



LANDSCAPE ECOLOGY: STUDY OF MEDITERRANEAN GRAZED ECOSYSTEMS

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ECOLOGICAL HISTORY OF THE CALIFORNIA MEDITERRANEAN-TYPE LANDSCAPE

James W. Bartolome
Department of Forestry and Resource Management
University of California, Berkeley

Résumé

Le present article passe en revue les effets a long terme de la geologie du climat et de l'immigration humaine sur les paysages Méditerranéens de la Californie.

L'histoire écologique du paysage Californien commence avec le phénomène de la tectonique des plaques qui a créé la geologie complexe des sediments marins et des roches metamorphiques et volcaniques. Ces processus, sous l'influence du courant froid de Californie, ont abouti au climat Méditerranéen caractéristique durant les derniers trois millions d'années. La faune et la flore natives de la Californie representent des groupes selectionnés dans l'éventail plus large des espèces qui etaient présentes et adaptés au climat à été pluvieuse avant le Pliocene à travers l'ouest de l'Amerique du nord.

Les oscillations climatiques durant les derniers 150,000 ans ont été considerables, avec de longues périodes d'avance glaciaire et un climat plus frais et plus humide mais qui conservait une période sécheresse estivale accentuée et avait des periodes plus chaudes et plus sèches qu'au present. Ces oscillations climatiques, qui se sont poursuivies durant l'Holocène, ont probablement en une influence récente importante sur l'étendue et la composition des types de vegetation dominés par Quercus et sur la végétation cotière, mais pas sur le "chapparal" ou la prairie.

L'influence humaine commence après 12000 B.P., à la fin de la dernière glaciation, et a sans doute provoqué l'extinction de quelques types de grands herbivores et une augmentation de la fréquence des incendies. L'influence humaine au cours des 150 dernières années se traduit par l'agriculture, l'urbanisation et l'introduction de nouvelles espèces plantes. L'introduction de l'agriculture et d'espèces nouvelles sont les deux facteurs les plus importants dans le changement de la dynamique et de la répartition des paysages.

L'interpretation des changements dans le paysage est étroitement liée à l'échelle temporo-spatiale considérée, les diverses causes de la dégradation des écosystèmes, de leur amélioration et la diversité régionale. La fiabilité des interpretations écologiques et les recommandations pour l'aménagement peuvent être améliorées en utilisant une approche qui met en relation les explications (holistique) et reductionistes pour la dynamique des paysages.

Summary

This paper reviews the long-term effects of geology, climate, and human immigration on California's Mediterranean landscapes.

The ecological history of the California landscape starts with the process of plate tectonics, which has created a complex geology of sea-floor sediments, metamorphic, and volcanic rocks. These processes, under the influence of the cold California current, developed the characteristic Mediterranean climate over the past 3 million years. California's

native flora and fauna represent groups selected from the larger array of species present in and adapted to the summer rainfall climate present before the Pliocene throughout western North America.

Climatic fluctuations over the past 150,000 years have been dramatic, with extended periods of glacial advance and cooler and wetter climates, although still with pronounced summer drought, and interspersed with periods warmer and drier than at present. These climatic shifts, which have extended into the Holocene, probably have had important recent impacts on the extent and structure of *Quercus* dominated vegetation types and coastal scrub, but not on chaparral or grasslands.

Human influences began after 12,000 BP, the end of the last major glacial advance, and included possible extinctions of large herbivores and increased fire frequency. Human impacts in the last 150 years have included cultivation, urbanization, and introduction of new species. Of these factors, cultivation and plant species introductions appear most important in changing patterns of landscape dynamics.

Interpretations of landscape change are strongly influenced by spatial and temporal scale, the differing causes of ecosystem degradation and improvement, and regional variability. The reliability of ecological interpretations and management recommendations can be improved using an approach which links holistic and reductionist explanations for landscape dynamics.

Introduction

This paper outlines the ecological history of the Californian landscape, linking natural factors to human impacts. The review describes long-term changes, emphasizing geology, vegetation, and climate; and concludes by identifying some weaknesses in information and theory.

A landscape is a diverse collection of more homogeneous sub-units called ecosystems (Forman and Godron 1986). Ecosystems are in turn comprised of biotic communities and their environment. The landscape approach explicitly allows for the detection and analysis of spatial and temporal pattern and inference about causal relationships, a central aim for ecologists. Changes in landscapes imply long term and often imprecisely understood processes, such as climatic change and prehistoric human impacts. Landscapes by definition include the range of natural disturbances in biotic communities (Urban et al 1987).

Ecologists tend to use a favorite set of temporal and spatial scales to detect pattern. This strategy is acceptable if the effects on ecological conclusions are recognized (Bartolome 1989). Normally, trends and fluctuations are detectable only at specific scales. As temporal scale becomes longer, the appropriate spatial scale to detect pattern also becomes larger, thus long-term changes are most effectively described over large areas.

For most of human history the Californian landscape remained pristine, free of human influence. Once people discovered North America about 12,000 BP, they began the extensive use of abundant natural resources that continued through about 1800 AD. In the late 18th century the Spanish pastoral system was imported via Mexico, beginning a progression towards more intensive resource use that continues today (Burcham 1957).

Management technology and resource management objectives have changed remarkably during the last 200 years. Today California has some of the most productive crop-

lands in the world. Recently, increasing conflicts among urban development, intensive agriculture, extensive pastoralism, and protectionism, have led to increasingly rigid distinctions among these various resource management objectives. The lack of a long-term perspective on the causes and interpretation of changes in the landscape contributes to conflicting goals and objectives for the public and for ecologists.

Geologic History

Most of the following information is taken from an excellent summary by Alt and Hyndman (1975) and from Norris and Webb (1976). Geologic history forms the foundation for understanding landscape development.

The Pacific Ocean and plate tectonics are the fundamental factors shaping the California landscape. In the Triassic period, about 220 million years ago, the North American and Pacific Plates collided, forcing ocean floor under the overriding western edge of the continent. This action eventually would produce the metamorphic and volcanic rocks of the major mountain ranges, the Sierra Nevada and the Klamath Mountains (Figure 1).

As the old sea floor surface of the Pacific was scraped off, it formed the most important basic rocks of the Coast Ranges, the sandstones, shales, and cherts of the Franciscan formation. Ultrabasic rocks from deeper ocean bottom were forced upwards through the Franciscan sedimentary layers to form serpentine soils with their often unique floras. Continued action of the two plates still distorts and elevates the coastal mountains which form the western edge of the Central Valley.

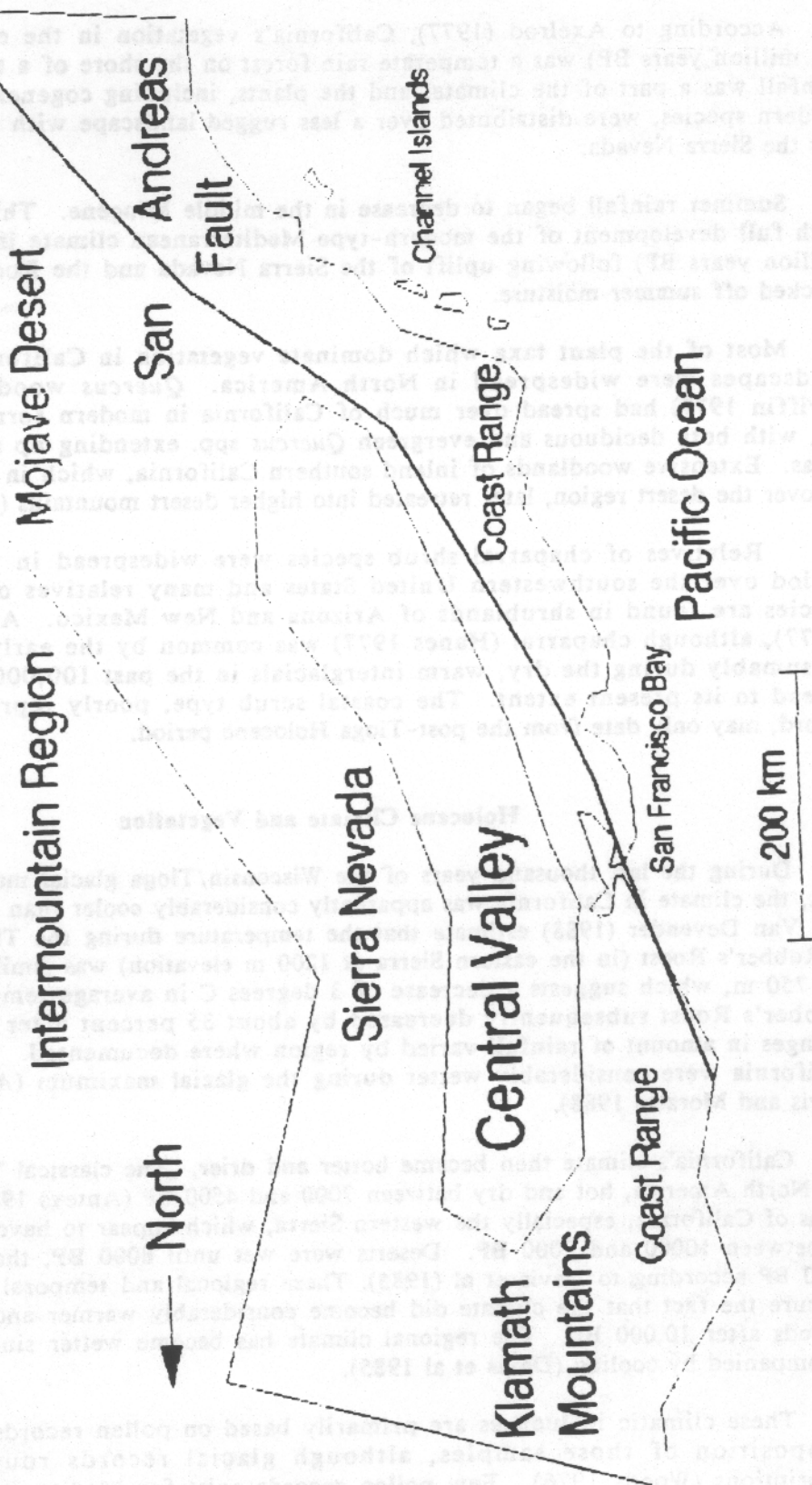
The Central Valley began filling with sediments, now hundreds of meters deep, in the Cretaceous period about 80 million years ago. Originally an inland sea, it filled with enough sediment to become mostly dry land by 1.5 million years ago.

Already a significant mountain range, the Sierra Nevada tilted and became several thousand meters higher in the Pliocene period. This uplift, beginning about 5 million years ago, had major effects on the regional environment. Also important, and relatively recent, was the beginning of movement of the San Andreas Fault, which in 15 million years moved granites from the southern Sierra Nevada to their present locations 500 km farther north, as far as San Francisco.

Geologic processes at a continental scale continue, but within the past 150,000 years, global climatic events have modified the basic geologic structure and associated landscapes in ways which modify the slower processes of plate tectonics. Important have been the changes in sea level associated with ice ages, which, with uplift of coastal lands, has produced distinctive coastal terrace landscapes. The most recent major glacial retreat began about 14,000 years ago, ending the Tioga glacial period in the Sierra, which generally corresponds with the late Wisconsin in North America and the Wurm in the Alps (Woods 1976). As glaciers melted, the rising sea level drowned the mouth of the Sacramento River to form San Francisco Bay.

Because so much of California's Mediterranean landscape rests on the unstable sedimentary rocks of the Franciscan formation, mass movement of soil is common. These movements are an integral feature of the landscape, which typically exhibits multiple landslides of varied ages but associated with intense rainfall events (Smith and Hart 1982). Removal of woody vegetation often leads to disastrous mass movement (Heady and Pitt 1979). Norris and Webb (1976) claim that slides on Franciscan substrate transport more material in the North Coast ranges than streams.

Figure 1. Location of California's Physical Features.



Pre-Holocene Climate and Vegetation

According to Axelrod (1977), California's vegetation in the early Miocene period (25 million years BP) was a temperate rain forest on the shore of a tropical sea. Summer rainfall was a part of the climate, and the plants, including cogenetic ancestors of many modern species, were distributed over a less rugged landscape with neither Coast Ranges nor the Sierra Nevada.

Summer rainfall began to decrease in the middle Miocene. This process culminated with full development of the modern-type Mediterranean climate in the late Pliocene (3 million years BP) following uplift of the Sierra Nevada and the Rocky Mountains which blocked off summer moisture.

Most of the plant taxa which dominate vegetation in California's Mediterranean landscapes were widespread in North America. *Quercus* woodlands and savannas (Griffin 1977) had spread over much of California in modern form by 5 million years BP, with both deciduous and evergreen *Quercus* spp. extending up and down the coastal areas. Extensive woodlands of inland southern California, which in the Pliocene extended over the desert region, later retreated into higher desert mountains (Axelrod 1977).

Relatives of chaparral shrub species were widespread in the Middle Miocene period over the southwestern United States and many relatives of present California species are found in shrublands of Arizona and New Mexico. According to Axelrod (1977), although chaparral (Hanes 1977) was common by the early Pleistocene, it was presumably during the dry, warm interglacials in the past 100,000 years that the type spread to its present extent. The coastal scrub type, poorly represented in the fossil record, may only date from the post-Tioga Holocene period.

Holocene Climate and Vegetation

During the last thousand years of the Wisconsin/Tioga glacial maximum, about 14,000 B.P., the climate in California was apparently considerably cooler than at present. McCarten and Van Devender (1988) estimate that the temperature during the Tioga glacial maximum at Robber's Roost (in the eastern Sierra at 1200 m elevation) was similar to that now found at 1750 m, which suggests a decrease of 3 degrees C in average temperature. Rainfall at Robber's Roost subsequently decreased by about 35 percent after glacial retreat. The changes in amount of rainfall varied by region where documented. Coastal and Southern California were considerably wetter during the glacial maximum (Adam and West 1983, Davis and Moratto 1988).

California's climate then became hotter and drier. The classical "altithermal" described for North America, hot and dry between 7000 and 4500 BP (Antevs 1948), does not fit some areas of California, especially the western Sierra, which appear to have had maximum aridity between 10000 and 7000 BP. Deserts were wet until 8000 BP, the coastal regions until 7000 BP according to Davis et al (1985). These regional and temporal variations should not obscure the fact that the climate did become considerably warmer and drier for significant periods after 10,000 BP. The regional climate has become wetter since 3000 BP, probably accompanied by cooling (Davis et al 1985).

These climatic influences are primarily based on pollen records and inference from composition of those samples, although glacial records roughly support these descriptions (Woods 1976). Few pollen records exist for Mediterranean-type vegetation in coastal California.

Axelrod (1977) claims that two major types, the *Quercus agrifolia* forest and the *Quercus douglasii*-*Pinus sabiniana* woodland have recently changed, the former extending over more of Southern California, the latter eliminated over much of southern California during the Xerithermic (Holocene period, 7000-4500 BP). Holocene reduction in the extent of *Q. douglasii* is supported by the apparently relictual populations in California's Channel Islands (Muller 1967).

California's Mediterranean climate in the past few millennia has been rather poorly described. From tree-ring records we know that there have been extended periods (several decades) of below average rainfall in the past 500 years (Fritts and Gordon 1980). However, the effects of those periods on the extent and structure of vegetation apart from a few thousand tree rings is unknown. Records are mainly from Intermountain Region locations at high elevation.

Between 1600 AD and the present, tree ring analyses reveal a major dry spell from 1760-1820 sufficient to have significant impacts on vegetation structure and distribution (Fritts and Gordon 1980). Another better documented dry period from 1860 to 1885 is often considered as a contributor to the demise of the native perennial grassland and replacement by Mediterranean annuals (Heady 1977).

Recently California's weather has been "normal" in the context of 100 years of record. The extreme and largely undocumented drought at the end of the 18th century was worse than that experienced in the well-publicized droughts of the late 1970s and late 1980s. Generally, the 20th century has been one of relatively high rainfall compared to the past 500 years. This record of tree-rings is also supported by the recent (700 BP to present) glacial advance (Woods 1976).

First Human Impacts

Human immigration into California about 12,000 BP had an unknown effect on the landscape. As with other areas of the world, the effects of human immigration into North America on flora and fauna are confounded with dramatic changes in climate. Speculation that mass extinctions of the megafauna after this time were the result of human hunters and their activities is supported inferentially but by little direct evidence (Martin 1973). A large and diverse fauna of grazing and browsing animals were present in California until a series of extinctions between 20,000 and 10,000 BP (Wagner 1989). These extinctions were concentrated in megavertebate genera, and distinctly non-random (Marshall 1988). Numbers of a few species, antelope and tule elk, remained high until the early 1800s (McCullough 1971).

Although fire was undoubtedly a tool used by prehistoric Californians (Sampson 1944), the impacts of deliberate burning on vegetation are not easily determined (Heady et al *In Press*). Fire frequency in Mediterranean types has changed significantly in the past 300 years, with fires much more frequent in the *Quercus* woodland between 1848 (before settlement) and 1948 than either before or after (McClaran and Bartolome 1989a).

During the first period of human occupation, several well-documented changes occurred in major ecosystem types adjacent to the Mediterranean zone. In the Intermountain region, shrub and woodland types showed remarkably rapid changes in dominant vegetation linked to climate and fire (Mehring 1986). *Artemisia tridentata* dominance shifted over a short period, and *Juniperus* Spp. moved hundreds of meters in

elevation over a few hundred years. Similar documentation is not available for Mediterranean-type vegetation, but such rapid changes were likely (Axelrod 1977).

Europeans: Their Livestock and Annual Plants

The introduction of livestock and crop agriculture into the California grassland has been exhaustively chronicled (Burcham 1957, Heady 1977, Heady et al *In Press*). The effects on woody types is much less documented, although extensive areas of chaparral and coastal shrub have been converted to crop or urban (FRRAP 1988) and areas of woodland have been thinned for range improvement or cleared for agriculture (Bartolome et al 1986).

The grassland was affected by the combination of several factors which cannot be properly evaluated independently: grazing, introduction of alien plants, and cultivation (Heady et al *In Press*). Grazing, beginning in the late 1700s along the coast and spreading inland, achieved heavy stocking levels by the mid-19th century, which weakened the native perennial grasses. The natives apparently did not evolve under heavy year-long grazing pressure (Heady 1977). Exotics, largely annual, and from the eastern Mediterranean, replaced the natives during the same period of livestock increase (Baker 1989).

Cultivation, which had been local around the coastal mission settlements, spread rapidly beginning in about 1860, further restricting range areas and eliminating native plants from several million hectares of grassland and woodland (Burcham 1957). Unknown areas of shrubs and trees were cleared.

Prehistoric Vegetation Compared to Present

The four major Mediterranean vegetation types in California have undergone considerable change since prehistoric times. Humans, changes in fire regime, and continuing long-term environmental trends have had significant but differing effects.

Grasslands: The grassland's original extent is unknown. Most grassland ecologists suggest an overall extent similar to the present grassland, exclusive of areas under cultivation (Heady et al *In Press*). Grasslands in California occupy an unusual climate, with pronounced summer drought, but are favored by geologic history. Because so much parent material is old sea-floor sediments, weathering produces fine-textured soils which often support grassland. The often unstable substrates favor herbaceous over woody vegetation. Areas with rolling topography and an underlying claypan, support unique vernal pool grasses (Heady 1977). The serpentine grasslands formed on soils derived from ultrabasic rock (Murphy and Ehrlich 1989).

The boundaries with *Quercus* savanna may have moved due to tree removal over the past 150 years, but the area involved is undetermined (Bartolome 1987). Suggestions of shrub invasion into former grasslands likewise account for only a small percentage of the total area (Wells 1962) and are likely to be compensated by grassland expansion.

The pristine grassland probably included perennial bunchgrasses with some native annuals: more annuals where drier, fewer where wetter (Heady 1977, Heady et al *In Press*); support for this notion is surprisingly weak. Only one study documents replacement of a native perennial grassland by annuals (Bartolome et al 1986). Now, the grassland is almost entirely dominated by annuals from the Old World, which form a new

stable vegetation type. Appearance and productivity of the landscape has not changed much, but species were replaced.

Known climatic changes are insufficient to account for alteration of the grassland dominants, as the present and past dominant species have sufficiently broad tolerance, as exhibited by present geographic distribution (Heady et al *In Press*) and physiological characteristics (Jackson and Roy 1989) to survive *in situ* the changes in climate characteristic of the past 100,000 years.

Changes in grazing pressure and fire are insufficiently known to determine the impacts on plant communities, although as a generalization, fire would favor native perennials, season-long use by livestock the annuals (Heady 1977). The biggest impact on vegetation was the plant introductions which altered the flora. The next biggest impact was cultivation.

Changes in grazing regimes resulting from activities of Europeans are not necessary to explain the replacement of the native grassland by exotic annuals. The biggest changes in grazing fauna and grazing impacts occurred between 20,000 and 10,000 BP, with loss of many taxa, long before livestock introduction. California's native grasses or close relatives have been present since the Pliocene, thus the Holocene release from grazing pressure by large ungulates was a short-term event. I believe that the native grasslands would have disappeared with introductions of exotic plants even without livestock grazing. The replacement of native perennials by annuals without grazing has been occasionally observed (Bartolome and Gemmill 1981).

Quercus savannas: The prehistoric extent of *Quercus* savannas is unknown, although the type was probably more widespread before the Holocene. Savannas were an especially widespread type through southern California in the Pliocene, retreating since, although with local extensions of *Quercus agrifolia* (Axelrod 1977). *Quercus* species are well-adapted to a variety of substrates, and California's upland *Quercus* species were selected for summer drought tolerance, resistance to browsing, and ability to resprout following fire.

Savannas were cleared for cultivation in many spots, particularly the *Quercus lobata*-dominated type (Burcham 1957). Much *Q. douglasii* savanna may have been cleared since settlement, raising the boundary of species distribution into foothills from the cultivated and settled valleys. The landscape has been altered dramatically in many areas: to cropland, to grassland, and to more open stands with few small trees. These changes, unlike those in the grassland, affected the sustainability of resource productivity. For example, soil stability and the soil nutrient cycle have been considerably disrupted. However, to put these changes in perspective, the Holocene period has seen widespread natural thinning of *Quercus* stands from woodlands into savannas.

The *Quercus* savanna understory has undergone the same type of replacement by exotic annuals as grasslands, but this change is undocumented, lacking a basis for good speculation about the original savanna understory. Changes in fire regime and grazing would have affected tree regeneration (McClaran and Bartolome 1989a), but are not well documented. The regional impacts of clearing on the understory are unknown.

Short-term changes in climate are unlikely to have an effect on mature trees, as savanna types are wide-ranging. For example *Quercus douglasii*-dominated ecosystems are found from 1000 to 300 mm mean annual precipitation (McClaran and Bartolome 1989b), a range which spans changes in average rainfall over the past few thousand years. Seedling survival and regeneration are more likely tied to climatic shifts, as

suggested by the regional differences in regeneration status of *Q. douglasii*, which is regenerating better in areas with higher rainfall (Muick and Bartolome 1986). *Q. douglasii* savanna stands at less than 750 mm annual rainfall could have established during the wetter periods of the past few thousand years, or even during the Tioga glacial period, with infrequent new establishment since. The trees that are now present range up to over 400 years in nominal age (Bartolome et al 1986), but may all be from sprouts following fire, not new plants established from acorns.

Chaparral: The chaparral, according to Axelrod (1977), has extended its range in the Holocene from an unknown prior extent. The major impact on chaparral has been the decline in summer rainfall over several million years, possibly with accompanying changes in fire regime. Chaparral plants have found a niche where sandstone parent material, and the resultant coarser-textured soils permit access to summer moisture. The shallower soils in a geologically active landscape also favor chaparral.

Perhaps aboriginal burning played a role in altering chaparral structure and extent in some areas, although non-anthropogenic fires were also common. Certainly recent, short-term effects of fire regime are important (Wells 1962, Davis et al 1988). Composition may have been altered by changes in the fire regime and may be continually altered by current prescribed burning systems. Obligate fire-following plants, narrowly adapted to specific fire regimes, may be in trouble. The long-term sustainability of the ecosystem is also undetermined. The effects of management on soil stability and water yield remain to be properly evaluated in the context of natural disturbances of the chaparral landscape. Fauna has apparently not been affected as much as in grassland and savanna types.

At a landscape scale, it seems unlikely that there have been major changes in chaparral. Grazing impacts are undetermined, as are short term climatic effects, but some ecologists suspect that grazing could affect structure in ways similar to fire (Axelrod 1977).

Coastal Scrub: This type extended in the Holocene, and is common on coastal terraces exposed by sea-level changes. The type has now retreated because of widespread cultivation and subsequent urbanization of coastal terraces in the past 150 years. The type is now heavily affected by development and changes in the fire regime (Westman and O'Leary 1986). Grazing and recent climatic changes seem to be less important than in other types.

The changes in landscape structure and extent since Europeans arrived were exceptional in the grasslands, rapid in some woody types such as the *Quercus lobatal* savanna, but less apparent in *Q. douglasii* savannas. The amount of change in shrub types is not accurately determinable.

Conclusions

Change permeates California's landscape, frequently producing short-term catastrophic effects. Fire, drought, human immigration, floral and faunal immigration, climatic change and extinction, have all been important since the Mediterranean-type climate first appeared following the Pliocene uplift of the Sierra Nevada. Some changes in the landscape have not accelerated appreciably during historic times. For example, the Holocene megafaunal extinctions involved replacement of more species at nearly the same rate as the subsequent changes resulting from introduction of livestock grazing following settlement by Europeans.

Three attributes of landscapes, ecosystems, and communities influence interpretation of the factors causing change. First, the investigator's choice of spatial and temporal scale will affect interpretation of change. Landscapes are most typically studied with respect to long-term regional or global factors, although the ecosystem scale also matches with climatic change or immigrations of new species (Heady 1975). Even when landscape change is abrupt, for example the landslides common in coastal California, the basic causal factors lie in the gradual development of unstable substrates which ultimately cause the event.

Second, a primary method used to interpret the causes of landscape change depends on similarities between recovery of an ecosystem following disturbance, and the process of degradation. If disturbance is a discrete event with an identified cause, for example cultivation, then the differences between degradation and recovery are obvious. Long-term changes in ecosystems, both degradation and recovery, are often assumed to represent mirror images of the same basic process, with similar causal factors. This is rarely the case. I am most familiar with examples of change in structure and productivity of rangeland ecosystems grazed by livestock. Here the processes of range deterioration (rarely observed) and range improvement (sometimes observed) are assumed to have the same basic causal mechanisms and a patterns. This assumption, which underlies the basic theory of American range science, is false for many rangeland ecosystems (Bartolome 1985).

In Californian *Quercus* spp., the causes for lack of regeneration and for successful regeneration are largely independent. The complex of environmental influences necessary for successful regeneration may be unrelated to the factor or factors which can prevent regeneration. Regeneration involves at least two different sets of factors and influences, which, to add to confusion, operate at different spatial and temporal scales (Bartolome et al 1987). The patterns and processes for directional change toward more new trees and fewer new trees are different.

Third, the unique properties of individual ecosystems limit general interpretations of landscape change. Even when controlling environmental factors can be identified at the proper temporal and spatial scale, predictability of response can be poor. Although Californian data sources are still very incomplete, the Holocene record of climatic change and vegetation change suggests considerable regional variability. One interpretation is simple lack of data, but another is that similar ecosystems respond differently to changes in climate. The role of unique historical accidents in ecosystem and community change is also underestimated. In Californian grassland ecosystems, the flora has completely changed in 150 years. Few of its present properties could be predicted based on previous structure and function (Huenneke and Mooney 1989).

The three attributes of landscape change which cause difficulties for study justify the value of landscape ecology for understanding change. However, this approach needs complementary support from reductionists (e.g. Harper 1967) to develop an understanding of cause and effect within the context of whole systems. The potential big losers will be those who attempt to manage landscapes, ecosystems, communities, and populations based on partial understanding of the past. The magnitude of future landscape changes are likely to soon equal those of the distant past. These changes cannot be properly managed by relying on analysis of past changes to predict the future under the influence of spatial and temporal scale, assumed similarities between landscape deterioration and improvement and chance.

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