

## Chapter 2 Ecological History

James Bartolome and Sheri Spiegel

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### Introduction

This chapter 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 seafloor sediments and metamorphic and volcanic rocks. These processes, under the influence of the cold Pacific Ocean current along the California coast, 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 adapted to the summer rainfall climate that was 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 oak-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, a period that 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 that links holistic and reductionist explanations for landscape dynamics.

### Landscape Change

This chapter 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 it concludes by identifying some weaknesses in information and theory.

Ecologists tend to use a favorite set of temporal and spatial scales to detect patterns. This strategy is acceptable if the effects on ecological conclusions are recognized (Bartolome 1989; Friedel 1994). Normally, trends and fluctuations are detectable only at specific scales. As temporal scale becomes longer, the appropriate spatial scale to detect patterns also becomes larger; thus, long-term changes are most effectively described over large geographic areas.

Defining a hierarchy of the scales is useful for detecting, describing, and understanding the patterns. Here we define a landscape as a diverse collection of more homogeneous subunits called ecosystems (Forman and Godron 1986).

Ecosystems are, in turn, comprised of biotic communities and their environment. Defining a landscape in this way explicitly allows for the detection and analysis of spatial and temporal patterns between and among ecosystems; it also allows for inference about causal relationships, a central aim for ecologists. Although nesting ecosystems within landscapes may not always be appropriate (Allen 1998; Wiens et al. 2002), it is useful for the discussion here. 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).

For most of human history, the Californian landscape remained pristine, free of human influence. Once people discovered North America around 12,000 BP, they began the extensive use of abundant natural resources that continued through about AD 1800. In the late 18th century, the Spanish pastoral system was imported via Mexico, beginning a progression toward 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 croplands 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 excellent summaries by Alt and Hyndman (1975), Norris and Webb (1976), and Harden (2004). Geologic history forms the foundation for understanding landscape development. The Pacific Ocean and plate tectonics are the fundamental factors that shape the California landscape. In the Triassic period, about 220 million years ago, the North American and Pacific Plates collided, forcing the ocean floor to subduct 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 (fig. 1).



Figure 1. Geologic regions of California.

As the old seafloor surface of the Pacific was scraped off, it accreted to North America's western margin and formed the most important basic rocks of the Coast Ranges, the sandstones, shales, and cherts of the Franciscan formation. Ultra basic rocks from deeper ocean bottom were forced upwards by the subduction of the Pacific Plate beneath the North American Plate, 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 that form the western edge of the Central Valley.

The Central Valley began filling with sediments, now thousands 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. The Great Valley Sea persisted longer in the San Joaquin Valley than in the Sacramento Valley (Harden 2004).

Already a low mountain range that was formed as a result of the subduction of the Pacific Plate, 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, over 15 million years, moved granites from the southern Sierra Nevada to their present locations 500 kilometers 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 that modify the slower processes of plate tectonics. There have been important changes in sea level associated with ice ages, which, with uplift of coastal lands, have 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 Nevada (Phillips et al. 1996), which generally corresponds with the late Wisconsin in North America and the Wurm in the Alps (Wood 1975). As glaciers melted, the rising sea level drowned the mouth of the Sacramento River to form the 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 and associated with intense rainfall events (Smith and Hart 1982). Removal of woody vegetation often leads to disastrous mass movement (Heady and Pitt 1979; Gabet and Dunne 2002). Norris and Webb (1976) claim that slides on Franciscan substrate transport more material in the North Coast ranges than do streams.

## 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 current manifestation of 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 that dominate vegetation in California's Mediterranean landscapes were widespread in North America. Oak woodlands and savannas (Griffin 1977) had spread over much of California in modern form by 5 million years BP, with both deciduous and evergreen oaks 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 over the southwestern United States in the Middle Miocene period, and many relatives of present California species are found in shrub lands of Arizona and New Mexico. According to Axelrod (1977), although chaparral was common by the early Pleistocene (Hanes 1977), 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 BP, 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 Nevada at 1,200 m elevation) was similar to that now found at 1,750 meters, which suggests a decrease of 3°C in average temperature. The 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 classic "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 Nevada, which appears to have had maximum aridity between 10,000 and 7000 BP.

Deserts were wet until 8000 BP and 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 the composition of those samples, although glacial records roughly support these descriptions (Wood 1975). Few pollen records exist for Mediterranean-type vegetation in coastal California.

Axelrod (1977) claims that two major types of vegetation, the *Quercus agrifolia* forest and the *Quercus douglasii*-*Pinus sabiniana* woodland, have recently changed; in the past, the former extended over more of southern California, while the latter was 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 is unknown, apart from a few thousand tree rings. Records are mainly from intermountain region locations at high elevation.

Between AD 1600 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 to be a contributor to the demise of the native perennial grassland and its 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 with the past 500 years. This record of tree rings is also supported by the recent (700 BP to present) glacial advance (Wood 1975).

### First Human Impacts

Human immigration into California at around 12,000 BP had an unknown effect on the landscape. As with other areas of the world, the effects on flora and fauna of human immigration into North America 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 with little direct evidence (Martin 1973). A large and diverse fauna of grazing and browsing animals was present in California until a series of extinctions took place between 20,000 and 10,000 BP (Wagner 1989; Edwards 2007). These extinctions were concentrated in

megavertebrate genera and were distinctly nonrandom (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; Anderson 2007), the impacts of deliberate burning on vegetation are not easily determined (Heady et al. 1991; Biswell 1999; Bartolome et al. 2007). Fire frequency in the Mediterranean-type has changed significantly in the past 300 years, with fires particularly frequent in the oak woodland between 1848 (before settlement) and 1948 (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). The dominance of *Artemisia tridentata* 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. 1991; Bartolome et al. 2007). The effects on woody types is much less documented, although extensive areas of chaparral and coastal shrub have been converted to crop production or urban development (FRAP 2010). Areas of woodland have been thinned for range improvement or cleared for agriculture

(Bartolome et al. 1986). In woodland areas neighboring the urban and agricultural areas, the frequency of lightning-induced fire has been suppressed in recent decades, resulting in dense growth that burns in extreme wildfire events that significantly affect woodland structure and function (FRAP 2010).

The grassland was affected by a combination of several factors that cannot be properly evaluated independently: grazing, introduction of alien plants, drought from 1862 to 1864, and cultivation (Heady et al. 1991; Bartolome et al. 2007). Grazing, beginning in the late 1700s along the coast and spreading inland, reached heavy stocking levels by the mid-19th century. 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; Minnich 2008). The area of shrubs and trees that was cleared is unknown.

### Prehistoric and Present-Day Vegetation

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 geology of the climate zones where California grasslands occur are favored by geologic history. Because so much parent

material is derived from old seafloor, weathering produces fine-textured soils that often support grassland. The often-unstable substrates favor herbaceous over woody vegetation. Areas with rolling topography and an underlying clay pan support unique vernal pool grasses (Heady 1977). The serpentine grasslands became established on soils derived from ultra-basic rock formed by the subduction of the Pacific Plate (Murphy and Ehrlich 1989).

In the present day, California's grassland is almost entirely dominated by annuals from the Old World, forming a new stable vegetation type. Appearance and productivity of the landscape has not changed much, but species have been replaced.

The grassland's original Holocene extent and composition, before European settlement, is unknown. Most grassland ecologists suggest an overall extent similar to the present grassland, exclusive of areas under cultivation (Heady et al. 1991; Bartolome et al. 2007). Recent evidence from phytoliths (siliceous bodies shed by grasses that persist in the soil for millennia) reveals that grasses were, in fact, present across this extent, but that they were not the dominant species except in coastal areas and along riparian corridors (Evetts and Bartolome 2013). Many contend that the pristine grassland was probably dominated by native annual forbs (Schiffman 2007; Minnich 2008). This contention represents a shift from previous thinking, in which native perennial bunchgrasses, particularly purple needlegrass (*Stipa pulchra*), were hypothesized to be the dominants (Bartolome et al. 2007). Native annuals were thought to fill the spaces between the bunchgrasses, with more annuals in drier areas and fewer in wetter areas (Heady 1977). Still others espoused shrubs as the former dominants, especially in the driest inland

locations (Keeley 1990, 2002; Hopkinson and Huntsinger 2005).

Reasons for the apparent decline of native perennial bunchgrasses have been sought. Major lines of conjecture include livestock grazing, drought, and cultivation (Bartolome et al. 2007). The native perennial grasses apparently did not evolve under heavy, yearlong grazing pressure (Heady 1977), but this has not been well studied (D'Antonio et al. 2007). A drought that occurred concurrently with intensive livestock grazing from 1860 to 1865 is thought to have been a major contributor to decline of native grasses. Tilling soil for cultivation, which directly kills the bunchgrasses, has also been implicated (Stromberg et al. 2007).

Over the past 150 years, the grassland's boundaries with oak savanna may have moved due to tree removal, but the size of the area involved is undetermined (Bartolome 1987). Shrub invasion into former grasslands has also been suggested as a factor, but this likewise accounts for only a small percentage of the total area (Wells 1962) and is likely to be compensated for by grassland expansion.

Known climatic changes are insufficient to account for the 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. 1991; Jackson and Bartolome 2007) and physiological characteristics (Jackson and Roy 1989)—to survive *in situ* the changes in climate of the past 100,000 years.

Changes in grazing pressure and fire frequency are insufficiently known, thus making it difficult to determine their impacts on plant communities; however, as a generalization, fire would favor native perennials, and season-long use by livestock would favor the annuals (Heady

1977). The biggest impact on vegetation came from the plant introduction that altered the flora. The next biggest impact came from 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 the loss of many wildlife and plant taxa, long before livestock introduction. California's extant native grasses or close relatives have been present since the Pliocene; thus, the release from grazing pressure experienced by large ungulates in the Holocene was a relatively recent event, which was only short-term because grazing was shortly subsumed by domestic livestock. We 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).

### **Oak Savannas**

The prehistoric extent of oak savannas is unknown, although the type was probably widespread before the Holocene. Savannas were an especially widespread type through southern California in the Pliocene; they have retreated since then, although with local extensions of *Quercus agrifolia* (Axelrod 1977). Oaks are well-adapted to a variety of substrates, and California's upland oaks were selected for summer drought tolerance, resistance to browsing, and ability to resprout following fire. Pollen studies show that the glacial periods' general expansion of conifers contrasted with interglacial dominance by oaks (Millar 1999; Byrne et al. 1991).

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, transformed to cropland, grassland, and 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 cycles have been considerably disrupted. However, to put these changes in perspective, the Holocene period has seen widespread natural thinning of oak stands from woodlands into savannas.

The oak savanna understory has undergone the same kind of replacement by exotic annuals as grasslands, but this change is undocumented, lacking a basis for solid speculation about the original savanna understory. Changes in fire regime and grazing would have affected tree regeneration (McClaran and Bartolome 1989a), but they 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 in areas with mean annual precipitation from 1,000 to 200 millimeters (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 millimeters 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 then. The trees that are now present range up to over 400 years in nominal age (Bartolome et al. 1986), but they 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 nonanthropogenic fires were also common. Certainly recent, short-term effects of fire regime are important (Wells 1962; Odion and Davis 2000). 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.

Livestock 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 vegetation 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 vegetation 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 lobata* 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 developed 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 the introduction of livestock grazing following settlement by Europeans.

Three attributes of landscapes, ecosystems, and plant communities influence interpretation of the factors causing change. First, the investigator's

choice of spatial and temporal scale affects the 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 the 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. We are most familiar with examples of change in structure and productivity of rangeland ecosystems grazed by livestock. Here the processes of range deterioration (rarely measured) and range improvement (sometimes measured) are assumed to have the same basic causal mechanisms and a pattern. This assumption, which underlies the basic theory of American range science, is false for many rangeland ecosystems (Bartolome 1989). The ecological concept of thresholds provides a theoretical foundation for hypotheses about the ecological processes that contribute to landscape degradation and recovery. To gauge where and when the threshold concept can be applied to range management, rangeland ecologists are testing threshold hypotheses in range settings (Bestelmeyer et al. 2013).

In Californian oaks the causes for successful and unsuccessful regeneration are largely independent. The complex of environmental influences necessary for successful regeneration may be unrelated to the factor or factors that can prevent regeneration. Regeneration involves at least two different sets of factors and influences, which, to complicate matters, 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 simply that we lack 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 have been predicted based on previous structure and function (Huenneke and Mooney 1989).

Despite these three attributes that hamper the study of landscape change, the study of landscape ecology remains valuable for interpreting change (e.g., Liu and Taylor 2002). 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 is likely to soon equal those of the distant past.

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