CLIMATE CHANGE AS AN ECOSYSTEM ARCHITECT:

IMPLICATIONS TO

RARE PLANT ECOLOGY, CONSERVATION, AND RESTORATION

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ABSTRACT

Recent advances in earth system sciences have revealed significant new information relevant to rare plant ecology and conservation. Analysis of climate change at high resolution with new and precise proxies of paleotemperatures reveals a picture over the past two million years of oscillatory climate change operating simultaneously at multiple timescales. Low-frequency oscillations are paced by cycles of the earth's orbit around the sun and the resulting solar heat that earth receives. These control multi-millennial cycles of glacial (~90,000 year) and interglacial (~10,000 year – the Holocene is one of many) periods with 10-15°C average differences. Despite the long duration of these cycles, transitions between periods have been abrupt, on the order of years to decades. Nested within the glacial/interglacial cycles are century-millennial climate oscillations, paced primarily by cycles in solar activity. These occur in quasi-1300 year periods and also have abrupt transitions between states, e.g., >8°C mean change in ten years. Further within these cycles are high-frequency interannual to decadal fluctuations, with mechanisms generated by ocean/atmosphere dynamics. Climate change thus functions as an important recurring agent of ecological and evolutionary change, with each scale of historic climate cycling tracked by changes in vegetation. Primary responses at multi-millennial scales are major migrations, range shifts, and population extirpations and colonizations (up to 1500 m elevation and across hundreds of km). Similar types of change but smaller magnitudes characterize mid-frequency climate variability, while annual and decadal climate oscillations provoke primarily changes in productivity and abundance of plants. The nature of climate change and the vegetation response have conservation implications on the nature of rarity, transience of native ranges and

plant associations, significance of population declines and increases, development of targets and references for restoration, and strategies for global warming.

INTRODUCTION

Conceptual views of the natural world influence tactical approaches to conservation, restoration, and management. Advances in ecological sciences during the 20th century about succession, disturbance, and spatial variability motivated a shift from viewing nature as static and typological to dynamic and processual. In turn, conservation and management matured from an emphasis on museum-like nature preservation to focus on maintaining variability and natural function. As a result, prescribed fires and managed floods, for instance, became important conservation tools, and recovery of ecosystem function as well as structure was added to restoration goals.

Important as these changes have been, static concepts still constrain our understanding of natural dynamism and limit our conservation successes. Recent advances in earth system sciences, which characterize recurrent climate change as a central physical force on earth, have not been fully incorporated into evolutionary and ecological theory, nor translated into conservation and management practice. In this paper, I briefly summarize the significant role of climate change as an ecosystem architect and an agent of change at micro- to macro-scales. From this perspective, vegetation response, including dynamics of rare plant demographics, persistence, population fluctuation, and disturbance relationships, is seen as occurring against a background that itself is changing – i.e., vegetation response becomes a "variable chasing a variable not a constant" (Jackson, 1997 citing Cowles, 1901). Using examples from California forest trees, I suggest ways in which integrating these concepts into rare plant ecology and conservation may lead to new interpretations and practices.

BACKGROUND – HISTORIC CLIMATE CHANGE

Changes in weather are familiar features of earth's surface, readily recognizable as diurnal variations, seasonal cycles, and annual differences that irregularly include extremes of drought, wet, heat, and cold. All forms of life are influenced by this variability in how and where they live, and mitigate adverse weather effects through conditioned responses and evolved adaptations. Cycles of climate change occur also over periods of decades to millennia, although until recently these scales have been little known and poorly understood. In the past two decades, new tools and an explosion of research in paleoclimatology have

revolutionized our understanding of historic climate, resulting in characterization of Quaternary (the last 2.5 million years, or 2.5 Ma) climate as highly oscillatory, with nested cycles occurring at short- (annual-decade), mid- (century-millennia), and long-term (multi-millennia) scales. Mechanisms that drive these oscillations, regulating periods of relative stasis, gradual change, and abrupt transitions, are becoming unified in global climate systems theory. Because much of this information hasn't been incorporated into ecological or conservation literature, I summarize primary patterns, mechanisms, and vegetation responses of the major climate-change cycles below (for textbook treatments, see Bradley, 1999; Cronin, 1999; Ruddiman, 2001).

Multi-Millennial Climate Cycles (Glacial/Interglacial, or Orbital, Cycles)

Until recently, reconstructions of Quaternary climate relied on geomorphic evidence such as glacial moraines, former sea levels, and historic lakeshore elevations as well as fossil remains of plants and animals. Collectively these led to early interpretations of the Pleistocene (0.01 – 2.5 Ma) as a long cold interval, or the "great ice period" of Agassiz. By the late 19th century, evidence for multiple glaciations accumulated and led to widespread description of four major glacial periods in the Pleistocene bracketed by warmer intervals. The ice ages were regarded as ending about 10 thousand years ago (10 ka) with the arrival of novel warmth of our recent epoch, called the Holocene to signify its difference from the Pleistocene. New climate proxies have been developed that have great precision, high resolution, and can be extended back in time thousands to millions of years. They reveal a far more complex climate history than previously understood. The most widely applied and useful proxies are carbon and oxygen isotopes taken from long ice cores retrieved from polar ice caps (Cuffey et al., 1995). Gases and atmospheric particles trapped in annual layers of ice faithfully record atmospheric conditions at the time of deposition. Cores drilled to the bottom of the ice sheets (>3000m) have yielded highly resolved information on over 40 climate variables for longer than 400,000 years. Analysis of these isotopes, especially ratios of oxygen isotopes ($\delta^{18}O$), which are robust indicators of surface air temperature, are now routinely used in other situations where undisturbed deposition occurs, such as lake beds, coral reefs, and sea floors, and where oxygen isotopes can be analyzed (e.g., from shells of micro-organisms). Studies of varying time depth around the world using these proxies, from a few decades to > 60 Ma (Zachos et al., 2001), have led to detailed global and regional reconstructions of historic climate.

Records that extend greater than 10,000 years collectively document that multiple major climate oscillations occurred over the past 2.5 Ma (Fig. 1, Wright, 1989; Raymo and Ruddiman, 1992). Unlike

inferences from geomorphic evidence, oxygen-isotope records show a repeating pattern of over 40 glacial/interglacial cycles occurring in two dominant modes, one of approximate 100,000 year duration, and an earlier one of 41,000 years duration. During the past 800 million years, glacial periods lasted 80-90 ka and interglacials lasted 10-20 ka, whereas prior to that the cold and warm phases were about equal length. Another important conclusion documented by the oxygen-isotope records is the overall similarity of the Holocene to past interglacials in overall length, trends, and temperature. From the many oxygen-isotope curves now available around the world, it has become clear that these major warm-cold oscillations of glacial/interglacial phases were expressed globally and more-or-less synchronously. Global temperature differences between glacial and interglacial periods averaged about 10-15°C (Petit et al., 1997); regional expression varied with latitude, elevation, and continentality, with Greenland extreme glacial-period temperatures at least 21°C colder than present (Cuffey et al., 1995). Dominance of glaciers and ice sheets was limited to high-latitude and mountainous regions.

The oxygen-isotope curves further reveal repeating structure to climate within glacial and interglacial phases (Lorius et al., 1990). Extensive cold glacial periods (stades) of the past were interrupted by warm phases (interstades) of about 1/3 the warmth of interglacials, and terminated abruptly into interglacials. At a coarse scale, interglacials, including the Holocene, began abruptly, peaked in temperature in early to middle cycle, and terminated in a series of steps, each with abrupt transitions, into cold stadials of the next glacial period. Collectively this yields the characteristic sawtooth pattern of Quaternary climate fluctuations (Fig. 1). Recognizing that the distinction between the Holocene and Pleistocene inaccurately describes fluctuations of past climates, climatologists now designate alternating climate phases by oxygen-isotope stage (OIS), assigning odd numbers to interglacials and interstadials and even numbers to cold glacial periods, starting with the Holocene as OIS 1.

A mechanistic cause for glacial/interglacial oscillations was proposed by Serbian mathematician Milatun Milankovitch (Milankovitch, 1941) long before detailed climate variability was observed. Milankovitch integrated knowledge about earth's orbit around the sun into a unified theory of climate oscillations. This has been refined and revised subsequently into a modern orbital theory that is widely accepted (Imbrie et al., 1992, 1993), although not without problems. Three major cycles of orbital variability recur over time (Fig. 2, Hays et al., 1976): (1) change in the shape of earth's orbit around the sun from elliptical to circular (eccentricity cycle; 100,000 years), (2) change in the angle of earth's tilt on its axis (obliquity cycle; 41,000

years), and, (3) change in time of year when the earth is closest to the sun (axial precession; 23,000 years). The amount of heat from the sun reaching the earth (solar insolation) at any point in time varies depending on the earth's position within each cycle. Milankovitch found that integrating the three cycles mathematically resulted in a curve over time of predicted temperature on earth that may explain glacial cyclicity. Subsequent analysis has revealed that these patterns of warm and cool strongly correlate with the observed oxygen-isotope curves (e.g., like Fig. 1). These were similar in shape and duration to the major glacial/interglacial cycles (called orbital or "Milankovitch" cycles) and to the shorter stadial/interstadial cycles (suborbital or "sub-Milankovitch" cycles). Differences within the Quaternary in primary pattern are related to dominance of one versus another of the suborbital cycles.

Although orbital variation has occurred for millions of years prior to the Quaternary, a highly oscillatory climate system like the last 2.5 Ma occurs only irregularly through time (Zachos et al., 2001). Possible factors contributing to Quaternary instability include (1) tectonic uplift, which generates high elevations and opportunities for ice accumulation (e.g., uplift of Tibet, Sierra Nevada, Colorado Plateau, Himalayas, Alps; Raymo and Ruddiman, 1992); (2) chemical weathering, which leads to declines in atmospheric carbon dioxide (Kutzbach et al., 1993); and (3) change in continental positions, which leads to altered ocean circulation and changed ocean/atmospheric relationships (Ramstein et al., 1997).

Abundant evidence worldwide indicates that life on earth has responded to glacial/interglacial climate shifts with similarly large, cyclic, and highly synchronous biotic changes. Vegetation response over time can be measured from sediment cores of lake and ocean bottoms, which contain continuous depositions of regionally local pollen (Faegri and Iversen, 1989). In other environments, macro-fossils of leaves and fruit preserved in sediments and packrat middens can be assessed (Betancourt et al., 1990). Collectively these paleorecords document that, at any one place, compositions of flora changed significantly in correspondence to major climate phases, often showing complete or near-complete species turnover and frequently documenting re-assemblage of similar groups of species during glacial or interglacial periods. In relatively flat terrain, such as in northeastern United States, eastern Canada, parts of Scandanavia, and northern Asia, species shifted latitudinally north and south many hundreds of miles, as modeled for spruce (*Picea*) in eastern North America (Fig. 3, Jackson et al., 1987). In mountainous regions, by contrast, such as western North America and western Europe, species responded primarily by elevational shifts as much as 1500 m, as indicated by conifers of the Great Basin and southwestern desert region (Fig. 4, Thompson, 1988, 1990;

Grayson, 1993). In regions where habitats were highly patchy, with steep and discontinuous gradients and obvious directional changes in latitude or elevation, species responded primarily by fluctuations in population size and minor shifts in location, as exemplified by oaks in California (Adam, 1988; Heusser, 1995; Millar and Skinner in prep).

A key characteristic of Quaternary paleoecology is the finding that species responded individually to particular climate cues with unique rates and sensitivities to individual climate variables. From this perspective, plant communities exist as transient assemblages of species that move individually through time and space following favorable climates and environments. The apparent re-coalescence of vegetation assemblages results from recurrence of similar climate conditions, although lags and differences in individual species responses, as well as stochastic events, give variation to the exact structure of plant communities at any one time (Webb, 1986; Davis et al., 1986).

Century- to Millennial-Scale Climate Cycles

Analyses of oxygen-isotope variation further revealed that oscillations of century to millennial length are nested within the major orbitally driven climate cycles. These were known first from a few well-studied individual climate events such as the Younger Dryas (Kennett, 1990), a 1000-year return to ice-age conditions that interrupted warming at the end of the last glacial period (11.5-12.5 ka); the Heinrich events (Heinrich, 1988), a series of short (100-1000 year) extreme cold intervals within the last glacial period; and the Dansgaard/Oeschger interstadials (Dansgaard et al., 1993), short warm intervals interspersed in the last glacial period. These climate periods, originally thought to be unique extreme events, are increasingly understood as part of an oscillation cycle that has been pervasive throughout glacial and interglacial periods for at least the last 130 ka (Bond et al., 1997). Periodicities of these oscillations, sometimes called “Bond cycles”, averaged 1340 years during the Holocene, 1536 years during the last glacial period, and 1480 years during the Eemian (previous interglacial). Characteristically, the events have stronger amplitude during glacial periods, where they express about 1/3 the temperature differences of full glacial/interglacial magnitude. Individual climate periods during the Holocene that exhibit millennial cycling of this nature include the warming of the 20th century (IPCC, 2001); the Little Ice Age (LIA, Grove, 1988; Overpeck et al., 1997), a minor ice advance and global cold period from AD 1450-1920; the Medieval Climate Anomaly (Stine, 1994; Hughes and Diaz, 1994), a warm, dry interval with regional variability from AD 900-1350; and the 8.2 ka cold event (Alley et al., 1997). Painstaking analysis at high resolution of several well known

intervals has documented that these oscillations begin and end extremely abruptly. Annual analysis, for example, of 150 years centered on the major collapse of ice at the end of the Younger Dryas cold event revealed that 15°C warming occurred in two 10-year periods (ca. 7-8°C each) separated by a 20-year plateau of no change (White et al., 2001). Similarly abrupt change is indicated for other transitions where analyses approach resolution adequate to detect rates (see examples in Cronin, 1999).

Of particular interest is the warming of the last 150 years. During the Little Ice Age, temperatures in western North America were on average 1°C colder than present, and glaciers in the Sierra Nevada were at their greatest extent since the end of the Pleistocene over 10,000 years ago (Clark and Gillespie, 1997). Warming since the late 1800s has been ca. 0.7°C globally (IPCC, 2001), with much of the increase occurring due to increases in minimum temperature. Mean annual temperatures in the late 1990s were warmer than any in the 20th century approximate those of the Medieval Climate Anomaly (Fig. 5, Esper, et al., 2002). Increases in the early part of the century are considered natural response to Bond cycling; continued warming and other changes since mid-20th century are widely believed to be due to anthropogenic increases in greenhouse gases (IPCC, 2001). Climate variables other than temperature have changed during the past 100 years, including increases in precipitation in the California region, and significant increases in climate variability, which led to increases in occurrence of and fluctuations between unusually extreme events (floods, droughts, tornadoes, etc.).

The natural mechanisms driving climate oscillations at the century-millennial scale are still highly debated and a topic of keen current interest. The relationship of extremely cold intervals within glacial periods to sudden surges of polar ice into high-latitude oceans, and resulting abrupt changes in global ocean salinity, first led climatologists to believe these intervals were driven by ice and ocean-circulation dynamics (Broecker et al., 1990; Clark et al., 2001). Recently, however, millennial cycles in the sun's intensity (mediated by sun spots and other changes at the sun's surface) have been shown to match the timing of the Bond cycles over the last 130 kyr with stunning precision (Bond et al., 2001). This has led climatologists to speculate that the trigger for century-millennial climate changes comes from outside the earth – that is, changes in the sun – and that changes in ocean circulation further regulate and abruptly communicate climate change worldwide. This new research points to tropical latitudes (tropical oceans) as the location of initial reception of solar switches. The relative expression of certain individual events, such as the LIA, which, although minor by glacial-age standards, brought a return in North America of the largest glacial

advance in over 10,000 years, was amplified by stochastic factors such as unusually high concentration of aerosols as a result of high global volcanic activity (Overpeck et al., 1997).

Significant and rapid response of vegetation to century-millennial scale climate change has long been documented for a few well known climate intervals at this scale. Before temperature proxies such as oxygen isotopes provided independent measures of historic climate, millennial-scale abrupt climate events were inferred from changes in vegetation. For instance, the Younger Dryas was known from changes in abundance of the arctic tundra plant *Dryas octopetala* (Jensen, 1935*)*. This species dominated paleofloras of western Europe during coldest ice ages and was being replaced by warm temperate vegetation as climate warmed at the end of the last major ice age. An abrupt short-lived reversal to full-glacial abundances of *D. octopetala* became known as the Younger Dryas, and was interpreted as a brief return to glacial climates. A similar earlier climate reversal, also described first by abrupt return to high *D. octopetala* pollen abundance, is known as the Older Dryas. Subsequent description of these and other periods of abrupt climate change using physical proxies such as oxygen isotopes has been found to correspond to significant changes in vegetation. An illustrative example is the abrupt changes in pine versus oak vegetation in southern Florida corresponding to Heinrich events (Fig. 6, Grimm et al., 1993). An important example from the California region comes from the work of Heusser and her colleagues, who demonstrated that abrupt changes in the dominance of oak versus juniper corresponded to rapid climate oscillations of the last 160 kyr (Heusser, 2000). In the Sierra Nevada, our work with limber pine (*Pinus flexilis*) shows colonization and extirpation events corresponding with the regionally recognized neoglacial period (3.5-2.2 ka), a post neoglacial dry period (2.2-1.5ka), Medieval climate anomaly (0.9-0.7 ka), the Little Ice Age (0.6-0.1ka), and the last 100 years. Major changes in population size and extent of pinyon pine (*P. monophylla*) also correspond to these century-long climate periods in the western Great Basin (Nowak et al., 1994).

Interannual- to Decadal-Scale Climate Change

Apparently random changes in weather from year to year are readily noted by even the most casual observer. In recent years, climatologists have defined systematic climate cycles and mechanisms that operate at high frequency, on scales from a few years to several decades. The best known of these is the El-Niño phenomenon, technically called the El Niño-Southern Oscillation (ENSO) for its worldwide and mechanistic basis (Diaz and Markgraf, 2000). Every several years, normal hemispheric trade winds that typically blow warm tropical ocean water westward across the Pacific Ocean stall and warm water instead

accumulates in the eastern Pacific Ocean. This leads to the presence of unusual water temperatures offshore from North and South America, which directly affects regional marine fauna and brings distinctive weather patterns to many regions of the world (called teleconnections). Monitoring ocean circulation temperatures through a network of ocean buoys has led to mechanistic understanding of annual variation in this phenomenon. Each year there is some degree of El Niño or its opposite effect, La Niña. Extreme events cycle on an approximate 2-8 year basis. Along the west coast of the North America, El Niño events bring unusually warm and wet fall and winters to central and southern California and unusually cold and dry weather to the Pacific Northwest, while the reverse occurs during La Niña events. The transitional position of northern California means that sometimes this region goes with the Pacific Northwest pattern, and sometimes with the California pattern (Redmond and Koch, 1991).

In addition to interannual phenomena like the ENSO cycle, climate oscillations on multidecadal (20-60 year) periodicities have been described recently. These are less well understood both from a descriptive and a mechanistic standpoint, but are the focus of intense current research. Many of these cycles affect particular regions of the world rather than globally. The Pacific Decadal Oscillation (PDO) is the best known quasi-cycle in western North America, is regulated by decadal changes in ocean circulation patterns in high-latitude Pacific Ocean (as opposed to ENSO's tropical locus), and yields climate effects and regional patterns similar to extended ENSO effects (Mantua et al., 1997; Zhanget al., 1997). Warm (or positive) phases are extensive (10-25-year) periods of El Niño-like conditions that alternate with cold (or negative) phases of La Niña -like conditions. PDO and ENSO interact to produce extreme events: the occurrence of a strong El Niño pattern in the tropical ocean during a warm PDO phase has resulted in a more extreme El Niño pattern than has occurred during a cold PDO phase (Gershunuv and Barnett, 1998).

Vegetation response to interannual cycling of ENSO has been better studied than decadal effects. Vegetation response to annual variability in warm/wet versus cool/dry years occurs primarily as changes in plant productivity and abundance within populations. The oscillations contribute to regional fire regimes, where fuel loads build during wet years and burn during dry years. These lead to meso-scale vegetation changes as ENSO itself cycles, and thus fire regimes change over time (Swetnam and Betancourt 1998; Kitzberger et al., 2001). Decadal climate and vegetation oscillation has been documented in secondary growth of trees, such as recurring droughts over the past 400 years that led to reduced ring-widths in ponderosa pine in New Mexico (Grissino-Mayer, 1996, Fig. 7), and the recurring pattern of ring-widths in

bigcone Douglas-fir (*Pseudotsuga menziesii*) that document PDO oscillations for the last 400 years; (Biondi et al., 2001). Our work with subalpine conifers in the Sierra Nevada documents that vegetation response to 20th century climate change occurred in decadal steps (Millar et al., 2000). In four independent studies, of meadow and snowfield invasion, and krummholz pine horizontal and vertical branch growth, we found that significant and threshold responses occurred during multi-decadal periods corresponding to phases of PDO.

Summary of Climate Change

This brief overview of climate leads to several conclusions: First, climate has *oscillated* between warm and cold, wet and dry regimes over the last 2.5 million years rather than been dominantly directional or stochastic. In broad terms our present warm period (Holocene) has been similar to interglacials of the past, and the last glacial period had many antecedents before it. Second, climate has oscillated simultaneously at *multiple and nested scales*, including interannual, decadal, century, millennial, and multi-millennial; mechanisms and the nature of expression differ depending on the scale, although the effects interact. Third, transitions between major and minor climate phases often occurred *abruptly* (a few years to decades), and were accompanied by significant changes in climate (e.g., 3-15°C). Finally, *vegetation responded to climate change* at each scale. Vegetation responses to annual/decadal variability are mostly in productivity, abundance, and local shifts in community composition, whereas responses at century/millennial scales involve major colonization and extirpation (migration and range shifts) events. Recurring climate changes at each scale thus exerts significant recurring evolutionary and ecological force on vegetation at multiple scales. Species have been exposed to fluctuating climate and rapid transitions for over two million years, and likely similar phases that punctuated the past 20 million years. Individual species follow their own ecological trajectories as climates cycle, leading to changes in community compositions that themselves form, dissolve, and (often) reform over time.

IMPLICATIONS TO RARE PLANT ECOLOGY AND CONSERVATION

Concepts of Sustainability

Ecological sustainability is a dominant current paradigm often used as an implicit or explicit goal in conservation, restoration, and management practice. Variously defined and defended, sustainability implies species, community, and ecosystem endurance and persistence over time (Lele and Norgaard, 1996). Operationally, sustainability has been difficult to describe, or to recognize when it is achieved. Sustainability is generally accepted to pertain when natural species diversity is maintained, species are well-distributed in

their native ranges and occur in historic abundances, community associations are maintained, and natural processes occur at reference intervals and conditions (Lackey, 1995; Hunter, 1996).

As a test of what has been sustained naturally in the past, my colleague and I assessed the paleorecord of Quaternary vegetation in the Sierra Nevada for losses, gains, changes in distribution, etc. (Millar and Woolfenden, 1999a). Accounting for limitations and biases of the paleorecord, we found that only a few conditions usually associated with sustainability pertained in the paleofloras of the Sierra Nevada. These included, (1) relative stability of the Sierra Nevada ecoregion, i.e., persistence of a distinct ecoregion over time, and, (2) persistence of overall species diversity at the scale of the entire Sierra Nevada ecoregion, with only one species, a spruce (*Picea* spp.), disappearing from the region about 500,000 years ago.

Beyond these two features, however, other conditions often associated operationally with ecological sustainability did not occur in the history of Sierra Nevada vegetation. At sub-regional scales within the Sierra Nevada, species diversity changed at timescales of centuries to millennia. Similarly, individual species ranges and population abundances shifted, often drastically. One example is giant sequoia (*Sequoiadendron giganteum*). Currently limited to small groves in limited sites of the southwestern Sierra Nevada, giant sequoia's range over the past 10-26 ka included the eastern Sierra Nevada (Mono Lake, Davis 1999a), and locations in the western Sierra Nevada that are both well above (to 2863m; Power 1998) and below (to 54m near the Central Valley, Cole 1983; Davis 1999b) its current range. Giant sequoia did not appear in its current location in the Giant Forest until 4500 years ago, and did not reach modern abundance until about 2000 years ago, i.e., about the age of the oldest living individuals (Anderson and Smith, 1994, Fig. 8). Another example is pinyon pine, which has a history of significant range shifts corresponding to major and minor climate periods. During the last glacial period, pinyon pine shifted far south into regions that are presently Mojave and Sonoran Deserts of southern California and Nevada. Its recolonization northward into the Great Basin and eastern Sierra Nevada has occurred in fits and starts over the past 10,000 years, and appears still to be in dynamic flux. Pinyon first arrived, for instance, in the floristic Great Basin 6500 years ago; in Slinkyard Valley near Monitor Pass 1400 years ago; near Reno 400 years ago; and to its current northernmost location (of western Great Basin populations) in the Pah Rah Range 200-300 years ago (Grayson, 1993).

Several other conditions often considered elements of ecological sustainability did not pertain in the paleorecord (Millar and Woolfenden, 1999a). Movement of individual species such as pinyon meant that

vegetation assemblages also changed over time and/or shifted locations as individual species followed climate gradients (Woolfenden, 1996). Vegetation communities appeared sometimes to shift locations, when individual species tracked climate coincidentally, and in other cases, changed composition and dominance relations. Non-analog communities (past vegetation assemblages that are not found today) also existed, such as the co-occurrence 20-30 ka in the Alabama Hills (southern Sierra Nevada) of yucca (*Yucca brevifolia*) and Utah juniper (*Juniperus osteosperma*) with an understory of *Artemesia tridentata, Purshia tridentata,* and *Atriplex concertifolia* (Kohler and Anderson, 1995). Historic fire regimes reconstructed from charcoal analyses in paleorecords also changed over time at multiple scales. Over the last 10,000 years, for instance, fire in mid-elevations of the western Sierra Nevada was a minor ecosystem architect. Beginning about 4000 years ago, charcoal records indicate increased local fires and effect on regional vegetation (Anderson and Smith, 1994, 1997). At scales of decades to centuries, Swetnam (1993) showed that fire regimes in giant sequoia forests shifted from frequent, light, and localized fires to infrequent, intense, and widespread fires in the last 1000 years following climate changes.

In sum, these and other records suggest that our current concepts of sustainability, with emphasis on persistence of species and communities within current ranges and in current population relationships and abundances, may not accommodate natural dynamics adequately. Species ranges have, and will continue to, shift naturally over small to large distances as species attempt to equilibrate with changes in climate. In the course of adjustment, plant demography, dominance and abundance levels change, as do vegetation associates and wildlife habitat relations. The recurring (oscillating or quasi-cyclic) nature of climate suggests that conditions of the past may recur, at least on coarse scale, and thus, if vagaries of chance pertain, vegetation shifts may also cycle. If there is any conclusion from the paleorecord it is that, at scales from years to millennia, ecological conditions do not remain stable nor are they sustained, but, by contrast, are in great flux (Jackson and Overpeck, 2000). The flux is not random, chaotic, or unlimited but directed by climate and interpreted by local environmental conditions. Resilience, at least in terms of species persistence, is met through the capacity of plants to track favorable environments as they shift over time, and through adjustment in range distribution, habitat, and population characteristics.

Concepts of Rarity, Population Decline, and Native Range

Rarity in plant species has often been linked to species history, for instance, recent speciation or paleo-relictualism (Rabinowitz, 1981; Fiedler and Ahouse, 1992). The perspective of Quaternary climate and

vegetation oscillations, however, illustrates that rarity may be transient and recurring, and may alternate with periods of widespread distribution. Oaks (*Quercus*) and junipers (*Juniperus*) illustrate this situation in California. Species of these genera faithfully tracked alternating temperature regimes of major and minor climate periods. During long glacial periods, for instance, *Quercus* abundance dropped drastically, and distribution of California species shrunk throughout their ranges to become rare species (Fig. 9; Adam and West, 1983; Heusser, 1995; Millar and Skinner, in prep.). By contrast, during warmest parts of interglacials (middle Holocene and middle Eemian), oaks expanded to reach distributions more widespread than at present. Juniper responded similarly but in complementary fashion to oaks: During long glacial times junipers expanded to become widespread and fragmented and contracted during warm interglacial periods (Adam and West, 1983; Heusser, 1995; Grayson, 1993). Oak and juniper expanded and contracted in similar nature but to lesser degree, with minor climate fluctuations occurring at the century-millennial scale, and significant changes in abundance occurring within as little as a decade (Heusser and Sirocko, 1997). The sensitivity of these genera to climate change led Heusser and her colleagues to call oak and junipers alternating endmembers of macrosuccesional dynamics.

The California coastal closed-cone pines, especially Monterey pine (*Pinus radiata*), provide another example of the transience of rarity. Rare at present, these species expanded and contracted in a meta-population pattern following historic climate shifts (Millar, 1999). In contrast to the oaks and junipers whose optimal conditions coincided with extensive climate periods, favorable climates for expansion of the coastal closed cone pines occurred briefly during transitions from glacial to interglacial periods and during short-lived interstadial periods (Heusser and Sirocko, 1997; Millar, 1999). Conditions of fuels and fire regimes that developed during these transitional times also contributed to temporary expansions in the range and abundance of these pines.

A final example of fluctuating species distribution size is in the redwood family (Taxodiaceae). From the perspective of deep time, directional trends seem obvious in this family, which experienced a peak in diversity and species distribution during the Mesozoic era. Modern species, including our coast redwood (*Sequoia sempervirens*) and giant sequoia (*Sequoiadendron giganteum*), appear as narrowly distributed relicts of significant directional changes over the past 60 million years that have diminished favorable redwood habitat at the continental scale. From the perspective of Quaternary climates and California distributions, however, these species have expanded and contracted significantly between relatively

widespread versus rare distributions following climate change. I have already described changes in giant sequoia's distribution and abundance that appear related to Quaternary climate oscillations, but in this context I emphasize change in abundance in addition to shifts in range extent. During the last glacial period giant sequoia had a larger distribution east and west of the Sierra Nevada crest and greater population abundance than its present interglacial rarity.

Coast redwood also fluctuated in population extent and abundance following cold/warm cycles, and was much more sparsely distributed than at present during climate periods when coastal fog did not develop and temperatures were too hot or too cold (Heusser, 1998; Poore et al., 2000). These conditions occurred, for instance, during glacial periods when ocean circulation patterns and air/ocean temperatures were such that winters were cold, summers were warm, and fog did not develop along the coast. Redwood expanded during mild, equable parts of interglacials when ocean temperature and circulation influenced development of coastal fog.

These examples and others suggest not only that rarity may be a transient and recurring condition in some plant species but that changes in population size (e.g., declines) and distribution (e.g., contractions) may be natural responses to climate change. The non-equilibrium nature and lags in adjustment mean that population increases or decreases may not appear to be "in synch" with current or recent climate change, and when rapid climate changes in different directions occur over short times, vegetation response may be particularly complex (Jackson and Overpeck, 2000). Depending on individual life histories and habitat requirements and the nature of climate change, populations may decline and contract in some species, or some parts of species' ranges, while others may increase or expand (Jackson and Lyford, 1999). Because plants, unlike animals, cannot "pick up and move", they migrate and shift in distribution by dying in some areas while expanding in others. These may be messy on the landscape – with patchiness and irregularity characteristic – making the effects difficult to evaluate while they're happening.

Finding base causes for changes in population size may be further hindered in that proximal causes for mortality or expansion may be local biotic or physical agents. These may seem sufficient to explain changes, but in fact are secondary effects triggered by changes in climate. Population declines may appear, for instance, as increases in natural pathogen- or insect-caused mortality in certain parts of ranges; these may occur in short-lived episodes (e.g., during droughts), but if viewed collectively, result in overall range adjustments. Many of the forest mortality events of western US in recent decades may be the result of this

combined with other effects, such as changes in fire regime. Conversely, on favorable edges of ranges, expansions may occur as periods of recruitment into certain habitats – these may also occur sporadically during especially favorable periods and thus the leading front will be ragged and irregular. Pinyon pine and juniper in the Great Basin are examples of such expansion (Nowak et al., 1994). Range adjustments are likely also to occur through changes in species density. For instance, an expected response of white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and other conifers in the California region to increases in temperature and precipitation of the 20th century (relative to the previous 450 years of the Little Ice Age) is to increase regionally in abundance and expand in range. This widely observed phenomenon has been attributed primarily to effects of fire suppression but, although fire is certainly part of the cause, climate may be far more significant than has been given credit.

A particularly challenging question becomes, "what is the native range of a species"? Native ranges have been the *sine qua non* of conservation. To define the range of a species is the basis for monitoring its condition, understanding favorable habitat, determining restoration targets, and indicting species as "exotic" (Jackson, 1997). Viewed against historic changes in distribution and natural flux, the native range of a species must be considered a relatively transient and dynamic phenomenon, readily capable of moving in space as climate shifts over the landscape (some habitats, by contrast, may be strikingly stable: e.g., serpentines?). Recognizing that non-equilibrium conditions exist and vegetation lags occur means that, like Lewis Carroll's Red Queen, vegetation chases a target (climate) that is itself changing, and may lag behind current conditions by large or small extent. Distribution ranges may be stable for relatively long periods if climate is in a stable phase and/or if the environment of a species offers considerable local heterogeneity (e.g., elevation, soil, aspect, hydrology gradients; Thompson, 1988). In these cases, shifts in climate may be tracked with relatively minor geographic changes. By contrast, in regions that are inelastic to change, for instance broad flat landscapes with little diversity, even small shifts in climate may bring large changes in population condition. In that the 20th –21st- centuries are experiencing considerable change in climate with high variability, we would expect species to be unstable also.

Defining niche requirements for a species may be better met by considering its range of historic climates and environments than by assuming the species is defined only by conditions of the current range. When this is analyzed over Tertiary timescales, for instance in giant sequoia, the current range describes not only a very small part of its former climatic range, but the current range is non-overlapping with previous conditions

(Fig. 10, Schorn, 2001). Changes over long times such as this may be due also to directional adaptation (evolutionary change) or loss of adaptation through population extirpation, although genetic studies indicate that a large percent of species-level diversity is contained within populations. When modern species are in contracted phases, such as the redwoods or closed-cone-pines, only very small portions of their genetic potential niche may be described by conditions of current ranges.

Reference Conditions and Restoration Targets: Discerning Natural from Human Caused Changes

Pre-disturbance conditions are often used as reference variability and as a description of desired conditions for restoration. In wildland situations of western North America, the pre-disturbance period has been equated most often with the one-two centuries prior to European/Asian settlement, i.e., AD 1700-1900. From a climate standpoint, this is a poor reference for modern conditions because the Little Ice Age occurred during these centuries, and the 19th century was the coldest part of it. Many of our current modern forests established during this time, and thus were influenced during their most formative recruitment stages by a climate condition that no longer pertains. Vegetation changes that have occurred during the last 150 years are not necessarily the result of human-caused impacts but also include natural adjustments to changing climate conditions.

Determining accurate causes for observed changes in species and population conditions is critical for proper assessment of status and for prescribing effective treatments (Millar and Woolfenden, 1999b). Causality is especially difficult to discern when natural and human-induced forces act in the same direction. As noted earlier, for instance, recent (last 150 years) climate changes and fire suppression, or climate change and insect/pathogen-caused mortality, have similar expected responses. An example comes from work in subalpine meadows (Millar et al., 2000). Invasions into meadows and other forest openings in the 20th century were determined by local land-managing agencies to be primarily a result of human-caused fire suppression, historic domestic sheep grazing, and/or road building effects. Treatments were set to reverse these invasions (i.e., remove trees from meadows and openings). Our evaluations of historic conditions, however, suggest that the invasions are explained by natural response to climate change since the Little Ice Age, including gradual warming and decadal-scale changes in precipitation. Human effects would cause similar responses, but in this case, they do not seem to have been involved.

Rather than a goal of returning species to former conditions (“re-storing” species), a climate-informed approach might attempt to understand the full niche breadth of a species (from the historic perspective),

species shifts related to climate change in the past, and historic distributions under climates similar to the present. Integrating this with knowledge of species responses under undisturbed modern conditions would give options for restoration (which I prefer to call "realignment"). I have attempted to consider questions such as these for Monterey pine (*Pinus radiata*, Millar, 1998, 1999). The shifting metapopulation behavior indicated for the Quaternary by paleorecords points to previous native distributions of Monterey pine at several locations along the California coast. Analysis of these historic periods and historic locations suggests that many other places than its current distributions near Año Nuevo, Monterey, and Cambria might be considered "neo-native" and be suitable as restoration sites. In many of these places (e.g., coastal state parks in northern California), Monterey pine has naturalized from ornamental plantings, and co-occurs with many of the associates found in its paleorecord. In some of these locations Monterey pine is being removed aggressively as an undesired exotic. Another example of an attempt to integrate historic knowledge to develop restoration targets is the Mono Lake case (Stine, 1990; 1991; Vorster, 1985), where information on past lake levels, historic climates, and a water balance model allowed projection of desired restoration lake levels for the present and inferred for future decades.

Global Warming and Conservation

The specter of global warming has raised much concern in conservation communities. As we now understand, this is not something coming in the future, but which we already are experiencing. Warming observed in the last 120 years is partly rebound in the natural Bond cycling events, superimposed on the longer periods of internal and orbital cycling to which earth is inextricably bound, and partly anthropogenic. As I have tried to describe, abrupt climate change and vegetation response to it have been common in earth's history. On the one hand, this is comforting to us as conservationists, in that plant species must be at least somewhat adapted to changes such as are occurring now. On the other hand, natural as they are, we may not like certain consequences, such as population and species declines, minor and major extirpations, shifts in native ranges, or changes in community composition. Accommodating these factors – if we choose to accept them -- will require rethinking our concepts about what and where is native habitat, what are "healthy" population sizes, what are causes of changes in population size, and when is change natural and acceptable. If we choose not to accept such consequences, we should know that our management and conservation efforts may run counter to natural process.

Clearly these arguments can be abused. Either intentionally or unintentionally they can be construed to imply that any change is natural and therefore acceptable. This is to misunderstand and misuse the arguments from paleoclimatology and paleoecology. History documents clear constraints to change, obvious bounds on capacities of species to adapt, and definite limits to native ranges, historic shifts, community associates, and changes in population sizes. Most important, however, is the fact that plants live now, even in our wildlands, in human-dominated landscapes. If a primary natural mechanism for species to accommodate climate change is by moving, human constraints now loom for many species as insurmountable obstacles. From fragmentation to land conversion, atmospheric pollution to exotic invasions, even conservation attitudes about where species ought to be (native ranges) and policies that set static land designations, human activities limit the potential of plants to move where they would naturally. Even our attempts at proactive conservation by modeling where species will move under simulated future climate conditions could back-fire. Although models of climate change at the global scale are relatively robust, regional and short-term changes are extremely difficult to estimate. If we misuse models by assuming they accurately predict geographic details, we may end up designating nature reserves where plants wouldn't have gone, and in the meantime developed, converted, or made uninhabitable other landscapes where plants would prefer to have gone. The novelty of modern anthropogenic impacts, both climate-related (e.g., greenhouse gases) and direct environmental effects, further limits both capacity for plants to adjust to change and our capacity to anticipate what may be best for them.

Although this paper will end having made only fragmentary suggestions for alternative strategies, my primary goal has been to alert the conservation community to new information from paleoclimatology about the way species and climate have acted in the past. I believe it will take the concerted efforts and open minds of many conservationists to integrate concepts of temporal dynamism fully into our practice and to develop more robust and enlightened approaches to protecting and maintaining natural biodiversity.

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FIGURES

Figure 1. Primary temperature fluctuations between glacial and interglacial periods of the past 2.5 million years derived from oxygen-isotope analysis of ice cores from the Greenland ice sheet. High values of $\delta^{18}O$ indicate cold temperatures (glacial periods) and low values indicate warm temperatures (interglacial periods). Our current interglacial period (Holocene) is at the far left, from 0-10,000 years ago). From Wright, 1989.

Figure 2. Primary orbital cycles of the earth, widely accepted as the mechanism for oscillating climates of the past 2.5 million years. Temperatures on earth vary depending on how much heat from the sun (solar insolation) reaches earth's surface. This in turn varies depending on the exact position of earth within each of three orbital cycles. Mathematical integration of the three curves produces a graph of temperature over time that closes matches temperature reconstructions from $\delta^{18}O$, e.g., Figure 1. A. Eccentricity cycle, or changes in shape of the earth's orbit from elliptical to circular (100,000 year cycle). B. Obliquity cycle, or change in tilt of the earth on its axis (41,000 year cycle). C. Axial precession cycle, or change in time of year of perihelion (when earth is closest to the sun; 23,000 year cycle). From Zachos, et al., 2001.

Figure 3. Shift in ranges of spruce (*Picea*) forests in eastern North America as they track changing temperatures from the Last Glacial Maximum to present . Reconstructed from pollen abundances in lake sediments for intervals of 3000 years. From Jackson et al., 1987.

Figure 4. Glacial/interglacial shifts in elevation for plant species of the Sheep Range, southern Nevada, showing current (interglacial, solid line) and past (glacial, pre-11ka, dots) elevation limits, and individualistic responses of species. From Thompson, 1988.

Figure 5. Radial stem growth (mm; black line) of long-lived trees, and confidence intervals (gray band) during the past 1200 years as a reconstruction of northern hemisphere surface air temperature. Graph is developed from 14 temperature-sensitive tree-ring chronologies of middle-latitudes sites. Modified from Esper, et al., 2002.

Figure 6. Correspondence in abundance of pine from Lake Tulane, Florida (indicated by pollen %, left panel) with millennial scale cold, or Heinrich, events of the last glacial period (indicated by % lithics, or ice-rafted rock debris, right panel). Data from Grimm et al., 1993; figure first produced by NOAA National Geophysical Data Center's Paleoclimatology Program (T.G. Andres, J.T. Andrews, and L.M. Lixey).

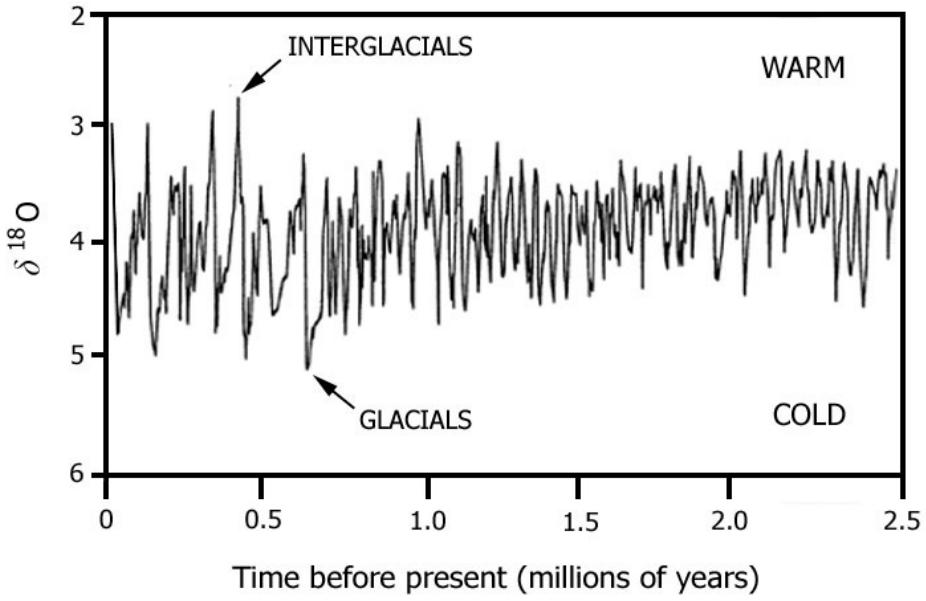
Figure 7. Decadal variability in precipitation for the past 2200 years as indicated in ponderosa pine/Douglas-fir (*Pinus ponderosa/Pseudotsuga menziesii*) tree-ring reconstruction of annual rainfall from western New Mexico. The drought of the 1950s is shown as well as droughts of equal and greater magnitude. Data from Grissino-Mayer, 1996; graphic modified and first produced by Connie Woodhouse, NOAA National Geophysical Data Center Paleoclimatology Program.

Figure 8. Changes in abundance and distribution of *Artemesia*, *Tsuga mertensiana*, *Sequoiadendron giganteum* and *Abies* over the last 15,000 years as summed from pollen analyses in western Sierra Nevada meadows. *Sequoiadendron* pollen reached its present abundance and native range at Giant Forest only in the last 2-3 ka. From Anderson and Smith, 1994.

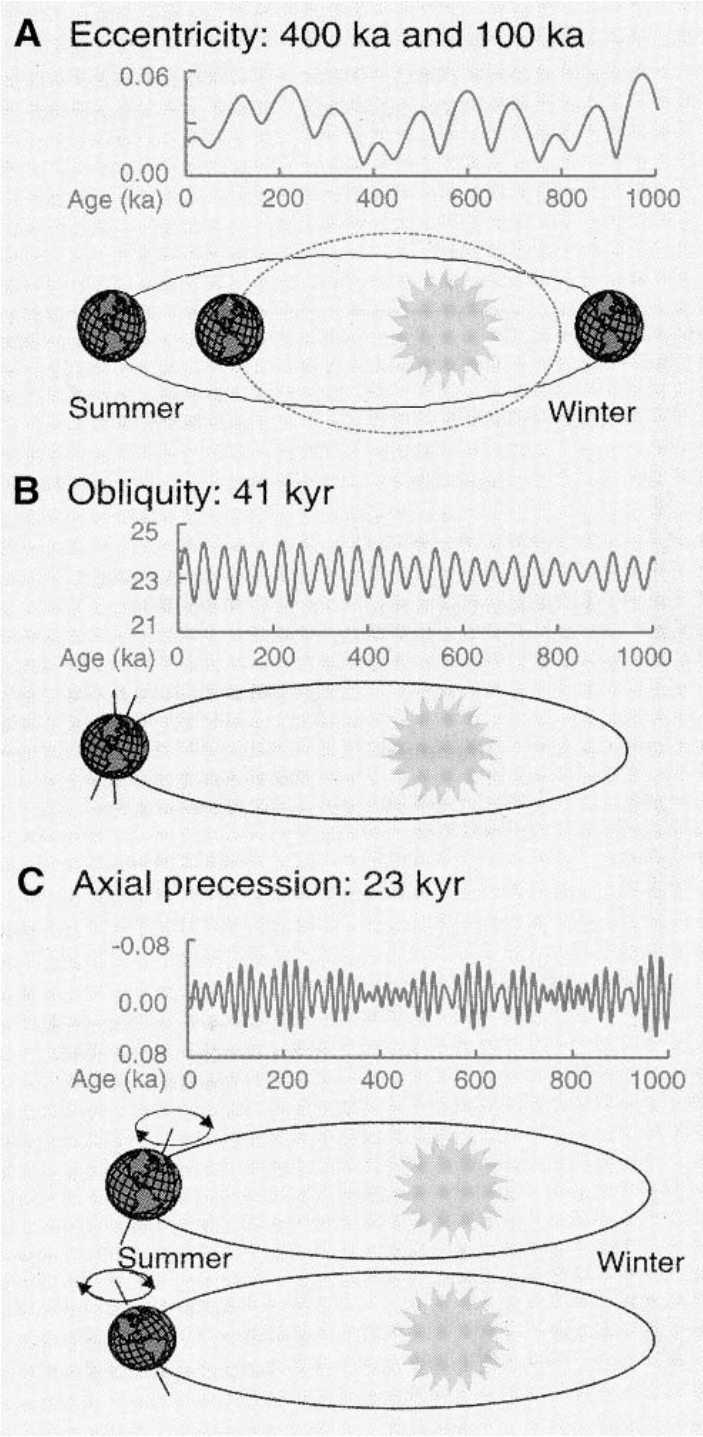
Figure 9. Correspondence of California oak (*Quercus*) abundance (pollen %) and temperature fluctuations recorded as variability in oxygen-isotope ratios indicating fluctuations between high and low abundance. Similar and synchronous patterns throughout the California oak ranges document species fluctuations between rare and widespread condition. A. 140,000 year record from Clear Lake, Lake County, CA in the north-central Coast Ranges (from Adam, 1988). B. 160,000 year record from Santa Barbara Basin, Santa Barbara County, CA (ODP 893A; from Heusser, 1995).

Figure 10. Change in climate space over 16 Ma for giant sequoia (*Sequoiadendron giganteum*), suggesting much broader range potential for the species than indicated by conditions of its present restricted range. Over this long time, intraspecific evolutionary change may explain some of the difference, but much is likely due to transience of physical conditions in the environment. From Schorn, 2001 using data from Jack Wolfe, 1999.

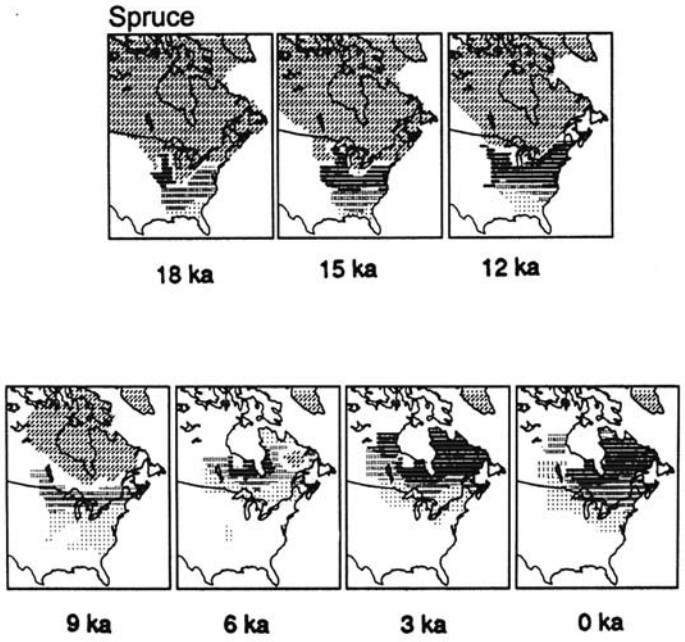
Millar, Figure 1



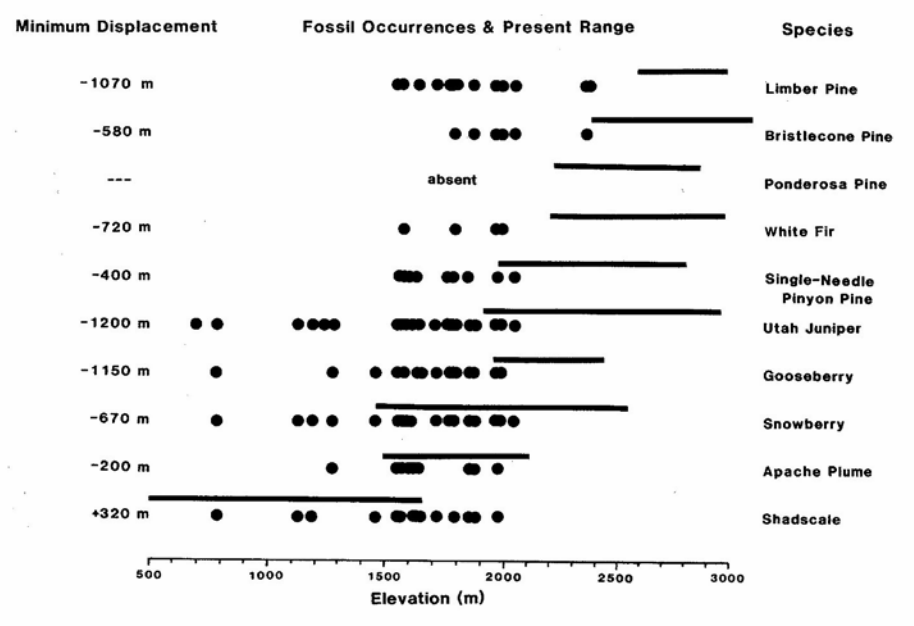
Millar, Figure 2



Millar, Figure 3



Millar, Figure 4



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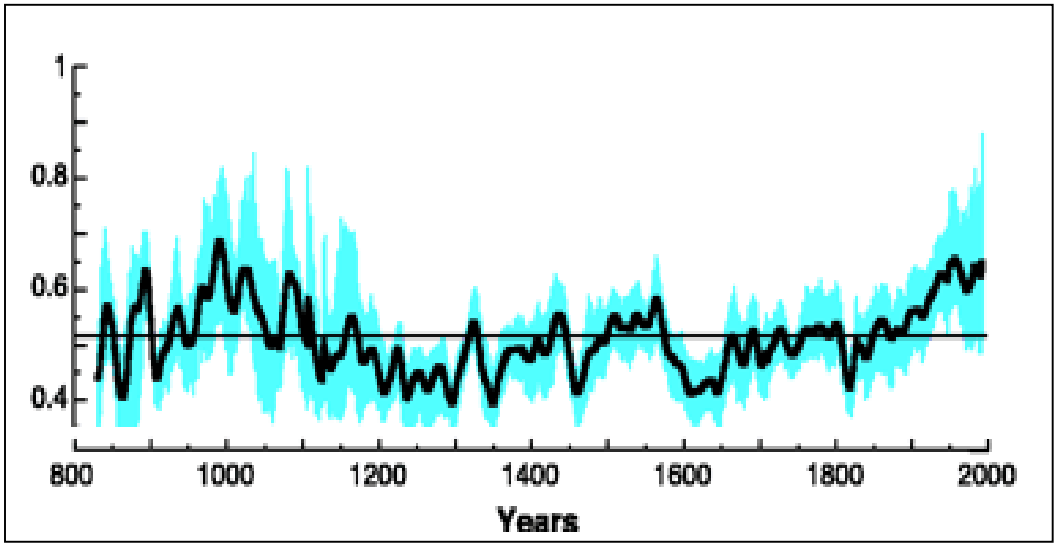
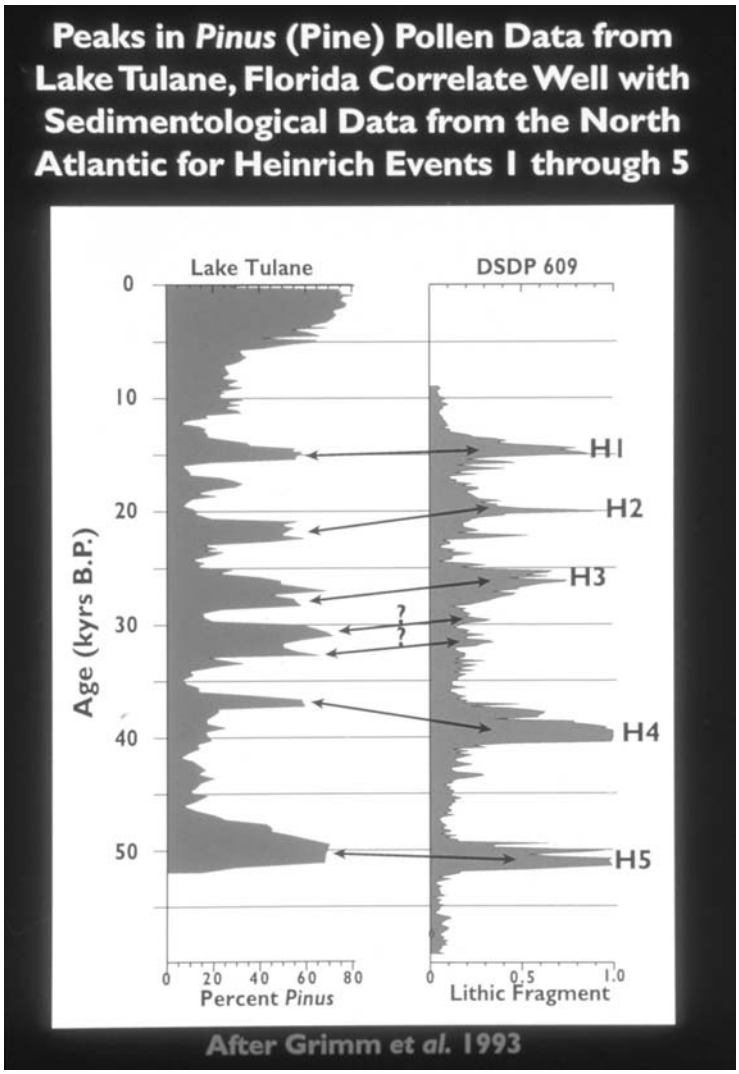
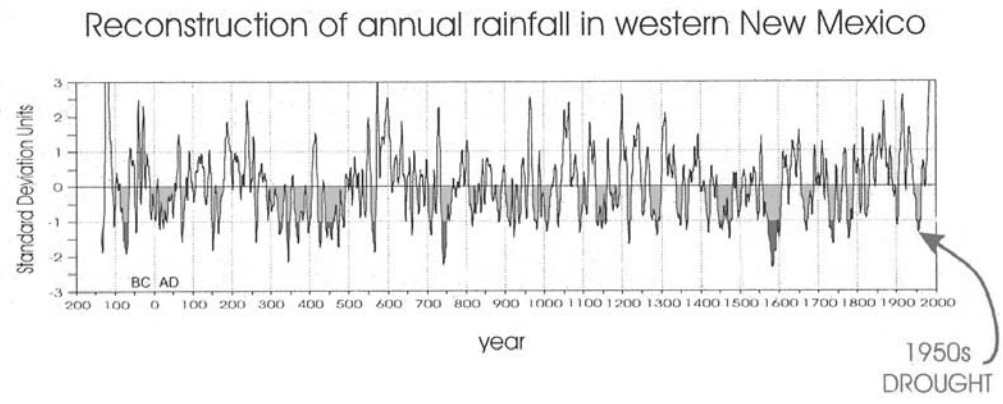


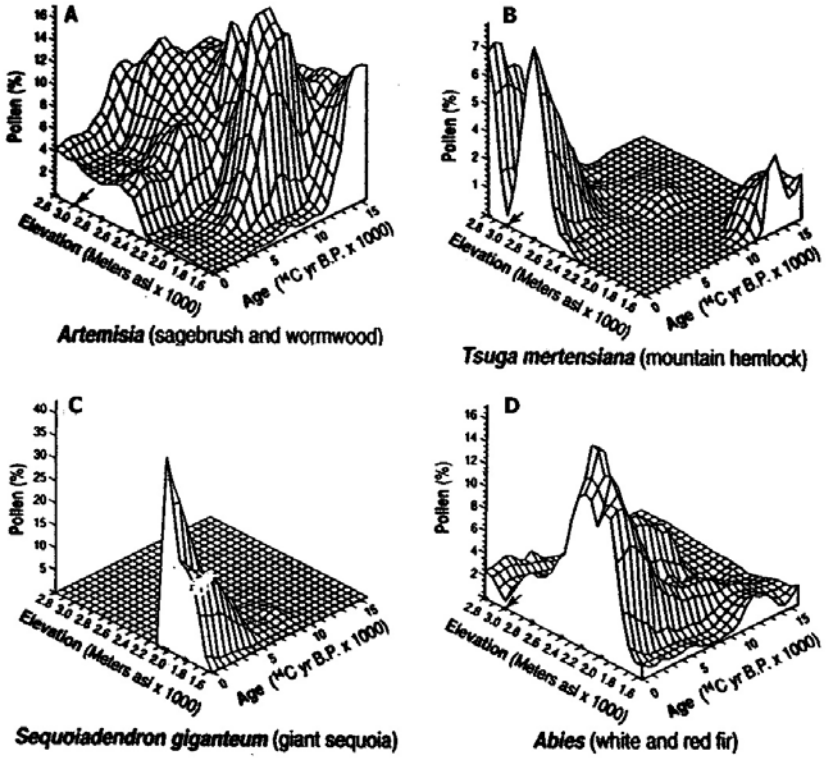
Millar, Figure 6



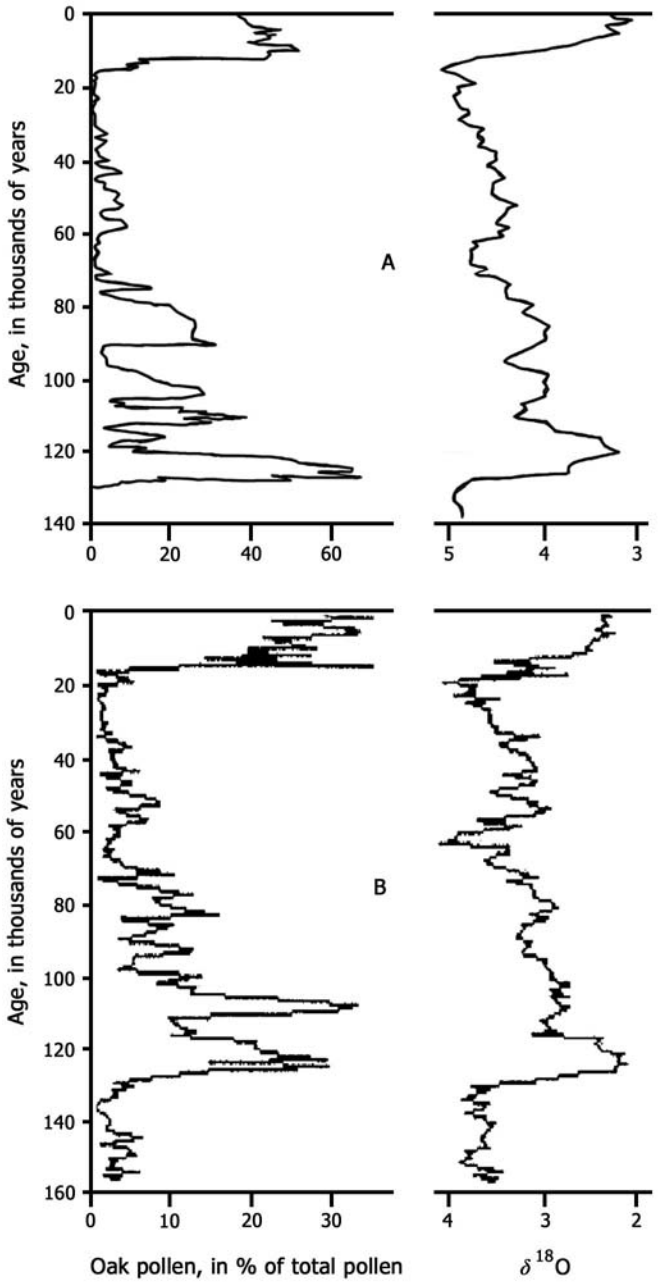
Millar, Figure 7



Millar, Figure 8



Millar, Figure 9



Millar, Figure 10