Sierra Nevada Forests: Where Did They Come From? Where Are They Going? What Does It Mean?

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Climate Change and Vegetation

The prospect of human-induced global warming has received centerstage attention from ecologists concerned about future ecosystems. While such effects deserve critical analysis, they are best understood in the context of natural climate change. Anthropogenic atmospheric effects are often discussed as if background climates were stable (Mahlman 1997). Even in the recent past, however, climates have changed at similar rates and magnitudes to predicted anthropogenic changes, catalyzing significant natural changes in terrestrial ecosystems. With or without the complication of human effects, implications of climate change to conservation and management planning are great. Over the past twenty years, advances in Quaternary sciences have significantly improved our understanding of historic climate and its influence on biota and planetary systems. Although resource ecologists increasingly engage this research, much of relevance remains to be incorporated into the thinking of forest science and management. In this paper, we briefly review the nature of historic climate change, summarize conclusions relevant to ecosystems of the Sierra Nevada, California, and suggest implications for managing Sierran forest ecosystems.

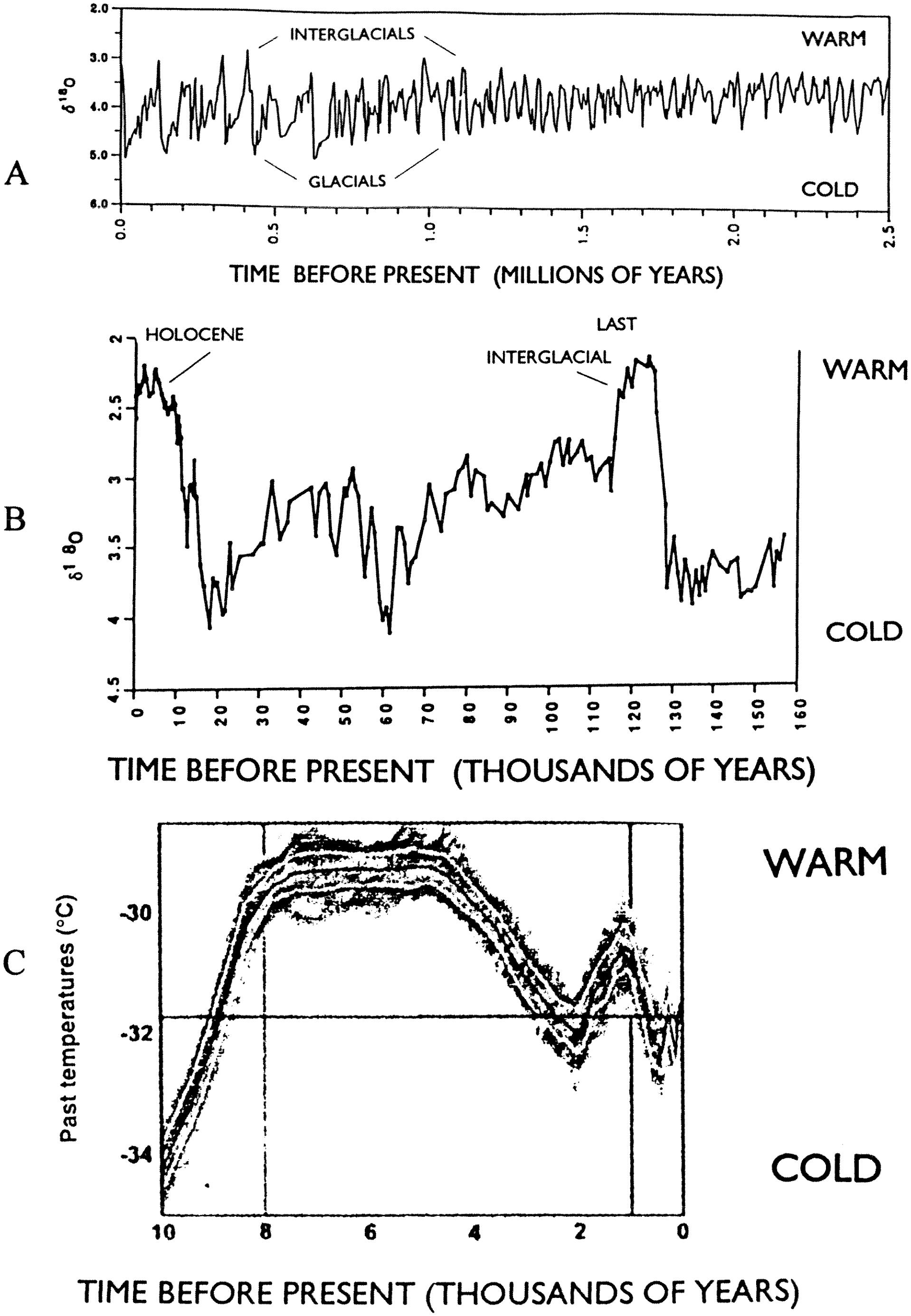
Quaternary Climate Change

A central finding from study of the Quaternary (the last 2.6 million years) is that historic climates have fluctuated in regular and hierarchic cycles at periods ranging from a few decades to 100,000 years. Characterization of these nested cycles is possible at increasingly fine time resolution (often annual) and over long times (the entire Quaternary) by analyzing oxygen-isotopes in long ice and sediment cores taken from ice caps and sea bottoms (Figure 1) (Wright 1989, Williams et al. 1993). Worldwide records cumulatively document about 50 primary oscillations between cold glacial and warm interglacial stages that distinguish the timespan of the Quaternary from earlier epochs (Figure 1a). The current climate period, known as the Holocene (0-10,000 years ago), is just one of many similar interglacial periods in the past. Average global temperature differences were about 10 degrees Celsius between these stages, with regional differences up to 20 degrees Celsius. These long-period oscillations relate to interactions of earth's orbit with internal global mechanisms (Broecker 1991, Imbrie et al. 1992, 1993).

Within the primary oscillations are cycles of shorter periods, from annual to a few millennia duration (Figures 1b and 1c) (Rind and Overpeck 1993). Initially, century-to-millennial scale cycles were thought to occur only during major glacial periods, and interglacials appeared more stable. Detailed study of the Holocene and the previous interglacial, however, documents that regular cycles of warm/cold periods continue through interglacials (O'Brien et al. 1995, Bond et al. 1997). Temperature differences of 3 to 6 degrees Celsius are recorded for these phases.

The hierarchic pattern of climate variability within the Holocene has been well characterized (Figure 1c), indicating overall warming from glacial conditions starting about 11,000 years ago to a period of maximum temperatures (2 degrees Celsius warmer than present) about 8,000 to 4,000 years ago (Dahl-Jensen et al. 1998). Since then, global temperatures have been gradually declining. Within this general cooling trend have been several short periods of anomalously warm and cold temperatures. Beginning about 900 A.D. and lasting to 1350 A.D., temperatures in many parts of the world were much warmer and drier relative to the general Holocene trend (Hughes and Diaz 1994). This event, known as the Medieval Warm Period, varied regionally in expression and intensity. Subsequent to the Medieval Warm Period, northern

Figure 1. Curves illustrating global temperatures on three timescales, showing values of oxygen-isotopes (high values of d^{18}O indicate cold temperatures; low values indicate warm temperatures)(A and B) and reconstructed temperatures (degrees Celcius) from the Greenland ice sheet (timescale reversed, C). A. The last 2.5 million yrs, from the North Atlantic ice cap, illustrating regular cycles of glacial and interglacial oscillations (from Wright 1989). B. The last 160,000 years, indicating temperatures cycles at finer resolution within the previous and current (Holocene) interglacials, and the last and beginning of the previous glacials from a sediment core taken below the Sta. Barbara Basin, California (from Kennett 1995). C. The last 10,000 years, showing warming in the early Holocene; general cooling since 4,000 years; warming of the Medieval Warm Period; cooling of the Little Ice Age, and warming of the last century (from Dahl-Jensen et al. 1998).


A
2.0
3.0
4.0
5.0
6.0
$\delta^{18}O$
INTERGLACIALS
GLACIALS
WARM
COLD
0.0
0.5
1.0
1.5
2.0
2.5
TIME BEFORE PRESENT (MILLIONS OF YEARS)
B
2
2.5
3
3.5
4
4.5
$\delta^{18}O$
HOLOCENE
LAST INTERGLACIAL
WARM
COLD
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
TIME BEFORE PRESENT (THOUSANDS OF YEARS)
C
-30
-32
-34
Past temperatures (°C)
WARM
COLD
10
8
6
4
2
0
TIME BEFORE PRESENT (THOUSANDS OF YEARS)

hemisphere climates cooled, and global temperatures declined abruptly from the background cooling trend an additional 2 degrees Celsius (Grove 1988). Known as the Little Ice Age, this phase lasted from 1400 to 1900 A.D. and has been considered the most abrupt climate change during the Holocene (O'Brien et al. 1995, Overpeck et al. 1997). A significant transition globally to warmer climates has occurred within the last century (Mann et al. 1998).

Very short cycle events include the El Niño/Southern Oscillation (ENSO) patterns (Diaz and Markgraf 1992). These are interannual and global in expression, although their effects vary by region. ENSO effects seem to have waxed and waned over the Quaternary, with the current intensification of the three to nine year cycle beginning approximately 5,000 years ago (Rodbell et al. 1999).

Another key aspect of historic climate is abrupt and rapid transitions, often occurring over a few decades to centuries, between major as well as minor periods (Adams et al. in press, Stocker 1998). The last interglacial, known as the Eemian, is increasingly used as an analog for what might occur in the Holocene future. It was punctuated by many short-lived, intensely cold, arid periods, with magnitude similar to the difference between glacials and interglacials. Transitions within the Eemian occurred over a few decades or less (Adams et al. in press). The Eemian ended with a rapid cooling event that took place in less than 400 years. Within glacial periods, brief expressions of the most extreme glacial conditions began and ended with sudden climate jumps taking just a few decades. For instance, the onset and termination of the Younger Dryas, a well-studied, 1,300-year glacial event just prior to the Holocene, occurred within 10 to 20 years (Mayewski et al. 1993). Sudden and short-lived warm events within glacial periods, known as interstadials, similarly began and ended in rapid climate jumps over only a few decades (Adams et al. in press).

Relevant to forest management is the abundant evidence documenting that terrestrial ecosystems have responded dramatically to these small as well as large climate shifts. On the glacial/interglacial scale, complete replacement of plant community types, massive species migrations and turnover of plant species diversity within communities were common (Prentice et al. 1991). In mountainous regions, species shifted elevationally as well as latitudinally in response to changing climates, while complex topographies offered opportunities for refugia and/or barriers to migration (Pitelka at al. 1997). Non-analog plant associations, that is, assemblages of species that do not exist in the present, are interpreted as indicating climate conditions that do not occur at present (Davis 1986, Webb 1986). This suggests that climate and biotic zones didn't just shift north and south, or up- and downhill during major transitions, rather they involved complex changes.

Short-term climate transitions had similar effects on biota. Usually these were lesser in degree and magnitude to glacial/interglacial cycles, although, for example, the 1,300-year Younger Dryas cold period triggered a return to full-glacial vegetation. Many examples exist of changes in species abundances and distributions, growth rates and mortalities, as well as fire regimes, and community compositions that correlate to short-period climate changes (Wright 1989).

Future Climate Variability

Despite the increasing understanding of the cyclic nature of past climates and the mechanisms that govern historic variability, accurate climate forecasting is not possible. This is partly because there are so many probabilistic elements, due to the chaotic nature of planetary systems. Analysis of the past is, however, highly informative. One lesson is the recognition that we currently are in a period of rapid climate change, and ecosystems are responding complexly to natural as well as anthropogenic effects. Further natural changes in global climate could occur on timescales of a few decades, catalyzing responses in ecosystems. Some climatologists view the recent Little Ice Age as an early sign of major climate deterioration that will characterize the rapid end of the Holocene, as such flip-flops have characterized the termination of other interglacials. Others infer that temperatures might have continued to decline beyond Little Ice Age minima if it weren't for anthropogenic complications of greenhouse gases (Mann et al. 1998). Others point to the anomalous late 20th century moisture regime as being the wettest half-century in the last two millennia, suggesting that the norm for this period is much drier (Graumlich 1993). A return to those average dry conditions might be expected. The role of humans and the interaction of greenhouse gases with the delicate, highly interdependent natural climate system could produce novel and unpredictable effects (Broecker 1999). Clearly change has characterized the past and is certain to continue. As managers, we need to understand how climate has affected vegetation, creating the conditions we inherit, and how we might best promote resilience of native ecosystems to unknown but certain future change.

Key Findings for the Sierra Nevada

Many of the trends described above in global conditions have been identified for the Sierra Nevada, although studies are patchy and incomplete. Without summarizing this information (see Woolfenden 1996a, Grayson 1993), we highlight key conclusions that provide context for managing biodiversity in the Sierra Nevada.

The Sierra Nevada Has Been a Distinct Bioregion for 2.6 Million Years

The Sierra Nevada at present is considered by most ecologists to be a distinct bioregion (e.g., SNEP 1996). This is recognized by the unique associations of plants and animals, united under broadly similar climates and soils, that currently inhabit the range, and that are distinct from ecosystems adjacent to it. But is this condition recent or ancient? The fossil and geological records suggest that the modern biota has been discretely Sierran for at least 2.6 million years. That is, the set of species currently in the Sierra Nevada appears to have existed within approximately the same perimeter throughout the Quaternary and has remained distinct from other groups of species adjacent to this area (e.g., McCarten and VanDevender 1988). This is not to say that the Sierran "boundary" has been in the same location, or coincidental over time for all species (nor is it a singular boundary today). The intersections with Great Basin, Mojave, Central Valley, and Cascadian regions have shifted somewhat at the edges of the range (with species acting individualistically) throughout the fluctuations of glacial/interglacial and minor periods. For instance, giant sequoia (*Sequoiadendron giganteum*) mixed-conifer forest appears to have moved downslope, possibly into the edges of the Central Valley during the late last glacial period, 26,000 to 11,000 years ago (Atwater et al. 1986, West et al. 1991). Piñon pine (*Pinus monophylla)* from the Sierra extended into what is now Mojave Desert on the fans and valley floors of the southern Sierra (Woolfenden 1996a). Aside from fuzziness of the edges, however, the Sierra Nevada has been a bioregion of high integrity for at least 2.6 million years.

Plant Species Diversity Changed Little over 2.6 Million Years

Not only has the Sierran bioregion been distinct, but Quaternary plant diversity appears to have changed little over time. This generality recognizes that the fossil record is an incomplete and biased documentation of species that existed, and that we can't compare total species diversities over time. We can, however, confidently point to species that have been lost from the range. Within the groups of plants well represented in fossil deposits (wind-pollinated trees, shrubs, grasses and forbs; riparian and aquatic species) only three taxa appear to have been present in the past that are not currently native. Two of these were at the periphery of the ancient range.

Only spruce (*Picea*) of uncertain affinity grew in the Sierra Nevada proper, and is now gone. It is known from early pollen records in the Lake Tahoe Basin (1.9 million years) (Adam 1973) and Owens Lake (800,000-650,000 years ago) (Litwin et al. 1997). The nearest extant spruce locations are a few outlier populations of *P. engelmannii* in the Klamath Mountains and in eastern Nevada and *P. breweriana* of northwestern California. At the margins of the Sierran bioregion, the Owens Lake pollen record indicates that a walnut species (*Juglans* spp.), likely allied to *J. arizonica*, grew sporadically in the Southern Sierra/Owens Valley prior to the Holocene (Woolfenden 1996b). The closest extant native walnuts (*J. hindsii* and *J. californica*) now grow in central and southern California. Rocky Mountain juniper (*Juniperus scopulorum*) occurred in packrat middens from the northern Owens Valley, dated about 16,000-20,000 years old (Koehler and Anderson 1994a). The nearest extant populations of this predominantly Rocky Mountain species are in eastern and southern Nevada.

Although in this paper we focus on historic vegetation, a discordance between faunal and floristic persistence is apparent. Whereas plant diversity in the Sierra Nevada changed little over the Quaternary, faunal diversity seems to have been affected by the extinction trends that were occurring episodically throughout the Northern Hemisphere during the last 10 million years. The most significant extinction phase of the Quaternary was the Rancholabrean, at 10,000 years ago, when 43 genera went extinct during only about 1,000 years (Webb 1989). Although we have only scattered evidence for large mammals inhabiting the Sierra Nevada, at least 10 extinct taxa left direct records in the western foothills (Edwards 1996), and dung spore (*Sporomiella*), an indicator of large grazing mammals, was present in glacial deposits until about 10,000 years ago at a high-elevation (2,219 meters) site in the southern Sierra (Davis and Moratto 1988). These suggest that at least some of the megafaunal taxa used the Sierra Nevada and that, similar to many regions, the Sierra experienced abrupt losses of faunal diversity in the late glacial period.

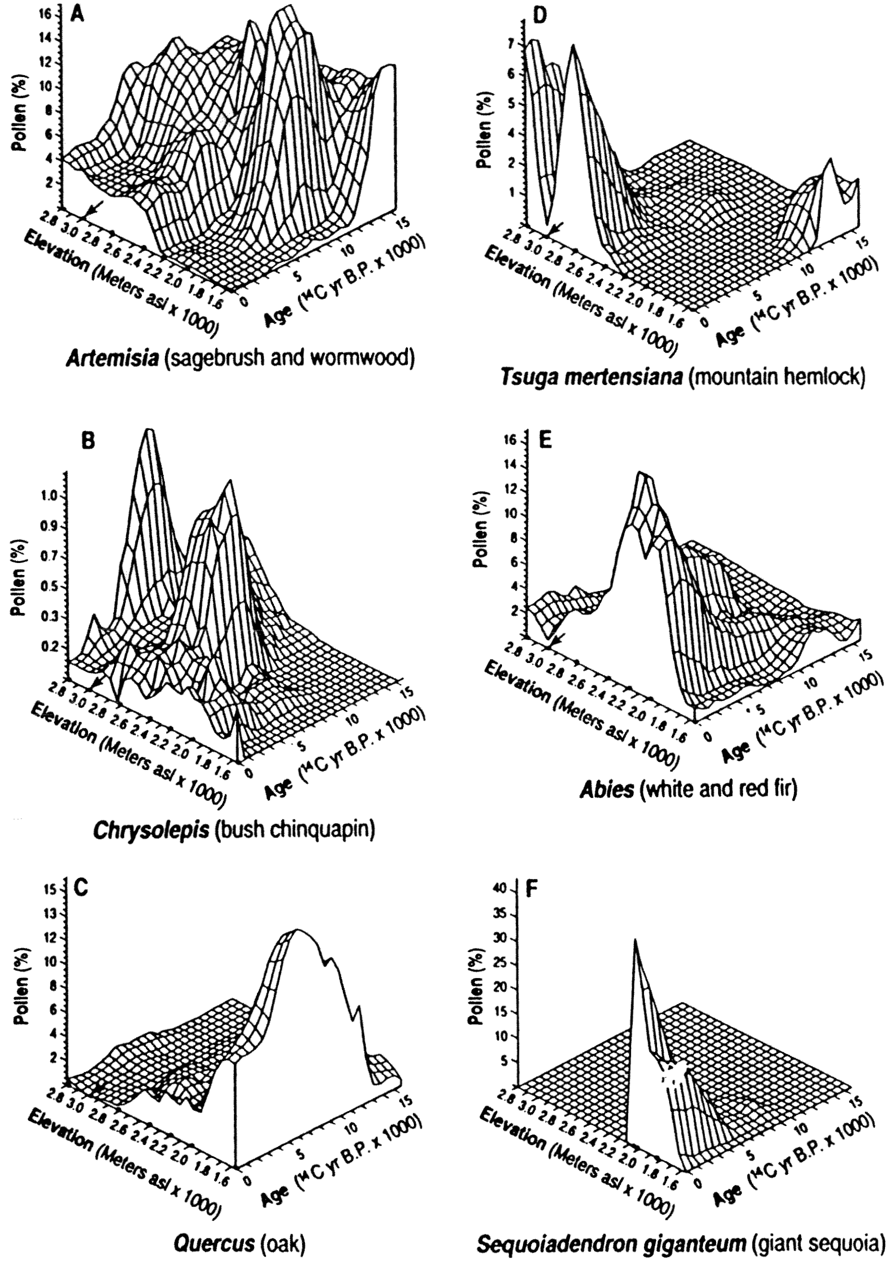
Species' Distribution Ranges and Abundances Changed Significantly

Contradicting the relative stability of species diversity and of Sierran bioregional boundaries is evidence for significant changes in species distributions and relative abundances within the Sierra Nevada over time. The most dramatic changes relate to glacial/interglacial fluctuations, although lesser changes occurred during minor climate shifts.

In some cases, fossil locations are geographically and ecologically distant from extant populations, indicating significant changes in range distribution. For instance, giant sequoia pollen is recorded in abundance from Mono Lake, in the central-eastern Sierra Nevada, at the end of the last glacial period, 10,000-11,500 years ago (Davis 1993). Because of giant sequoia's limited pollen dispersal, its presence in such abundance strongly indicates that giant sequoia grew near Mono Lake. This location is far distant and on the opposite side of the Sierran crest from the modern species, and lies currently within arid sagebrush (*Artemesia*) steppe communities. Giant sequoia has also been documented outside its range in the western Sierra. Abundant pollen found in Tulare Lake in the southern San Joaquin drainage between 26,000 and 11,000 years ago was interpreted to mean that giant sequoia extended into low-elevation riparian woodland along the Kern River (Atwater et al. 1986, West et al. 1991). Similarly giant sequoia pollen occurred in a packrat midden (920-1,270 meters) at Kings Canyon well below its current range during full glacial times (Cole 1983). The site lies now in oak (*Quercus*)/piñon pine/chaparral woodland. Giant sequoia pollen from East Lake at 13,000 to 11,500 years ago (Power 1998) and Exchequer Meadow (Davis and Moratto 1988) at about 10,680 years ago documents locations for the species between and above current outlying groves. Notably East Lake, at 2,863 meters and within subalpine habitat, is well above the current elevational limit of the species. The absence of giant sequoia from its current location also points to species' movement. Giant sequoia was absent from pollen records at Log Meadow in the Giant Forest of Sequoia National Park until trace amounts began to be evident around 9,000 years ago (Anderson 1994). Cumulative evidence suggests that giant sequoia has not occupied its present location until about 4,500 years ago (Figure 2) (Anderson and Smith 1994).

Holocene species changes are commonly marked by significant elevational, topographic, and other ecologic differences from present ranges. Only a few of many examples are noted here. Shifts in treeline provide direct measure of species' responses to climate. Classic studies by LaMarche (1973) document 150 meters cumulative downslope movement of bristlecone pine (*Pinus longaeva*) in the White Mountains over the last 4,000 years, with greatest recent decline in the Little Ice Age. Treeline in foxtail pine (*P. balfouriana*) has similarly shifted 100 meters downslope in the southern Sierra Nevada during regionally synchronous periods over the last 4,000 years (Scuderi 1987, Graumlich and Lloyd 1996). In the central Sierra Nevada, records from sediments in several high-elevation lakes document movement of upper range limits in red fir (*Abies magnifica*), mountain hemlock (*Tsuga mertensiana*), and lower limits in whitebark pine (*Pinus albicaulis*) (Anderson 1990). The dynamics of these shifts track major and minor climate trends of the Holocene. Lake sediments and packrat middens from lower elevation westside sites reveal movement of species up- and downslope within the general forested zones as well. These are summarized by species response curves over time (Figure 2) (Anderson and Smith 1994) that cumulatively document the recency of current ranges.

Within current distribution ranges, abundances of species changed significantly over time. Fir (red [*Abies magnifica*] and white [*A. concolor*]) provides a well documented example, often being a marker for distinct timeperiods. Abundance of *Abies* pollen changed significantly over time in the Owens Lake record, increasing during the termination of the last interglacial (Woolfenden 1996b). During the late glacial, red fir was common at a low-elevation midden



Artemisia (sagebrush and wormwood)

Chrysolepis (bush chinquapin)

Quercus (oak)

Tsuga mertensiana (mountain hemlock)

Abies (white and red fir)

Sequoiadendron giganteum (giant sequoia)

Figure 2. Diagrams showing movements of six taxa over time as represented by percent pollen at seven sites in the central and south-central Sierra Nevada. Elevation axis is from east side (left) of the Sierran crest (arrow) to the west side of the range (right). Age axis is thousands of years before present (radiocarbon estimate) (from Anderson and Smith 1994).

site (920-1,270 meters) in Kings Canyon National Park now dominated by oak/pine/chaparral (Cole 1983). From the mid-Holocene (4,000 years ago) to present, *Abies* has been increasing in abundance at many mid-high elevation locations throughout the Sierra Nevada, for instance, at Osgood Swamp (Adam 1967), Dinkey and Exchequer Meadows (Davis and Moratto 1988), Balsam Meadows (Davis et al. 1985), Lake Tahoe (Davis 1996), Lake Moran (Edlund 1991, Edlund and Byrne 1991), Barrett Lake, and Starkweather and Tioga Pass Ponds (Anderson 1990) (Figure 3).

Plant Community Compositions and Distributions Have Changed Significantly

The most dramatic conclusion from the Sierran Quaternary fossil record is how much and how often plant communities have changed, and how these changes have occurred over relatively short times. Plant communities moved in location and changed in diversity as a cumulative result of individual taxa responding to climate gradients. Non-analog communities have been found in several situations, suggesting novel climate conditions, migrational lag, and the role of chance events. At a coarse scale, vegetation in the Sierra Nevada appears to have remained relatively stable for periods of millennia, then rapidly changed to new conditions. At finer resolution, plant communities also tracked decadal- and century-long climate events. Significant species migration and rearrangements of community compositions occurred most commonly during transitional phases.

Examples that correspond to glacial/interglacial oscillations occur at many sites throughout the Sierra Nevada (Anderson et al. 1997). The main effect illustrated by long records covering many oscillations (e.g., Adam et al. 1990, Litwin et al. 1997) as well as shorter records is of major replacement at mid-high elevations from sagebrush steppe/juniper to pine/mixed conifer forests (Figure 3). More than 11 sites above 1,500 meters on the west and east sides of the range and covering the last glacial/interglacial interval document such shifts (Woolfenden 1996a). For many west side sites, the closest modern community analogs are currently in the eastern Sierra. Examples of non-analog vegetation include a full-glacial Utah juniper (*Juniperus osteosperma*)/Yucca (*Yucca brevifolia*) community in the southern Sierra (Koehler and Anderson 1994a) and a high conifer diversity forest in the central Sierra from the last glacial/interglacial transition (Smith and Anderson 1992).

Within the last 10,000 years, plant community shifts in many mid-elevation sites reflect drying and warming of the early to mid-Holocene (8,000-4,000 years ago) (e.g., Koehler and Anderson 1994b, Davis et al. 1985, Davis and Moratto 1988, Edlund 1991). Fir/pine forests that had developed during the earliest Holocene (as climates warmed from full glacial) shifted to in-

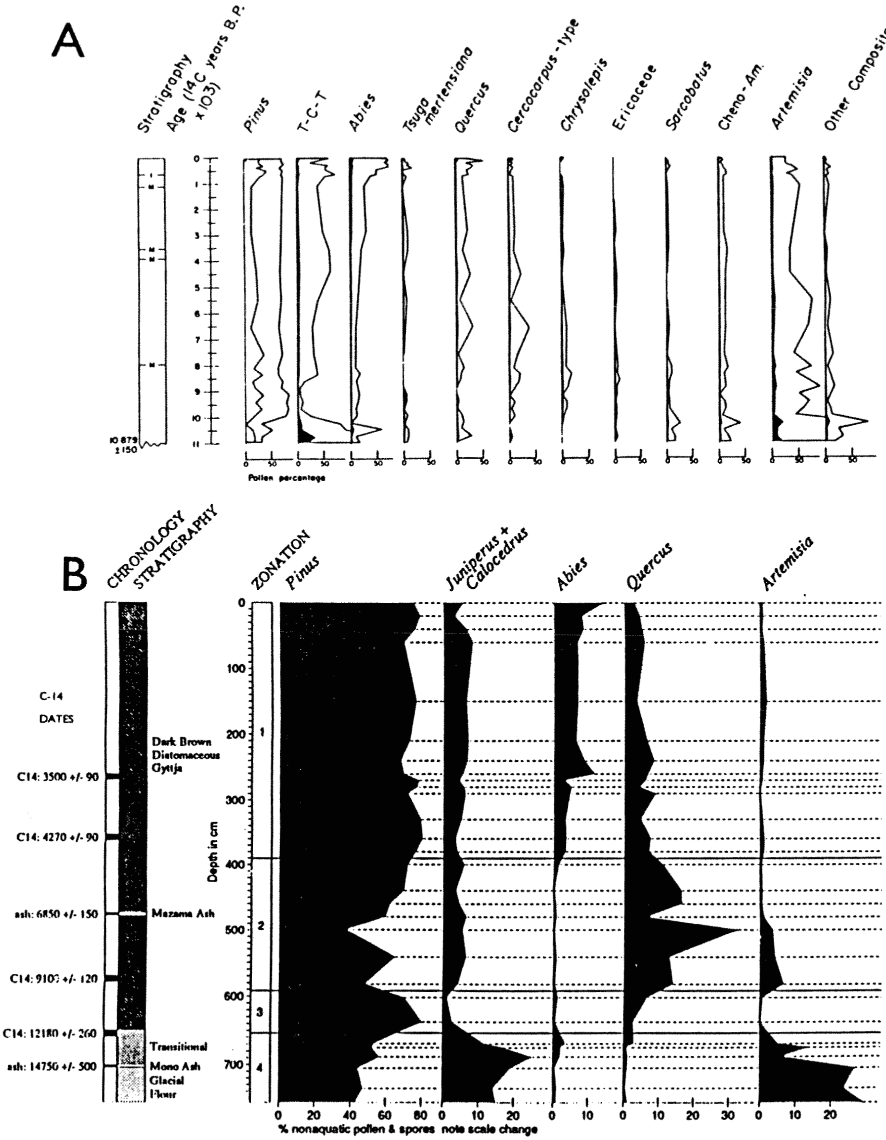


Figure 3. Diagrams showing percent pollen of different species over time in sediment cores taken from two westside Sierran lakes (Edlund 1991, Edlund and Byrne 1991). Note change at glacial/interglacial boundary near bottom of both records in dominance from sage/juniper (here "TCT"= Taxodiaceae/Cupressaceae/Taxaceae) to mixed conifer with high pine/fir and change in abundance of fir over time. A. Starkweather Pond (elevation 2,438 m) in southcentral Sierra Nevada near Devils Postpile National Monument. Age axis is thousands of years before present. From Anderson 1990. B. Lake Moran (elevation 2,107 m) in the North Fork of the Stanislaus River. Discrete dates are noted at left.

cense-cedar (*Calocedrus decurrens*)/sage/oak forests during the mid-Holocene, interpreted as be increasingly sparse and open due to prevailing warm, dry climates. At higher elevations, upper montane mountain hemlock/red fir forests were replaced by shrub communities (Anderson 1990).

Starting about 4,000 years ago, this trend reversed, reflecting the general cooling that has dominated climates since the mid-Holocene (Figure 1c). Many paleoecologists consider this to be the time when modern vegetation communities began to develop in the Sierra Nevada (e.g., Adam 1967, Smith and Anderson 1992, Anderson and Smith 1997), as present species ranges (e.g., Figure 3) and plant community locations became established and community diversities assembled.

Tree-ring studies document short-period trends within the general cooling of the last 4,000 years. Although other vegetation studies in the Sierra include this period, often they do not resolve recent and short-term changes because sampling intervals are too long. Studies in the southern and eastern Sierra Nevada provide evidence for two recent century-long climatic anomalies that correspond to the Medieval Warm Period (MWP) and Little Ice Age (LIA) (Figure 1c). The MWP, documented in the Sierra Nevada for 900 to 1350 A.D., has been characterized as a warm, dry period. Two persistent droughts (900-1100 A.D. and 1200-1350 A.D.) within this period are well documented from lowstands recorded in Mono Lake and other lakes and rivers in the eastern and high Sierra (Stine 1990, 1994).

Vegetation response to this period is seen as an abrupt decline in treeline of foxtail pine in the southern Sierra Nevada (Scuderi 1987, Graumlich and Lloyd 1996) and bristlecone pine in the White Mountains (LaMarche 1973). Growth rates of foxtail pine and western juniper (*Juniperus occidentalis*) were also significantly and persistently affected during this time (Graumlich 1993, Scuderi 1993). Changes in forest development occurred in fire regimes (Swetnam 1993) and an increase of *Abies* in high elevation communities (Anderson 1990). Changes in behavior of aboriginal peoples in the Sierra have also been interpreted as response to warm, dry climates (Moratto et al. 1978).

The Little Ice Age, or Matthes glaciation, has been dated in the Sierra Nevada as 1450 to 1900 A.D., although climate was not uniform during this period (Matthes 1941, Birman 1964, Stine 1996); the coldest period was in the 1800s. Several phases of cold and possibly dry climates created conditions for what is now considered likely the only glacial advance in the Sierra for over 13,000 years (Clark and Gillespie 1997). Throughout the high Sierra, glacial moraines provide evidence that the Matthes glaciation was significant, in magnitude approaching half the size of the most recent full-glacial advance.

The Little Ice Age is recorded as a decline in foxtail pine treeline in the southern Sierra Nevada (Scuderi 1987, Graumlich and Lloyd 1996) and bristlecone pine in the White Mountains (LaMarche 1973). That complex and apparently opposite climate anomalies such as the MWP and LIA, can catalyze similar changes in vegetation, such as treeline decline is discussed by Graumlich and Lloyd (1996). Persistent decline in tree-growth occurred during this period in foxtail pine and western juniper (Graumlich 1993, Scuderi 1993). At Starkweather Pond, subalpine communities more typical of the late glacial (11,000 years ago) replaced upper-montane mixed-conifer communities that had been present for several millennia prior (Figure 3) (Anderson 1990). Shifts in community dominance from red fir to lodgepole pine (*Pinus contorta*) have been interpreted in a montane eastside forest and in meadow floristics to result from LIA climate change (Millar and Woolfenden in press).

Considerable evidence has mounted to document an abrupt climate transition of the last century, starting in the latest 1800s and signaling an end to (or temporary excursion from) the LIA (summarized in Mann et al. 1998). Evidence from records of glacial retreat indicates temperature has increased an average 0.5 to 1.5 degrees Celsius since the late 1800s; most of this is interpreted as due to warmer summers. Few studies of vegetation change in this period have been done in the Sierra Nevada, however, that discern climate from anthropogenic effects. Tree-ring evidence in the southern Sierra Nevada indicates that the transition from the Little Ice Age has also been wet: the wettest 50-year period of the last millennium is documented from the last century (Graumlich 1993). Doubled growth rates of whitebark pines at treeline (J. King and L. Graumlich personal communication) and significant, persistent increases in growth rates of foxtail and lodgepole pines in the Sierra Nevada (Graumlich 1991, Graumlich and Lloyd 1996) and bristlecone pine in the White Mountains (LaMarche 1974) occurred since the late 1800s. Treeline ecosystems expanded upslope in Lassen National Park (Taylor 1995). Changes in montane meadow hydrology and floristics (Wood 1975) have been attributed to rapidly warming climates.

Many biotic effects of this transition are likely confounded with environmental effects of modern settlement since the two conditions coincide. In the Sierra Nevada, non-Indian human influence began in the mid-late 1800s (SNEP 1996). Many of the anthropogenic effects mimic or amplify what might be expected from environmental response to recent glacial retreat and to warming and wetter climates. These include increases in *Abies* abundance at mid elevation, changes in forest mortality and fire regimes, shifting forest structure, invasion of trees into meadows, and changes in meadow hydrology. It is important to separate human from natural effects, not just for the justice of proper attribution of cause, but to understand how current ecosystems are responding to environmental changes, and thus, how to align forest management with current rather than past environmental conditions.

Fire Regimes Reflect Long- and Short-term Climate Changes

Fire regimes appear to have tracked long and short climate periods in the Sierra Nevada and fire has changed in importance as an ecosystem process over time. Anderson and Smith (1997) divide the last 8,700 years into two primary fire periods (Figure 4A). Very low charcoal abundances occurred in seven meadow sites from mid-elevations within the mixed-conifer zone of the central to southern Sierra Nevada 8,700 to 4,500 years ago, suggesting that fire had negligible importance. From 4,500 years ago until early this century, charcoal was continuously abundant throughout the records, interpreted as meaning that during the Holocene fire has been a significant ecosystem architect only in the last 4,500 years (Anderson and Smith 1997). Lack of fire in the early to mid-Holocene was attributed to warm, dry conditions that created open, sparse forests with low biomass and low flammability. Wetter climates subsequently led to denser forest conditions, greater biomass, higher fuel loads, and higher fire frequencies. Intensification of the El Niño/Southern Oscillation pattern in the middle Holocene (Rodbell et al. 1999) may also have catalyzed the change to high importance of fire in the current interglacial (Anderson and Smith 1997).

Within the last 1,000 years, fire regimes also fluctuated at century-long scales reflecting changes during the climate phases of the Medieval Warm Period and Little Ice Age. Firescar evidence from giant sequoia shows significant increases in fire frequencies and decreases in fire sizes for the period from 800 to 1300 A.D. (the MWP), and significant decreases in frequencies and increases in fire size from 1400 to 1860 A.D. (the LIA) (Figure 4B) (Swetnam 1993). Swetnam interprets these patterns to suggest that, although dry years trigger fires at an annual scale, decadal and century patterns respond to trends of summer temperatures, reflecting persistent high temperatures in the MWP and low temperatures in the LIA. The MWP pattern is corroborated in charcoal abundances from meadow sediments (Anderson and Smith 1997).

Fire-history studies of shorter-lived conifers indicate that fire regimes during the LIA (referred to as the pre-settlement period) varied among forest types and geographically across the range (summarized in Skinner and Chang 1996, Kilgore 1973). Scattered fire-history studies in various forest types and locations indicate that high heterogeneity of Sierran physical environments and biotic conditions contributed to development of spatial mosaics of fire regimes during this period (Skinner and Chang 1996). For westside mixed-conifer forests, for instance, including its many subtypes, fire regimes in general were characterized by high fire frequencies (median fire-return intervals from 5 to 18 years), with large fire perimeters but high spatial heterogeneity in intensity and patch size within fires (Skinner and Chang 1996). Low intensities were most common, and there is little evidence that stand-terminating events oc-

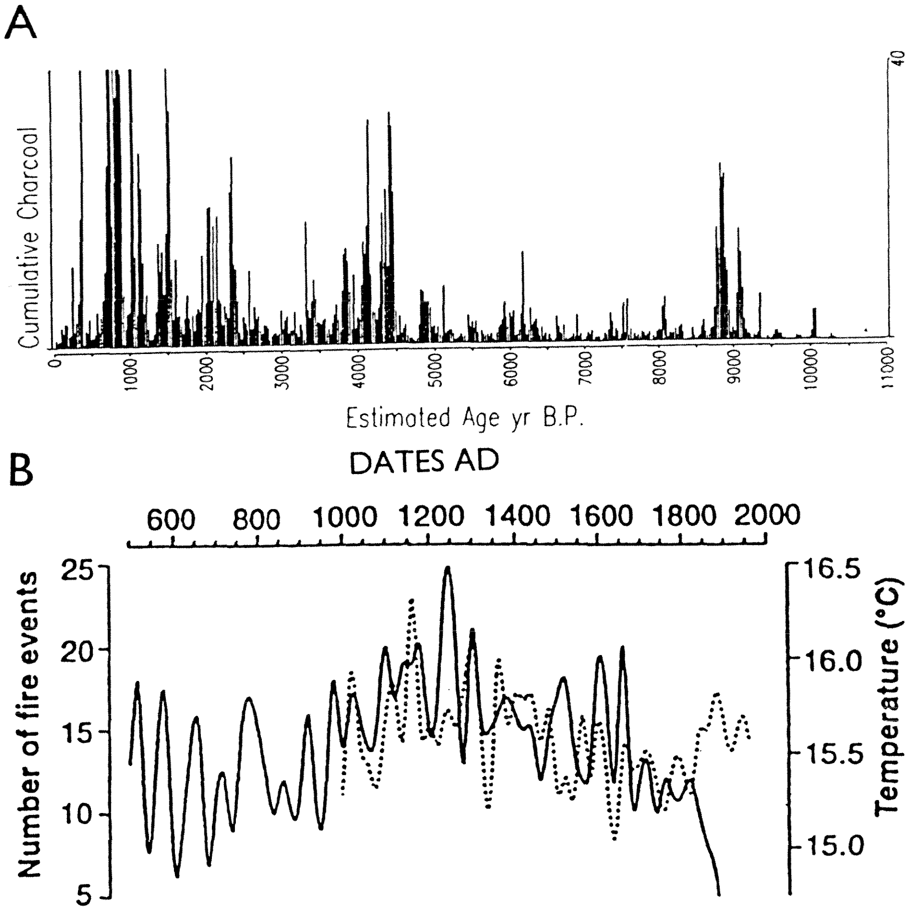


Figure 4. Changes in historic fire regimes at two timescales in the Sierra Nevada (modified from Swetnam 1993). Timescales are reversed. A. Composite charcoal record over the last 11,000 years based on sums from seven meadows in the central and southern western Sierra. Charcoal abundance axis measures cumulative area (mm^2) of microscope thin sections. Time axis is years before present (from Anderson and Smith 1997). B. Reconstructed variation in number of fire events from tree-ring analyses over past 1,500 years of five giant sequoia stands in the southern Sierra Nevada (smoothed solid line) and reconstructed summer temperatures (dotted line), showing increase in fire events during the Medieval Warm Period, decrease in the Little Ice Age, and near absence of fires in the recent fire-suppression period.

curred in patches larger than tens of hectares. Although little direct evidence exists, fire-return intervals in riparian areas for this period seem to be several times longer than adjacent upland areas (Skinner and Chang 1996). In some parts of the range of mixed-conifer type, fires appear to have created uneven-aged landscape structure composed of very small even-aged patches

(Bonnicksen and Stone 1981). For the most part, however, little direct evidence exists to indicate forest structure at the landscape scale and this critical component is inferred (Toth et al. 1994, Skinner and Chang 1996, Franklin and Fites 1996).

Studies of this time period offer the most detail on natural fire regimes, and thus are commonly used to provide baseline reference for restoring currently fire-suppressed forests. The long-term perspective of the last millennium and the Holocene reminds us, however, that the climate of these pre-settlement forests was anomalous (Little Ice Age) for the last 13,000 years. Relative to the impacts of fire suppression in the 20th century, natural variation in fire regimes may seem small. In using fire information from the Little Ice Age, however, managers should be aware of differences between such "reference" and current conditions, and adjust goals about desired conditions accordingly.

Current Ecosystems Are Novel Due to the Presence of Exotics

In an evolutionary sense, exotic species are taxa that arrive in ecosystems from remote locations and have not shared a co-evolutionary history with native taxa in the new habitats. Although exotics are usually considered to be introduced by humans, many natural introductions act like exotics. The arrival of *Homo sapiens* in North America and rapid spread over only a thousand years at the beginning of the Holocene is an example. Another is the sudden arrival and rapid spread of creosote bush (*Larrea tridentata*) from South America into the Sonoran and Chihuahuan Deserts of North America about 21,000 years ago, and into the Mojave Desert about 10,000 years ago (Grayson 1993). Both species arrived suddenly from distant continents into North American communities where native species had co-evolved (without them) for millions of years. Another trait commonly attributed to exotics occurred with these examples as well: their arrival catalyzed, or was influential in effecting, rapid and significant ecological transformations. Although controversy has raged over exact cause (Martin and Klein 1989), there is little doubt now that the arrival of the exotic hunter, *H. sapiens*, was a primary factor in many of the Rancholabrean megafaunal extinctions of North America (Ward 1997, Flanney 1999). Similarly, the arrival of *Larrea* transformed North American warm deserts, for today it is the dominant species over vast desert tracts.

Exotics introduced during the settlement period in the Sierra Nevada (since 1769 [Barbour and Major 1988]) compose a small but significant percentage of the modern flora and fauna of the Sierra Nevada, distinguishing them from historic ecosystems: 15 non-native vertebrates compared with 398 native taxa, and 300 to 400 non-native plants compared with 3,500 native taxa are now established in the Sierra Nevada (Graber 1996, Shevock 1996, Shevock personal communication, Schwartz et al. 1996). These are non-randomly distributed in Sierran ecosystems, and have variable ecological effects on the communities in which they are established. Most altered are valley oak grasslands and foothill oak woodlands, riparian and aquatic zones at low to mid-elevations, and the eastern slope (Schwartz et al. 1996). Within these zones, exotic plants and animals have aggressively displaced native taxa and triggered significant ecological transformations (Sierra Nevada Ecosystem Project 1996, Graber 1996, Standiford et al. 1996, Schwartz et al. 1996).

Implications for Management in the Sierra Nevada

As in other parts of the Southwest, old-growth forests have long been a major conservation issue of the Sierra Nevada. Management of the public forest (primarily in U.S. Forest Service and National Park Service jurisdiction) has been highly controversial in recent years. Several attempts at developing long-term regional guidelines have begun (USFS 1995, 1996); another major effort is currently underway, called the Sierra Nevada Framework (Connaughton and Lee current volume). What can we learn from Sierran paleoforests and past climates that might inform management of these ecosystems today?

Ecological Sustainability

The concept of ecological sustainability has been at the heart of forest management philosophies and social choice for more than a decade. Despite its popularity, sustainability has proven nearly impossible to characterize operationally, primarily because it embodies the inherent contradiction of a yearning for stasis within an undeniably dynamic world. By stepping back several timescales, we can ask what has been sustained in Sierra Nevada ecosystems over the past two million years and what dynamics have enabled these to persist. This perspective hints at what sustainability might be, or might not be, in Sierran ecosystem management.

As elaborated in this paper, two conditions that appear to have persisted over time are the integrity of the Sierra Nevada as a bioregion and the diversity of plant species that compose the bioregion. These are usually included as assumptions of sustainability in conservation planning, and they underscore the importance of "patrolling the borders" of the bioregion for invasions, removing exotic species and preventing new invasions, countering extinction trends, and supporting the habitat needs to maintain healthy populations of native species.

On the other hand, the historic record does not support assumptions that sustainability involves stable species abundances within locations; unchanging species range distributions or extents; stable plant community diversity and distributions; or pre-settlement conditions as a baseline. Contradicting many current sustainability objectives, the historic record indicates high variability of species abundances within locations, changes in species extent and distributions (especially at geographic and ecological margins), changing species diversity within plant communities, movement of plant communities around the range, and changing fire regimes over even relatively short times.

In sum, the historic record informs our concept of sustainability in the Sierra Nevada by showing what has remained relatively stable and what has changed. Although management goals to maintain native plant diversity have historic precedence, maintaining steady-state plant communities and vegetation structure may be successful only over small scales and short timespans, and with concerted effort. Sustaining larger Sierran landscapes in this way or striving toward a single desired landscape condition over the long term is not compatible with historic perspective and likely not feasible. By contrast, focusing sustainable management on the "maintenance of the dynamic capacity [of an ecosystem] to respond adaptively" (Costanza et al. 1993) acknowledges that certain kinds of changes are typical in Sierran ecosystems. Sustainability in this context could be viewed as conditions that retain the capacity of forests to shift adaptively in species composition and abundance, patch size and location, and spatial arrangement over the landscape in response to regional climates as well as local disturbance. Because changes such as these may be expressed on management scales as forest mortality and invasion events, we may want to re-examine conclusions about the causes and meaning of such things as changing abundances of white fir, its increasing representation in young age classes throughout many mid-elevations Sierran forests, episodic forest mortality, the role of "catastrophic" fire, changes in Sierran meadows, or apparent species declines or instability of marginal populations. Because there is evidence that plant recruitment and establishment are highly sensitive phases to climate (Lloyd 1997), disturbance events may catalyze reorganization of vegetation during periods of climate change such as the last century (Whitlock 1992, Wigand et al. 1995). These and other situations have often been considered the undesired result of human effects; they may as well be a result of natural changes (Figure 3).

Old-growth Forest: What Is It?

Part of the controversy over Sierran old-growth forests lies in the difficulty to consistently determine exactly what and where it is. As habitat for native wildlife, key structure of native plant communities, guardian of watersheds, and source of fuel, fiber and spiritual value, old-growth forests have been described in several ways. An historic perspective may offer insight. Because forest structure is not directly revealed in the historic record, it must be inferred. We acknowledge that much of what follows in this section is speculative, but feel its importance warrants the risk.

Sierran forests of recent millennia don't fit a traditional model of succession. Old-growth forest stands are most clearly described in forested ecosystems where disturbance (most commonly stand-replacing fire) and successional development are in relatively simple relationship: major disturbance is followed by establishment, stand development, maturity and old-growth phases, as the dominant and tolerant trees age (e.g., Spies 1997). Disturbance resets the cycle. Mature and old-growth stages are characterized, among other things, by a dominance of old trees and long time since disturbance.

Although forests in some regions, such as the western Cascades of the Pacific Northwest, may approach this model, many Sierra Nevada forests of recent millennia appear to have been far different, and the traditional model may actually confuse understanding of forest development. This is due largely to the nature of fire in Sierran forests over the last 4,000 years and variation of fire regimes over space and time. It is also due to high soil and topographic mosaicism, high plant species diversity and other varying factors related to elevation and latitude. A cohort of trees in almost any forest type growing to old-age had a wide range of possible trajectories, including the likelihood of many repeat entries of fire of varying intensities, sizes, and intervals. Thus for many Sierran forest types, over the last 4,000 years and at landscape scales, fire has not acted as a reset factor for succession, but rather an ongoing architect of patch type. It seems that "resetting" is not a dominant event in recent Sierran forest development. Rather frequent disturbance has interacted with changing climates and environmental variation and stochasticity to shape a continuing development of heterogeneous patch types over space and time.

From this it follows that many Sierran forests of the last millennia were characterized by a large number of patch types distributed in mosaic pattern over the landscape, with pattern varying by forest type and location. Some patches may have had dominantly young trees (resulting from small areas of high intensity fire) and could be considered early successional; more often patches would be mixed-age classes and mixed structural diversity, depending on the particular fire history of the area. Individual trees persisted to old age within many different patch settings, ranging from dense near-evenage stands of old trees to scattered, even solitary, old trees surrounded by trees of mixed ages and densities. The large number of patch types that contained old trees, and variability among forest types and across the physical environment, contribute to the difficulty we have in fitting a traditional old-growth model to Sierran ecosystems.

Sierran forests of recent millennia appear to be characterized also by patch types shifting in structure, size and species composition over time (at annual to century scales). This fluidity seems the result of the history of disturbance interacting with changing regional climates. Over several decades to centuries, a mid-size Sierran watershed under natural fire regime seems likely to experience considerable shifting of patch types. Even species presence in any general location has duration of only a few generations of the dominant tree species (Figure 2).

In sum, it is speculative but consistent to infer that forest structure and plant communities have been highly fluid over the past decades to millennia, and these patterns likely existed during previous interglacials, interspersed by many millennia of forests conditioned otherwise by glacial climates. This is not to conclude that Sierran forests have been so changeable that "anything goes" in forest management. Rather, we concur that traditional successional models of old-growth do not capture the full range of conditions that historically contained old trees and old-tree habitats. Instead of a successional model that emphasizes old-growth, an original- or old-forest model, based on interpretations of how forest ecosystems might develop and change in the early 21st century without the dominant presence of humans, may be useful as a reference to guide management. Such original forests would begin to be described by the elements above: many and diverse patch types containing a wide range of age and structural classes pertinent to forest type and local environment, high landscape heterogeneity, frequent but variable disturbance, and shifting mosaic of patches and species abundances and composition over time. Collectively the patch types, their landscape arrangement and fluidity, would constitute Sierran old forests. Similar descriptions of remnant Sierran old forests have been given by Franklin and Fites (1996) and of historic forests by Skinner and Chang (1996).

Landscape Allocations

Land management of public forests in the Sierra Nevada, as elsewhere in the Southwest, has been highly zoned. Parcels of land are allocated for specific management priorities and activities, such as wilderness, wildlife habitat (spotted owl, goshawk, marten), other significant features (special interest areas, natural areas), riparian zones, recreation designations, and extractive uses (timber, grazing, minerals). Recently, alternatives have been suggested (USFS 1995, 1996, SNEP 1996, Connaughton and Lee current volume) that emphasize the importance of the whole landscape to ecosystem functioning and advocate management with minimal zoning.

Other factors aside, the historic record favors a whole-landscape management approach. The record suggests that the Sierran bioregion has remained distinctive with a characteristic species diversity over millennia, but this has been achieved at the scale of the whole bioregion, or at least large portions of it. There is little to no evidence from the historic record that suggests spatial continuity or stasis of forest patch types or size, species abundance (or even presence), of plant community composition, or of fire regime. To the contrary, there is evidence for shifting boundaries of these elements at many timescales. Fluidity in species boundaries and plant community structure and composition has been a dominant feature in Sierran ecosystems, and may be a significant mechanism enabling species sustainability over time. With changing climates, species have responded by dying in some places and invading others. They have found refugia within the environmental diversity of the range in unexpected places; such relict populations appear to serve as important sources for rapid recolonization when favorable climates again shift over them (Pitelka et al. 1997). Zoned approaches assume landscape stability of the elements they are designed to protect, and impose a rigidity that is counter to natural process (Hunter et al. 1988, Pitelka et al. 1997).

In the context of forest policy, many factors enter into decisions about how and whether to zone lands. Although most of these are beyond the scope of this paper (involving trust, cost, operational feasibility, etc.), we raise a final ecological consideration. Whether explicit or not, many approaches to science-based ecosystem management make choices about how much to mimic nature. On the one hand are those that recommend a strong "patterned after nature" approach to restoration and management of ecosystems (e.g., Costanza et al. 1992), including, for example, implications we advance in this paper regarding the natural historic behavior of Sierran landscapes. An assumption in this approach is that by maintaining and restoring the natural land mechanism, we do the best for all the parts and pieces (Leopold 1949). Nature is considered too complex for humans to either understand completely or to know better than to take a course that deviates from natural pattern and process.

For nature to run its course requires, however, that we can both create conditions for this to happen and that we accept the consequences. These include fluidity of biota across the landscape or changing species abundances and distributions, including loss of populations in some places or species migrations into other parts of the range. They also include the potential for dramatic mortality events, periods of large and catastrophic fires, ecological type conversions, significant changes in water output on yearly and decadal levels, potential rangewide shifts in age structures of forests, etc.

Does society want this or can it afford such variance? Although there are many arguments, the implication of stasis expressed by ecological sustainability suggests society does not or cannot. The stability desired does not seem consistent with patterns naturally experienced in the Sierra Nevada.

Added to this is the question of whether the capacity for historic dynamism even exists or is possible anymore in the Sierra Nevada. The arrival of the exotic *H. sapiens*, especially the recent wave in the late 1800s, has altered the landscape drastically and seemingly permanently. The addition of hundreds of exotic plants associated with human settlement, many having already converted ecosystems, create very different biotic conditions than anything seen in the last 2 million years of Sierran history. These changes may well render the lessons from prehuman history less meaningful, and to ignore the significant changes that have occurred as a result of human invasion would be myopic. Even aside from policy decisions about land allocation that enforce rigidity, a high degree of stasis is already imposed on Sierran ecosystems by the network of human development across the Sierra, including rural communities and urban interface, roads, dams, etc. Under such constrained conditions, would a designer-approach to management, such as forcibly maintaining ecosystems garden-like within predetermined land allocations, be more likely to achieve societal goals?

To us, it seems that the Sierra Nevada is in a middle ground regarding the potential to pattern successfully after nature versus an engineered landscape. For, notwithstanding human alterations, at many spatial scales Sierran ecosystems are still relatively wild, or rather, wild enough to be realigned with natural process such that working within natural pattern and process seems likely to be successful. If so, the more we are able to provide ecological flexibility over the entire landscape in achieving desired goals, the more likely we are to provide capacity to adapt to changing conditions. This seems most likely to happen in a management context without strict spatial zoning or enforced or static forest structure. If, for whatever reasons, an approach with strong zoning is favored, natural ecosystem functioning can be promoted by setting ecological goals for the lands outside the specific zones (often called matrix lands) as well, and by allowing flexibility to reallocate zones as conditions change. This, in effect, allows the whole landscape to be used to attain ecological goals, even if management emphasis differs by allocation.

Increasing attention to historic concepts is helping to translate ideas such as these into practice. The importance of paleoecological dynamics in plant community and forest development, the individualistic nature of species, and the role of climate as an ongoing architect and disturbance agent have been discussed for specific aquatic and terrestrial ecosystems (e.g., Davis 1990, Sprugel 1991, Smol 1992, Tausch et al. 1993). Paleoecologists are now investigating forest responses over short timescales that link annual forest dynamics with climate change (Davis et al. 1998). Quantitative models that simulate changing climate with historic vegetation response for large (Prentice et al. 1992) and small (Campbell and McAndrews 1993) areas and timespans will prove useful in exploring future management scenarios. Applications have focused on biodiversity conservation at broad scales (Hunter et al. 1988), maintenance of ecosystem health (Tausch 1996), and incorporating natural ranges of variation into landscape analysis (Stephenson 1994, Millar 1997, Swetnam in press). Whole landscape approaches generally are favored by those taking a paleoecological perspective (Foster et al. 1996). For the Sierra Nevada, these have been translated into planning scenarios that emphasize fine-scale forest mosaic over the whole landscape and high flexibiity (SNEP 1996), such as the Distributed Forest Conditions strategy for old forests, and emphasis on landscape analysis for watershed management. Such designs impose considerable management challenge, but paybacks in ecosystem resilience and adaptability make them worth increasing application.

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