3 Biodiversity and Ecosystem Functioning in Mediterranean-Climate California

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3.1 Introduction

Rapid population growth and land development in California have already contributed, largely through habitat destruction, to a significant loss of biodiversity (Jensen et al. 1990). These obvious alterations in our flora and fauna have led to increasing concern about further losses of species diversity resulting from fragmented populations and from the introduction of non-native species and concern about the impact of losses in genetic diversity arising from reduced population sizes (Keeley 1993). In addition, predicted climatic changes are likely to alter landscape patterns of diversity with unknown consequences on regional ecosystem processes.

We believe this is a matter of concern for all citizens because of our dependence upon the proper functioning of natural ecosystems. Not only do these ecosystems have aesthetic, recreational, and scientific value, they play fundamental roles in regional landscape processes that are required for the air we breath, water we drink and food we eat. However, it is unclear exactly how these known and anticipated changes in biodiversity might alter or have altered the functioning of Californian ecosystems; specifically, the transfer of water, nutrients and carbon. The reasons for this include a depauperate body of knowledge on the basic population biology of most native species, the lack of full understanding of the mechanisms underlying the assemblage of species in communities, and the paucity of studies that have attempted to relate population biology or community ecology to ecosystem function.

In this chapter we address the question of how biodiversity affects the functioning of natural ecosystems in California. *Ecosystem function is defined as the set of processes which maintain natural systems through the transfer of energy, matter and information.* These processes are regulated by species and the biotic interactions that characterise ecological systems (see Hobbs et al., Chap. 1, this Vol.). We know relatively little of how individual taxa affect ecosystem processes and far less of how their role in the system affects the overall functioning of the system. While this region has a relatively rich source of scientific studies on the flora and fauna, nearly all have focused on one or a few species and a single level of

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organisation such as either populations or communities. Some of these studies provide clues about the effect of individual species on certain ecosystem processes, however, such studies have not addressed the question of how biodiversity per se, i.e. the numbers and kinds of species assembled at one time in one place, affects ecosystem functioning. Thus, any attempt to answer the question posed here must rely upon induction and extrapolation. We will briefly review past and present patterns of biodiversity in the State. The extent to which species affect ecosystem processes that control functioning is explored and the evidence for functional groups of ecological equivalents is analyzed. Critical to answering this question is whether species are redundant in the roles they play and the extent to which seemingly minor "players" are linked to ecosystem processes. Lastly, we will focus on evidence that diversity affects ecosystem functions such as carbon gain, water balance and nutrient cycling.

3.2 Patterns and Determinants of Diversity

Diversity encompasses a hierarchy of scales, and each level of diversity, from genetic diversity to gamma diversity, produces effects at other levels. Thus, processes affecting one level will invariably alter other levels of diversity. Climatic and topographic change, particularly over the past million years, has created our particular pattern of landscape (gamma and beta) diversity. Today, both landscape and community (alpha) diversity of plant and animal species is influenced by disturbances such as fire, urbanisation and invasive organisms. For example, the anthropogenic impact on fire frequency has altered the balance of species composition within communities and the distribution of communities across the landscape. Urbanisation has had a profound impact on the fragmentation of habitats, and invasives are potential threats to native species. These changes are of concern because the persistence of populations, particularly in the face of global climate change, may ultimately be determined by existing patterns of diversity. In other words, communities are a storehouse of diversity, some of which may not be tied to the proper functioning of ecosystems now, but could be critical under future conditions.

3.2.1 Historical Determinants of Floristic Diversity

The California Floristic Province, which encompasses the mediterranean-climate region to the west of the Sierra Nevada and other interior ranges, extends over 1500 km from Oregon to Baja California (Fig. 3.1).

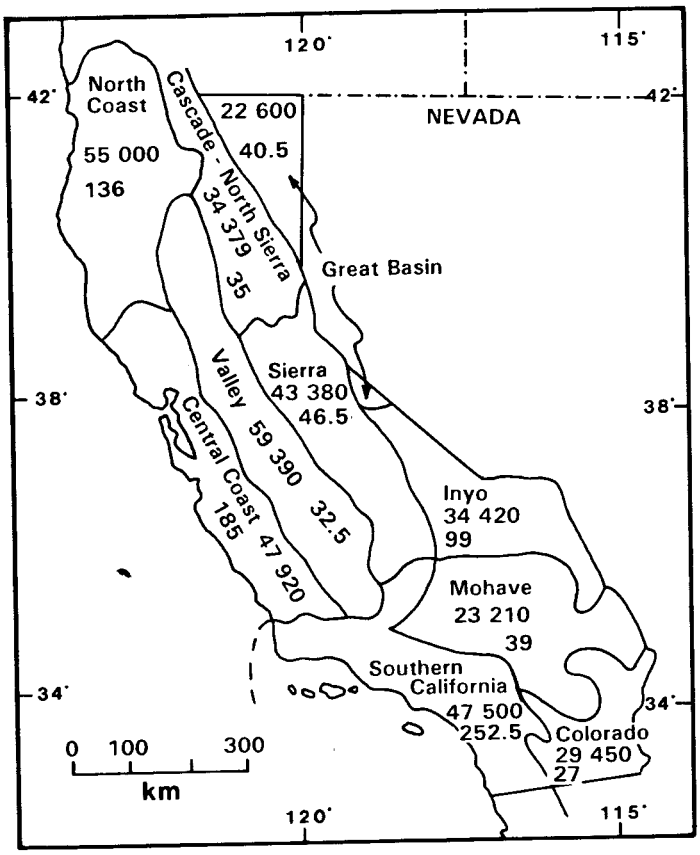

Fig. 3.1. Floristic regions of California. The *larger number* in each region represents its area in km^2. The *smaller number* indicates the number of endemics in 70 large and intermediately sized genera. The area west of *heavy line* is the California Floristic Province. (Raven and Axelrod 1978)

Historically, this broad latitudinal gradient comprised an ecotone between the Arcto-Tertiary geoflora to the north and the Madro-Tertiary geoflora to the south (Axelrod 1958; Raven and Axelrod 1978). During the Miocene (25-15 Ma B.P.) central California included both xeric adapted Madro-Tertiary and mesic adapted Arcto-Tertiary species. These elements segregated in a mixture of community types with Arcto-Tertiary species restricted to cooler habitats, such as high elevations and north-facing slopes or in southern California in riparian habitats (Sauer 1988). During Pleistocene shifts between warm-dry and cool-wet climates, elements of both assemblages mixed as climate forced a cycle of latitudinal migration and retreat (Axelrod 1981, 1986). Beginning in the Late Pliocene,

increasing topographic relief, generated by the uplift of the Sierra Nevada and other ranges, had profound impacts on local climates and created many novel combinations of environmental characteristics (Raven and Axelrod 1978; Axelrod 1981). Other geological features of the region, such as unusual substrates like serpentine, have further increased the number of habitats (Raven and Axelrod 1978; Axelrod 1981). Thus, modern plant assemblages represent unique mixtures of species derived from both geofloras.

The present mediterranean climate of California is the result of a climate shift of diminishing summer rains and warmer, drier conditions beginning in the early Pleistocene (Axelrod 1981, 1986; Raven and Axelrod 1978). This, coupled with the glacial/interglacial shifts in climate, resulted in an ecological disequilibrium, which has been the driving force behind the rapid speciation in many characteristic Californian taxa such as *Ceanothus, Arctostaphylos* and *Phacelia* (Stebbins 1976; Raven and Axelrod 1978). In addition, the spread of the summer-drought climate affected wildfire frequency, which has had an impact on speciation patterns in some taxa (e.g. Wells 1969; Keeley and Keeley 1988). Concomitantly, with the shift from a summer-rain to a summer-drought climate, many taxa were eliminated, leading to a marked decline in diversity at the generic level (Axelrod 1973, 1975). The summer-drought conditions would have eliminated many more taxa, but the newly uplifted Sierra Nevada provided mountaintop refugia for taxa such as *Picea, Abies* and *Sequoiadendron*, which were eliminated from lower altitudes and lower latitudes (Warter 1976; Johnson 1977a; Axelrod 1981). Due to the moderate winter temperatures of the mediterranean climate, California also has been a refuge for previously widespread taxa such as *Sequoia*, which were eliminated from colder parts of western North America (Stebbins and Major 1965; Raven and Axelrod 1978).

During the warming of the Xerothermic (8000 - 4000 B.P.) regional climate changes of as little as 1°C had additional profound effects on present-day species distributions (Johnson 1977b; Raven and Axelrod 1978; Axelrod 1981). Taxa migrated north and west into previously cool wet areas and remain today as endemic taxa or northern extensions of a broader southern distribution (Stebbins and Major 1965; Raven and Axelrod 1978; Axelrod 1981). Such climatic patterns may have played a role in the wide disjunctions observed in the distribution of some taxa; e.g. populations of the madrone tree, *Arbutus menziesii*, in southern California are interpreted as relicts of a former widespread distribution pattern, which were left when the species retreated northward due to increasing aridity.

In summary, the flora of California has undergone periods of rapid speciation as well as recombinations of species assemblages. These factors account for the preponderance of endemic plant taxa in the different

floristic regions of California (Fig. 3.1) and are certainly important determinants of our present patterns of diversity at all levels. Clearly, large-scale changes in landscape diversity have occurred, with marked shifts in patterns of diversity at other levels. The effect of such changes on ecosystem function are unknown.

3.2.2 Historical Determinants of Vertebrate Diversity

Near the end of the Pleistocene, during a brief period between 11200 and 10800 B.P., over 70% of the genera of large mammalian herbivores in North America became extinct (Owen-Smith 1987; Diamond 1992). In California, this included four genera of megaherbivores (>1000 kg) and many smaller herbivores such as cervids, bovids, antilocaprid, camelid and equid species. In addition, this period also saw the extinction of numerous carnivores, including canids, ursids, and felids, and a diverse raptorial and scavenging aviafauna (Stock 1930; Lundelius et al. 1983).

Climate change cannot account entirely for these extinctions, since massive extinctions did not accompany prior glacial/interglacial periods (Graham 1992). Several other arguments can be made against the climatic explanation for this massive extinction event. Based on Pleistocene fossil floras, it appears that suitable climates did not disappear but rather moved northward and in the process there were few extinctions of plant species on which these megaherbivores depended. Additionally, many of these mammalian taxa were very widespread across North America (Lundelius et al. 1983), suggesting tolerance of a broad climatic regime.

The coincidence of these extinctions with the populating of North America by humans skilled in hunting large prey is used as evidence to support the hypothesis that humans were directly responsible (Martin 1984). Simultaneous changes in climate may have hastened the extinction process (Johnson 1977b), since escalating summer droughts would have forced species to congregate near water, making them easy targets for increasingly larger populations of humans 11000 B.P. (Johnson 1977a). However, the human overkill hypothesis fails to account for the massive extinction of many species which were not likely targets of human predation.

Owen-Smith (1989) has proposed the "keystone herbivore" hypothesis to explain the extinction of the diverse fauna not directly a target of human exploitation. Based on the principles derived from studies of megaherbivores in Africa, he suggests that these Pleistocene mammals were the source of massive disturbances, which would have maintained widespread landscape diversity. The mosaic of habitats thus created may have been critical to the survival of other herbivore species. Today, megaherbivores in Africa are postulated to be an important link in nutrient cycling, acting

to keep nutrients near the soil surface where they are easily reincorporated into primary production (Botkin et al. 1981). Thus, Pleistocene megaherbivores would have had a massive impact on nutrient cycling and regrowth after grazing and trampling and this in turn may have been critical to the production of suitable habitats for other species (Owen-Smith 1987; Edwards 1992). With the extinction of the megaherbivores, many of these habitats would have disappeared and been replaced by unsuitable habitat comprising a greater abundance of evergreen woody plants that were less nutritious or toxic (Guthrie 1984). Additionally (as observed today in African ecosystems), with the demise of the major disturbance-creating megaherbivores, shrublands and woodlands would have expanded, leading to more widespread catastrophic wildfires (Owen-Smith 1988).

Since the arrival in southern California of the first Europeans, large mammals, the grizzly bear (*Ursus horribilis*) and the pronghorn antelope (*Antilocarpra americana*) have been eliminated from cismontane California. Many other large carnivores and herbivores have undoubtedly shrunk in numbers due to habitat destruction and lack of corridors between habitat fragments. More recently, due to stream channelisation in the early part of this century, salmon (*Salmo* spp.) spawning has been eliminated from southern Californian rivers.

In conclusion, over a geologically brief period of time there has been a dramatic decline in faunal diversity in California. Based on analogous contemporary megaherbivore-dominated systems, it seems certain that this loss of biodiversity had a profound impact on those ecosystems' capacity for transfer of water, nutrients and energy, and these extinctions had a domino effect, causing further extinctions. The remaining fauna is not only a small subset of the Pleistocene fauna, but it is also a subset of the smallest members of that fauna. Thus, it appears that these changes in ecosystem functioning did not impact all growth forms in a like manner. Apparently, much of the contemporary fauna was represented in the Pleistocene fauna and is likely to have undergone shifts in distribution and abundance. Almost certainly the patterns of natural disturbance have changed, changing also the landscape diversity and distribution of plant communities. Loss of the megaherbivores would have resulted in greatly altered patterns of nutrient cycling and, since sclerophylly is a functional response to decreased nutrient availability (Gulmon and Chu 1981; Mooney 1986), may have reinforced the climatically induced trend toward the dominance of sclerophyllous shrubs and trees.

3.2.3 Present Patterns of Plant Diversity

The vascular flora of mediterranean-climate California includes approximately 5050 species, 30% of which are endemic and 15% are naturalised non-native species (Mooney et al. 1986a). The annual growth form represents a sizable proportion (27%) of the flora and nearly half are endemic to the region (Raven and Axelrod 1978). Diversity of the total flora is highest in mountainous areas but growth forms show different patterns (Richerson and Lum 1980). Trees are proportionately more diverse in the northern coastal areas, herbaceous perennials are most diverse in northern coastal and montane regions, shrub diversity is highest in central and southern coastal areas, whereas annuals are most diverse in the Central Valley and southern coast ranges. Many of these annual species are temporally sporadic in occurrence, arising after wildfires in chaparral or after heavy rainfall in the desert. Due to their ephemeral nature, communities dominated by annuals show marked seasonal changes in diversity.

Present day gamma diversity patterns of Californian vegetation including the total flora and its various life-forms and taxonomic subdivisions can be predicted by climatic and topographic variables, and thus serve as a reasonable test of proposed environmental hypotheses of diversity regulation (Richerson and Lum 1980). The actual relationship between environment and diversity patterns was more complex than might be supposed. Topographic heterogeneity had a strong effect, however, weather variables accounted for the bulk of the diversity patterns in the models used. The results were unexpected in that favourableness indices (mean weather variables) were generally more important than indices of seasonality or irregularity. These results suggest that favourableness hypotheses deserve more theoretical and empirical attention.

There are a number of large (>50 spp.) endemic-rich genera in the state; including woody taxa (*Arctostaphylos, Ceanothus*), suffrutescent or herbaceous perennial taxa (*Eriogonum, Penstemon, Lupinus, Astragalus, Carex*), and mostly annual taxa (*Phacelia, Cryptantha, Mimulus*). Many of the species in these genera show remarkable morphological similarity with congeners, suggesting some level of redundancy or ecological equivalency.

Cody (1986) has addressed this possibility by looking at species turnover as a function of distance in the two largest shrub genera in California. In the genera *Ceanothus* and *Arctostaphylos*, about a quarter of the species in the former genus are restricted to one or two counties, and 40% of the species in the latter genus are local endemics (with ranges less than 50000 km^2). In both genera the percentage of species turnover among 1/2° x 1/2° latitude-longitude quadrats (about 50 x 50 km) along the coast is nearly linear (Fig. 3.2), with a 4-5% turnover per unit shift in distance over a 500 km interval. However, species turnover from coastal points (Santa Cruz,

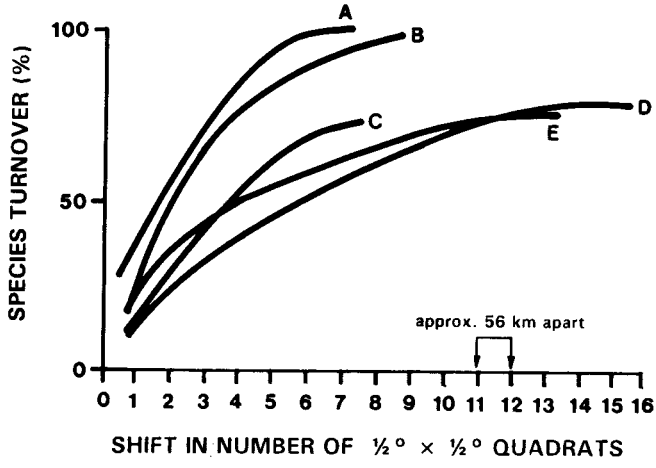

Fig. 3.2. Species turnover rates in *Ceanothus* and *Arctostaphylos* in 0.5° x 0.5° latitude-longitude quadrats, expressed as a percentage of the species that the sites have in common. Santa Barbara/Santa Cruz to inland transects illustrate coast to interior changes (**A**, **B**, **C**), and coastal transects illustrate latitudinal changes (**D**, **E**). (Cody 1986)

Santa Barbara) inland, over a steeper climatic gradient together with topographical changes, is much steeper – about 20% per unit shift in distance. The steeper gradient reflects greater sediment heterogeneity and climate heterogeneity which comes about through local topographic effects on fog distribution. These patterns suggest finely tuned morpho-physiological types adapted to fairly specific ecological conditions, dictated by sediment and climate, and would argue against the notion of redundancy in these large genera.

Even within the same community there is evidence that pairs of morphologically similar annual species of *Cryptantha* and *Lotus* are separated by micro-topographic niche differences, one species of each pair is restricted to gaps and the other to beneath the chaparral canopy (Shmida and Whittaker 1981). Regional differences in shrub composition of coastal sage scrub was suggested as a factor accounting for herb species diversity as herb species seem to prefer associating with different shrub species (Westman 1987).

3.2.4 Present Patterns of Insect Diversity

For natural ecosystems, there is relatively limited data on diversity and abundance of most invertebrate groups. Powell and Hogue (1979) estimate that there are 28000 insect species in California but, outside of agricultural

systems, relatively few of these have been studied in any detail. Flying insect communities in chaparral appear to follow marked seasonal patterns with greatest biomass and diversity in late spring (Atkins 1977). Summer drought appears to be a major limiting factor to these invertebrates, as the lowest diversity is observed at the end of the summer drought in October (Atkins 1977). This would also be supported by the report that flying insect abundance on the pole-facing slopes peaks later in the season than on equator-facing slopes (Cody 1974). Clear microsite differences are seen in the distribution of aphid galls (Sholes and Beatty 1987) and are evident by the restriction of biting-flies to humid ravines, a phenomenon well-known to chaparral field biologists.

Ground-dwelling insects in chaparral reach peak diversity and biomass peak much later, in September (Saiz 1977), suggesting that the limiting factors operating in the understorey are different than those in the canopy. In Saiz's study, which lasted 2 years, only 118 species were reported, primarily beetles. It is unclear how closely this approximates the total invertebrate ground-dwelling fauna. In California, it is estimated that there are 206 ant species (Snelling pers. comm. reported in Cody et al. 1977) and Hunt (1977) noted marked elevational differences in ant diversity, with more than double the diversity at 1000 m than at either coast or montane (2000 m) sites. Some of this diversity, however, may be tied to greater plant community diversity sampled at the mid-elevation site (Force 1990).

Caterpillars, moths and butterflies make up the major component of the foliage consuming trophic level in California and are relatively well known. Powell (1992a) has been conducting a census of the lepidopteran fauna in coastal central California at the Big Creek Reserve near Monterey. In total, 810 species of lepidoptera (60 butterflies and 750 moths) have been recognised, and it is estimated that this represents approximately two-thirds of the total Lepidopteran fauna. Adults of 17% of the microlepidoptera at Big Creek, and 9% of all moth species are diurnal, and these are primarily pollinators.

There is some evidence that lepidopteran diversity is tied to plant diversity. For example, Brown (1987) has shown that butterfly diversity is highly correlated with floral diversity in California and Baja California. He suggests that this is because these macrolepidopterans are highly host-specific. Powell (1992a) has made an intensive examination of the larval food plants for a community of microlepidoptera (Fig. 3.3). There are confirmed host plants for 171 insect species at his study site in Monterey and, based on other studies, the host is inferred for 96 additional species. Thus, host plants for about 65% of the recorded microlepidopteran species in the fauna are documented, and known detritivores (34) raise the total number of insect taxa accounted for to 73%. Powell (1992a) found that these species use only 67 native and 3 alien genera, or about 32% of the

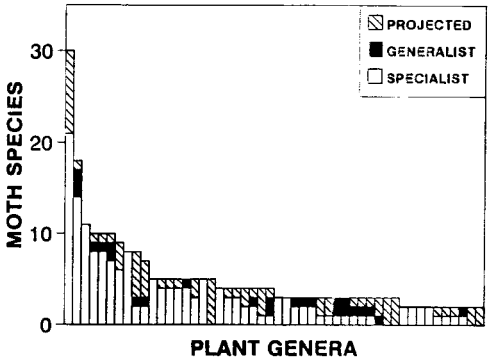

Fig. 3.3. Number of moth species recorded feeding or projected to feed on genera of vascular plants at Big Creek Reserve, California. Each *vertical column* represents one genus, from *left to right*: *Quercus* (31 moth species), *Ceanothus* (18 spp.), *Salix* (11), *Baccharis, Gnaphalium, Arbutus* (10 each), *Arctostaphylos* (9), *Alnus* and *Lupinus* (8), *Artemisia* (7), etc. Remaining 19 plant genera are host to a single species. (Powell 1992a)

native plant genera at Big Creek. It is possible that the remaining moth species that are unaccounted for use many of the other 70% of the flora. However, in a comparable study at the Antioch National Wildlife Refuge in Contra Costa County the pattern is similar. Antioch is a much simpler community with about 110 native plant species in 87 genera, and Powell (1992a) could account for 86% of the microlepidoptera fauna, but they utilize only about 48% of the native plant genera.

Detailed studies of a single shrub species *Eriogonum fasciculatum* in chaparral revealed that as many as 100 genera of insects were recorded from daytime collections and the species composition of nighttime collections was quite different (Swisher 1979).

Bees represent the primary pollinators in California. There are over 1200 native species and it is estimated that they pollinate 95% of the insect-pollinated plants in California (Force 1990). Bees are particularly abundant in chaparral, and Moldenke (1976) suggests that this can be attributed to the fact that most are ground-nesting and the understorey of chaparral, devoid of low ground cover but protected from wind, is the ideal environment. Force (1990) suggests that wind poses an obstacle to pollinating insects and accounts for the decrease in insect pollinators near the coast. Not surprisingly, pollinator diversity, as well as insect abundance in general, rises with increasing biomass of the floral resources (Cody et al. 1977).

Several studies have documented successional changes in insect communities. In mature chaparral insect diversity is generally greater than

in the immediate postfire years (Moldenke 1977; Force 1981) and there are marked successional shifts in insect guilds (Force 1982). For example, predatory insects are particularly abundant after fire and parasitic insects increase over time. Also, pollinators are abundant immediately after fire but are gradually replaced by phytophagous insects. There are at least two groups of insects that are the invertebrate equivalent of postfire annual plants. These fire-following insects include species of beetles (*Melanophila*) (Barr and Linsley 1947) and flies (*Microsamia*) (Kessel 1947). Thus, there is reason to believe that insect diversity and trophic structure is tied to plant diversity, climate and disturbance.

3.2.5 Present Patterns of Vertebrate Diversity

There are fewer than 150 species of amphibians and reptiles in California (Laudenslayer et al. 1991) and the best studied are the lizards, which comprise about a third of these taxa. In general, alpha diversity is relatively low, although even so, species sub-divide the habitat by micro-topography (Cody et al. 1977). Relative to Chilean matorral, Californian lizard communities have lower alpha and beta diversity, but greater gamma diversity.

Excluding rare visitors, the Californian avifauna comprises approximately 450 native species, although a large percentage of these are associated with the marine environment (Laudenslayer et al. 1991). Besides the Californian condor (*Gymnogyps californianus*), only the yellow-billed magpie (*Pica nuttalli*) is endemic to the state. The Passiformes or perching birds comprise more than 40% of the total avifauna and nearly 65% of the terrestrial bird fauna. Relatively few of the passerines are restricted to just a single plant community, although exceptions include the Californian gnatcatcher (*Polioptila californica*) which is restricted to coastal sage scrub (Atwood 1993) and the wrentit (*Chamaea fasciata*) and Californian thrasher (*Toxostoma redivivum*) which occur only in chaparral (Cody 1973). The narrow restricted distribution of the latter species inspired Grinnell (1917) to coin the now famous term "ecological niche" to describe the thrasher's role in the chaparral community.

Focussing largely on the Passiformes, Cody et al. (1977) showed a very marked turnover of species across the landscape with a peak in species turnover per habitat in mid-elevation chaparral (Fig. 3.4). In addition, alpha diversity changed markedly in different plant communities, reaching a peak in plant communities with the greatest biomass (Fig. 3.4). The association between avian diversity and plant biomass is tied to different foraging opportunities provided by communities of greater stature. For example, Dutton (1981) found that during the breeding season in chaparral 27 bird

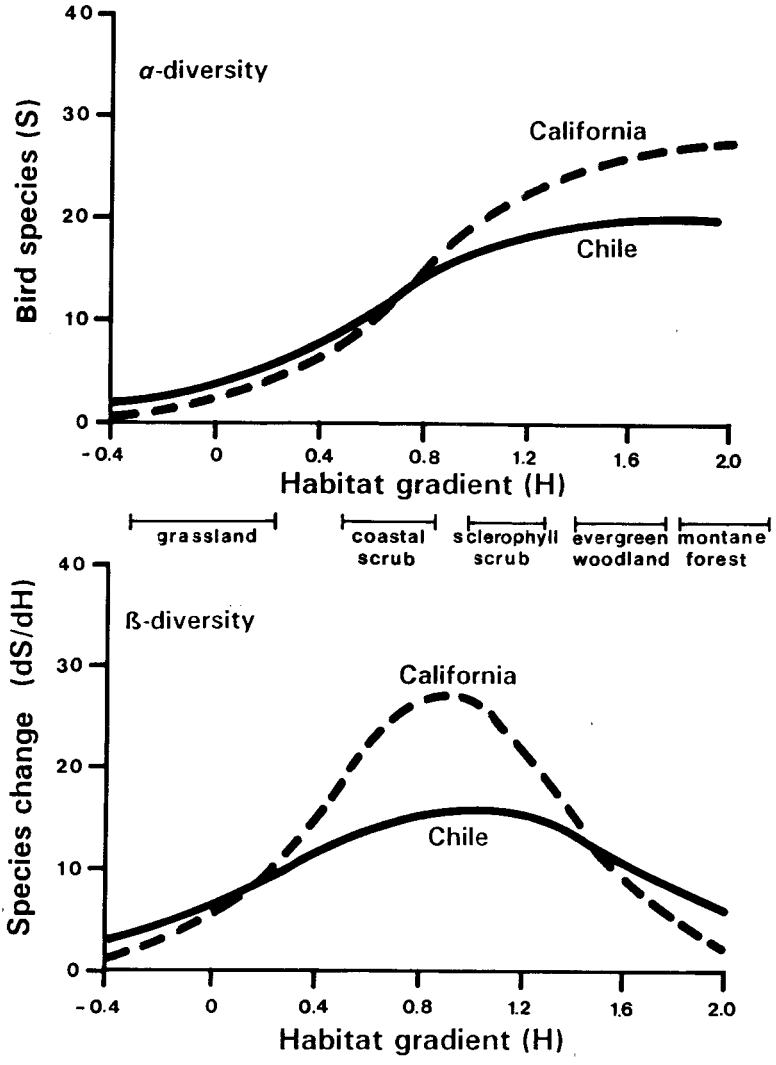

Fig. 3.4. Bird diversity in California and Chile. *Above* Alpha diversity plotted as a function of position on the habitat gradient. *Below* Beta diversity plotted as a function of position on the habitat gradient (Cody et al. 1977)

species partitioned resources primarily by differential foraging height in the shrub canopy.

The California gnatcatcher is an extreme habitat specialist restricted to coastal sage scrub vegetation (Atwood 1993). Due to rapid urbanisation and destruction of this community, the gnatcatcher is a federally listed

endangered species. Not only is it restricted to coastal sage scrub, but there is evidence that it is restricted to particular sub-associations. For example, it is apparently absent from *Salvia mellifera*-dominated sites (Atwood 1993) and even within communities there is evidence of shrub preferences.

Temporal changes in avifauna diversity have been reported following wildfires in chaparral. In recent burns, Wirtz (1979) showed that breeding bird species diversity increased over unburned chaparral. Five years after fire, species composition of burned chaparral was still decidedly different from mature stands (Yoder 1976), and as noted above for insects, there were marked changes in the trophic guilds of birds present in burned and mature chaparral. However, bird density may be higher in burns due to a decrease in territory size resulting from increasing food resources such as seeds and insects. In fact, Alten (1981) observed that initial postfire bird diversity was correlated with insect diversity, but as the stand aged this did not hold.

There are approximately 210 species and subspecies of native terrestrial mammals in California of which rodents (Rodentia) comprise 57% (Laudenslayer et al. 1991). Evidence indicates that environmental complexity is an important and general determinant of animal diversity in the state. Additionally, small mammal diversity may vary seasonally or annually. For example, rodent communities in coastal sage scrub experience fluctuations in the relative abundance of species and the variable presence of rare species results in temporal fluctuations in species diversity (McCloskey 1972).

Unlike birds, which are capable of more efficient utilisation of different levels in the canopy, mammal diversity does not increase with increasing plant biomass in California (Cody et al. 1977). Rather, much of the small mammal diversity in California is accounted for by local differences between habitats (beta diversity) and thus gamma or landscape diversity is relatively low.

3.2.6 Diversity Patterns of Fungi

For the more conspicuous fungi it is estimated that there are perhaps 4000 species of Basidiomycetes, 300 species of slime molds and 1000 species of lichen (Jensen et al. 1990). According to Armstrong and Platt (1993), there has been a dramatic decline in the lichen flora of southern California, due largely to air pollution.

Microscopic fungi in our systems have not been studied in great detail but some generalisations are possible. Any given site may have a dozen or more genera represented in the soil and, as with other taxonomic groups, there are widespread generalist species as well as highly specialised species.

In a study of different vegetation types on Mount Diablo in northern California it was observed that the genus *Penicillium* could be divided into species that were nearly ubiquitous in time and space and species that were highly specialised to different vegetation types and even to different types of chaparral, dependent upon the shrub dominant (Fordham 1977). The effect wildfires have on fungi and other soil microbes is not exactly clear. Apparently there is an initial dieback but they may come back in greater mass early in succession (Dunn et al. 1985).

3.2.7 Patterns of Genetic Diversity

Life history mode has had a profound influence on patterns of genetic diversity and this has most likely been important in adapting to the radical climatic shifts since early Pleistocene. Speciation in plant genera such as *Arctostaphylos* and *Ceanothus* was driven by increasing aridity and increasing probability of fire. Wells (1969) suggested that adaptive radiation of these genera is tied to the evolutionary loss of the resprouting mode, and this is supported by the observation that the majority of the species are obligate seeders, which do not resprout after fire. Obligate seeders have greater numbers of sexually produced generations, resulting in greater genetic recombination, which in turn contributes to more rapid speciation. A consequence of this life history mode is the potential for greater fine-tuning to the aridity of the summer-drought climate. Thus, it is not surprising that obligate seeders are far better able to tolerate drought stress, both as seedlings and mature shrubs, than resprouting taxa (Keeley and Keeley 1988). This may also explain why several resprouting species of *Arctostaphylos* produce obligate seeding populations on the most arid borders of their distribution (Keeley, unpubl. data).

The differences in life history mode have observable effects on patterns of genetic variation. Within the genus *Arctostaphylos*, populations of obligate seeding species tend to be morphologically homogeneous relative to populations of resprouting species. Each new generation of obligate seeders arising after fire is the product of genetic mixing, recombination and intense selection. Populations of resprouters, on the other hand, are far more heterogeneous and appear to represent a collection of morphologically distinct clones, many of them potentially quite ancient (Keeley pers. observ.).

Related perhaps to the rapidity of evolution, as well as the shifting climatic pattern which maintains ecological disequilibrium, woody taxa such as *Arctostaphylos* and *Ceanothus* have not evolved fertility barriers (Raven 1973). These shrubs are largely outcrossing and where species distributions overlap, hybrid swarms are common (Dobzhansky 1953;

Gottlieb 1968; Keeley 1976; Ellstrand et al. 1987) and there is evidence that hybrids and backcrosses may segregate out in the landscape in different microhabitats (Ball et al. 1983). Also, such hybrid swarms may represent a reservoir of genetic variation poised to colonise newly available habitat which is provided by disturbance such as fire. Genotypes of individuals on the margins of populations, where the potential for hybridisation exists, are likely to differ from those in the center (Bazzaz 1986). Patterns of variation in *Arctostaphylos* strongly support this idea and it undoubtedly accounts for the taxonomic difficulty of the group. For example, the very widespread resprouting *A. glandulosa* has had more than a dozen subspecific epithets assigned, apparently because of previous hybridization events (Keeley, unpubl. data). They persist as clones and are not swamped out by genetic recombination.

On the other hand, some clonal species may be genetically depauperate. For example, the very rare southern Californian *Nolina interrata* is a rosette-forming subshrub represented by only a few widely scattered populations. Genetic analysis suggests that one such population of 2000 rosettes is apparently composed of just a single clone (Bauder 1993), a particular problem for this dioecious species.

In the herbaceous flora, annuals are the obligate seeders and perennials are analogous to resprouters; however, the annual turnover in generations has led to internal barriers to hybridization (Raven 1973). Thus, we find that annuals are less variable genetically (Karron 1991). For example, genetic identities among seven populations of the annual *Pentachaeta lyonii* range between 1.00 and 0.990, and mean heterozygosity ranged from 0.000 to 0.058 (Arias et al., unpubl. data). This endangered species is endemic to the Santa Monica Mountains of southern California and has been reported from fewer than 50 locations (California Natural Heritage Program Natural Diversity Data Base 1991). The lack of variability within this species does not necessarily reflect decreasing population sizes, but may instead be related to its life history strategy. *Pentachaeta lyonii* appears to expand preferentially into disturbed areas on a temporary basis, persisting until resources become limiting as a result of increasing competition (Keeley and Keeley 1993). Such a life history, which restricts reproduction to periods of favourable conditions is similar to that exhibited by chaparral annual species (Swift 1991) and desert annuals (Mulroy and Rundel 1977) and would increase reproductive isolation of populations responding to localized changes in resource availability. Relative to long-lived species, annuals are more likely to have locally adapted populations and are replaced more rapidly as we move from one habitat to the next, i.e. they exhibit greater beta diversity.

An appreciable portion of theoretical population biology is based on the temporal and spatial variations in the frequency of different chromosomal

inversions in *Drosophila pseudoobscura*. Thus, the effect of chaparral wildfires on such genetic changes is of some interest. Moore et al. (1979) demonstrated that the gene arrangements of the third chromosome of *D. pseudoobscura* were unchanged in populations of mature chaparral and recently burned chaparral. What is remarkable is that the frequency of various inversions observed by Dobzhansky in the 1950s have remained relatively stable, despite repeated wildfires and colonization by closely related species. Thus, the ecological role of genetic variation in some species is far from resolved.

Smith (1978) studied allele frequencies between populations of the deermouse *Peromyscus californicus* and suggested that the pattern of geographic variation may have been affected by historical events and the potential exists that fragmentation of the central coast region may have contributed to isolation of the northern populations.

3.2.8 Effect of Wildfire Frequency on Landscape Diversity

Wildfires play an important ecological and evolutionary role in many Californian ecosystems and potentially affect biodiversity. It is clear that species are not equally adapted to all fire frequencies and there is evidence that entire ecosystems may be replaced by altering the burning regime. The landscape mosaic predicted by Owen-Smith (1989) for the Pleistocene environment of southern California would have had a very discontinuous fuel load. This landscape heterogeneity predicts a more heterogenous fire environment than that created today by massive stands of contiguous fuels. This, coupled with anthropogenic ignitions, has increased the fire frequency (Wells 1962), with the result that many shrublands have been replaced by non-native annual grasslands (Fig. 3.5), and this has had measurable impacts on vertebrate diversity patterns (Lillywhite 1977). Such increased disturbance has possibly increased landscape diversity and, due to the dynamic nature of shrubland displacement and re-invasion, there is much temporal diversity in the landscape (Fig. 3.6).

In montane regions, apparently decreased fire frequency has likewise altered ecosystem processes and potentially altered community characteristics (Rundel 1971; Kilgore and Taylor 1979).

Predicted climate changes may alter fire frequency, and Parsons (1991) has suggested that with a predicted increase in lightning ignitions (perhaps as much as 26%) the potential exists for profound landscape changes that might accompany such an increased source of fire ignition.

Fig. 3.5. Vegetation mosaic in southern California coastal ranges. Grasslands are dominated by non-native annuals and have displaced native perennial grasslands on the alluvial flats in the *foreground* and have displaced coastal sage scrub on the *slopes.* (Keeley 1990)

3.2.9 Effect of Alien Species' Invasions on Native Flora and Fauna

Invasion and establishment of alien species has had a profound impact on Californian ecosystems and has altered diversity patterns at all levels from genetic to landscape diversity (Mooney and Drake 1986; Groves and di Castri 1991; D'Antonio and Vitousek 1992). Genetic diversity of native species is often affected through hybridization with invasive taxa, as is the case with southern Californian cacti following the introduction of *Opuntia* from Mexico (Benson and Walkington 1965). Sometimes regional movement of plant material can affect local taxa. For example, the island cherry, *Prunus lyonii*, endemic to offshore islands, is widely planted and seeded in southern California and readily hybridizes with the mainland *Prunus ilicifolia* (Keeley, unpubl. data). Intraspecific effects are possible when locally adapted gene complexes are disrupted by the intentional introduction of foreign ecotypes in community restoration projects (Ledig 1992); however, such introductions could have a beneficial impact on populations that are genetically depauperate due to demographic bottlenecks.

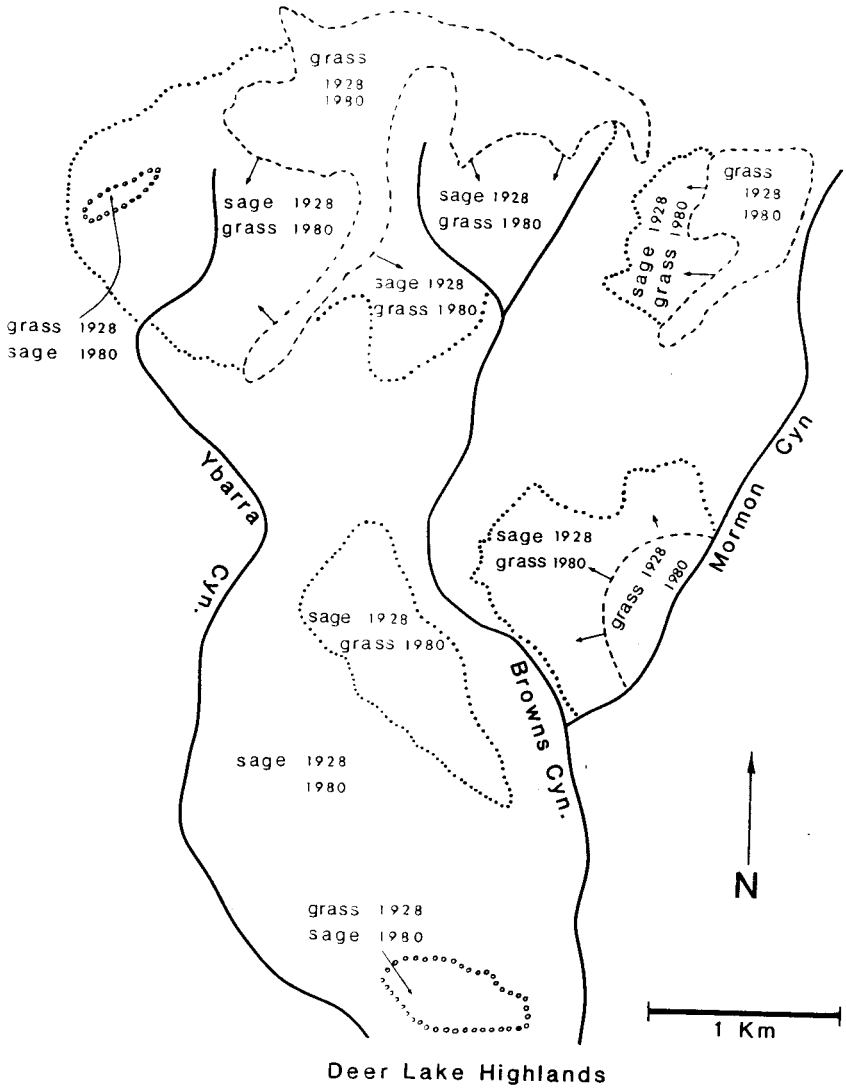

Fig. 3.6. Historical and present-day distribution of grasslands and coastal sage scrub (as of 1980) on a portion of the Oat Mountain Quadrangle, Los Angeles Co. (Freudenberger et al. 1987)

Invasives may also impact community diversity patterns by causing the extirpation of native species. For example, in chaparral the diversity of herbaceous species has been shown to be drastically reduced by the management practice of seeding the alien grass *Lolium multiflorum* (Keeley et al. 1981; Nadkarni and Odion 1986). Likewise, avian community

diversity in California may have been altered by the introduction of the European Starling, *Sturnus vulgaris*, which was introduced in 1890 in New York and arrived in California in 1942. It competes with native hole-nesting species such as bluebirds, titmice, nuthatches, swallows, wrens, woodpeckers and nuthatches (Vuilleumier 1991). Although a total of 19 bird species have been introduced to California, nearly all are restricted to urban environments and only the starling has successfully invaded the chaparral (Vuilleumier 1991).

Ecosystem effects of feral sheep and goat introduction on coastal islands of southern California are horrific. The effect of uncontrolled overgrazing and trampling have denuded many of the island ecosystems (Van Vuren and Coblentz 1987) and often invoke the image of a lunar landscape. These introductions into an environment devoid of the necessary predator diversity illustrate clearly the impact of simplified community structure on ecosystem stability.

Invasive species can also affect landscape diversity as illustrated by the relatively rapid and widespread establishment of annual grasses and forbs (e.g. *Avena, Bromus, Hordeum, Lolium, Brassica and Erodium*). Today, annual grasslands persist under a wide range of topographic and edaphic conditions. They have replaced shrublands after repeated fires and replaced perennial grasslands under regimes of overgrazing and drought (Fig. 3.5). Under both conditions the landscape has changed from one dominated by native perennials to non-native annuals.

A consequence of this invasion is the destruction of much of the native grassland community. The invasion of the pristine Californian Valley Grassland illustrates how rapidly and thoroughly an alien flora can dominate another landscape. The process began in earnest in the late 18th century and was nearly complete by the middle of the 19th century. Perhaps what is most unique about Californian annual grasslands is the comparative stability of this ecosystem dominated by non-native annuals with relatively little threat of being displaced by natives.

The precise effect of this invasion on grassland biodiversity is unknown. The pristine prairie in California was dominated by perennial bunchgrasses in genera such as *Stipa, Poa, Koeleria* and others although there is evidence that they seldom exceeded 50% ground cover (Keeley 1990). The interstitial spaces between the bunchgrasses would have been filled by native annuals and geophytes. Replacement of the native flora by introduced species has most likely reduced the diversity of life histories and phenologies in Californian grasslands. The earliest flowering non-native species flower later than the earliest natives and the latest-flowering non-natives flower earlier than the summer active natives (Chiariello 1989). Reduced growth form and life history diversity in modern annual grasslands have potentially created a very different environment for

foraging animal species. It has been demonstrated in southeastern Arizona that native grasslands invaded by non-native grasses have a significantly lower variety and abundance of indigenous grasses, herbs, shrubs, grasshoppers, rodents and birds than pristine grasslands (Bock et al. 1986).

In California, invasion by non-natives has most likely resulted in a more homogenous pattern of landscape diversity. Most annual grass species have a great deal of ecological and geographical breadth. However, the native grassland community exhibited much diversity across the state with replacement of the widespread *Stipa pulchra* by other native species on different sites (Beetle 1947). For example, moister sites were dominated by *Muhlenbergia rigens* and drier interior sites by *Aristida* and *Oryzopsis*. On rich alluvial soils were rhizomatous species of *Elymus* and *Agropyron*, on gravelly ridges and serpentine, *Sitanion jubatum* dominated, and alkaline flats were dominated by the rhizomatous perennial *Distichlis spicata* and the bunchgrass *Sporobolus airoides*.

Ellstrand (pers. comm.) has suggested that this colonization event may have had a profound impact on the ability of ecological communities to respond to pollution and global climate change. Native perennials as a group naturally harbour high levels of genetic diversity and are largely outcrossers whereas the invasive annuals are genetically less diverse and are typically selfers. However, this analysis is complicated by the greater adaptive potential of the annual life cycle. Predictions for future climate change indicate that the rate of temperature rise in the Central Valley of California may approach 5°C over the next 75 years (Jensen et al. 1990). Almost certainly, perennials will be unable to adapt or migrate rapidly enough to such unprecedented rates of change, and thus these introduced annuals may spread even further.

3.2.10 Effect of Habitat Fragmentation on Patterns of Diversity

Rapid population growth in California has resulted in widespread habitat destruction throughout the state; consequently, remaining natural areas represent habitat islands often without corridors between (Swift et al. 1993). Several studies have investigated the effect of such fragmentation on biotic diversity and have inferred effects on the functioning of these systems.

Soulé et al. (1988) did an island biogeographic study of specialist bird species in chaparral habitat fragments in coastal urban areas of San Diego County, California. These fragments are portions of canyons that have been insularized by encroaching development on canyon rims and in canyon bottoms. An archipelago of "islands" of native chaparral vegetation has been formed with fragments ranging in size from less than 1 hectare to hundreds of hectares and of varying ages up to 80 years.

They found a significant negative partial correlation between species diversity and fragment age (time since insularization) and a positive correlation between a species' density and the number of habitat fragments it currently occupies. They concluded that populations of species that naturally occur at lower density become extinct more rapidly than do those of more abundant species, i.e. species differ in their vulnerability to extinction. Additionally, Bolger et al. (1991) compared the species-area relationship in unfragmented chaparral habitat with that in urban chaparral fragments and confirmed that rapid population extinction of resident bird species had occurred in these fragments. A strong positive correlation between the relative persistence ability of a species and its density remained even after correcting for the sampling effect of area. Bird species present in species-poor fragments were nested subsets of those in species-rich fragments. Once isolated, these fragments degrade with time as a result of invasion by alien plants.

Effect of habitat fragmentation on plant diversity in these same coastal scrub communities has been studied by Alberts et al. (1993). They found that for 25 isolated patches of coastal scrub vegetation in San Diego County, the variance in native plant species number was best accounted for by size and age variables, with larger and more recently isolated patches supporting more species. Fragments with longer perimeters contained more ruderal weeds, whereas older fragments and those with artificially supplemented water sources supported higher numbers of escaped ornamentals.

Human disturbance, including clearing of vegetation, addition of non-natural water supplies, and disruption of fire regimes, has probably contributed to the loss of natives and subsequent invasion of alien plants into fragments. Obviously, any change in the flora could potentially upset the community structure of animal communities. Other factors that could affect these communities include the introduction of "subsidized" predators such as domestic cats (*Felis domestica*) and dogs (*Canis domesticus*) which are effective predators of native bird and mammal populations (Wilcove et al. 1986). Soulé et al. (1988) proposed that in less disturbed habitats large predators such as the coyote (*Canis latrans*) may reduce the populations of medium-sized nest predators such as the opossum (*Didelphis virginianus*). In small, highly disturbed fragments the large predators go extinct and populations of "meso-predators" increase, causing increased nest predation. In this instance the coyote is considered a "keystone" species (see Hobbs et al., Chap. 1 Sect. 1.4 this Vol. for a definition), which, when locally extinct has profound impact on the biotic diversity of other animal guilds. It remains, however, to develop a general conceptual framework that will predict which kinds of organisms play key roles in different kinds of ecosystems. With such knowledge, if extirpation of these keystone

organisms cannot be avoided, their roles could potentially be replaced by other species or other forms of ecosystem management.

Despite the lure of Soule's "keystone coyote" hypothesis, not all subsequent studies have supported it. Langen et al. (1991) found that the predation rate of artificial birds' nests was highest in an unfragmented site. Among fragments, predation was higher at moderately disturbed than at highly disturbed sites. These results suggest that nest predator species diversity or density is reduced in disturbed chaparral fragments and that nest predation is probably not the most important cause of the observed loss of chaparral breeding bird diversity in habitat fragments.

All of these studies suggest the important role of habitat size in affecting faunal and flora diversity. Consistent with this is the finding by Sauvajot and Buechner (1993) that for 12 habitat fragments in the Santa Monica Mountains of southern California variation in bird and mammal species richness and relative abundance were not correlated with proximity to development. These studies illustrate how chaparral habitat very close to urban development can have important conservation value.

It is apparent, however, that direct alteration of a site during development has a very destructive effect on biodiversity (Sauvajot and Buechner 1993). However, in a study of central Californian suburban bird populations, Vale and Vale (1976) found that both numbers of species and numbers of individuals increased with time after development, although most of the increase in species diversity is concentrated in the initial years following housing construction. Garden plantings seem most influential in determining the distribution and density of birds, but other factors (e.g. the presence of bird feeders) may also be important. When compared to the pre-suburban habitats adjacent to the suburbs studied, the residential neighbourhoods supported larger numbers of both species and individuals and potentially could visit adjacent habitats and have a detrimental influence on these communities.

3.2.10.1 Fragmentation and Ecosystem Processes

Ecosystem functioning of habitats may be altered by fragmentation and proximity to urban development. For example, pollinator services may be greatly upset by insecticide application in adjoining agricultural fields. In southern California, much of the landscape is dissected by golf courses which have a myriad of indirect impacts on ecosystem processes. For example, increased human activity and noise may reduce raptor and other predator activity in adjoining grasslands and scrub. Loss of these predators could threaten plant species sensitive to uncontrolled rodent and rabbit populations. The threat may be exacerbated by the fact that summer

drought acts as a natural check on these predator populations. Golf courses provide a high nutrition food resource during the summer, which contributes to the maintenance of unnaturally high rodent and rabbit populations. Not only are predation rates increased under such conditions but, due to the connectedness of these natural and unnatural systems, these habitats will be nutrient- enriched by movement of animals between the golf courses and the grasslands. In native grasslands, such nutrient enrichment is known to favour non-native weeds at the expense of native species (Keeley 1990).

Theoretical considerations predict a negative impact of subdivision on regional species numbers when species interactions are strongly positive or mutualistic (Gilbert 1980). Conversely, subdivision is particularly likely to increase diversity when strong negative interactions occur among species and otherwise threatened species are able to escape in space and time. Few, if any, empirical tests have examined diversity in otherwise comparable areas differing only in the degree of subdivision. Numerous species-area studies indicate that diversity should be maximized in single contiguous areas, whereas patch models often predict regional co-existence and thus enhanced total diversity, resulting from spatial subdivision of habitat (Soulé and Simberloff 1986).

This problem was investigated experimentally in a Californian annual grassland by isolating experimental areas of 64 m^2, subdivided into 2, 8 and 32 subunits, with each subunit separated by intensive grazing (Quinn and Robinson 1987). Species richness and species evenness of flowering plants increased with increasing subdivision, with approximately 40% more species in the most subdivided treatment than in the least. It was concluded that aboveground interspecific competition appears to be an important causal mechanism. There is evidence of strong "priority effects" in which dominant species pre-empt particular plots and prevent the establishment of competitors. Late-emerging and low-growing species occur primarily on plot edges and the greater relative perimeter of the more subdivided treatments may contribute substantially to their greater diversity.

A far-reaching consequence of habitat fragmentation is the decreased potential for plant migration in response to impending climatic change which could result in large scale changes in gamma diversity. Movement of species between interior ranges and coastal ranges during the Xerothermic most likely involved movement along watercourses (Axelrod 1981). In addition, these watercourses probably acted as localized mini-refugia (particularly in southern California) (Sauer 1988), allowing taxa to persist in California which otherwise might have been lost during warming over the last million years. Large-scale elimination (89% of valley riparian habitat has been lost as a result of habitat conversion) and alteration of such natural corridors (Mooney 1983; Jensen et al. 1990) may have

eliminated important migration routes for plant and animal species responding to climatic change with shifts in population distribution.

3.3 Biodiversity and Community Structure and Function

Functional linkages between different trophic levels in a community are common and important to evaluating the degree to which biodiversity controls functioning of entire ecosystems. MacArthur (1955) argued that more complex communities were also more stable. Complexity may be defined by the diversity of species or the diversity of pathways energy takes to reach a particular population. The examples chosen here illustrate the difficulty of lumping species into "functional groups", as species within such a group may be tightly linked to species in quite another functional group (Schulze and Mooney 1993).

3.3.1 Plant Linkages with Other Trophic Levels: Oaks as a Case History

Perhaps more than any other element, oaks (*Quercus* spp., Fagaceae) play a fundamental role as keystone species in Californian mediterranean-type ecosystems (MTEs). They affect plant and animal diversity through impacts on the functioning of food webs and as important functional links between other ecosystems.

Species of oaks are critical food sources for a myriad of fungal and animal species, including aboriginal peoples (Pavlik et al. 1991). Oaks are utilized by a diverse array of herbivores. Most obvious are the granivores, that depend upon acorns as an important part of their diet. Some, such as the scrub jay (*Aphelocoma coerulescens*), in turn play critical roles in the dispersal and caching of acorns. Without their assistance, oaks could not persist on steep slopes, as gravity tends to carry acorns to the bottom of ravines (Grinnell 1936). Studies in other parts of North America reveal that, although jays feed exclusively on acorns during the fall, they are unable to exist entirely on this diet. Consumption of acorns infested with the acorn weevil larvae is critical to counteracting the effects of acorn tannins and this accounts for their apparent subsistence on just acorns during the fall caching season (Johnson et al 1993). Oaks sustain these much-needed dispersers during the interim periods of acorn crops by the array of insect larvae specialized on oaks. One of these is the Californian oak moth (*Phryganidia californica*) that feeds on the coast live oak (*Quercus agrifolia*). Peaks of herbivore damage occur during the summer drought as the oak moth preferentially feeds on the less nutritious mature foliage, as

a means of circumventing quantitative plant defenses such as condensed tannins (Mauffette and Oechel 1989). Populations of the oak moth are controlled by a virus which is always present but increases in populations over time, possibly contributing to a cyclic pattern of oak moth infestation (Baker 1965). Mycorrhizal fungi, which proliferate on oak roots, produce mushrooms that are important food sources for insects and vertebrates.

Another granivore is the acorn woodpecker (*Melanerpes formicivorus*), which stores acorns in small holes that it drills in storage trees known as granaries. Trees are sometimes riddled with holes and this provides needed entrance for insects and microbes, which play a critical role in the decomposition process of dead trees. Similar ecosystem services are provided by sapsucker woodpeckers (*Sphyrapicus* spp.) that tap living oak tissues for sap.

All oaks harbor gall-forming wasps, and in the western USA oaks are host to more than 140 species (Brown and Eads 1965). All are in a single family of Hymenoptera, the Cynipidae, and most are restricted to oaks. This appears to represent an ancient association, as black oaks and white oaks have their own separate cynipid fauna. In some species of wasp there is an alternation of generations in which bisexual populations generate asexual populations, separated in time and space, and each generation produces a different gall on a different part of the plant. Gall larvae are often parasitized by other species of wasps, and the galls themselves may harbour other insects long after the original resident has left.

Evergreen and deciduous oak species play different roles in the landscape. Some animals are dependent upon the perennial nature of the foliage in evergreens, both as food and shelter, whereas other species may require the dense litter layers that develop under deciduous species. All oaks play an important role as substrates for lichens, and mistletoes and lichens may be important sources of nesting material for an array of bird species.

In savanna landscapes oaks are linked to the functioning and biodiversity of surrounding grasslands through their impact on the light regime and on nutrient cycling (Gordon et al. 1989; McClaran and Bartolome 1989; Callaway et al. 1991; Welker et al. 1991) In shrubland habitats scrub oaks may play critical roles as shelter for animals that graze the adjacent grasslands (Davis and Mooney 1985; Hobbs and Mooney 1986) as well as facilitating the establishment of more mesic trees such as coast live oaks (Callaway and D'Antonio 1991; Keeley 1992a).

On coastal slopes oaks act as fog-collectors, contributing significant amounts of dew precipitation, which affects the water budget of the site. Seedling recruitment by other species may be dependent upon this added moisture.

Oak communities also play key roles in the linkage of communities. For example, as seasonal food sources for birds that migrate from montane

environments during the fall when acorns are dispersing, such as the large flocks of band-tailed pigeons (*Columba fasciata*) that seek out the massive acorn crops that occur in mast years. Phainopeplas (*Phainopepla nitans*) move in winter from their desert environments to obtain mistletoe berries. Mistletoes also provide a critical food source for migratory frugivores such as waxwings (*Bombycilla* spp.).

3.3.2 Vertebrate Communities

MacArthur (1972) hypothesized that competitors in communities of species that depend on a common limiting resource are likely to develop divergent resource utilizations. He concluded that abundances of competitors will equilibrate at a configuration minimizing a quantity which is the difference between the amount of resources produced by an environment and the amount utilized by the community. If too much of one type of resource is left unused, then a new species that uses the resource efficiently can invade the community, thereby reducing the ratio. Similarly, a particular species that depends on a rare resource will be rare or absent. In short, this theory provides a method for predicting species abundances from knowledge of the availabilities and species utilizations of critical resources. The theory has implications for the role of biodiversity in the functioning of communities and ecosystems, and predicts that loss of biodiversity from an ecosystem will prevent complete utilization of resources.

Price and Waser (1984) compared predicted changes in rodent abundances with those observed over the two and one-half years following a fire in a topographically uniform area of California coastal sage scrub vegetation. They used microhabitat-specific capture frequencies as resource-utilization functions for each species, because structural microhabitats appear to be related to underlying resources that limit rodent populations. Resource-availability functions were derived from censuses of vegetation and other structural features on burned and unburned sides of the permanent grid. Predictions from MacArthur's theory were upheld in that (1) abundances of each species on one side of the grid relative to the other correlated significantly with relative K values on the two sides of the grid (K values were calculated as the overlap between microhabitat utilization and availability functions); (2) relative abundances of the five rodent species on the burned side of the grid were correlated with those predicted from relative K values; and (3) the total microhabitat utilization of the rodent community on each side of the grid matched overall microhabitat availability on that side well and matched availability on the other side poorly. These results provide support for a potentially powerful protocol for predicting identities and relative abundances of co-existing species.

One means of evaluating the extent to which redundancy occurs in natural ecosystems is to look at the manner in which animal guilds utilize plant resources in their environment. Studies to date are consistent in demonstrating that co-existence of rodent communities is a function of the manner in which species divide up resources. For example, Meserve (1976a, 1976b) studied the food habits of seven species of rodents in a Californian coastal sage scrub community. Laboratory feeding experiments using the cafeteria method indicated different patterns of food preference from wide acceptance of shrubs, forbs, and grasses (*Dipodomys agilis*) to lower preferences for shrubs and high preferences for grasses (*Reithrodontomys megalotis, Peromyscus eremicus* and *P. californicus*) to relatively narrow acceptance of only grasses (*Perognathus longimembris).* Other dietary axes that act to separate these rodents include a high utilization of insects and *Eriogonum fasciculatum* by *Reithrodontomys*, a generalized diet for *Perognathus maniculatus*, and a specialization on various seeds, flowers, and fruits, by *P. californicus* and to a lesser degree by *P. eremicus*.

Additional factors affecting co-existence include differences in nest sites, e.g. *Dipodomys* burrows in sandy soils whereas some other species do not use burrows. *Peromyscus* species are dependent upon free water while *Perognathus* and *Dipodomys* are independent of free water. Also, species have horizontal and vertical differences in spatial preferences within the coastal sage scrub, which contribute to differences in resource exploitation.

One type of observation that is suggestive of incomplete redundancy is that microhabitat specializations do not disappear entirely when competitors are removed (Price 1978). Additionally, it is unlikely that removal of one species from a community will be exactly compensated for by increased consumptive biomass of another species. For example, Brown and Munger (1985) found that *Dipodomys* spp. removed from a site are not replaced by equivalent consumptive biomass of other small granivores. The reason for this is probably one of efficiency: no two species will have exactly equal efficiency at utilizing a particular food type. Hence, loss of one species means lower net efficiency by the remaining species. For example, less consumption means less rapid biomass recycling, which means less fertile soil, which translates into reduced plant productivity.

3.3.2.1 Rodents and Plant Community Structure

There is tremendous potential and at least a few documented cases in which rodents are linked to processes that would impact plant species diversity. Seed predation is ubiquitous and widespread and by its sheer force would seem to be potentially capable of affecting plant diversity. One study

showed that predation of *Arctostaphylos* seeds was significantly greater on one species than another (Keeley and Hays 1976) and this could potentially affect not only community composition but genetic diversity for fruit size since rodents selectively removed the largest seeds. In annual-dominated communities, rodents that selectively remove large-seeded species have been shown to have a profound effect on plant species diversity (Samson et al. 1992).

The bare zone between mature chaparral or coastal sage scrub and grassland, possibly controlled in part by allelopathic inhibition (Muller et al. 1964), owes its existence on some sites to rodent and rabbit predation (Fig. 3.7) (Bartholomew 1970). These animal activities not only control community boundaries but may play roles in nutrient linkages between communities.

Postfire herbivory also has the potential for markedly impacting plant diversity. Studies by Mills (1983, 1986) have shown that small mammals consistently prefer seedlings of *Ceanothus greggii* over *Adenostoma fasciculatum*. When seedlings were protected from herbivory, *Adenostoma* seedlings experienced higher mortality. Quinn (1991) demonstrated that *Ceanothus greggii* dominated a site several years after fire in an area fenced from small mammals; however, in an adjacent unenclosed site this species was replaced by *Adenostoma fasciculatum*. Quinn (1986) has shown a similar phenomenon with *Ceanothus crassifolius*.

The potential exists in mediterranean-climate vegetations for marked control of vegetation structure by rodent guilds. Brown and Heske (1990) studied the more xeric desert scrub habitat which shares many of the same Heteromyidae genera, such as *Dipodomys* and *Perognathus*, with more coastal communities in truly mediterranean-climate vegetations. In their study, 12 years after three species of *Dipodomys* were removed from plots, density of tall perennial and annual grasses increased about three-fold, and rodent species more typical of this community had colonized the site. They concluded that species of *Dipodomys* were a keystone guild: through seed predation and soil disturbance they have major effects on biological diversity and biogeochemical processes. In this case the "keystone" organism was not a single species, but a guild of three taxonomically related and ecological similar *Dipodomys*. In their study there was some evidence of redundancy in that removal of the largest of the three species had significant effects on the distribution of other rodents, but it required the removal of all three species to cause wholesale changes in vegetation. This study was significant because it demonstrated that the eight common and several rare species of rodents that remained after *Dipodomys* had been removed clearly did not play the same keystone role and were not able to prevent the conversion of scrub to grassland.

Fig. 3.7. Bare zone between coastal sage scrub and grassland with rodent-proof exclosure in bare zone in the *foreground*

Changes in important carnivores may have indirect impacts related to foraging strategies of predators and prey. If nocturnal predators such as coyotes are removed and diurnal predators such as hawks remain, this could change the balance between nocturnal prey such as kangaroo rats and diurnal prey such as squirrels. Since the former are granivores and the latter herbivores, we might expect these changes to impact the vegetation composition.

Removal of large carnivores may also have regional impacts in that it reduces the across-habitat connectance, which potentially decreases food-web stability. This is particularly so in southern California, where the juxtaposition of grasslands and woodlands may be needed to sustain raptors

that forage in grasslands but require woodlands for shelter (M. Price, pers. comm.).

3.3.3 Invertebrate Communities

3.3.3.1 Pollinator Linkages

In a detailed study of pollinator communities along an altitudinal transect of 15 community types across central California, Moldenke (1975, 1979a,b) concluded that competition between plants for pollinators increases the blooming season of plant species in pollinator-limited environments. This has the effect of increasing the percentage of the flora that is blooming during any given week. It was noted that some of the least important contributors to community floral biomass are the most heavily visited by pollinators and vice versa. In other words, species that have limited control of ecosystem functions such as energy flow, may be strong controllers of ecosystem processes such as pollinator resources.

Competition for pollinators was further suggested by the observation that self-compatible plant species not visited by pollinators and therefore forced to self, are highest at the peak of blooming. Additionally, this competition for pollinators is revealed in the disproportionate occurrence of genetically incompatible annual species flanking the anthesis peak, while a disproportionate abundance of self-compatible perennial species occurs at the anthesis peak.

A mechanism that permits successful outcrossing at the peak of blooming is the exceptionally high number of plants serviced by specialist-feeding bees which allows for pollination even when a plant species is in low density or when competing species may have successfully usurped all the generalist pollinators. Specialized feeding habits of course would not evolve in bees, if it were not competitively forced upon them by competition for their floral resources as well; more species of specialist-feeding bees are in fact active during the peak synchrony of anthesis than at any other period.

Moldenke concluded that while there is a tendency for specialization in most environments, it is only in the most predictable or stable environments that the loss of both behavioural and genetic flexibility, associated with specializing, is a viable strategy.

Extreme specialization has long been noted between all species of the genus *Yucca* and moth species in the genus *Tegeticula* (or *Parategeticula*) (Powell 1992b). It is curious that almost all of the many *Yucca* species from Nevada to Florida are pollinated by a single species of moth, yet each of the three of Californian *Yucca* species is pollinated by a different species

of moth. Such extreme specialization illustrates a marked degree of co-evolution between insect and plant.

3.3.3.2 Herbivore Linkages

Factors controlling diversity of insect communities are not well understood. One approach is to determine the degree of niche overlap. This was addressed in a very detailed study of microlepidoptera on its host, the California live oak (Opler 1974). In these herbivores the question is complicated by the fact that species interact as adults as well as larvae. On this host there are 35 species of foliage-feeding microlepidoptera; 18 external feeders and 17 leaf miners (see also Fig. 3.3). These groups segregate out on young and mature foliage, respectively. All of the leaf miners are host-specific, some being restricted to coastal sites and some interior. Opler found relatively little niche overlap in these moths, as species on the same tree exhibited trophic and temporal separation.

Another approach is to separate ecological from biogeographical processes. Regional (gamma) herbivore richness is defined as the total number of herbivore species associated with a host plant in any part of its range and local (alpha) richness is the number of species associated with a host population at a single site. Understanding the mechanisms operating on community diversity requires an understanding of the relationship between these two variables. When local ecological interactions are weak and herbivore species are widespread, the correlation between richness at these two spatial scales should be strong. If local interactions are strong and herbivore species have restricted ranges due to habitat specialization, the correlation should be weak.

Cornell (1979, 1985, 1986) attempted to separate these two factors in a study of Californian cynipid oak gall-forming wasps. Different oak species support significantly different numbers of cynipine species on trees of a given size. Cornell found that within oak species, tree height and the number of cynipine species available to colonize trees explains much of the variation in cynipine richness among trees. However, there is no evidence of vertical or horizontal zonation; upper tree canopies support the same species as the lower canopies. Those species found in smaller trees are either random or non-random subsets of those in larger trees.

On the other hand, the total number of cynipine species associated with each oak species (regional richness) varies widely among five oak species and correlates significantly with cynipine richness on individual trees in multiple regressions with tree size. Path analysis indicates that regional richness is correlated with richness on trees exclusively through increasing the species pool from which the assemblage on individual trees is drawn

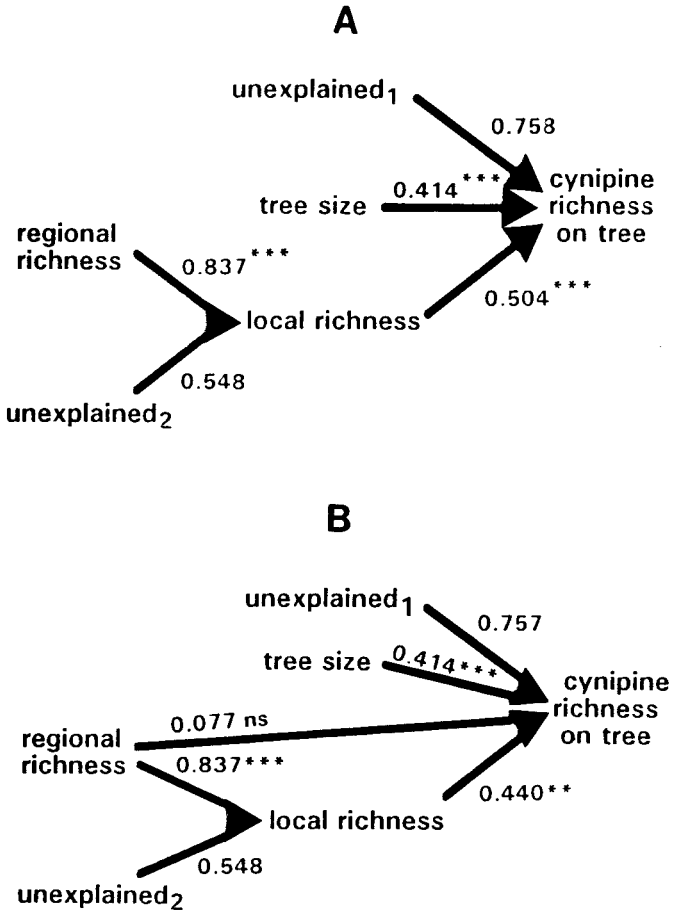

Fig. 3.8. Path analysis to determine the contribution of regional richness of cynipine wasp species to cynipine richness on trees either via its influence on local richness (**A**), or directly (**B**). *Numbers* associated with *arrows* are path coefficients. (Cornell 1985)

(Fig. 3.8). In other words, there is an unabated increase in alpha diversity as gamma diversity increases, suggesting that excess niche space is available on host oaks for additional cynipine species, and that limits to similarity of co-existing cynipines have not been reached. This indicates that sufficient information on the causes responsible for local herbivore richness cannot be gained by studying the local host population in isolation. The spatial dynamics of the system are such that measures of the regional pool from which the local assemblage is drawn must also be taken. However, cynipine habitat specialization and local interactions are not

predictable from regional richness, but may influence local richness on certain oak species independently of regional richness.

3.3.3.3 Parasite Linkages

Although widespread in North America, Lyme disease has a unique vector system in Californian chaparral. The western black-legged tick, *Ixodes pacificus*, gives the disease to several hundred people each year. This tick species picks up the disease, borne by a spirochete *Borrelia burgdorferi*, from the dusky-footed woodrat *Neotoma fuscipes*. However, only 1-5% of the *I. pacificus* ticks are infected, a number that epidemiologists believe is too low to maintain a spirochete reservoir in the woodrat population. Recently, Brown and Lane (1992) demonstrated that the disease cycle requires a second tick species, *I. neotomae*, which does not bite humans but is responsible for maintaining high levels of the spirochete in the woodrat population. Thus, Lyme disease can only exist in areas where the spirochete, the woodrat, both ticks, and humans co-exist.

3.4 Biodiversity and Ecosystem Function

Here we explore the hypothesis that different patterns of community diversity affect the efficiency of resource use in two Californian ecosystems. The resources considered are water, light energy and nitrogen, and resource use efficiency is defined as the ratio of the amount of resource taken up to the amount available. There are reasons to believe that communities should converge towards a set of species that produces a higher resource use than any other mixture of species (MacArthur 1972). Loss of biodiversity thus translates into less efficient resource utilization.

3.4.1 The Annual Grassland Ecosystem

Close to one-fifth of the Californian landscape is covered by grasslands, most of which are dominated by non-native annuals (Huenneke 1989). Biodiversity of grasses and forbs plays an important role in efficient exploitation of resources in this ecosystem. Factors affecting diversity patterns included unpredictable annual weather patterns, spatial distribution of resources and disturbance by animals and fire.

3.4.1.1 Disturbance, Predation, Inundation and Grassland Diversity

Grassland community structure is strongly controlled by disturbances. Gopher mounds, for example, have been shown to create special microhabitats within the annual grasslands and result in very different survivorship curves for different species (Hobbs and Mooney 1985). Clearly, species sort out along a disturbance gradient by their very different regeneration niches and some species even require gopher disturbance to enable them to establish and remain within the community. Thus, gopher activity maintains a higher overall community diversity and this is predicted by the model of Hobbs and Hobbs (1987).

Further, the disturbance regime creates a complex pattern of microsites which are most suitable for different species in different rainfall years (Hobbs and Mooney 1991). Domestic livestock grazing has the potential for upsetting this balance since it leads to exclusion of gophers (Hunter 1991), and although it creates bare soil of a different nature (Table 3.1), there is evidence that canopy gaps created by grazers and gopher mounds favour the same species (Peart 1989). The effect of grazers such as rodents and livestock on altering community composition has been documented by Talbot et al. (1939) (Table 3.2).

Harvester ants (*Veromessor andrei*) likewise have the potential for affecting the diversity of grasslands through their preference for seeds of non-dominant species (Hobbs 1985). In addition, ant nests alter the chemical and physical properties of the soil by elevating temperatures and levels of phosphorous, potassium and nitrogen, relative to the surrounding soils (Beattie 1989). Thus, loss of the ant guild could potentially greatly alter the community composition in these grasslands. It is unknown whether other seed-eating guilds, such as the Heteromyidae rodents, that compete with ants, have similar preferences.

In some respects, selection for diverse approaches to resource exploitation has resulted in a sort of co-evolutionary dance with other microbial and animal guilds that, in turn, select for greater diversity. For example, grasshoppers can affect the quality of their own host plants through feeding, potentially influencing biomass, resource allocation and the actual distribution of the individuals in the host plant population (Joern 1989). Perennials and C_4 species may tolerate grazing better than annuals or C_3 species. In addition, different weather patterns may generate different phenological patterns, both in plants and in their predators, and consequently the vulnerable species one year may not be the same in the next year. For example, larvae of the butterfly, *Euphydryas editha bayensis* depend on precise coupling between the host-plant phenology and larval development. Very wet years can uncouple this relationship by retarding larval development and result in localized extinction (Chiariello 1989).

Table 3.1. Mean percentage ground cover (and standard error) in grazed and ungrazed areas at Vina Plains Preserve, Tehama Co., California. (Hunter 1991)

Cover type	Ungrazed (n = 100)	Grazed (n = 50)
Bare soil	9.62 (1.2)	28.60 (3.3)
Gopher mounds	7.05 (0.9)	0.67 (0.5)
Rock	1.25 (0.4)	1.09 (0.3)
Vegetation	81.92 (1.3)	68.03 (3.3)

Table 3.2. Fluctuations in composition of annual grasslands under different treatments. (Talbot et al. 1939)

Plot	Treatment	Year	Total		Four most abundant species			
			Forbs	Grasses	*Erodium* spp.	*Bromus hordeaceus*	*Avena barbata*	*Bromus rigidus*
			Per cent of cover					
1	Rodents	1933	98	2	86	1	T	T
	and	1935	4	96	3	20	72	4
	livestock	1937	1	99	0	10	1	88
	excluded	1938	20	80	1	10	10	60
2	Only	1933	99	1	80	T	0	T
	livestock	1935	15	85	14	75	10	T
	excluded	1937	4	96	2	85	8	T
		1938	20	80	0	55	20	T
3	Grazed by	1933	98	2	82	T	T	T
	livestock	1935	79	21	50	5	T	T
	and	1937	67	33[a]	50	0	0	T
	rodents	1938	43	57[a]	10	24	T	T

T (Trace) = values less than 1%

[a] Includes *Juncus bufonius*

Impacts of herbivory by rodents has the potential for producing substantial changes in vegetation composition. Not only are there qualitative differences in food preferences but peaks in animal abundance may vary from year to year such that peaks may occur in winter one year and in summer the next year (Lidicker 1989). A classical example of herbivory's effect on biodiversity is preferential feeding on the imported Klamath weed (*Hypericum perforatum*) by the introduction of certain *Chrysomela* beetles as biological control agents which resulted in the return of native bunchgrasses (Huffaker 1951). Thus, herbivory has the potential for

creating a heterogenous selective landscape that would select for higher biodiversity.

Grasslands are also quite resilient to wildfires and such perturbations play an important role in eliminating invading shrubs and thus maintaining the herbaceous nature of this community. Wildfires also have the potential for altering the balance between different taxa (Larson and Duncan 1982; Parsons and Stohlgren 1989).

Inundation of grassland depressions which are underlain by an impervious hardpan support a unique vernal pool flora adapted to the seasonal alteration of winter inundation and summer drought. These azonal communities support a rich endemic flora and non-natives have not permanently established in most vernal pool communities. Unpredictable rainfall results in pools that remain filled for variable lengths of time from year to year and species appear to segregate out spatially and temporally according to the average water duration period (Fig. 3.9). (Zedler 1987). It could be argued that full exploitation of resources in this community is dependent upon this diverse array of plant strategies. Based on detailed comparison of carbon gain in representatives of this flora it has been argued that co-existence of this diverse community is enhanced by a disequilibrium process that favours some species in very wet years and others in dry years (Keeley and Sandquist 1991).

3.4.1.2 Grassland Diversity and Patterns of Resource Utilization

Biomass production in the annual grassland ecosystem is largely controlled by patterns of precipitation and temperature. Pitt and Heady (1978) described the impact of variation in weather patterns over an 18-year period on standing crop, cover and botanical composition. Typically, standing crop increased as the growing season progressed from March to June, although some species declined during this period and were replaced by other species. They also found that consistent precipitation following fall germination, and again during the period of rapid plant growth in spring, contributes to a "grass year", whereas quite a different set of conditions would favour forbs, e.g. biomass of *Erodium* spp. correlated with dry fall conditions.

Other researchers have likewise found evidence of significant niche differentiation in grassland species that could impact total net production for the community. For example, in laboratory studies, Hufstader (1976) showed marked differences in mean maximum, mean median and mean minimum temperatures necessary for maximum biomass production in two seemingly ecologically equivalent species of *Bromus*. In the field Johnston and Lathrop (1978) showed temporal segregation of *Erodium obtusiplica-*

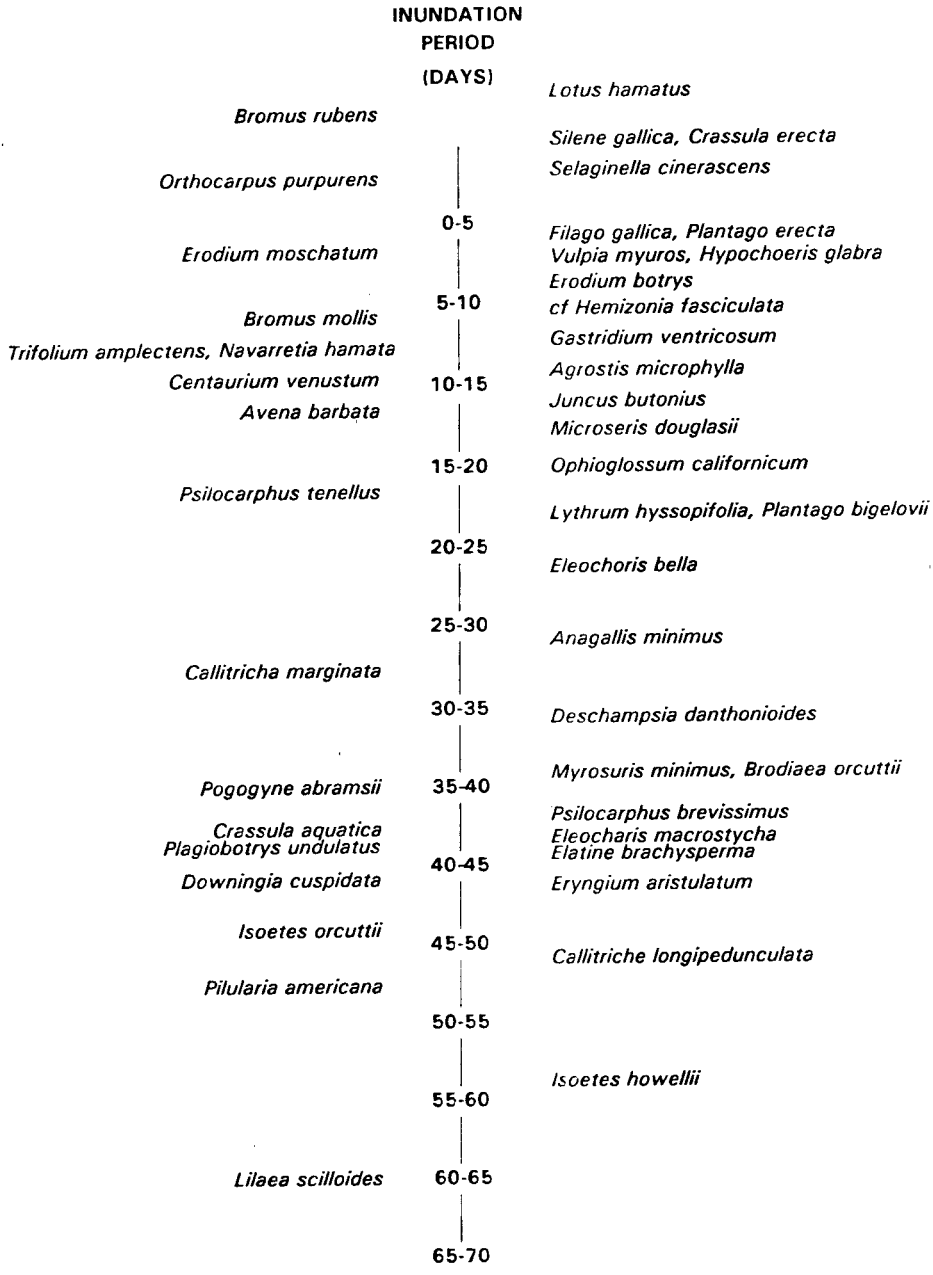

Fig. 3.9. Average water duration class for common vernal pool species for Kearney Mesa, southern California. (Zedler 1987)

tum, Avena barbata and *Holocarpha virgata* (Fig. 3.10). Elongation and phenological development of each species were correlated with temperature, daylength and soil moisture, and manipulated association experiments indicated that competition effects are not totally responsible for temporal phase segregation in the annual grassland. Martin and Harding (1981) showed that total reproductive rates of sympatric populations of two species of *Erodium* were greater than allopatric populations, further supporting the notion that species have evolved finely tuned differences in the manner in which they exploit the environment and that intra-specific competition is generally more intense than inter-specific.

Growth form diversity also leads to greater utilization of resources. Jackson and Roy (1986) showed that different annual patterns of rainfall and timing and duration of summer drought had markedly different effects on annual grasses compared to perennial grasses. It is to be expected that in exceptionally wet years perennial bunchgrasses would predominate and in exceptionally dry years annuals would succeed.

Marked phenological differences in the annual flora have been demonstrated by Gulmon et al. (1983) and Mooney et al. (1986b). Species differ in rooting depth and thus are separated by the portion of the soil profile where water is primarily extracted. This has a profound effect on flowering phenology and acts to extend the period of energy capture (Fig. 3.11). These species can be viewed as comprising two functional groups; the early flowering annuals and the late flowering annuals. Field studies have shown that if one or the other of these functional groups is removed from a site, it will result in decreased productivity (N. Chiariello, pers. comm.).

Marshall and Jain (1969) showed density-dependent differences in exploitation of resources by the nearly indistinguishable, and seemingly redundant species, *Avena fatua* and *A. barbata*. An analysis of the relative fitness of the two species in mixed populations indicated that they could successfully cohabit over the range of densities studied due to frequency-dependent selection favouring *A. barbata* in relative rarity.

Chiariello and Roughgarden (1984) have shown the potential for evolution of intra-genomic diversity as a mechanism of optimizing carbon allocation in ecotypes of an annual grassland plant that are either vernal or autumnal. Their results showed that autumnal ecotypes delay reproduction to later in the year as a means of reducing seed predation and this has transformed into different patterns for storage carbon.

Seed dormancy is one means of avoiding inter-specific competition and enhancing the distribution of different species in time in a manner that increases the exploitation of the environment. Jain (1982) showed that there was much variability in germination behaviour of five grass species and two legume species, and seasonal dormancy of *Avena* and *Bromus* was

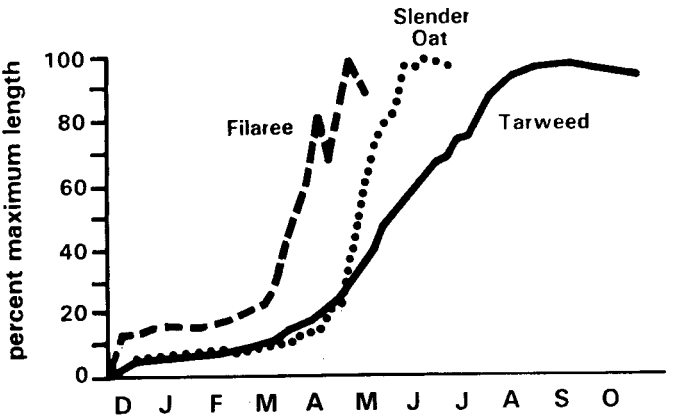

Fig. 3.10. Seasonal change in leaf length in filaree (*Erodium obtusiplicatum*), slender oat (*Avena barbata*) and tarweed (*Holocarpha virgata*). (Johnston and Lathrop 1978)

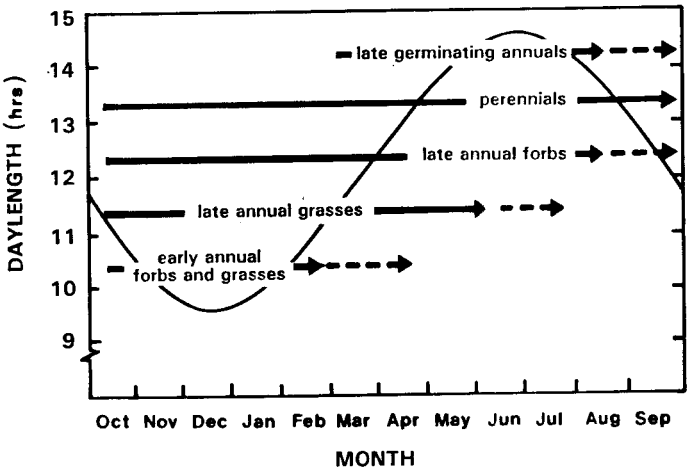

Fig. 3.11. Functional groups of grassland species based on phenological patterns. (Chiariello 1989)

highly correlated with the patterns of a probable rainstorm at different sites during the summer months. There is evidence that some of this variation is carried over between generations as maternal effects (Ewing 1981). In some cases a single species may diversify its germination behaviour. Stamp (1990) showed that *Erodium brachcarpum* seeds produced late in the fruiting period are likely to germinate in the year of seed production,

whereas seeds produced early in the season are larger, with a thicker seed coat and are likely to germinate in subsequent years.

Also, in this nitrogen-limited system there is microsite heterogeneity of inorganic-N availability. This arises because some microsites may be nitrate-depleted due to inherent spatial variation in the NH^{4+} pool available to ammonium oxidizers and because in some microsites microbial assimilation may out-compete plant assimilation (Davidson et al. 1990). Growth form diversity may play an important role in the spatial distribution of ammonium due to differences in amounts of standing dead and thus the amount retained against leaching. For example, prostrate forbs disarticulate and possibly decompose more rapidly than annual grasses, which stay erect in dry air. Grazers will contribute even more to this heterogeneity of nutrient pools (Center et al. 1989). Growth form diversity underground will also carry with it different competitive abilities in different seasons. Therefore, differences in nitrogen assimilation rates between species (Hull and Mooney 1990) and between annual and perennial grasses (Joffre 1990) may play important roles in affecting N cycling processes of this ecosystem. Differences between species may change during the year as demand for nutrients changes, and these will be affected by relative growth rates and by photosynthetic rates that determine the carbon available for nitrogen assimilation (Schimel et al. 1989).

The important role of biodiversity in exploiting this heterogenous micro-landscape of nutrient pools is suggested by experiments that show loss of native diversity and invasion by non-native weeds when this heterogeneity is buffered by the more or less even distribution of nutrients (Huenneke et al. 1990). In fact, McCown and Williams (1968) have presented experimental verification that under favourable nutrient conditions *Bromus mollis* becomes the superior competitor for light because of its greater stature and more erect leaf habit, but under nutrient-stressed conditions leaf area is considerably reduced and *Erodium botrys* becomes the superior competitor. Hull and Muller (1976) also demonstrated that *Bromus* species were superior under enhanced nutrients whereas *Avena* species had superior production under well-watered conditions, and Hobbs et al. (1988) showed that this superiority of *Bromus* under high nutrient conditions was over forbs as well.

Species specific differences in degree of mycotrophy may also play a critical role in the exploitation of soil nutrients. It appears that much of this annual flora is mycorrhizal (Chiariello et al. 1982; Hopkins 1987) and there are apparent differences in the dependence upon mycotrophy between different species and different growth forms (St. John 1993). These differences may have important ramifications for successional processes and interactions between ecosystems. Preliminary data suggest that many of these annuals and successional subshrubs such as *Diplacus, Eriogonum* and

Artemisia are facultatively mycorrhizal, whereas chaparral climax shrubs are often obligately mycorrhizal.

3.4.2 The Chaparral Ecosystem

This evergreen shrub vegetation dominates much of the Californian landscape, particularly on mountain slopes below 1500 m. Wildfires are an important disturbance factor in this community and they have a profound impact on many ecosystem processes.

3.4.2.1 Regeneration, Disturbance and Biodiversity

Grubb (1977) has suggested that maintenance of species richness in plant communities may be tied to differences in their regeneration niche. The regeneration niche of chaparral species can be represented by two functional groups; those having "disturbance-dependent" recruitment and those with "disturbance-avoiding" recruitment. In the first group, opportunities for recruitment and population expansion are restricted to a narrow window of time immediately after fire e.g. *Ceanothus* species in the subgenus *Cerastes*. In the latter group are species that survive fires by resprouting, but opportunities for recruitment and population expansion occur in the absence of disturbance e.g. shrub species of *Quercus*. These two functional groups have different patterns of survivorship as chaparral ages (Fig. 3.12).

Although species within each of these functional groups share many life history characteristics, they are not ecologically equivalent; individual species are often displaced geographically, as described above (Cody 1986).

Most communities are a mixture of these two functional groups and the relative success of one group over the other will vary with the pattern of disturbance. When the fire-return interval is very short, many disturbance-dependent taxa are unable to regenerate due to insufficient time for regenerating the soil seed bank. For example, fires in consecutive years can cause the localized extinction of some shrub taxa (Zedler et al. 1983). As fire frequency increases, many native species that regenerate after fire, are replaced by non-native weedy annuals (Fig. 3.13). This fact is well known to land managers who, for many years, have used high fire frequency for type-conversion of chaparral to annual grassland (Sampson 1944; Arnold et al. 1951). Species that resprout after fire are generally less sensitive to high fire frequency than obligate seeding species, and depending upon the particular species, they may have disturbance-dependent recruitment or disturbance-free recruitment.

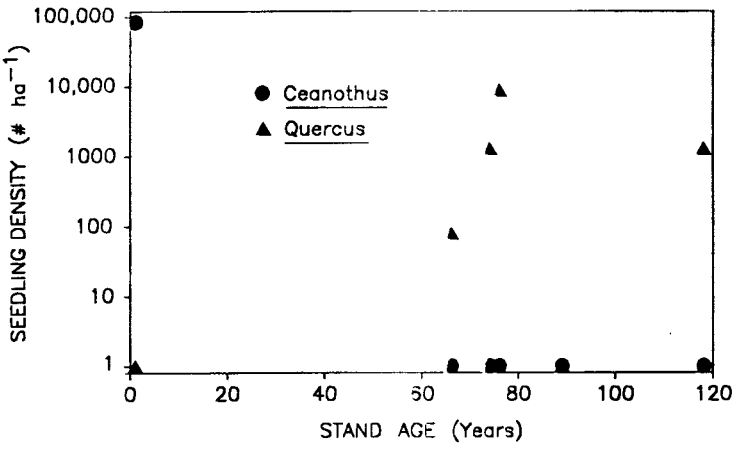

Fig. 3.12. Seedling recruitment and adult mortality as a function of stand age for *Ceanothus* and *Quercus*. (Keeley 1992a,b)

Extended fire-free periods are required for reproduction by species with disturbance-avoiding recruitment. Species in this functional group fail to recruit in postfire environments, and other gaps, because their seedlings are sensitive to drought stress (Davis 1989); thus recruitment is most successful under the canopy of older chaparral (Keeley 1992a,b).

Transition matrices provide a useful means of examining the effect of different fire frequencies on community composition of these two recruitment functional groups (Keeley, unpubl. data). By iteration we can model the demographic consequences of different recruitment modes in the disturbance-dependent mode of *Ceanothus* and the disturbance-avoiding mode of *Quercus*. Although *Ceanothus* suffers marked decline in older stands, their seed bank is capable of great persistence, making them reasonably resilient to long fire-free periods (Fig. 3.14A). The highly conservative resprouting mode of *Quercus* makes these shrubs relatively resistant to fire; however, seedling regeneration is markedly reduced by disturbance (Fig. 3.14B).

With this model we can predict how the demographic characteristics of these two functional groups will affect long-term community composition. If this transition matrix is iterated over repeated fire cycles of short and long fire return intervals we find substantial differences in the density of *Ceanothus* and *Quercus*. Over a period of repeated cycles of fires every 30 years, *Ceanothus* has the potential for population expansion (Fig. 3.15A). If fires are too frequent, *Ceanothus* declines due to insufficient time to accumulate a soil seed bank, and if fire frequencies are too infrequent, *Ceanothus* declines due to adult mortality and natural deterioration of the

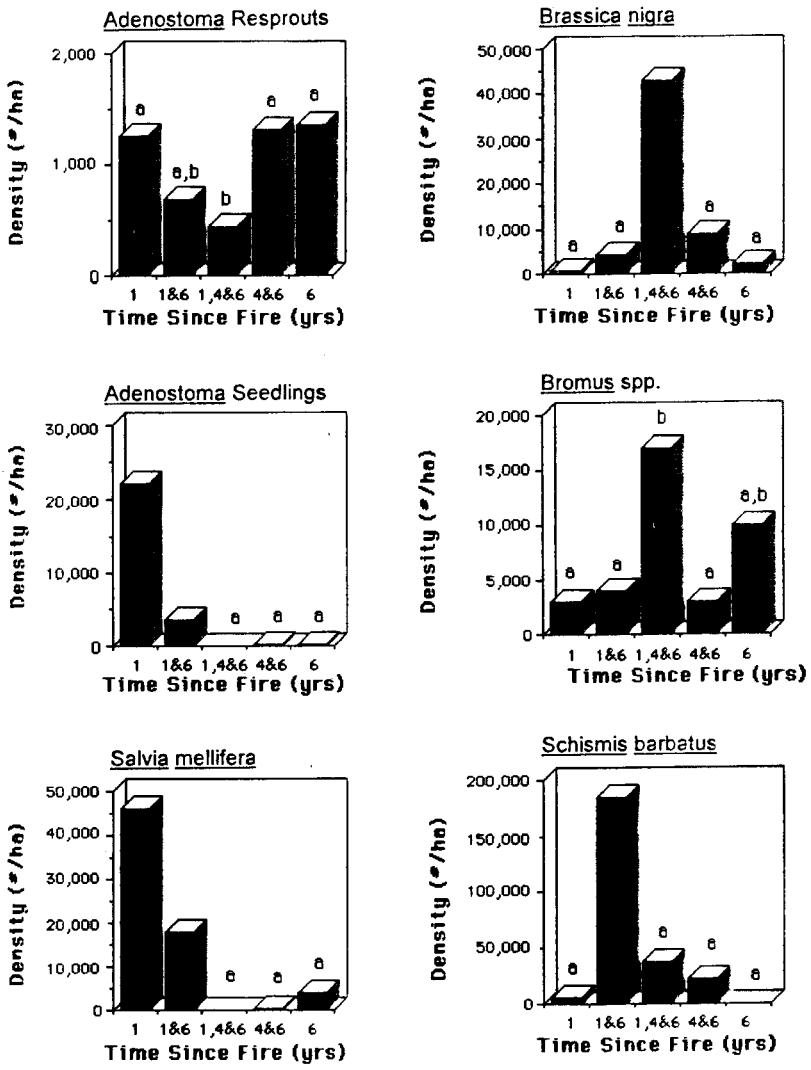

Fig. 3.13. Density of native shrubs and non-native annuals on sites subjected to different burning frequencies in southern California mixed chaparral. Each *bar* represents a different site subjected to burning during the indicated years of a 6-year cycle. Statistically significant differences are denoted by labels above the *bars*. (Haidinger and Keeley 1993)

soil seed bank (Fig. 3.15A). *Quercus* illustrates a more conservative pattern. It is largely unaffected by short or long fire-return intervals (Fig. 3.15B) and, in fact, will increase at fire return intervals of 150 years.

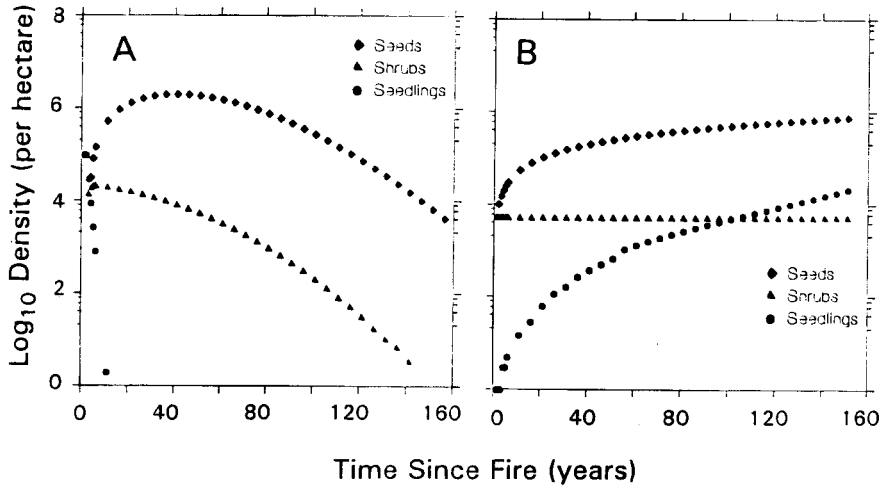

Fig. 3.14 A,B. Predicted sizes for state variables, shrubs, seeds, seedlings + juveniles for (**A**) *Ceanothus* and (**B**) *Quercus*. Transition probabilities and initial population sizes were based on values from the literature. (Keeley unpublished)

Under the conditions of these transition matrices, if fires occur at 30-year intervals, *Ceanothus* potentially could dominate, whereas at intervals of 100 years it declines and *Quercus* potentially dominates (Fig. 3.15A,B). Today, the shorter fire cycle is more typical of most chaparral sites due to the influence of humans on ignition of wildfires (Keeley 1982). Under natural conditions there are reasons to believe that, due to the stochastic nature of lightning ignitions, both short and long fire-return intervals were experienced by chaparral taxa. If we model such conditions (Fig. 3.15C) it is apparent that alternating long and short fire-return intervals result in an equilibrium in the density of *Ceanothus* and *Quercus*. In chaparral, co-existence of these functional groups is most likely enhanced by variable burning regimes, and thus biodiversity may be tightly linked to exploitation of the full range of fire regimes.

3.4.2.2 Diversity, Water Balance and Chaparral Functioning

In this summer-drought climate, water plays a critical role in the functioning of the chaparral ecosystem. Soil-water balance is intimately associated with the plant water balance and is a function of patterns of soil characteristics, precipitation, runoff, interception in the canopy, stemflow, throughfall, and infiltration. Plant water balance is intimately tied to potential plant biomass production and strongly affected by different plant characteristics (Fig. 3.16), and, not surprisingly, species differ in their sea-

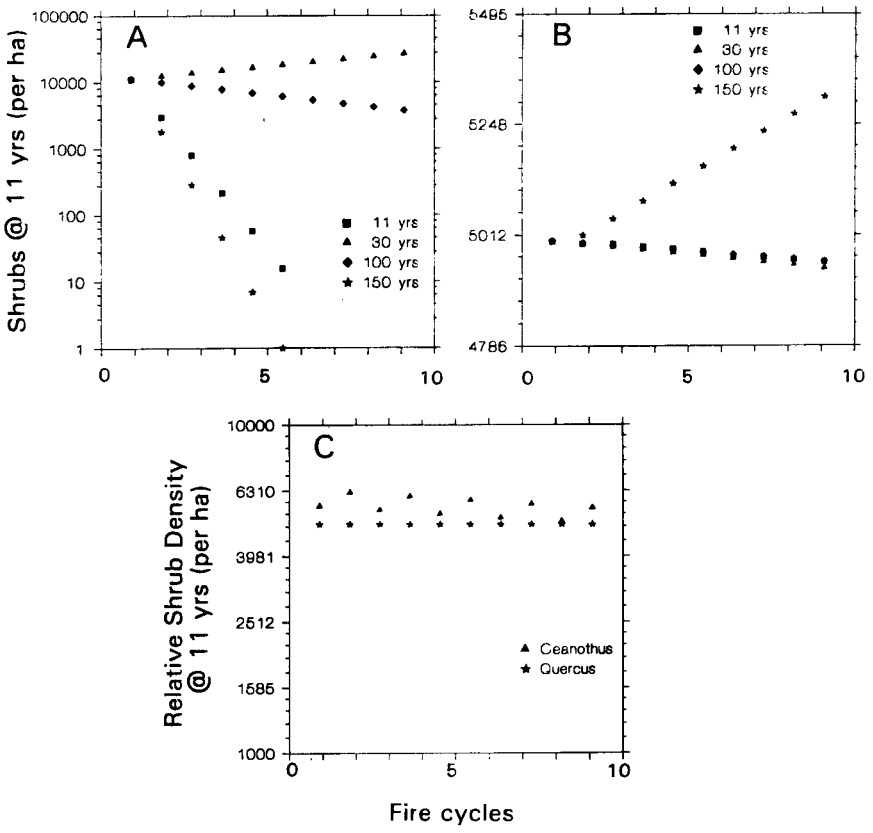

Fig. 3.15. A-C. Predicted shrub population density after 11 years at different fire-cycle return intervals for (**A**) *Ceanothus*, (**B**) *Quercus*, or (**C**) both taxa under an alternating fire regime of 30 and 100 years. Fire was introduced at the designated interval by multiplying the state vector of population size by a new "fire" transition matrix. (Keeley unpublished)

sonal patterns of water use (Poole et al. 1981). Water use efficiency (transpiration/precipitation) likewise varies between species and sites. Consequently, water capture efficiency for a site is strongly controlled by vegetation composition (Patric 1961) and different combinations of species may more fully utilize available soil moisture.

Chaparral can be categorized into different functional groups based on the mode of tolerating summer drought. Shrubs such as *Quercus, Rhamnus* and *Prunus* persist on arid chaparral sites, not because they are extremely drought-tolerant but rather due to their deep root systems, which penetrate fractured substrates and persist from one fire cycle to the next by resprouting; they survive summer drought because they are drought-

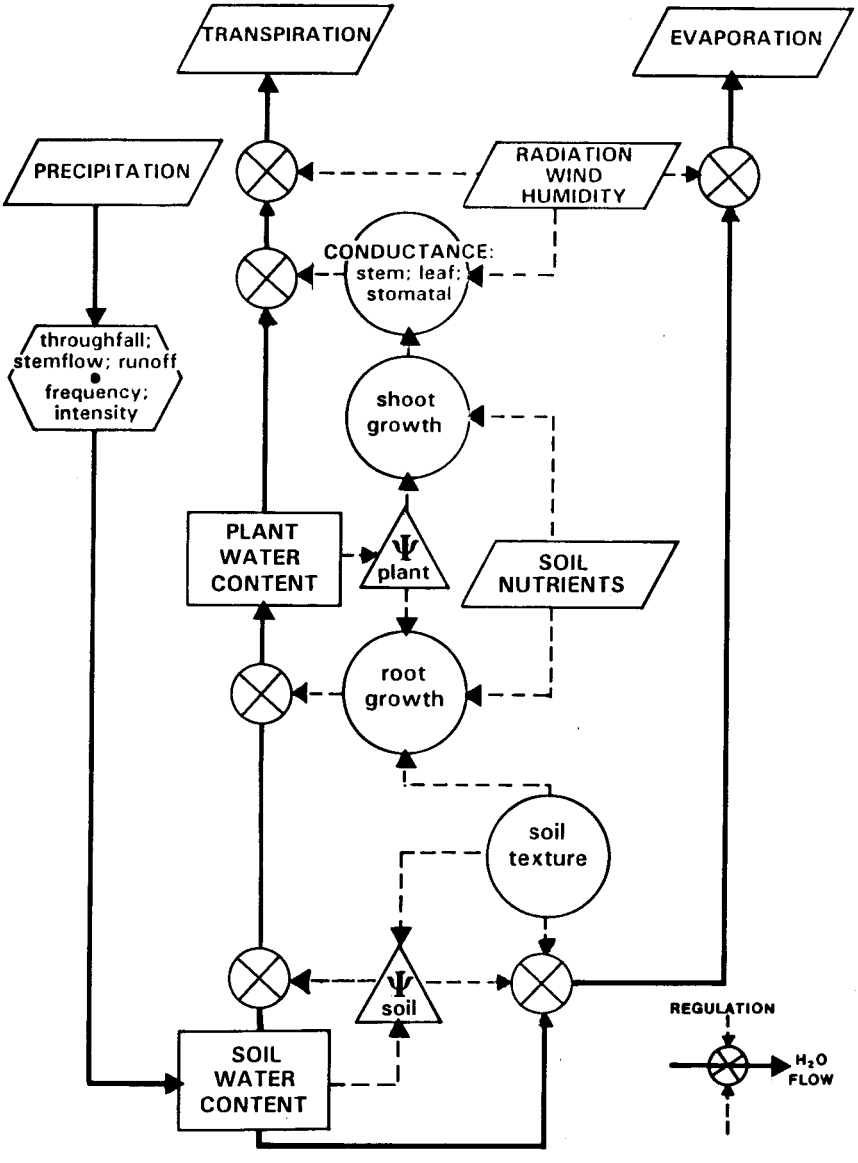

Fig. 3.16. Flow diagram of water through the soil-plant-atmosphere system, and controlling plant and environmental variables. *Heavy lines* flows of water; *broken lines* controls; *boxes* water storage; *circles* control variables; *psi* water potential. (Miller 1983)

avoiders. On the other, hand shrubs such as *Ceanothus* and *Arctostaphylos* are more drought-tolerant, but, because they regenerate after fire from seed, they have relatively shallow root systems. The vast majority of chaparral sites comprise mixed stands of deeply rooted and shallow rooted shrubs, which exploit water in very different ways. For example, on all but the most mesic sites, soil moisture is apparently insufficient to support pure stands of deep-rooted *Quercus*. The shallow-rooted *Ceanothus* fill in spaces between the *Quercus* and contribute shade and litter, both of which are required for *Quercus* seedling recruitment (Keeley 1992a).

The water balance for a site is markedly different after wildfires and is exploited differently by the diversity of growth forms normally present. Fire-following annuals, with rapid growth rates and fibrous roots exploit a very different part of the soil column than shrub seedlings or resprouts (Miller 1983). Seasonal patterns introduce a stochastic factor that makes some growth forms more efficient in years of light, evenly distributed rain, and other forms more efficient in years of heavy, infrequent storms. Also, subsurface topography, which may be quite heterogenous on a micro-topographic scale (Kummerow et al. 1981), means that sites most suitable for one species may be juxtaposed with sites more suitable for another. Very marked species-specific differences in growth rates of roots are just one way in which species may differ in their ability to exploit these microsite differences (Miller 1983). Although data are lacking, it is likely that the diversity of growth forms on a site will impact water yield following wildfires.

Other watershed processes tied to water yield include peak water flow, erosion and sedimentation. These likewise are linked to community composition through the diversity of root growth forms present on a site and are readily altered by disturbance such as fire or artificial type conversion. For example, in the San Dimas Experimental Forest of southern California, burned watersheds that were seeded and converted to annual grassland had an eightfold increase in landslides and sediment production (Knight et al. 1984). Such impacts are temporary and in the long term, converted water sheds yield greater stream flow, although other site factors, such as evaporative losses, increase greatly (Rowe and Reimann 1961).

3.4.2.3 Diversity, Nutrient Cycling and Chaparral Functioning

For many species, leaf nitrogen content and photosynthetic capacity are highly correlated (Field and Mooney 1983). In chaparral, fertilizer application studies indicate some species such as *Adenostoma fasciculatum* are more nutrient-limited than others such as the nitrogen-fixing *Ceanothus* species (McMaster et al. 1982). The highest concentrations of soil nutrients

tend to be in the upper soil layers (Christensen and Muller 1975), thus, shallow-rooted shrub species may have a competitive advantage. Rooting depth, of course, will impact water relations and thus different growth forms carry with them different trade-offs. This is most evident in the relationship between nitrogen use efficiency and water use efficiency (Fig. 3.17).

Fire acts to recycle nutrients tied up in organic matter but also generates substantial losses; up to two-thirds of the total nitrogen in litter and soil are lost during an intense fire (DeBano et al. 1979). Wet- and dry-fall inputs are so low that it may take >60 years to replenish these losses, although in polluted regions of southern California nitrogen input may be 10-20 times greater than elsewhere (Schlesinger and Gray 1982). Postfire successional species on many sites are nitrogen-fixers, e.g. annual *Lupinus* spp. or the subshrub *Lotus scoparius* (Rundel 1983), and of lesser importance is asymbiotic nitrogen-fixing microbes (Dunn and Poth 1979).

Also critical to the nitrogen balance in chaparral is the postfire annual flora that captures much of the mineralized nutrients that would otherwise be lost in runoff. The fire-specialist species are a highly diverse group and only occur on burns; disappearing after the first or second year. Other species in the postfire flora are less specialized and persist for much longer after fire. There is evidence that these two groups of species have very different nitrogen utilization strategies (Swift 1991). It appears that fire specialists such as *Phacelia brachyloba* and *P. minor* preferentially utilize ammonium and are apparently adapted to taking advantage of the high soil ammonium levels immediately after fire. These fire specialists, however, have much lower nitrogen-use efficiency than generalist species, that persist later in succession, such as *Cryptantha intermedia, Phacelia cicutaria* and *Brassica nigra.* It is unclear what the ecosystem impact would be if one or the other of these groups were eliminated from the chaparral, but it is possible that this diversity of postfire annuals plays an important role in the chaparral nutrient cycle. In light of the fine-scale pattern of soil nutrient distribution after fires (Rice 1993), a diversity of structural and functional growth forms may play a key role in the nutrient cycle of chaparral. Failure to retain or return nitrogen to a site potentially could result in site degradation to less diverse forms of chaparral such as *Adenostoma fasciculatum* dominated chaparral.

3.4.2.4 Energy Capture, Resource Use and Biodiversity

Photosynthetic capacity is one of the principal determinants of primary productivity. On a landscape scale, different plant attributes contribute to dramatic differences in predicted carbon gain along gradients of moisture

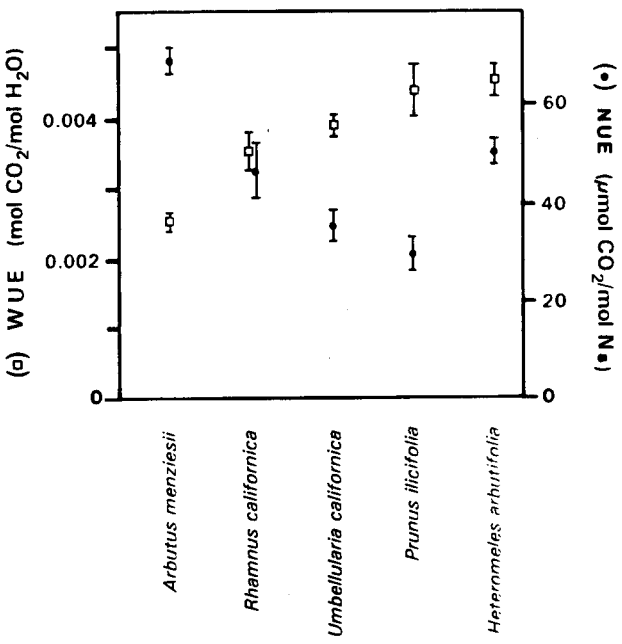

Fig. 3.17. Water-use efficiency (*WUE*) and nitrogen-use efficiency (*NUE*) in five Californian evergreen shrubs. Species range from those typical of moist sites on the *left* (viz. *Arbutus menziesii*), to those typical of dry sites on the *right*. (Field and Davis 1989)

and temperature (Oechel et al. 1981). There is a strong correlation between total seasonal carbon uptake and percentage cover of a species at a particular site, suggesting that no single species is best adapted to all parts of the landscape (Fig. 3.18). Increased growth form diversity results in a seasonal increase in duration of plant growth at a site (Fig. 3.19).

Chaparral taxa differ greatly in their ability to maintain net carbon gain under stress. In general, there are apparently physiological constraints that result in species capable of net photosynthesis under water stress being sensitive to light stress and vice versa (Oechel et al. 1981). In other words, shrubs seem to fall naturally into either functional groups of either drought-adapted or shade-adapted species. On a local scale one might predict that a mixed chaparral community would be more likely to optimize resources than monotypic stands of any single species.

In order to look at the role of biodiversity on resource utilization in chaparral, Miller et al. (1978) designed an ecosystem simulator called MEDECS. This multi-compartment model simulated seasonal patterns of resource use and demonstrated that shrub species had very different daily and seasonal patterns of uptake of water, solar energy and nitrogen. In ad-

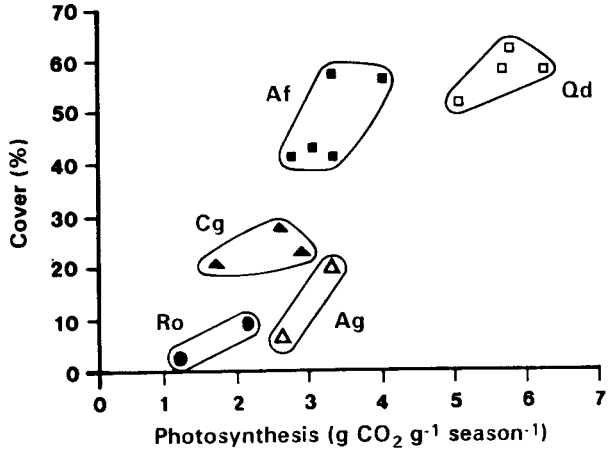

Fig. 3.18. Relationship between total seasonal photosynthesis and percentage cover of a species at a site from various elevations *Af Adenostoma fasciculatum*; *Qd Quercus dumosa*; *Cg Ceanothus greggii*; *Ag Arctostaphylos glauca*; *Ro Rhus ovata*). (Oechel et al. 1981)

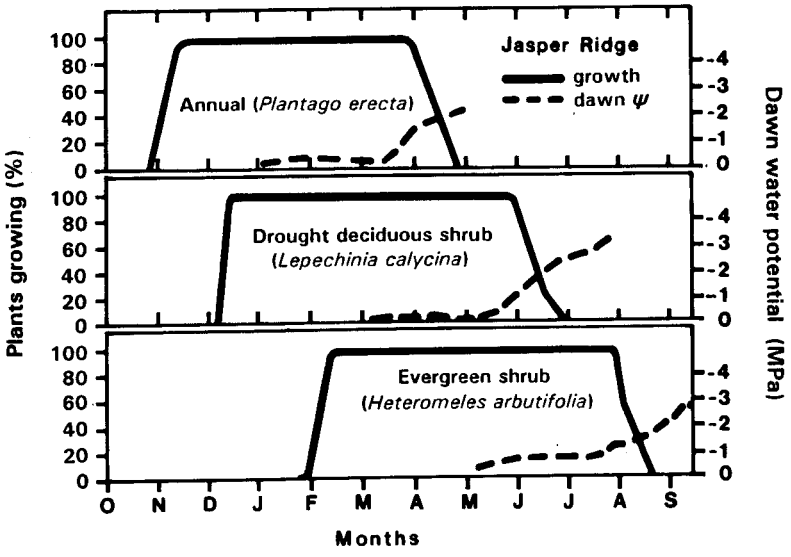

Fig. 3.19. Growth, and dawn water potentials of three different growth forms of mediterranean-climate plants from northern California. (Mooney 1983)

dition, simulations were run with various combinations of four species competing for light, water, nitrogen, and phosphorus. Unfortunately, Miller et al.'s (1978) simulations would predict quite different conclusions

dependent upon assumptions 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 this, their models are an important avenue for exploring the question of biodiversity and ecosystem function. 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 (Fig. 3.20A). However, for other aspects of resource use, such as nitrogen uptake, single species exhibited greater resource use than mixed communities (Fig. 3.20B). Thus, these simulation did not consistently predict that resource use by mixed species chaparral would be greater than 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.

3.5 Conclusions

In mediterranean-climate California, biodiversity is viewed as having an impact on ecosystem functioning in two fundamental ways. In grassland and chaparral there is reasonably good evidence that ecosystem functions, such as transfer of water, nutrients and carbon, are sensitive to the reductions in diversity of growth forms (above- and belowground), phenologies, physiologies and recruitment strategies. Species that are ecologically redundant in one character, e.g. recruitment mode, typically are not ecologically equivalent to the same taxa in other characters. Additionally, ecosystem processes, including trophic level linkages, are considered relevant ecosystem functions, since without them, ecosystems cannot persist. It is worth noting that some species may have limited control of ecosystem functions such as energy flow, but may be important controllers of ecosystem processes such as pollinator resources.

An impressive illustration of the key role played by certain species in ecosystem functioning is the massive extinction of late Pleistocene mammals, where loss of certain megaherbivores had a cascading effect, possibly causing the extinction of much of the mammalian fauna of California.

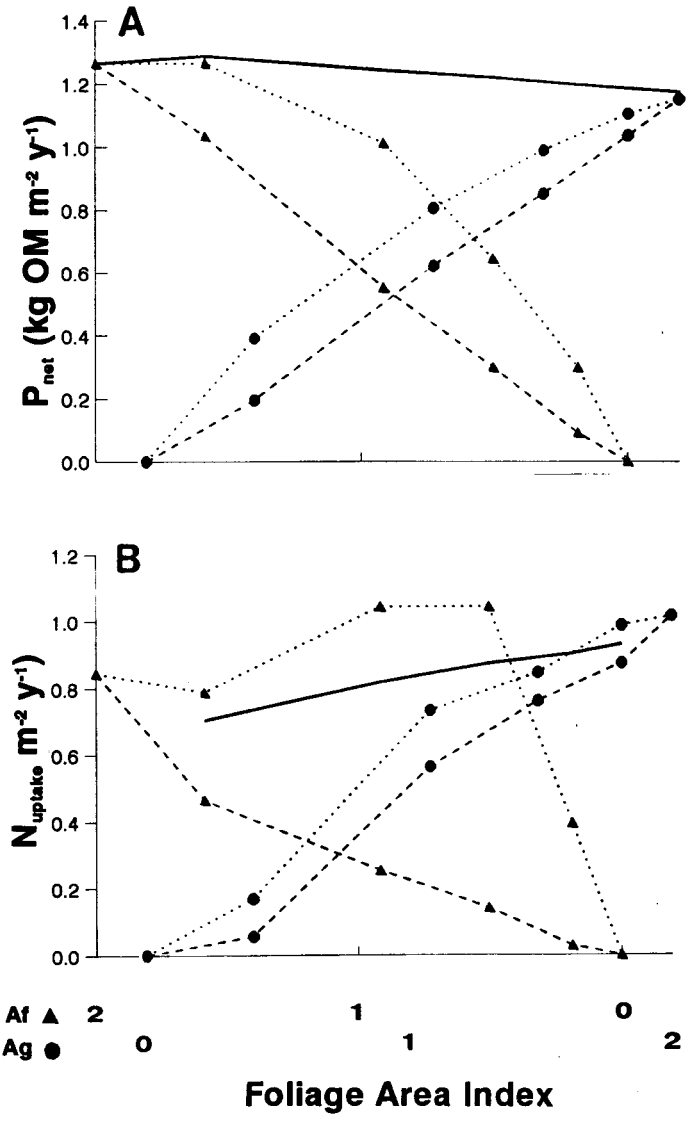

Fig. 3.20 A,B. Simulated patterns of **A** net photosynthesis and **B** total N uptake by *Arctostaphylos glauca* (*circles*) and *Adenostoma fasciculatum* (*triangles*) growing alone (*dotted line*) or with the other species (*dashed line*). The *solid line* is the sum of the two species growing together with a constant foliage area index of 2. The foliage area index of *A. glauca* increases from left to right (2 to 0). The differences between the *solid* and *dashed* lines of a species represent the effects of competition on the species. (Miller et al. 1978)

3.6 Future Research Needs

A definitive answer to the question of the role of biodiversity and ecosystem function requires experimental work specifically designed to address this question. Presently one such study is underway with the annual grassland ecosystem at Jasper Ridge (N. Chiariello, pers. comm.). Extending such studies to native ecosystems, such as chaparral and oak woodland would be important to the broader picture of biodiversity and ecosystem functioning in California. Due to problems inherent in large-scale manipulations of such communities, it may be logistically more feasible to utilize natural experiments that have manipulated biodiversity through grazing or type conversion projects and compare carbon, water and nutrient budgets for sites of differing diversity. While such an approach may tell us much about the functional significance of alpha diversity, other approaches may be necessary in order to evaluate other scales of diversity. Transplant studies that examine the degree of redundancy in species which appear to be ecological equivalents would be one way of examining the functional significance of gamma and beta diversity.

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