The Paleohistory of California Oaks[1]

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Abstract

Oak woodlands are a fixture of California geography, yet as recently as 10,000 years ago oaks were only a minor element in the landscape. The first fossil evidence for California's oaks is in the early Miocene (~20 million years ago) when oaks were present across the west, intermixed with deciduous trees typical of eastern North America. As climate became drier, species dependent upon summer precipitation went locally extinct and oaks retreated west of the Sierra Nevada. During the Pleistocene (the last 2 million years) oak abundance declined during cool glacial periods and expanded during warm interglacials. After the last glacial maximum (~18,000 years ago), oaks expanded rapidly to become the dominant trees in the Coast Ranges, Sierra Nevada foothills, and Peninsular Ranges. During the Holocene (the last 10,000 years) oaks in the Sierra Nevada were most abundant during a warm dry period between 8000 and 6000 years ago. Native American use of fire to manipulate plants for food, basketry, tools, and other uses helped maintain oak woodlands and reduce expansion of conifers where these forest types overlapped. Fire suppression, initiated by the Spanish and reinforced during the American period has allowed oak woodland density to increase in some areas in the Coast Range, but has decreased oaks where pines are dominant. Extensive cutting of oaks has reduced their populations throughout much of the state.

Key words: California, oak woodlands, paleoecology, *Quercus*, vegetation history

Introduction

Oak woodlands characterize much of the California landscape, but widespread oak communities are of relatively recent origin in the state. During most of California's geologic history, oaks were absent or much more limited in their distribution. Fossil evidence shows that species conforming to modern California oaks were present in western North America by about 10 million years ago, but their range shifted into the state within the last few million years as the summer-dry Mediterranean climate developed and strengthened. During the last 100,000 years, oaks were only a minor element of the landscape, most likely persisting as isolated refugia.

At the end of the last ice age, about 10,000 years ago, oaks rapidly expanded creating the woodlands of today. Even during this time period, climate change has influenced the range and distribution patterns of oak woodlands, such that in some locations, woodlands have only been in place for the last few thousand years. Evidence of the first appearance of humans in California also dates to about 10,000 years ago, so that the expansion of oak woodlands after ice ages coincides with a period of human land use. Native Californians lived throughout the oak woodlands and evidence suggests that their practice of frequently burning the landscape influenced the development of the open oak savannas commonly described in the earliest European accounts. Within just the last 2 centuries, intensive resource use has extensively altered the distribution and abundance of oak woodlands throughout most of their range in California.

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Early Miocene (20-16 Ma)

California oaks were not originally part of a summer dry Mediterranean climate, but appear to have evolved under a summer rainfall regime. California oak history begins in the Pacific Northwest in the Early Miocene, between 20 and 16 million years ago (Ma), with the first fossils that can be compared with modern oaks (Wolfe 1980). The presumed ancestors for black oak (*Q. pseudolyrata* - *Q. kellogii*) and valley oak (*Q. prelobata* - *Q. lobata*) are found in Oregon (fig. 1), not California (Chaney 1920).

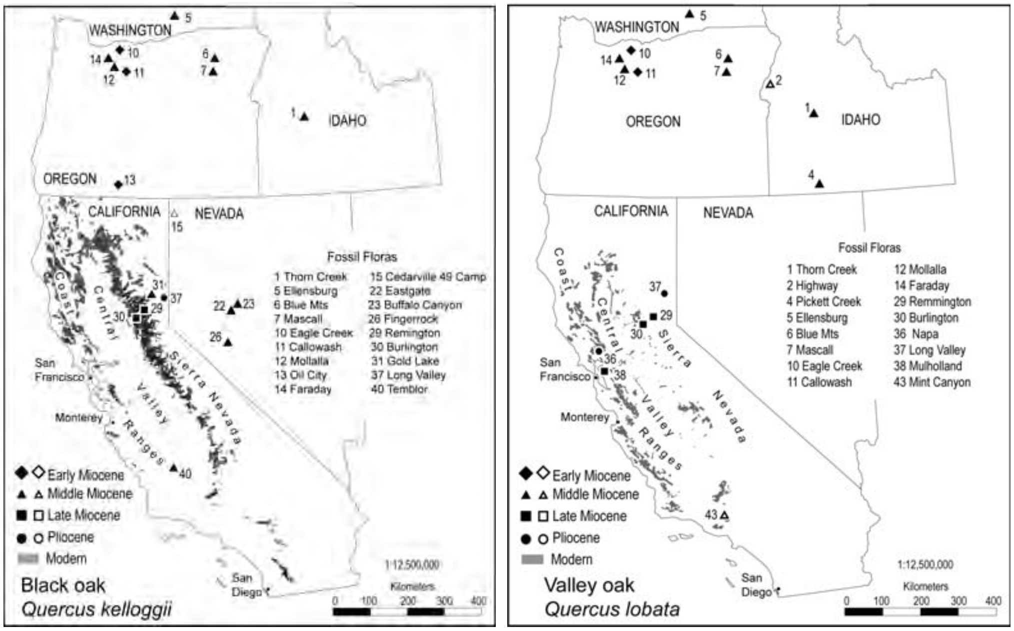

Figure 1—Distribution maps of the fossil localities and modern ranges of black oak (*Quercus kelloggii*) and valley oak (*Q. lobata*). Filled symbols represent sites where there is greatest confidence in the fossil identification and open symbols are sites with the least confidence following table 1.

These oaks grew with a diverse mix of species within genera now commonly found in either east Asia: ginko (*Ginko*), zelkova (*Zelkova*); the eastern United States hickory (*Carya*), tulip tree (*Liriodendron*), sweet gum (*Liquidambar*), elm (*Ulmus*) and magnolia (*Magnolia*); or now confined to riparian habitats in the west, such as maple (*Acer*) and beech (*Fagus*) (Axelrod 1983). As summer rainfall disappeared through the late Cenozoic, most deciduous broadleaf species went locally extinct, but California's oaks survived (Axelrod 1973). Today's native species must have been pre-adapted to summer drought and were able to persist in the region as summer rainfall diminished and the climate became more Mediterranean (Blumler 1991).

Table 1—Middle Miocene (M Mio) and Early Miocene (E Mio) floras mentioned in the text with the best known age in millions of years. Chronology follows Woodburne and Swisher (1995), and Schorn (unpublished data)

Site #[a]	Site name	St.	Age	Qa[b]	Qk	Qw	Qc	Qe	Ql	Qd
M Mio										
33	Table Mt.	CA	10-11					X		
2	Highway	ID	10-11				X		X	
5	Ellensburg	WA	10-11		X[c]				X	
14[e]	Faraday	OR	11		X				X	
4[e]	Pickett Creek	ID	11				X		X	
3	Hog Creek	ID	11-12				X			
43	Mint Canyon	NV	12	x[d]		x		x	X	
24	Aldrich	NV	13				X			
1	Thorn Creek	ID	12-14		X		X		X	
20	Fallon	NV	13-14			X	X			
9	Trout Creek	OR	13-14				X			
12	Mollalla	OR	13-14		X				X	
25	Stewart Spring	NV	14			X	X			
6	Blue Mts.	OR	14-15		X		X		X	
27	Esmeralda	NV	14-15				X			
17	Chloropagus	NV	14-15			X	X			
19	Purple Mt.	NV	14-15				X			
16	Gilliam Spring	NV	15.5				X			
28	Cedarville Pit Riv.	CA	15.5	x						
15	Cedarville 49 Cmp	NV	15.5	x	x					
31[e]	Gold Lake	CA	15-16		X					
8	Succor Creek	OR	15-16				X			
7	Mascall	OR	15-16		X		X		X	
21	Middlegate	NV	15-16			X	X			
22	Eastgate	NV	15-16		X	X	X			
23	Buffalo Canyon	NV	15-16		X	X	X			
26	Fingerrock	NV	16		X	X	X			
40	Temblor	CA	16				X			
41	Tehachapi	CA	16				X	X		
E Mio										
13	Oil City	OR	16-18		X					
11	Callawash	OR	16-18		X				X	
10	Eagle Creek	OR	18-20		X				X	

[a] Site# refers to site identification numbers in figures 1 and 2.
[b] Species are: Qa = *Q. agrifolia*, Qk = *Q. kellogii*, Qw = *Q. wislizeni*, Qc = *Q. chrysolepis*, Qe = *Q. engelmanii*, Ql = *Q. lobata*, Qd = *Q. douglasii*, *Quercus agrifolia*, *Q. douglasii*, and *Q. engelmanii* are not mapped.
[c] X = fossil present that conforms to the modern species.
[d] x = identification determined ambiguous by the author.
[e] Unpublished floras examined at the University of California Museum of Paleontology paleobotany collection.

Middle Miocene (16 – 10 Ma)

By the beginning of the Middle Miocene ~16 Ma, two additional oaks comparable to modern species are found in the fossil record (fig. 2), canyon live oak (*Q. hannibali* – *Q. chrysolepis*) and interior live oak (*Q. wislizenoides* – *Q. wislizeni*). The vast majority of oak woodlands were still outside of the present area of California, in

Nevada, Idaho, Oregon and Washington (Axelrod 1956, Axelrod 1973, Axelrod 1995, Axelrod and Schorn 1994).

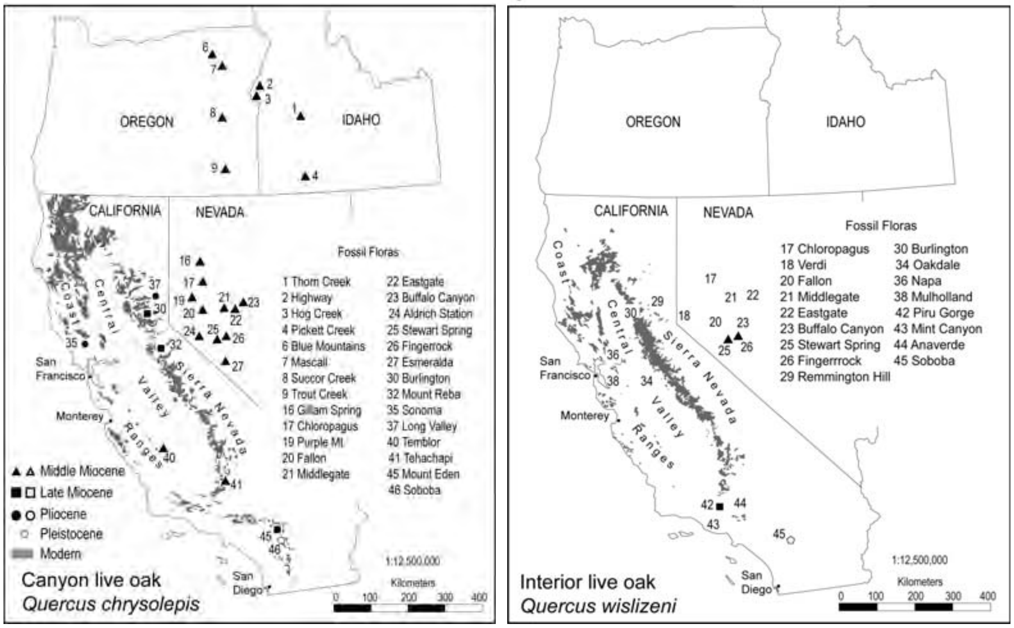

Figure 2—Distribution maps of the fossil localities and modern ranges of canyon live oak (*Q. chrysolepis*) and interior live oak (*Q*. *wislizeni*). Filled symbols represent sites where there is greatest confidence in the fossil identification and open symbols are sites with the least confidence following table 1.

Only two species were confidently present in California during the Middle Miocene, black oak found in the southern Coast Range and north of Lake Tahoe, and canyon live oak near the Tehachapi (Axelrod 1939, Renny 1972) in southern California (table 1, figs. 1 and 2). In the Tehachapi, oaks grew alongside laurels (*Persea*), suggesting a wetter climate than now. These two species had the widest distribution pattern of all the oaks, also being found in Nevada, Oregon, Idaho and in the case of black oak, southern Washington (Smiley 1963).

In Oregon, black oak, valley oak and canyon live oak grew with eastern deciduous species as well as redwoods, indicating mild temperatures with wet summers (Axelrod 1973, Chaney 1959). Fossils with lobed oak leaf morphology resemble both valley oak and Oregon white oak. These two species may have had similar progenitors in the Pacific Northwest that diverged sometime after the Middle Miocene, with valley oak becoming restricted to California.

Interior live oak fossils were restricted to Nevada during the Middle Miocene (fig. 2) where they co-occurred with canyon live oak and black oak along with deciduous species indicative of a summer wet climate, including ancestors of madrone (*Arbutus*), walnut (*Juglans*), *Eugenia* (extinct), birch (*Betula*), maple (*Acer*), buckeye (*Aesculus*), persimmon (*Diospyros*) hickory (*Carya*), elm, (*Ulmus*) and zelkova (*Zelkova*) (Axelrod 1956, 1973, 1985).

Late Miocene (11 – 5 Ma)

By the late Miocene, California oaks became restricted within the present boundaries of the state. Reliable fossil evidence for each species can be found within or near some portion of the species present boundaries (table 2; figs. 1 and 2), indicating that the mild and humid climate of the Early Miocene had begun to give way to a more seasonal Mediterranean climate.

Table 2—Pleistocene (Pleist), Pliocene (Plio) and Late Miocene (L Mio) floras mentioned in the text with the best known age in millions of years. Chronology follows Woodburne and Swisher (1995), and Schorn (unpublished data)

Site #[a]	Site name	St.	Age	Qa[b]	Qk	Qw	Qc	Qe	Ql	Qd
Pleist										
46	Soboba	CA	1-2			x	x			
Plio										
35	Sonoma	CA	3-4	X[c]			X	x		X
36	Napa	CA	3-4	X		X			X	
37[e]	Long Valley	CA	4		X		X		X	
L Mio										
42	Piru Gorge	CA	5-6			X				x
44	Anaverde	CA	5-6			X				
45	Mt. Eden	CA	5-6	X			X	X		X
18	Verdi	NV	6			x		X		
38	Mulholland	CA	6-7			X			X	
32	Mt. Reba	CA	7				X			
34	Oakdale	CA	7-8			X				X
30[e]	Burlington Ridge.	CA	8-9		X	X	X		X	X
29	Remington	CA	8-9		X	X			X	X
39	Black Hawk	CA	9	x[d]				X		

[a] Site# refers to site identification numbers in figures 1 and 2.
[b] Species are: Qa = *Q. agrifolia*, Qk = *Q. kellogii*, Qw = *Q. wislizeni*, Qc = *Q. chrysolepis*, Qe = *Q. engelmanii*, Ql = *Q. lobata*, Qd = *Q. douglasii*, *Quercus agrifolia*, *Q. douglasii*, and *Q. engelmanii* are not mapped.
[c] X = fossil present that conforms to the modern species.
[d] x = identification determined ambiguous by the author.
[e] Unpublished floras examined at the University of California Museum of Paleontology paleobotany collection.

The Remington flora (Condit 1944) and adjacent Burlington flora in the west central Sierra Nevada held five species of oak, including canyon live oak, black oak, interior live oak, valley oak and the first appearance of blue oak (*Q. douglasoides* – *Q. douglasii*) (table 1). Chaparral species from several genera were present, including manzanita (*Arctostaphylos*) and buckbrush (*Ceanothus*), providing the first evidence of a diverse oak woodland associated with chaparral shrubs. Summer rainfall types present included maple (*Acer*), buckeye (*Aesculus*), sweetgum (*Liquidambar*), laurel (*Persea*), and elm (*Ulmus*), indicating that although oaks and chaparral were present, the landscape was still not comparable to modern oak woodlands (Axelrod 1973).

The first fossils that have been attributed to coast live oak (*Q. lakevillensis* – *Q. agrifolia*) appeared about 5 to 6 Ma on the northwest slopes of the San Jacinto Mountains in southern California (Axelrod 1937, 1950a, 1950b). Coast live oak was only found at its southern limit, although this species is uncommon in the fossil record indicating that it was either rare, or difficult to differentiate.

Pliocene (5 – 2 Ma)

The major Pliocene sites are located within the modern distribution of the species today. The Central Valley was a large inland sea in the early Pliocene (Johnson and others 1993) that would have modified temperature and precipitation patterns but prevented colonization of the Central Valley and created a barrier to dispersal. Mixed oak woodland appears to be well developed at the Sonoma and Napa localities (Axelrod 1944, 1950c) with blue oak associated with interior live oak, coast live oak, canyon live oak and valley oak. Most of the fossils suggest a modern forest typical of the Coast Range with redwood (*Sequoia*), Douglas fir (*Pseudotsuga*), alder (*Alnus*), tan oak (*Lithocarpus*), sycamore (*Platanus*) and shrubs such as mountain mahogany (*Cercocarpus*), buckbrush (*Ceanothus*) and manzanita (A*rctostaphylos*). Several fossils stand out as exotic, including elm (*Ulmus*) and laurel (*Persea*), suggesting persistence of a climate wetter than today.

Pleistocene (2 Ma – 10,000 yr B.P.)

Evidence for oak woodland abundance and distribution during the Pleistocene comes from pollen data. Oak pollen percentages are lowest during glacial maxima and stadials (cool periods) and highest during warm interglacials and interstadials (fig. 3).

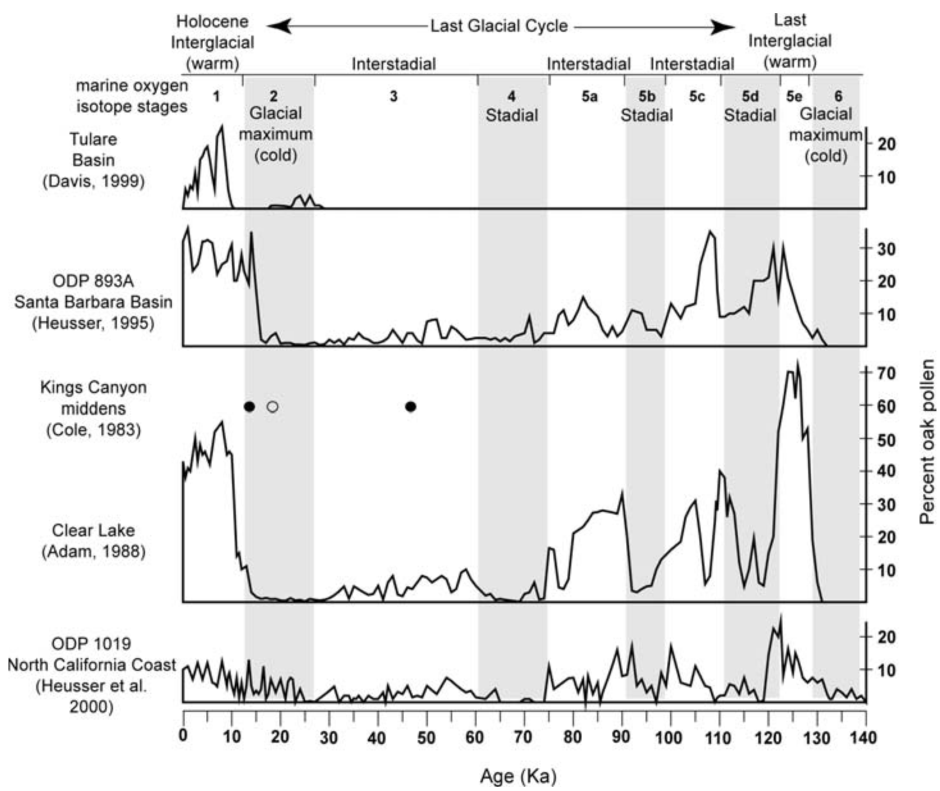

Figure 3—Pleistocene age pollen diagrams for sites in California recording oak. Filled circles represent packrat midden samples with oak pollen and open circles represent samples with no oak pollen. Time series are based on independent age models. Marine oxygen isotope stages (1-6) follow Bradley (1999). Gray bands identify cold periods (stadials and glacial maxima).

Along the northern California coast, oak pollen is most abundant during the Holocene and the last interglacial (about 125 Ka – thousand years ago; Heusser and others 2000). During glacial maximums, oak pollen abundance is very low. Although glacial cycles include a great deal of climate variability, the duration of cool/wetter phases is longer than warm/dry phases. Interglacials persist for 10,000 to 15,000 years while glacials last 90,000 to 100,000 years. Oak woodlands were regionally important during interglacials, but nearly disappear from the landscape for long periods of time during periods of glacial advance.

The Clear Lake (404 m elevation) record in the northern Coast Ranges supports this interpretation (Adam 1998). During colder conditions pines, sagebrush and juniper dominated the landscape. Shifts from oak dominance to oak absence were abrupt (Adam and West 1983) suggesting that when the climate became wet and cold, oak woodlands were quickly replaced by pine forest, but when climate became warm and dry, oaks rapidly reestablished. Similar evidence has been presented from the southern Coast Ranges (Heusser 1978, 1995; Poore and others 2000).

If oak woodlands were largely absent from their present range during glacial epochs, it is natural to ask where they were. The most likely answer is in isolated refugia such as rocky south facing slopes. There is no clear evidence of refugia, but wood rat middens *Neotoma* (packrat) in Kings Canyon in the Sierra Nevada foothills (920 to 1270 m elevation) had oak pollen during warmer interstadials which was then absent during the coldest period of the glacial maximum (Cole 1983). After the glacial maximum, oaks recolonized the area, suggesting migration from a source area not too far away. The pattern of nearly continuous expanses of oak woodlands in the Coast Ranges and around the Central Valley is a recent phenomenon. During ice ages low elevation California would have been characterized by coniferous forest. The characteristic Mediterranean climate of California with its oak covered rolling hills has only existed for brief periods during interglacial cycles like the one we enjoy today.

Holocene (10,000 years ago to historic)

The earliest evidence of human occupation in California suggests an arrival date of ~11,500 years ago. (Aikens 1978), though direct Native Californian influence on oak woodlands is largely restricted to the last few thousand years. Studies from the modern day upper elevational limit of black oak in the Sierra Nevada provide a consistent story of vegetation change (Davis and Moratto 1988, Edlund 1996, Smith and Anderson 1992). The late Pleistocene was dominated by juniper and/or incense cedar, sagebrush and pine with very little oak, suggesting an open landscape with a cooler drier climate than today. Beginning about 10,000 years ago oak began to increase (fig. 4), reaching a maximum between 8,000 to 6,000 years ago, then slowly declining while pine and fir increased. Oaks remained a minor component in the montane forests of the Sierra Nevada until the late Holocene when evidence suggests that burning by native Californians once again favored an increase in oak woodlands at the expense of conifers (Anderson and Carpenter 1991).

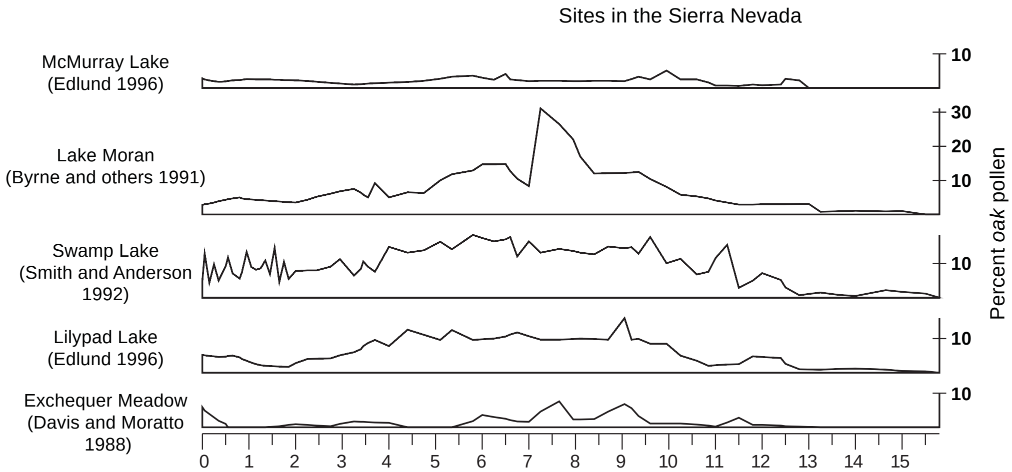

Figure 4—Sierra Nevada Holocene age pollen diagrams for oak sites in California. Time series are based on independent age models.

Coastal sites show a steady increase in importance of oak following the end of the ice age, reaching maximum levels about 8,000 – 7,000 years ago, remaining high throughout the Holocene (Byrne and others 1991). While low elevation oak woodlands (blue oak, valley oak, coast live oak and interior live oak) became well established in the mid-Holocene, higher elevation oak populations (black oak and canyon live oak) became a minor component of the lower montane forests (fig. 5).

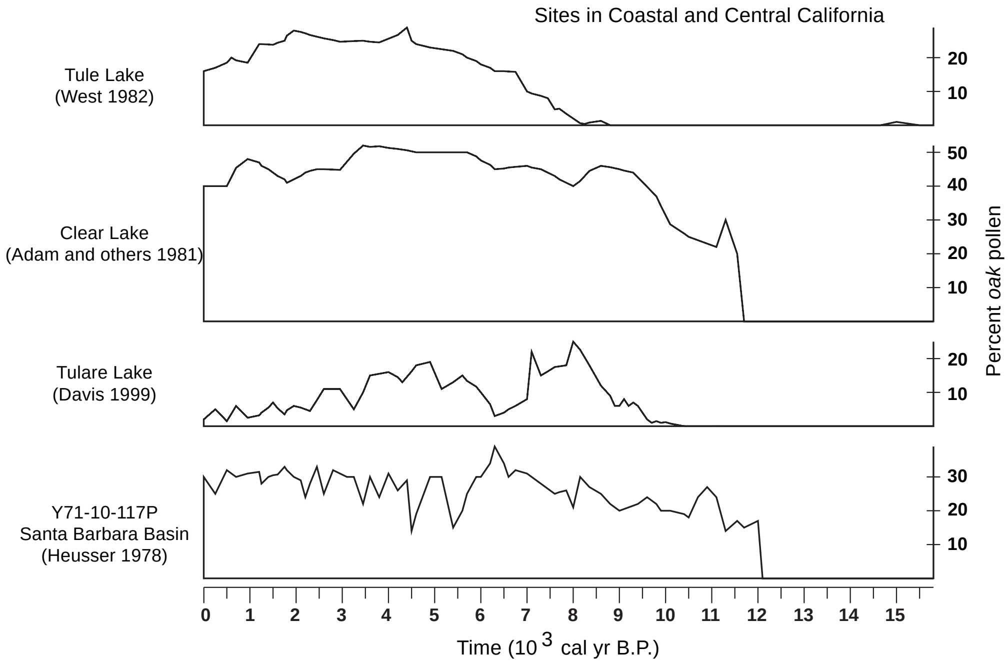

Figure 5—Coast Range and San Joaquin Valley Holocene age pollen diagrams for sites in California recording oak. Records vary in length. Time series are based on independent age models. Data digitized from published pollen diagrams.

A record from Tulare Lake in the San Joaquin Valley shows that beginning about 8,500 years ago oak woodland replaced pinyon-juniper woodland and sagebrush (Davis 1999). Oaks remained common while water tables were high, but after 3000 years ago, lower water tables and severe dry conditions caused oaks to decline, replaced by drought tolerant saltbush species (Davis 1999). The evidence suggests that recent climate changes have influenced oak woodland distribution patterns, such that oaks were probably more widespread in the San Joaquin Valley 3,000 years ago.

The Influence of native Californians on oak woodlands

Although new studies are being made to quantify the role of Native Americans on forest structure, at this time their influence on oak woodlands must largely be inferred from observations made at the time of initial contact, oral histories of elders, and landscape changes that have been documented since the demise of the native populations. California Indians set fires for the purpose of clearing ground to gather acorns, promoting secondary growth used for basketry materials, clearing brush for hunting, and facilitating collection of seeds (Anderson 2005, Blackburn and Anderson 1993). Acorns are the most abundant plant food found in archaeological sites throughout central California (Anderson 2005), confirming that oaks have been important to California Indians for a long time. Fires, set by California Indians, are believed to have been the major factor in determining the type of vegetation found by Europeans when they arrived in California (Stewart 2002).

Pollen studies of Woski Pond in Yosemite National Park provide some of the clearest physical evidence that anthropogenic influences were important in maintaining oak woodlands in the Sierra Nevada (Anderson and Carpenter 1991). This record shows an increase in oaks and decrease in pine beginning about 650 years ago coinciding with a shift from the Tamarak complex to the Mariposa complex, characterized by a larger population and greater reliance on acorns. Forest clearance through burning would have favored expansion of oaks and improved conditions for gathering acorns. Open oak woodlands increased during a cool wet climate period (referred to as the Little Ice Age) when pines and firs would have typically been favored. Oak woodlands predominated in Yosemite Valley as a result of Indian-set fires rather than climate change (Reynolds 1959).

In the absence of periodic burning, ponderosa pine (*Pinus ponderosa*) is successional to black oak, and within the lower montane forest, the typical forest structure today is one of young, tall ponderosa pine and white fir (*Abies concolor*) overtopping old black oak. Young black oaks are uncommon. Large complexes of bedrock mortars at 2100 m elevation (Bennyoff 1956) near the upper treeline of black oak today suggest the montane forest included many more oaks in the past.

Frequent burning by California Indians to manipulate the landscape was not confined to the Sierra Nevada, but has been documented throughout the state (Anderson 2005). At least 35 tribes in California used fire to increase the yield of desired seeds, drive game, and stimulate growth of specific plants (Reynolds 1959). More studies are needed to determine the extent to which Native American use of fire may have expanded oak woodlands in the recent past.

The Impact of European settlement on oak woodlands

Franciscan missionaries constructed a chain of 21 missions and nine settlements in Alta California between 1769 and 1821 A.D. (Gerhard 1982). The distribution of Franciscan missions between 1769 and 1821 A.D followed the distribution of coast live oak, termed *encina*, (*Q. agrifolia*) and valley oak (*Q. lobata*) termed *robles* (Rossi 1980). Although the Spanish introduced many herbaceous weedy species that completely transformed the understory layer in oak woodlands, there is no clear evidence that the mission period, or the subsequent period of Mexican control, had any significant impact on the distribution or abundance of California oak woodlands (Mensing 1998). The Spanish introduced laws to prevent setting fires (Timbrook and others 1982), which may have benefitted oak recruitment and survival in coastal environments where frequent fires set by California Indians would have regularly killed seedlings.

Following the Gold Rush in 1849, impacts on oak woodlands intensified. First, along all major river corridors in the Central Valley where valley oaks dominated riparian woodlands, oaks were nearly completely removed for use as fuel and clearing for agricultural land. Second, oak woodlands were extensively cleared for agriculture and range improvement in rich agricultural lands of the Coast Ranges, southern California, the Sacramento and San Joaquin Valleys. Third, in wildland settings, forests and woodlands increased in density with improved fire suppression efforts. In some communities, oaks increased with the absence of fires, whereas in others oaks have been out competed by conifers. Finally, urbanization has expanded into oak woodlands fragmenting wildland habitat. Changes in land use practices have led to poor oak regeneration in many but not all woodlands, but the factors that result in low regeneration rates are not fully understood.

Despite challenges with recruitment, clearing, and changes in fire, oak woodlands remain the iconic California landscape. The long-term history of oak woodlands in California illustrates that they have persisted through millions of years of climate change and thousands of years of human impacts.

Acknowledgments

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