario of aridification and desertification in MTEs is considered, climatically induced land degradation would be less rapid in Chile, South Africa and Australia than in California and the Mediterranean basin.

7.3.2 Substrates

South Africa and southern Australia have landscapes which are older than those of the Mediterranean basin, California and Chile. The latter regions were subjected to mountain-building events as late as the Tertiary and Quaternary, while in the former it is only the coastal belt of marine deposits which are that young. The pattern of winter rainfall that has existed in MTEs throughout the Cenozoic era (Deacon 1983) has, however, driven soil-forming processes to produce many similarities between different regions. Soils are often calcareous, or moderately to strongly leached, with low availability of several nutrients, especially, phosphorous. Wild fire, a feature common in MTEs, also influences the cycling of soil nutrients, especially that of nitrogen and phosphorus. Nitrogen is easily lost through volatilization or the physical loss of post-fire debris, and is probably maintained in the long-term by nitrogen fixation (Rundel 1983; van Wyk et al. 1992).

7.3.3 Vegetation

Vegetation in the different Mediterranean-climate regions has been described as convergent, especially in terms of the sclerophyllous shrubs that dominate many of the plant communities (Mooney 1977; Cody and Mooney 1978; Cowling and Campbell 1980; Milewski 1983). The vegetation types considered as "typically Mediterranean" are usually chaparral in California, maquis and garrigue in the Mediterranean basin, mattoral in Chile, kwongan in Australia, and fynbos in South Africa. As Barbour and Minnich (1990) correctly point out, there are many differences between these vegetation types. Many communities in all these regions conform with Specht's (1979) definition of heathlands – evergreen sclerophyllous communities on nutrient-poor soils with, but not necessarily dominated by, heaths of the order Ericales. The heathland concept has been criticized because it demands the simplistic categorization of shrubland types in terms of soil nutrient status (Cowling and Holmes 1992). Within each region there is a considerable degree of variation in the composition and structure of the shrub vegetation, and a range of other vegetation types is also present. For example, Tomaselli (1981) lists 15 variants of matorral vegetation in the Mediterranean basin, and Hanes (1981) gives nine variants of chaparral in California. The basic fynbos and kwongan types can also be split into innumerable different floristic and geographic variants, and there is a range of other shrub types present in both areas (George et al. 1979; Beard 1984; Cowling and Holmes 1992).

Table 7.2 Emphasis placed on different functional groups of animals at the plant–animal interaction MEDECOS VI symposium (Thanos 1992)

Animal group	Number of papers
Invertebrates	
Herbivores	5
Pollinators	4
Dispersers	1
Multiple topics	7
Birds	
Dispersers	4
Multiple topics	8
Mammals	
Small mammals and marsupials	4
Other natural fauna	3
Domestic livestock	10
Reptiles and amphibians	0

There has been considerable discussion of the floristic diversity of Mediterranean-type shrublands, particularly in South Africa and Australia (see Hobbs *et al.* 1995a; Richardson *et al.* 1995). What is frequently overlooked is that the heavily grazed woodlands and shrublands of the Mediterranean basin have perhaps the greatest alpha-diversity of any temperate plant community (Naveh and Whittaker 1979; Blondel and Aronson 1995). The diversity in these communities derives from the large numbers of annuals capable of surviving the multiple stresses of drought, fire, grazing and cutting.

Since the variety of vegetation types present in each region contributes to the overall biodiversity of that region, more detailed research on the total vegetation mosaic, both within each region and comparatively across regions, seems appropriate.

7.3.4 Fauna

Concepts of convergence in MTEs rest for the most part on similarities in climate and vegetation across the regions. There is no apparent history of a parallel investigation of the faunal components of MTEs, nor is there any compelling evidence that regions with Mediterranean-type climates are useful geographical units for the basis of such studies. The MEDECOS VI conference in Crete was dedicated to plant–animal interactions, but even there the
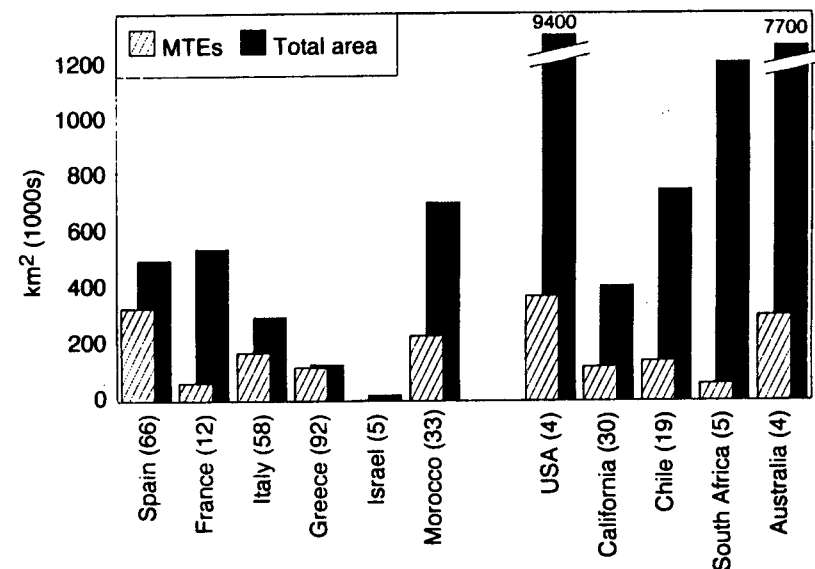
Figure 7.2 The relative extent of a Mediterranean-type climate in a selection of Mediterranean basin countries and those of the other four Mediterranean-climate regions. These areas represent Köppen's Csa and Csb regions as mapped by Müller (1982)

major emphasis was on the practical issues of domestic livestock (Table 7.2). Hobbs *et al.* (1995a) make the point that regional faunal diversity in western Australia, which is lower than the floristic diversity, is not strongly influenced by adaptation of species to MTEs. It is, they argue, more a consequence of biogeography, and the fact that the fauna comprises species adapted primarily to other adjacent and more extreme biome types. They (Hobbs *et al.* 1995a) illustrate this point with the reported low levels of endemism for mammalian vertebrates (20%) and for birds (5%), while Blondel and Aronson (1995) offer a similar picture and explanation for the Mediterranean basin, with 25% and 14% endemism for mammals and birds, respectively. Glaciation during the Pleistocene comprised a set of events which probably had a marked influence on animal diversity in all of the MTEs, but especially those in the northern hemisphere. The dramatic climate changes that occurred during that period (1.2 million to 20 000 years before the present) are thought to have lead to widespread extinctions in all of the MTE regions, especially of the large herbivores. Fuentes *et al.* (1995) refer to the possibility of open niches in central Chile that have resulted from extinction of mammalian species during climatically harsh times, followed by a climatic improvement but with insufficient time for either

adaptation, or influx of species past the severe geographical barriers of sea, mountain and desert which isolate the region. The rising influence of *Homo sapiens* during the latter part of the Pleistocene had further effects through hunting, an action which has been linked to the disappearance of dwarf hippopotamus and elephant in the Mediterranean basin (Attenborough 1987; Diamond 1992; Blondel and Vigne 1993).

Insect diversity has been poorly studied in all of the regions, apart from in the context of agricultural management. The functional importance of insects in MTEs is, however, recognized directly in terms of the vectors of dispersal for pollen and propagules, and indirectly for its collaborative role in plant evolution. Bees are especially important pollinators in California (Keeley and Swift 1995) and Chile (Fuentes *et al.* 1995), while the keystone role of ants as dispersers of seed has been noted both in Australia (Milewski and Bond 1982; Hughes and Westoby 1990) and South Africa (Slingsby and Bond 1985; see also Section 7.4.4 below).

7.3.5 Humans in MTEs

In spite of climatic and vegetational similarities, development in the five regions has not been parallel, and different political, historical and cultural influences are all discernible.

The first and most obvious difference between countries (as currently delineated) containing Mediterranean-climate zones is the proportion of each comprising MTEs (Figure 7.2). These proportions, making adjustments of productivity in the remainder of the country, may be taken as a rough measure of the importance of MTEs in those countries. Apart from the obviously different anthropological histories on the five continents involved, it is also possible to group Mediterranean-climate regions according to their current status in modern global economic terms – the "developed" and the "developing" countries (Figure 7.3). Of the four regions outside of the Mediterranean basin, California and Australia are distinctly developed, while Chile and South Africa have strong developing elements to their economies and socio-political structures. The Mediterranean basin, on the other hand, represents a range of countries across an extensive spectrum which, in terms of several indicators, brackets the global set of MTE regions.

The economic indicators in Figure 7.3 suggest the different abilities of countries to invest in scientific research – the stronger the economy, the more resources there are available for basic research. This is not a fully quantifiable relationship, since resources for scientific research are not in all cases tied to broad aggregate economic indicators. Ecological work in Chile and South Africa, for instance, has benefited from a concentration of resources directed by residual colonial structures and value systems, while
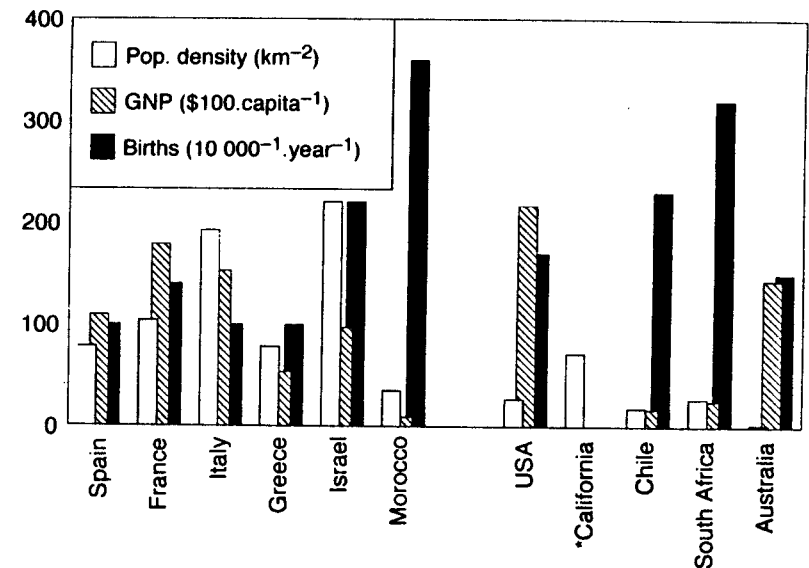
Figure 7.3 A bar chart of a cluster of socio-economic information for a selection of Mediterrean basin countries and the other four MTE regions, showing: population density per km^2; the Gross National Product in hundreds of US$ per capita; the annual birth rate per 10 000 of the population (Europa World Yearbook 1994). The GNP and birthrate for California are taken to be reflected by those of the USA as a whole

such investment was not made for basic science in the poorer countries of the Mediterranean basin.

MTEs therefore constitute an interesting and global set of systems, in some ways convergent, and in others divergent. This is a favorable situation for many lines of comparative exploration into how ecological diversity is impacted by human activities, and how its productivity supports human populations even in a technological age.

7.4 INFLUENCES OF DIVERSITY ON SYSTEM FUNCTION IN MTEs

In this section we offer some examples of diversity and function in MTEs, and place them in the context of the model by Noss (1990), who proposed that diversity has three components, the compositional, the structural and the functional, each covering a range of scale from the molecular to the landscape. We do this by considering the different components and scales of

diversity in the five Mediterranean-climate regions, and where possible highlight the traceable links to system function. System properties which are emergent, such as resilience, stability and sustainable exploitability, are inferred from these observed patterns and relationships. Most of the examples used below can be found in Davis and Richardson (1995).

7.4.1 Landscape diversity and productivity

A loose global network of free market economies is the backdrop against which much of today's science is being done. Utility of system components is therefore usually a strong motivation for conservation. In the case of biodiversity, landscapes which offer a stable mosaic of opportunity for human exploitation are considered desirable and worthy of conservation. In the Mediterranean basin, humans have for hundreds of years derived sustained benefit from functional attributes of ecosystems, and have been responsible for the maintenance of biodiversity for this reason. Blondel and Aronson (1995) refer to the long tradition of mixed agricultural production where rural communities historically combined cultivation with animal husbandry and the harvesting of products from natural forests in what the ancient Romans called the *ager–saltus–silva* (field–pasture–forest) system. These integrated systems relied on the diversity of terrains and climates which could support them. Such stable systems existed from the Middle Ages until the mid-18th century in southern France (Blondel and Aronson, 1995), and until more recently in southern Spain and Portugal as the "dehesa" or "montado" systems (Joffre *et al.* 1988). The apparent stability and sustainability of these systems appears to have been linked to the ecological diversity they comprised. Nevertheless, specialized forms of land-used have become more common, and selected aspects of system productivity has altered landscapes quite radically. With regard to forest products particularly, these range from the selective elimination of deciduous oaks for charcoal used in the French glass-blowing industry prior to the 1789 revolution, to the decimation of forests for shipbuilding during Roman times (Thirgood 1981). Other landscape transformations have included clearing of littoral zones for cereal crops, with later conversion to vineyards, and more recently to the concrete of urban and suburban environments. In all these instances, biodiversity has been altered to manipulate system function in terms of productivity for human utility. What still needs to be assessed is: (i) the degree to which these transformations have affected the stability of those systems; (ii) to what extent input of energy is required for maintenance of the new system states; (iii) what degree of degradation and loss of potential function has been incurred by changes in diversity; (iv) whether or not system shifts are reversible.

7.4.2 Functional mechanisms of biodiversity

Ecological insights into system function, especially in terrestrial systems, are widely recognized as difficult to obtain because of the connected nature of most ecosystems. Relationships involving only a small number of system components can usually be described, while the bulk of the system's functional attributes remain undetermined. Improving techniques in observation, experimentation and analysis are, however, affording better and better opportunities for expanding quantitative knowledge of system function in relation to compositional and structural diversity.

Nevertheless, Springett (1976) provided some early evidence for the identifiable role of species diversity in ecosystem function in Western Australia. In that study, the diversity and abundance of soil microarthropods and litter decomposition were compared between natural woodlands and plantations of *Pinus pinaster*. No clear relationship was found between arthropod abundance and decomposition, but there was a significant correlation between species diversity and decomposition rates. This relationship indicated a large effect at low diversity values, but a tailing off of the response at higher levels. This supports the theoretical model of an asymptotic relationship between diversity and function, as suggested by Vitousek and Hooper (1993), and the notion that a certain minimum numbers of species (or types of species which may be referred to as functional groups) may be required for full ecosystem function. While additional species may add little to the ability of the system to support the essential processes, they may still provide an important insurance against disturbance and change (Hobbs *et al.* 1995b).

Based on observations at a broader scale, chaparral vegetation in southern California has provided the opportunity to gain some insights into the temporal role of diversity in system function during the post-fire period of that fire-prone vegetation. Fire is essential for the release and recycling of nutrients tied up in mature vegetation. However, released nutrients are vulnerable to loss from the system by volatilization and with post-fire runoff. As much as 66% of nitrogen in the soil and litter layer can be lost from a chaparral system during an intense fire (DeBano *et al.* 1979), and natural input levels are so low that full replacement of soil nitrogen could take more than 60 years for pre-fire levels to be reached where industrial pollution makes no contribution (Schlesinger and Gray 1982). Rundel (1983) has pointed out that on many chaparral sites symbiotic nitrogen-fixers such as annual *Lupinus* species, or the subshrub *Lotus scoparius* are post-fire pioneers, while less efficient asymbiotic microbiota still play an important role in rebuilding nitrogen pools (Dunn and Poth 1979). Also assisting in maintaining the nutrient balance on recently burned sites are members of the post-fire annual flora, which through rapid

growth are able to capture nutrients which might otherwise be lost with runoff. These organisms represent a highly diverse group of fire-specialists that occur only on burned sites, and then disappear after one or two years. Generalists persist for much longer after fire. Swift (1991) provides evidence that fire-specialists and generalists have very different nitrogen utilization strategies. Fire-specialist plant species such as *Phacelia brachyloba* and *P. minor* appear to have a preference for ammonium nitrogen over nitrate nitrogen, thereby being able to take advantage of high levels of the former found in the post-fire environment. On the other hand, their nitrogen-use efficiency is much lower than more persistent generalist species such as *Cryptantha intermedia, Phacelia cicutaria* and *Brassica nigra*. The exact role of these broad groups of species in nutrient relations of chaparral systems is not clear, but the fine-scale pattern of soil nutrient distribution after fires (Rice 1993) may require a great deal of structural and functional diversity for all of the key nutrient cycling processes to occur. Without the full complement of post-fire nutrient cycling functions, a chaparral system may degrade into one of a less diverse type, such as that dominated by *Adenostoma fasciculatum*.
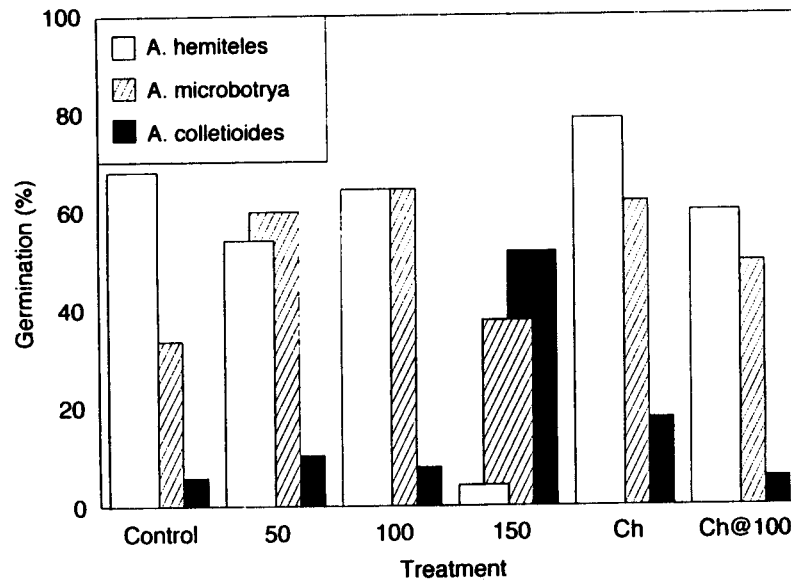

Figure 7.4 Germination responses of *Acacia* species in a laboratory experiment following different heat (50, 100 and 150°C) and charcoal (Ch) treatments (Atkins and Hobbs, 1995)

7.4.3 Functional groups

A topic which has been debated extensively recently, the relevance of which can be seen in the above discussion of nutrient cycling in chaparral, is that of *functional groups* (Walker 1992). The concept of a functional group rests on the notion that organisms which are taxonomically distinct can be functionally similar. An obviously coherent functional group is the set of plants that forms symbiotic relationships with nitrogen-fixing bacteria – these are most notably legumes (Rundel 1989), but it includes many other taxa. In MTEs, nitrogen-fixers are epitomized by the genera *Ceanothus, Lotus* and *Cercocarpus* in California (Hanes 1977), *Apalathus* and *Psoralea* in South Africa (Lamont 1983), *Trevoa trinervis* in Chile (Rundel 1983) and many species of *Acacia* and *Casurina* in Western Australia (Lamont 1983). Blondel and Aronson (1995) report that nitrogen fixers are not common in the Mediterranean basin, but *Coriaria myrtifolia*, which forms dense stands under evergreen oaks in southern France and Spain, and *Myrica* species may be important fixers of nitrogen (Rundel 1983). Leguminous plants usually form root nodules in association with the bacterium *Rhizobium*, while other taxa such as *Casurina* and *Myrica* will nodulate in response to infection by actinomycetes, and *Macrozamia*, the Australian cycad, forms corraloid nitrogen-fixing roots in association with blue-green algae (Lamont 1983).

In eucalpyt woodlands in southwestern Australia, a suite of six to ten *Acacia* species make up what can be construed as a functional group of nitrogen fixers. There is apparent functional equivalence within the group since all are morphologically similar, and all fix nitrogen. However, this similarity disappears when their response to disturbance is considered. Studies of a subset of these species have indicated that seeds of different species have markedly different responses to elevated temperatures similar to those expected during fire (Figure 7.4). It is well known that seeds of some species require a high temperature treatment to stimulate germination (Bell *et al.* 1993), while seeds of other species are intolerant of high temperatures. Some of the *Acacia* species were inhibited and others stimulated by high temperatures, and subtle differences in temperature response were evident. Thus, different species will be stimulated to germinate depending on the severity of the fire. The diversity within the nitrogen-fixing group thus provides insurance against the complete loss of that group in the face of variations in disturbance intensity. In this example we have been able to show interlinkage between the composition of the system (*Eucalyptus* and *Acacia* spp.), its structure (a woody plant community with cycles of accumulating fuel) and some of the ecosystem processes (fire and the flux of nutrients, and the flow of genetic information from one generation to the next). An emergent property of the mechanistic portion of the system,

embodied in an otherwise tightly constituted functional group, is the resilience that the whole system is able to manifest over time in response to unpredictability in the pattern of disturbance by fire. There are probably other equally important emergent properties which have not yet been quantitatively described, such as stability/mestastability, elasticity, plasticity and predictability.

Functional grouping, it is evident, must be regarded as relative (Davis *et al.* 1994). Clearly a drought-adapted nitrogen fixer will be in a different water-use group to one suited to mesic conditions, and one could only substitute for the other under a limited set of conditions (Hobbs *et al.* 1995b). This relativity of functional grouping is well demonstrated by the observed dynamics of predator–prey relations in an arid Chilean MTE, described by Jaksic *et al.* (1993) and Fuentes *et al.* (1995). In that study a set of 10 predators (four falconiform hawks, four owls and two foxes) were monitored together with their prey, which comprised eight small mammal species (seven rodents and one marsupial). Within each of these sets, animals were recognized as belonging to one of a few trophic guilds; prey species were either granivores, insectivores, folivores or omnivores (with possible preferences), while the predators were classed as either omnivore or exclusive carnivore. Over the 5-year period of the study, the annual rainfall varied from 58 mm to 513 mm (with a long-term average of 206 mm). Associated with these wet and dry years were troughs and peaks in primary production and small mammal population size. Contrary to expectation, small mammal populations within supposed trophic guilds did not irrupt synchronously when high precipitation promoted plant growth. Instead, only populations of *Phyllotis darwinii* (a granivore), *Akodon olivaceus* (a granivore/omnivore) and *Marmosa elegans* (a marsupial insectivore) irrupted, while those of *Oryzomys longicaudatus* (a granivore) and *Akodon longipilis* (an insectivore/omnivore) did not. In addition, during the relative drought years, five of the eight small mammal species disappeared from the study site. These were *O. longicaudatus, A. longipilis* and the three folivores *Abrocoma bennettii, Octodon dregus* and *Chinchilla laigera*. Fuentes *et al.* (1995) interpret these observations as evidence for little redundancy in the supposed guilds, and claim that these groups could not be functionally equivalent. The results therefore suggest that functional groups, should they exist for the prey species, cannot be defined in trophic terms alone.

Within the trophic guilds of predators, on the other hand, indications of functional equivalence were much stronger. The two carnivorous owls, *Bubo virginianus* and *Tyto alba*, preyed on the same species at approximately the same frequencies, while the omnivore guild comprising the two *Pseudalopex* foxes (*P. culpaeus* and *P. griseus*), the owls *Athene cunicularia* and *Glaucidium nanum*, and the falcon *Falco sparverius*, also displayed consistently similar feeding habits. The three large falcons (*Buteo polyosoma, Geranoaetus*

melanoleucus and *Parabuteo unicinctus*) were also consistently carnivorous. During the lean years, predator species started to disappear when small mammal numbers dropped to below 100 individuals ha^{-1}. Although there was a reasonable match between the carnivorous diets of the three larger falcons and three of the owls, it was the former group that disappeared from the study site first. Even the omnivorous falcon *F. sparverius* disappeared before its owl counterpart *A. cunicularia*. Of the four predator species that remained at the study site when prey numbers were low, three (the two foxes and the owl *G. nanum*) were omnivores, and only one species (the owl *T. alba*) was a carnivore. Of the six species which migrated away from the site during the lean years, five were carnivores. Fuentes *et al.* (1995) believe that this pattern suggests a high degree of functional equivalence amongst the recognized guilds, but concede that the "acid test" of density compensation within guilds has yet to be performed on this system.

In a review of this work on predator–prey relationships, Wiens (1993) made a further interpretation regarding the relative nature of functional equivalence. He interpreted the early disappearance of the falconiform species during the lean years as a fine-tuning of the functional grouping, and a teasing apart of the broad trophic niche occupied during the good years by both owl and falcon species into separate and narrower niches (Figure 7.5). Taken to its logical conclusion, separation of functional attributes between species along different axes reduces ultimately to an argument about niche breadth.
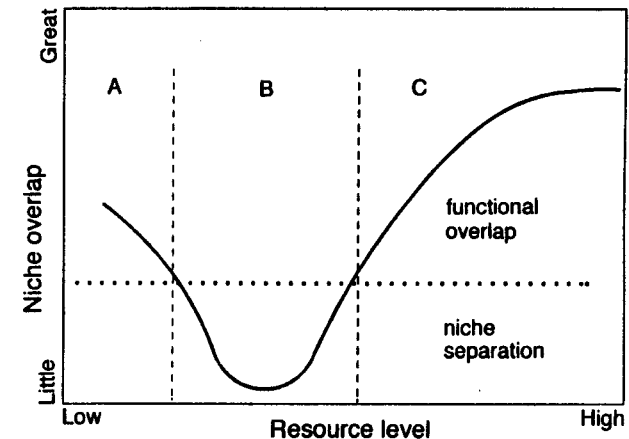

Figure 7.5 The relationship between resource availability and the overlap of niche spaces, based on observations in a Chilean predator–prey system, and demonstrating the relative nature of niche breadth. Resource levels, A, B and C reflect conditions of starvation, specialization and opportunism, respectively, in a prey species. Redrawn from Wiens (1993)

differentiation (*sensu* Hutchinson 1958). The existence of such niches in Californian MTEs has been elegantly demonstrated by Cody (1986). Along one set of transects which intersected the main axis of the coastal mountains (representing steep environmental gradients) and another running parallel to the coast (representing shallow gradients over latitudinal environmental changes), he determined the turnover of species in the diverse genera of *Ceanothus* and *Arctostaphylos*. The replacement sequences of species along these two sets of gradients were correspondingly steep for the steep gradients, and shallow for the shallower ones, which Cody (1986) interprets as evidence for niche separation in the two speciose genera investigated.

7.4.4 Keystones

The epithet *keystone* can be applied to a component, or sometimes a process of a system, the removal of which would cause disproportionate changes to the system (Lamont 1992; Bond 1993). The keystone quality is therefore a concept which links diversity to system function in a particular way, suggesting that maintenance of species richness per se is not always a reliable measure of system stability, and that other species, or even suites of species, may rely on the presence of the putative keystone. In the Australian review of biodiversity in MTEs (Hobbs 1992), Lamont (1992) presented a multilevel interpretation of keystones, drawing on interactions in natural systems to illustrate his model. In that model, depicted in a sketch as a mediaeval-style building, he pointed to three levels of keystones in a Jarrah forest: first-order keystones have only one species dependent on them; second-order keystones support whole suites of species (the example given is N$_2$-fixing bacteria which support all nodulating legumes); a third-order keystone is one without which the whole system would collapse. For this third-order keystone, Lamont (1992) cites the case of *Gastrolobium bilobum*, a major nitrogen-fixing plant which also stabilizes soil and provides food and shelter for small vertebrates, such as the small marsupial *Bettongia penicillata*. Germination of *G. bilobum*s seeds depends on the action of a suit of ectomycorrhizae, which in turn rely on *Bettongia* for dispersal, as well as for facilitation of spore germination in passing through the animal's gut. Without *G. bibobum*, it is reasoned, the Jarrah forest system would collapse.

An example of a keystone component in a MTE of the Cape, South Africa, is provided by the recent work on myrmecochory (seed dispersal by ants) (Bond and Slingsby 1984; Bond and Stock 1989; Bond *et al.* 1992). Over 1300 fynbos plants (20% of the flora) produce seeds which have a protein-rich elaiosome that attracts indigenous ants. The indigenous ants habitually forage for the seeds, which drop close to the parent plant, and haul them away to their nests where the elaiosomes are eaten. The seeds are

then abandoned in the nest, affording them protection against granivores and the heat of intense fires. The ants function as dispersers and protectors of seed, and myrmecochory can therefore be regarded as a keystone process which is necessary for the continued survival of the many fynbos plants. The vulnerability of this keystone process was recently shown when the alien Argentine ant, *Iridomyrmex humilis*, invaded parts of the fynbos. This ant is smaller but more aggressive than the indigenous seed-gathering ants, and regularly displaces the latter. The Argentine ants eat the elaiosomes on the soil surface and do not bury the seeds. In fynbos invaded by this species, seedling regeneration of ant-dispersed plants after fire is much less successful than in uninvaded fynbos (Bond and Slingsby 1984). Besides threatening many fynbos plants with extinction, the collapse of this ant–plant mutualism could have ecosystem-level effects since ant-dispersed plants are often dominant components of fynbos shrublands. Proteaceous species are generally deeper rooted than other members of fynbos communities (Higgins *et al.* 1987), and local extinction would probably therefore also induce a marked change in the hydrology of the host systems. Thus *I. humilis* may be considered a keystone invader with negative system impact.

7.4.5 Biodiversity and its support of human utility

There are many illustrations of the role that biodiversity can play in the functioning of ecosystems. In some cases the diversity of components themselves, or the structure they provide, may be absolutely essential for the stability and resilience required for the impacts of natural or human perturbation. In some instances, however, altered diversity of ecosystems may act to enhance their human utility. In Chile, for instance, the production side of the honey industry comprises the honeybee, *Apis mellifera*, and a flora from which the raw materials of honey production are obtained. This system has been investigated by Varela *et al.* (1991) and reported in Fuentes *et al.* (1995), and has provided considerable insight into the roles that biodiversity can play. Firstly, in a survey of the pollen collected by bees throughout the year, it was shown that regardless of the number of plant species in flower, which were up to 90 at any one time, bees only used up to 15 of them. This suggests a functional saturation of diversity along the lines of the Vitousek and Hooper (1993) model referred to in Section 7.4.2. A second lesson was derived from the fact that the bulk of pollen collected by bees was contributed by a limited number of plant species (Varela *et al.* 1991). *Galega officinalis* (Fabaceae), *Lithraea caustica* (Anacardiaceae) and three members of the Brassicaceae (*Hirschfeldia incana, Raphanus sativus* and *Rapistrum rugosum*) were in this category, for which a seasonal replacement series of pollen supply was observed during the early southern hemisphere summer, the bulk of pollen was supplied by the Brassicaceae species in October, by

L. caustica in November/December, and by *G. officinalis* during December/January (Fuentes *et al.* 1995). Of the significant pollen contributors, more than 50% were introduced species (including the Brassicaceae and *G. officinalis* mentioned above). This indicates that altered diversity plays a major role in the functioning of the ecosystems in central Chile which produce honey for human consumption – remembering too that the main protagonist, *Apis mellifera*, is also an introduced species.

A similar scenario can be presented for the fynbos region of South Africa. In that case the Cape honeybee (*A. mellifera capensis*), a fynbos race of the European honeybee (Hepburn and Jacot-Guillarmod 1991), is indigenous, while many of the plant species that provide it with pollen and nectar are aliens. Introduced plant species used by the Cape honeybee include *Eucalyptus, Acacia*, citrus fruits and deciduous fruits, as well as many herbaceous species (Anderson *et al.* 1983), resulting in a far more productive honey industry than would be the case without them.

7.4.6 Intraspecific variation and system function in the Mediterranean basin

In the Mediterranean basin, taxonomically well-known groups of species have been shown to have large amounts of intraspecific variation. Linking this variation to function, however, has been difficult. The common pasture grass, *Dactylis glomerata*, for instance, comprises a complex which includes as many as 15 diploid types, three tetraploids and one hexaploid, the latter being confined to North Africa (Lumaret 1988). Stebbins and Zohary (1959) interpreted the differentiation of tetraploid forms of *D. glomerata* to be the result of autopolyploidy in diploids from both temperate and Mediterranean groups, and an ecological adaptation to the different climatic regions. High environmental heterogeneity in the Mediterranean basin is seen as the selective force behind higher MTE ecotypic variation of this species than in the topographically more uniform part of its range (Lumaret 1988). Adaptations to Mediterranean conditions include morphological traits that support water-saving mechanisms, as well as seed retention throughout the summer drought. Variations in water relations and other physiological characteristics of this species along gradients of water stress are more or less correlated with trends in four different enzyme systems (Roy and Lamaret 1987). Intraspecific variation can therefore be seen as the raw material for evolution, which in turn provides functional plasticity at the system level and ensures persistence of ecosystems.

Another important feature of many Mediterranean plants is the presence of volatile essential oils in their tissues. Well-known examples are thyme (*Thymus*), mint, basil, parsley, fennel, sage, rosemary, lavender, coriander, oregano, rue, bay leaves (*Laurus nobilis*), wormwood (*Artemisia* spp.), fenugreek, sesame, saffron, licorice, onions, shallots, chives and garlic. The

majority of these are grouped in the Lamiaceae, Apiaceae and Asteraceae. While these species are clearly of culinarily functional value to humans, the role of plants containing volatile aromatic compounds in ecosystems is complex and not fully understood. On the one hand it is thought that these highly flammable oils are linked to the fire ecology of Mediterranean basin systems, but they may also: (i) be a defence against herbivores, bacteria and fungi; (ii) inhibit competitor establishment through allelopathy; (iii) mimic insect pheromones to attract pollinators; (iv) reduce water stress by providing antitranspirant action (Margaris and Vokou 1982). In *Thymus*, one of the best-studied of aromatic genera, there is significant variation in oil content between species, as well as genetically controlled variation within species. Gouyon *et al.* (1986) found that the distribution of intraspecific variability in oil content (chemotypes) in *Thymus vulgaris* is probably strictly determined by the environment. However, they also found that there is a high turnover of chemical polymorphism across very short distances, which makes up a mosaic persistent in time. However poorly it is understood, diversity at the intraspecific level is clearly implicated with the maintenance of system function.

7.4.7 Pleistocene herbivores in the Californian palaeolandscape

In California, near the end of the Pleistocene, there was a massive extinction event in the large mammalian herbivore fauna; over 70% of the genera were lost during a brief period of a few hundred years. This was apparently precipitated by the depletion of large megaherbivore populations through human impacts (Martin 1984). This resulted in a cascade of extinctions involving other mammals in the trophic chain (Owen-Smith 1989). It was proposed that an important role of the megaherbivores was the maintenance of landscape diversity; the loss of this faunal component resulted in loss of habitats required by other herbivores, and hence the loss of food resources for carnivores, which ultimately greatly altered the functioning of these ecosystems (Keeley and Swift 1995).

7.4.8 Formation shifts in South African MTEs

Until recently the prevailing view was that the boundaries between major vegetation formations in the southern and southwestern Cape of South Africa were controlled by edaphic factors and moisture availability (see review in Cowling and Holmes 1992). However, recent studies revealed the dynamic nature of boundaries between forest and fynbos, fynbos and grassland, fynbos and renosterveld, and renosterveld and grassland, and the boundary between stands of natural vegetation and thickets of alien trees and shrubs. In all cases, changed disturbance regimes (notably fire and
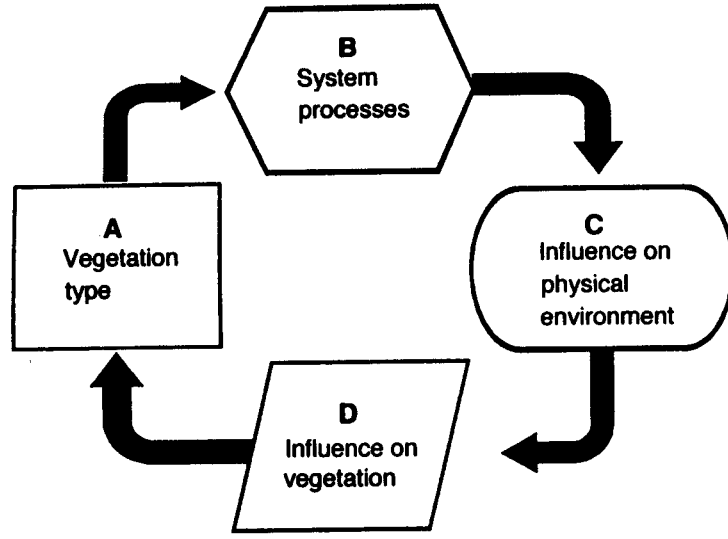
Figure 7.6 A model of the feedback loop which connects system processes with vegetation type in MTEs. This figure refers to the observed dynamics of natural vegetation and that dominated by invasive alien plants in MTEs of the fynbos region of South Africa, as described in Table 7.4

grazing intensity) have caused shifts in the boundaries between formations (Richardson et al. 1995).

Ecosystem functions such as net primary productivity and standing phytomass, water production, fire behavior, fire-induced soil water-repellency, and sediment yield and nutrient cycling are very different in the major natural and alien vegetation formations of the Cape floristic region (CFR). These differences are attributable to the structural and functional characteristics of the assemblages, rather than to the biodiversity of these formations per se (Richardson et al. 1995). Changing patterns of land use can and do influence the boundaries between the major formations in the CFR. The replacement of species-rich fynbos by species-poor indigenous forest or stands of a few alien tree species has major effects on ecosystem function. Such vegetation changes are often rapid and irreversible (Bond and Richardson 1990), and their effects are pervasive (Figure 7.6). For example, the recent invasion of the region by many bird species from adjacent biomes is an indicator of profound alterations to many ecosystem features caused by man-induced vegetation change. Intentional or naturally occurring formation shifts offer excellent opportunities for studying the effects of changes in biodiversity on ecosystem function (Table 7.3).

Table 7.3 Dynamics of natural and transformed MTEs in the fynbos region of South Africa, showing feedback influences of functionally different vegetation types (after Richardson et al. 1995)

A Vegetation description	B System processes	C Influence on physical environment	D Influence on vegetation	Metastable vegetation type (= A)
Even-aged sclerophyllous shrubland with with high species diversity but low structural diversity	Production of acidic litter Regular loss of nutrients through volatilization in fires	Acid and nutrient-poor soils (effective podzols)	Selection for fire-adapted species Even-aged vegetation	Fynbos: a fire-prone vegetation adapted to nutrient-poor environments
Evergreen forest with closed canopy and sparse understory	Nutrients contained in a shallow litter layer	Low light penetration Moderately nutrient-rich soils Low flammability	Understory (fynbos) species suppressed by low light Tree seedlings can establish due to low incidence of fires	Indigenous evergreen Afromontane forest
Vegetation invaded by alien Acacia spp.	Regular fires enrich soil surface with cations and phosphorus Nitrogen fixation by invaders compensates for losses by volatilization	Thicket formation shades understory Soil water depleted by invaders Allelochemical substances produced by invader	Slower-growing indigenous species out-competed for light, nutrients and water by N₂-fixing invasive Acacia spp.	Alien Acacia thicket – the dominant species dependent on substrate-type

7.4.9   Land fragmentation in the wheatbelt of western Australia

During the phase of agricultural development in western Australia, natural ecosystems were replaced with extremely simplified agricultural ones. The major difference between the two is a dramatic simplification in composition and structure at all organizational levels, and a reduction in the number of functional groups present in the agricultural system (see also Swift and Anderson 1993).

The native ecosystems were dominated by a diverse array of perennials with a variety of structural and functional adpatations to periodic drought and low nutrient availabilities (Lamont 1984; Groves and Hobbs 1992). The prevalent agricultural system consists mainly of annual crops and pastures. The options available for energy, water and nutrient capture in a heterogeneous and uncertain environment have thus been reduced. This means that patterns of energy capture are altered since there is no plant cover for half the year. Water uptake and evapotranspiration are reduced compared with those of perennial-dominated communities, since rooting patterns and growth periodicities are altered. There is no longer a diversity of rooting depths and modes which take up water from different soil layers and at different times of year. This leads to less efficient utilization of rainfall, more lateral and vertical water movement, and hence rising watertables and the transport of soil-stored salt to the surface (McFarlane et al. 1993). Nutrient transfers are also significantly different, since the plants mostly lack specialised roots or symbionts, decomposer communities are greatly simplified, and increased leaching and soil erosion lead to greater exports from the system (Hobbs 1993; Hobbs et al. 1993; Lefroy et al. 1993a). The agricultural system is thus very "leaky" compared with the natural system, and net flows of energy, water and nutrients in and out of the system are considerably greater (Hobbs 1993; Swift and Anderson 1993). The agricultural system also lacks resilience and is vulnerable to disturbances such as drought, flooding or insect attack.

Land degradation problems of salinization and erosion are directly related to the poor ability of the agricultural system to capture energy, use water and retain nutrients. Arresting the decline of the agricultural system thus requires a replacement of some of the compositional, structural and functional diversity which was lost on transformation to agriculture. An approach to this has been developed by Lefroy et al. (1993a,b) which is based on increasing the amount of perennial vegetation in the agricultural landscape. The effect of this is to push the agricultural system back in the direction of the natural system, and to tackle imbalances in energy, nutrient and water transfers simultaneously. The approach is thus one of increasing the complexity of the landscape (which can be viewed as increasing biodiversity at this scale) by reintroducing functional groups which had been removed during agricultural development.

7.4.10   Modelling the influence of diversity on system function

In order to look at the possible role of plant interactions on resource utilization in chaparral, Miller et al. (1978) designed an ecosystem simulator which they dubbed MEDECS. This multi-compartment model simulated seasonal patterns of resource use in chaparral plants, and demonstrated that different shrub species had very different daily and seasonal patterns of water uptake, solar energy capture and nitrogen uptake. Simulations were run with various combinations of four species competing for light, water, nitrogen and phosphorus.

Using different combinations of two species, Adenostoma fasciculatum and Arctostaphylos glauca, Miller et al. (1978) showed that mixed communities had greater net photosynthetic production than monotypic communities. However, for other aspects of resource-use, such as nitrogen uptake, single species exhibited greater resource-use than mixed communities. Thus, these simulations did not consistently predict that resource-use by mixed-species chaparral would be greater than that by single-species communities. Rather, with respect to certain resources there may be a single optimum physiological type for any given site. However, even if this were true, landscape heterogeneity may select for greater biodiversity, dependent upon whether plants experience a coarse-grained or fine-grained environment.

However, these simulations by Miller et al.(1978) would predict quite different conclusions depending on what assumptions are made about root distribution and subsurface topology. Thus, an important factor that prevents accurate predictions about the ecosystem function of biodiversity in chaparral is the lack of information on underground conditions. Despite these shortcomings, the models referred to are illustrative of an important avenue for exploring questions of biodiversity and its relationship to ecosystem function.

7.5   MTE RESEARCH AND THE GLOBAL FORUM

Critics sometimes argue that funding of, and attention to, MTE research is disproportionate because they occupy only about 2% of the Earth's land surface according to Köppen Cs climate zones (Müller 1982), or less than 1% using the more narrowly circumscribed definition of Aschmann (1973). This supposes that importance is a linear function of area, which implies that the collective GNP of all MTEs is approximately 4% that of the USA (Europa World Yearbook 1994). MTEs, however, have some distinctive industries associated with them which play keystone roles in the economies of some areas. South Africa's deciduous fruit industry is centred in the country's winter rainfall (Mediterranean-climate) region, as is its wheat

production. Many countries of the Mediterranean basin are also reliant to a large extent on natural ecosystems to draw income from tourism in addition to agriculture, and it might be interesting to calculate the extent to which the southern Californian movie industry relies directly and indirectly on attributes of the region's Mediterranean-type climate.

The history of ecological research in Mediterranean-climate regions reported in this chapter is far from complete, yet it should be evident that the research community involved with MTEs comprises a cohesive collegium which has made considerable investment of its diverse skills in the search for new ecological paradigms. MTE research therefore provides a scientific perspective well integrated with patterns of human need, and provides scope for developing visions of policy and planning for sustainable management of a wide spectrum of natural and human-impacted systems (Davis and Rutherford 1995).

MTEs must also not be viewed in isolation – a factor implicit in the production of this volume. Criteria which delineate boundaries of activity and interest are often, for practical reasons, arbitrary. What comprises an MTE is by no means unequivocal or closed to interpretation. There are generally recognized points of convergence around which more comparative MTE work is done, and which relate to similarities of climate and sclerophyll shrub vegetation. However, affinities with differently composed systems are many, both in terms of vegetation type, and in broad geographical terms (Figure 7.7). Mountain fynbos of the South African southwest, for instance, is also regarded as a heathland vegetation (Moll and Jarman 1984), as is the kwongan of Western Australia. Matorral of central Chile intergrades northward into arid shrublands (Fuentes et al. 1995), while jarrah (*Eucalyptus marginata*), karri (*E. diversicolor*) and marri (*E. calophylla*) define a recognized forest-type vegetation in Mediterranean-climate western Australia (Dell et al. 1989). The temperate forests of southern Europe also penetrate well into the Mediterranean basin, and several oaks of California (*Quercus douglasii, Q. engelmanii, Q. agrifolia, Q. wislizenii* and *Q. lobata*) form a distinctive savanna vegetation type in winter-rainfall California (Pavlik et al. 1991; Huntsinger and Bartolome 1992). Climatic gradations from the precisely defined areas (Aschmann 1973) into sub- and non-Mediterranean climate regions create equally fuzzy boundaries. Those areas of transition are clearly places where research overlap is not only possible, but is necessary for a more complete understanding of the systems on either side. In terms of structural and functional perspectives as well, MTEs can be seen to overlap with many other system types (Figure 7.7). Knowledge about fire behavior is a well-established area of MTE research which overlaps significantly with forestry systems (Conrad and Oechel 1982), while agroecosystem research in Mediterranean-climate regions is an important activity in most of the regions, and one where interaction between different interest groups can yield a valuable flow of information.
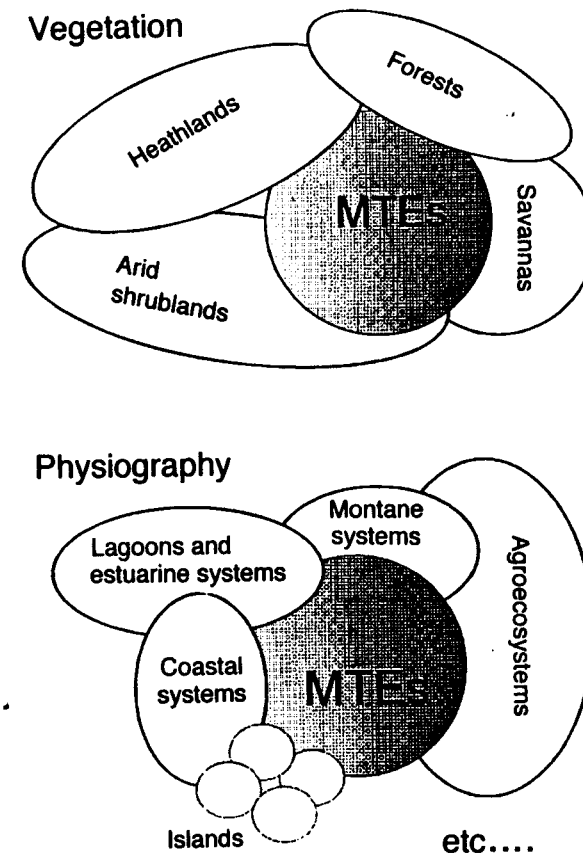
Figure 7.7 MTEs overlap with other system types with regard to both the composition and structure of their vegetation (above), and their physiographically dictated function (below)

In this chapter, the question of biodiversity's effect on ecosystem function has, through the absence of previous focus, been restricted to indirect investigation, as all the scientifically based information presented has been collected to answer different questions. It may be fair to ask whether there is another way to approach the question. The degree of interrelatedness between the many driving forces and their driven counterparts may make it an impossible task to confront head-on. The ultimate usefulness of ecological knowledge to environmental management practice relies to a large extent on the resolving of perceived ecological complexity into the simpler units of testable models and tractable strategies. Continued work by specialists on MTE subsystems, guided by the important overarching concepts of

biodiversity, will help to clarify ways in which we should be asking the questions about how diversity affects ecosystem function. An MTE protocol for well-designed experimental research into the links between diversity and system function is the next task.

7.6 SUMMARY

Quantitative and focused research into the effects of biodiversity on ecosystem function has not yet gained momentum in MTEs. This chapter has therefore reviewed some of the imaginative ways in which ecologists in these systems have been able to interpret existing data. This has been a useful exercise, and has provided valuable insights into how that quantitative research might be conducted, and what some of the pitfalls might be.

There is evidence, at the smallest scale considered here, that species diversity can be very important in determining the way that some MTEs function, even though its influence may be limited to specific temporal or spatial windows. For instance, the diversity of soil microarthropods appear to be important in litter decomposition (Section 7.4.2), while the nitrogen economy of some fire-driven systems is dependent on the synchrony of a particular component (viz. N-fixers) in the diversity of post-fire vegetation. The latter example illustrates that the temporal dimension of diversity can be an important and very influential factor in total system function.

Another aspect of the topic is the buffering value of diversity. This has been illustrated by a model of interaction between an apparently homogeneous functional guild of post-fire reseeding plants, each with slightly different germination behaviour, and the stochastic nature of wild fires (Section 7.4.3). This intermittent function, which might be described in terms of *action windows* of diversity, can also be seen in the example of predatory–prey systems, where niche overlap has been interpreted as varying functionally with resource availability. On a different scale, the biological invasions which are so prevalent in MTEs can be seen as agents which directly alter native patterns of diversity. It has been shown that these can produce distinct changes in important system processes (Section 7.4.8 on fynbos system shifts).

The ultimate concern of humanity about the biophysical consequences of altered diversity is the way in which it might affect our own survival. It does not yet seem that this question can be answered directly, but the current review of MTE research throws some light on the diversity and intensity of impacts that humans have imposed on the systems they exploit. In western Australia (Section 7.4.9), for instance, landscapes that a short while ago were impressively rich in native species have been transformed over a very short period to monospecific stands of wheat. These artificial systems now

seem unable to sustain basic ecosystem processes. In contrast, the Mediterranean basin has been developed by humans over millennia, and the diversity of human approaches and techniques during that period has conformed much more closely to the natural diversity and function of landscapes, apparently protecting and stabilizing their productivity for human use where mixed small-scale agriculture survives (Section 7.4.1).

It is still unclear whether in order to predict the effects of biodiversity change on ecosystem function we need a better designed set of experiments generating more data, or a paradigm shift which can provide a better understanding of ecological complexity. The work on MTEs suggests that both are probably necessary.

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