Chapter 15

Climate Change and Paleoecology: New Contexts for Restoration Ecology

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In this chapter, we explore linkages between two fields that have been little acquainted yet have much to say to one another: restoration ecology and climatology. The limited discourse between these fields is surprising. In the last two decades there have been significant theoretical breakthroughs and a proliferation of research on historical climate and climate-related sciences that have led to an overhaul of our understanding of Earth's climate system (Smith and Uppenbrink 2001). These new insights are relevant to restoration and ecology—so much so that fuller understanding could trigger rethinking of fundamental principles.

Climate Variability as an Ecosystem Architect—In Perspective

Conceptual views of the natural world influence tactical approaches to conservation, restoration, and resource management. The phrase *climate change* usually connotes global warming, greenhouse gas impacts, novel anthropogenic threats, and international politics. There is, however, a larger context that we must begin to understand and assimilate into restoration ecology theory—that is, the role of the natural climate system as a pervasive force of ecological change.

Advances in environmental sciences during the mid-to-late twentieth century on ecological succession, disturbance, and spatial and temporal variability motivated a shift from viewing nature as static and typological to dynamic and process driven. In turn, restoration ecology and practice matured from emphasis on museum-like nature preservation to maintaining variability and natural function (Jordan et al. 1990). As a result, prescribed fires and managed floods, for instance, became important restoration tools, and recovery of ecosystem function, composition, and 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. The recent advances in climate-system sciences characterize recurrent climate change as a central physical force on Earth and significant agent of physical, ecological, and even cultural change at micro- to macroscales. From this perspective, climate is a macrodisturbance element, or the background stage of change on which evolutionary and successional dynamics play out. Such dynamism has only begun to be incorporated into evolutionary and ecological theory, and remains largely untranslated into conservation and restoration ecology. As a result, resource analyses and prescriptions, such as evaluation and diagnoses of ecological change, determination of baselines and evaluation of change in monitoring, and development of targets for restoration, may have limited applicability.

In this chapter, we bring forward new ideas in paleoclimatology and paleoecology that are relevant to restoration ecology. In so doing, we hope to foster discussion about fundamental goals and purposes in restoration that result from dialog between the fields. Our examples draw from western North American plant communities, but generalities from these extend to other areas and are supported by theoretical treatments (e.g., Jackson and Overpeck 2000).

Earth's Climate System: A Paleoclimatology Primer

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 these fluctuations have been little known and poorly understood. Until recently our knowledge of past climates came mostly from interpreting their indirect effects on the Earth's surface—for example, glacial moraines as evidence of past ice ages, coastal terraces as clues to former sea levels. Collectively these led to early interpretations of the Pleistocene (0.01–2.5 million years ago) as a long, cold interval—the "Great Ice Age" of Agassiz (1840). By the late nineteenth century, evidence for multiple glaciations accumulated and led to widespread description of four major glacial periods in the Pleistocene bracketed by brief warm intervals. The ice ages were regarded as ending about 10,000 years ago with the arrival of novel warmth of our present epoch, called the Holocene, or Recent, to signify its difference from the Pleistocene. Because the climate of the Holocene was interpreted as distinct from the past, Pleistocene climate processes were viewed as having little relevance to the present.

In the past two decades, new tools with high precision and resolution, new theory reliant on high-speed computing capacity, and a critical mass of empirical research have revolutionized understanding of Quaternary (the last 2.5 million years) climate. Quaternary climates are now understood as being far more variable and complex than previously imagined (Bradley 1999; Cronin 1999; Ruddiman 2001). The most widely applied and useful proxies first derived from long ice cores retrieved in polar ice caps (Cuffey et al. 1995). Gases and atmospheric particles trapped in ice faithfully record atmospheric conditions at the time of deposition. Due to annual layering and the ability to date layers accurately, analysis of thin sections at regular intervals yields high-resolution historic climate information for continuous time series. Cores drilled to the bottom of continental ice sheets (e.g., Greenland) have yielded highly resolved information on more than 40 climate variables that extend over 200,000 years (Lorius et al. 1990). The most important are isotopes of oxygen. Ratios of heavy to normal oxygen isotopes ($\delta^{18}O$) quantify the relative amount of oxygen stored in land ice relative to seawater, and provide robust indicators of surface air temperature at the time the isotopes were trapped in the ice. Analysis of these and other climate-related isotopes are now routinely extracted from other situations where undisturbed deposition occurs, such as lake beds, coral reefs, and sea floors sediments. Other climatologically important indicators retrievable from ice and sediment cores include greenhouse gases (CO_2, CH_4) and atmospheric aerosols that indicate dust and volcanic ash. Studies of varying time depth around the world, from a few decades to over 60 million years ago (Zachos et al. 2001), have led to detailed global and regional reconstructions of historic climate, which cumulatively provide new insight on the causal nature of climate variability.

Multimillennial Climate Cycles: Glacial/Interglacial or Orbital Cycles

Taken together, these long, highly resolved records collectively document the repeating, cyclic nature of climate over the past 2.5 million years (Figure 15.1) (Wright 1989; Raymo and Ruddiman 1992). Unlike earlier assumptions of persistent Pleistocene ice, oxygen-isotope records show a repeating pattern of over 40 glacial/interglacial cycles. A startling insight revealed by the oxygen-isotope records is the overall similarity of the Holocene to previous interglacials in length, trends, and relative temperatures; our Recent is not wholly novel after all. 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 10°–20°C (Petit et al. 1997). Compare this to 0.7°C, the twentieth-century increase. (IPCC 2001).

The oxygen-isotope curves further reveal a repeating structure of climate variability 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 one-third the warmth of interglacials, and they 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 stades of the subsequent glacial period. The cumulative effect is a sawtooth pattern typical of Quaternary climate records around the world (Figure 15.1).

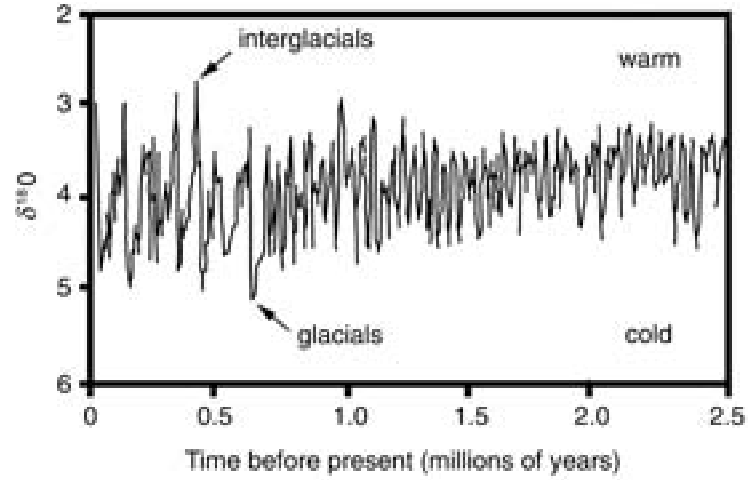


FIGURE 15.1 Primary temperature fluctuations between glacial and interglacial periods of the past 2.5 million years derived from oxygen-isotope analysis of ice cores from the Greenland ice sheet. High values of _^{18}O indicate cold temperatures (glacial periods), and low values indicate warm temperatures (interglacial periods). Our current interglacial period (Holocene) is at the far left, from 0 to 10,000 years ago. From Wright 1989.

A mechanistic cause for climatic oscillations was proposed by Serbian mathematician Milatun Milankovitch (1941) long before detailed paleoclimate variability had been documented. Milankovitch integrated knowledge about Earth's orbit around the sun into a unified theory of climate oscillations. This has been revised subsequently into a modern orbital theory that is widely accepted as the pacemaker for the ice ages (Imbrie et al. 1992, 1993). Three major cycles of orbital variability recur over time (Figure 15.2) (Hays et al. 1976): (1) change in the shape of Earth's orbit around the sun from elliptical to circular (100,000 years);

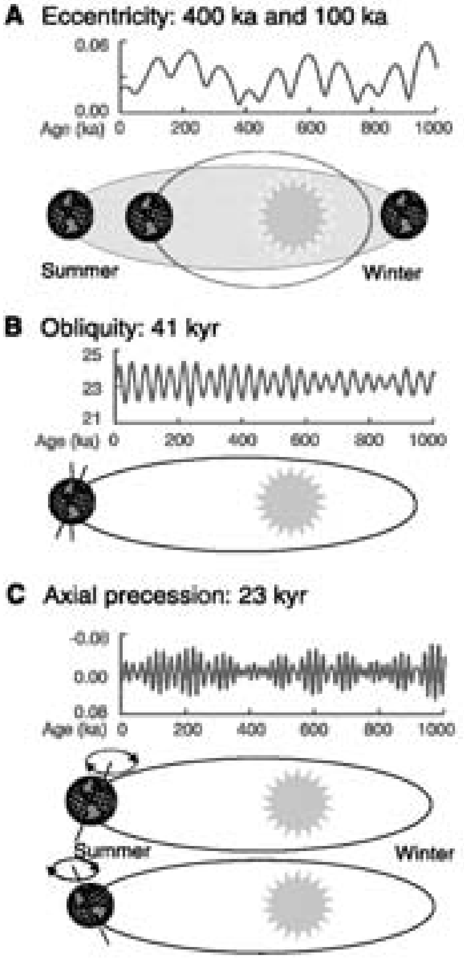


FIGURE 15.2 Primary orbital cycles of the Earth, the fundamental mechanism for oscillating climates of the past 2.5 million years. Temperatures on Earth vary depending on how much heat from the sun (solar insolation) reaches Earth's surface. This in turn varies, depending on the exact position of Earth within each of three orbital cycles. Mathematical integration of the three curves produces a graph of temperature over time that closely matches temperature reconstructions from _^{18}O (e.g., Figure 15.1). (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.

(2) change in the angle of Earth's tilt on its axis (41,000 years); and (3) change in time of year when the Earth is closest to the sun (23,000 years). The amount of heat from the sun reaching the Earth (solar insolation) at any point in time varies with the Earth's position in each cycle. Integrating the three cycles mathematically results in a curve over time of predicted temperature on Earth that corresponds to the observed oxygen-isotope curves (e.g., Figure 15.1).

Century- to Millennial-Scale Climate Cycles

Analyses of oxygen-isotope variation at finer temporal resolution further reveal century to millennial length oscillations nested within orbitally driven climate cycles. These were known first from a few well-studied climate events, such as the interval known as the Younger Dryas (Kennett 1990), a 1,000-year return to ice age conditions that interrupted warming at the end of the last glacial period (11,500 years – 12,500 years ago); Heinrich events (Heinrich 1988), a series of short (100 years–1,000 year), extremely cold intervals within the last glacial period; and Dansgaard/Oeschger interstadials (Dansgaard et al. 1993), brief, abrupt, warm intervals during the last glacial period. These climate events are increasingly understood as part of a pervasive oscillation pattern, called "Bond cycles," documented for at least the last 130,000 years (Bond et al. 1997). Bond cycles average 1,300 years– 1,500 years, meaning that for each warm or cold phase (each ca. 700 years), the warmest and coldest half-phases last 300 years –400 years (Figure 15.3). Climate intervals during the Holocene that exemplify Bond cycles include the Little Ice Age (LIA), a minor ice advance and global cold period from A.D. 1450 to 1920 (Grove 1988; Overpeck et al. 1997); the Medieval Climate Anomaly, a warm, dry interval with regional variability from A.D. 900 to 1350 (Hughes and Diaz 1994; Stine 1994; Esper et al. 2002); and the 8,2000-year cold event (Alley et al. 1997).

Painstaking analysis at high resolution of several well-known Bond intervals has documented that oscillations often 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

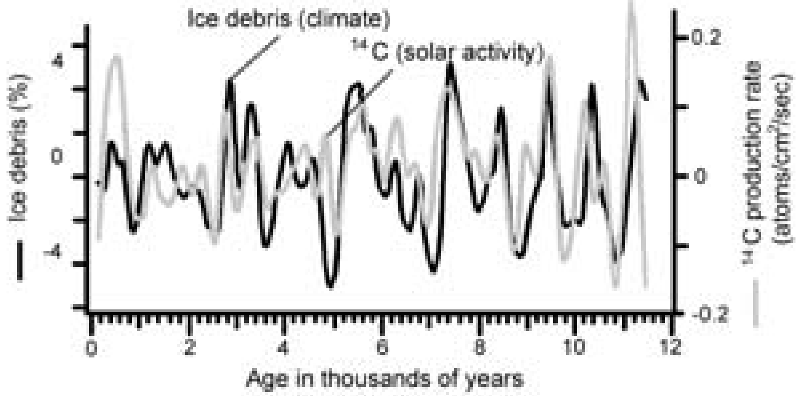


Figure 15.3 Century-millennial scale oscillations, or Bond cycles, have been pervasive at least through the Holocene and last major glacial age. Individual events have long been recognized, such as the Little Ice Age (1450–1900 CE) and the Younger Dryas (11,500–12,500 years ago), but these are only recently understood as part of a systematic cycle. Correlations with solar activity suggest a sun-driven mechanism for this climate pattern. From Bond et al. 1997, 2001.

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 detectable change (White et al. 2001).

Of particular interest is the warming of the twentieth century. During the preceding four-century-long Little Ice Age, temperatures in western North America were on average 1°C colder than present; glaciers in many western North American mountain ranges 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 with much of the increase occurring due to increases in minimum temperature (IPCC 2001). Increases in the early part of the century are now widely accepted as natural climate forcing, whereas continued warming since mid-twentieth century can be explained only by recent anthropogenic-induced greenhouse gases (IPCC 2001).

The natural mechanisms driving climate oscillations at the century-millennial scale are a topic of great 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 on the sun's surface) have been shown to match the timing of the Bond cycles over the last 130,000 years with high precision (Figure 15.3) (Bond et al. 2001). This has led climatologists to speculate that a trigger for century-millennial climate changes comes from outside the Earth—that is, changes in the sun—and that resulting changes in ocean circulation subsequently regulate and abruptly communicate solar signals worldwide.

Interannual- to Decadal-Scale Climate Change

In recent years, climatologists have defined high-frequency climate cycles operating on scales from a few years to several decades. The best known of these is the El Niño pattern, called the El Niño-Southern Oscillation (ENSO) for its interhemispheric expression and ocean-based cause (Diaz and Markgraf 2000). Every several years, 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. Each year there is some degree of El Niño or its opposite effect, La Niña. Extreme events cycle on a 2-year to 8-year basis (Figure 15.4). El Niño events bring different conditions to different parts of the world. For instance, they portend unusually warm and wet falls and winters in central and southern California, and unusually cold and dry weather in the Pacific Northwest. The reverse occurs during La Niña events.

Climate oscillations on multidecadal (20-year to 60-year) periodicities have also been described recently. Like ENSO, these act regionally but have effects on distant locations. The Pacific Decadal Oscillation (PDO) is a recently characterized multidecadal cycle affecting western North America. It appears to be regulated by decadal changes in ocean circulation patterns in the 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; Zhang et al. 1997). Warm (or positive) phases are extensive (10-year to 25-year) periods of El Niño-like conditions that alternate with cool (or negative) phases of La Niña-like conditions.

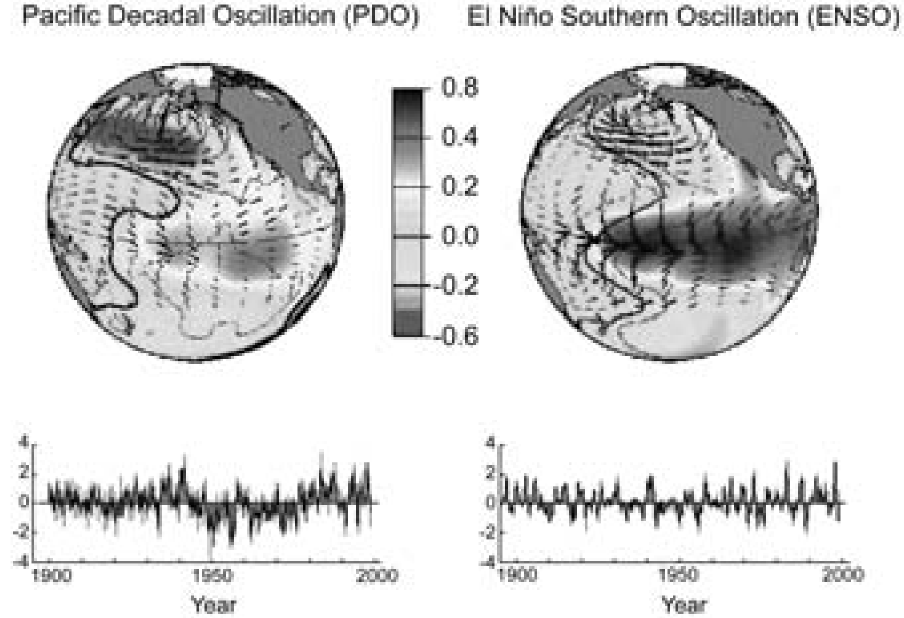


Figure 15.4 The El Niño/Southern Oscillation (right) and Pacific Decadal Oscillation (left) are internally regulated, ocean-atmospheric patterns that affect climate on interannual (ENSO) and multidecadal (PDO) scales. Positive ENSO (El Niño)and PDO periods bring systematically warm, wet conditions to certain parts of the world, while negative ENSO (La Niña) and PDO bring cool, dry conditions. PDO and ENSO interact such that during times of positive PDO, El Niño signals are enhanced, and the reverse is true during negative PDO decades. PDO regime shifts, such as in 1976, can be abrupt, with dramatic physical and ecological effects. From Mantua et al. 1997; http://tao.atmos.washington.edu/pdo/.

Other ocean-mediated multidecadal patterns affect other parts of the world, such as the North Atlantic Oscillation, and the Arctic Oscillation (Cronin 1999).

Climate Change as an Ecosystem Architect

Abundant evidence worldwide indicates that life on Earth has responded to climate change at each of these scales. Changes in biota over time can be measured in many ways, such as from sediment cores taken from wet areas including meadows, bogs, lakes, and ocean bottoms. In dry environments, packrat middens preserve macrofossils, while in temperate forests tree-ring records archive annual tree growth. In ocean environments, annual coral layers record ecosystem responses.

At *multimillennial* scales, paleoecological records collectively document that, at any one place, compositions of flora changed significantly in correspondence with major climate phases, often showing complete species turnover and recurring patterns of similar groups of species or species with similar adaptations alternating between glacial and interglacial periods. In relatively flat terrain, such as in the northeastern United States, eastern Canada, parts of Scandinavia, and northern Asia, species shifted latitudinally north and south many hundreds of kilometers, as modeled, for example, for spruce (*Picea*) in eastern North America (Figure 15.5) (Jackson et al. 1987). In mountainous regions, by contrast, species responded primarily by elevational shifts, as indicated by conifers of the Great Basin and southwestern desert region, which shifted as much as 1,500 m (Figure 15.6) (Thompson 1988, 1990; Grayson 1993). In regions where habitats were highly patchy, with steep and discontinuous gradients, species responded primarily by fluctuations in population size and minor geographic shifts in location, as exemplified by oaks in California (Adam 1988; Heusser 1995). Areas occupied by continental ice caps were often revegetated via rapid colonizations from refugia (Brubaker and McLachlan 1996).

Significant and rapid response of vegetation to *century*-scale climate change is also well documented. Before temperature proxies such as oxygen isotopes provided independent measures of historic climate, millennial-scale abrupt climate events were inferred from changes in flora and fauna. For instance, the Younger Dryas cold interval was known from changes in abundance of the arctic tundra plant *Dryas octopetala* (Jensen 1935). This species dominated paleofloras of western Europe during the 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 (in contrast to an earlier interval known as the Older Dryas), now recognized as a phase of the Bond cycles.

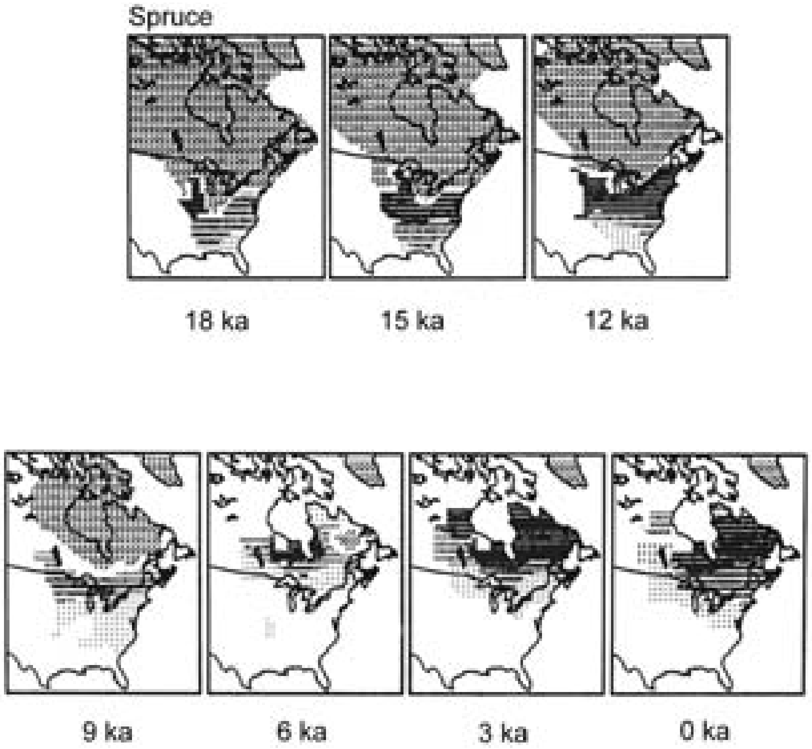


FIGURE 15.5 Shift in ranges of spruce (*Picea*) forests in eastern North America as they track changing temperatures from the Last Glacial Maximum to present. Reconstructed from pollen abundances in lake sediments for intervals of 3,000 years. From Jackson et al. 1987.

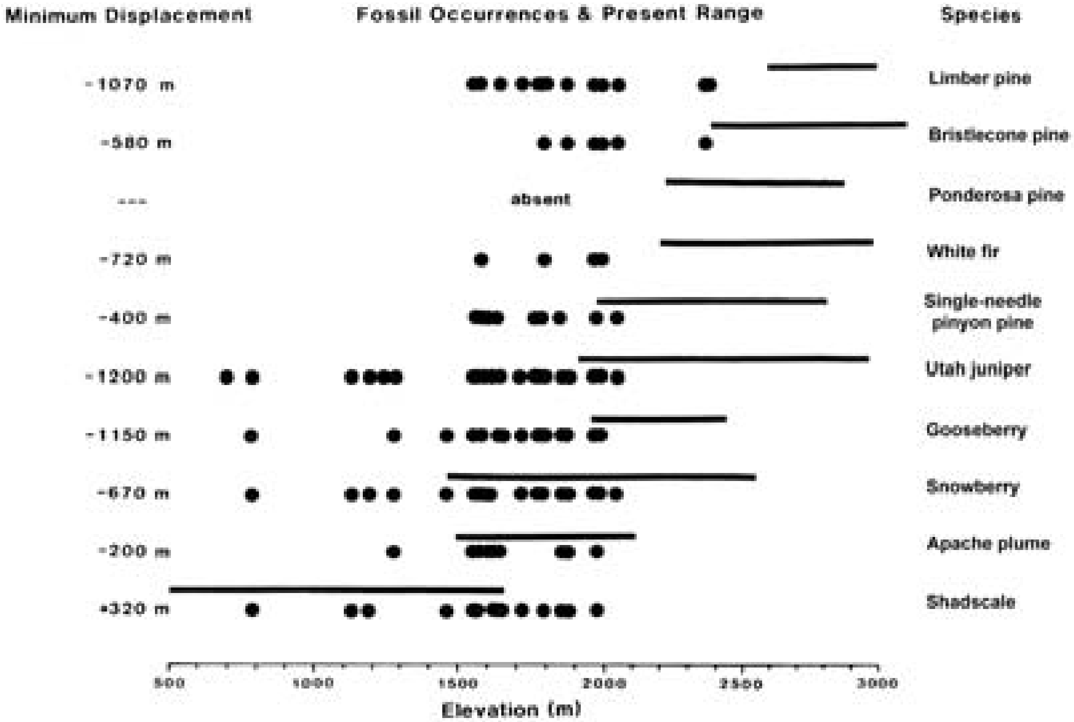


Figure 15.6 Glacial/interglacial shifts in elevation for plant species of the Sheep Range, southern Nevada, showing current (interglacial, solid line) and past (glacial, pre-11,000 years ago, dots) elevation limits, and individualistic responses of species. From Thompson 1988.

Many examples now show fluctuating changes of vegetation corresponding to Bond cycles. An illustrative example is the abrupt change in pine versus oak vegetation in southern Florida that corresponds to Heinrich events (Figure 15.7) (Grimm et al. 1993). Another example from the California region comes from the work of Heusser (2000), who demonstrated that abrupt changes in the dominance of oak versus juniper corresponded to rapid climate oscillations of the last 160,000 years. In the Great Basin of North America, major changes in population size and extent of pinyon pine (*P. monophylla*), and changes in floristic diversity, correspond to Bond-scale, century-long cycling (Tausch et al. 2004). Whereas recurring patterns emerge at coarse scales, species responses are individualistic, lags are common, and non-analog patterns frequent, so that population increases or decreases may not appear to be "in synch" with climate change, especially when climate changes are extreme and abrupt (Jackson and Overpeck 2000).

Vegetation responds also to *interannual* and *decadal* variability. At ENSO scale, changes occur primarily 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 mesoscale 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 oscillations have been well 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 (Figure 15.8) (Grissino-Mayer 1996), and the recurring pattern

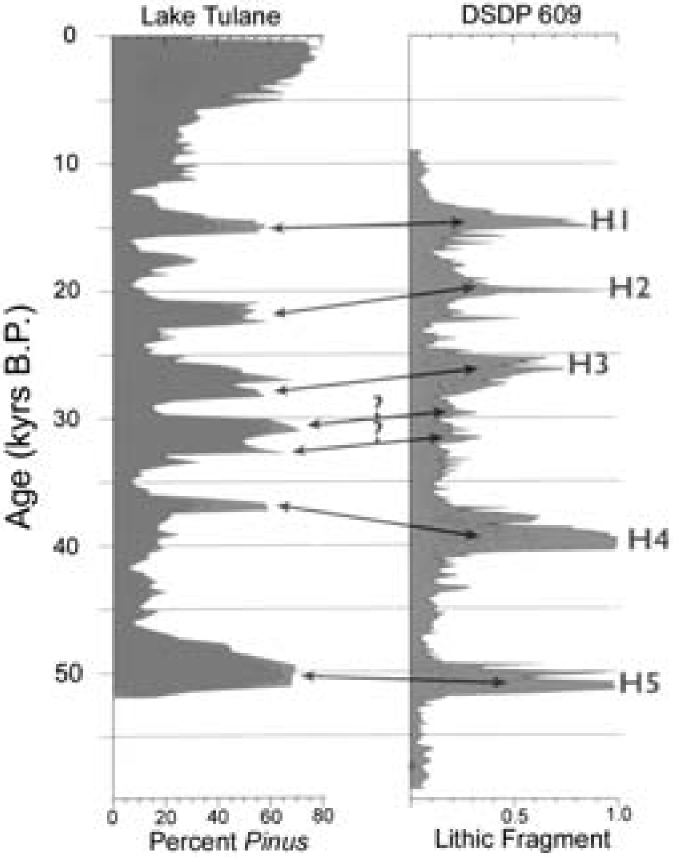


Figure 15.7 Correspondence in abundance of pine from Lake Tulane, Florida (indicated by pollen ‰, left panel) with millennial scale cold, or Heinrich, events of the last glacial period (indicated by ‰ lithics, or ice-rafted rock debris, right panel). Data from Grimm et al. 1993; figure first produced by NOAA National Geophysical Data Center's Paleoclimatology Program (T. G. Andres, J. T. Andrews, and L. M. Lixey).

of ring-widths in big-cone Douglas-fir (*Pseudotsuga macrocarpa*; Biondi et al. 2001), mountain hemlock (*Tsuga mertensiana*; Peterson and Peterson 2001) and subalpine fir (*Abies lasiocarpa*; Peterson et al. 2002) that correlate with PDO for up to 400 years in the past. Vegetation type conversions from meadow to forest, changes in species growth rates and crown morphology, and changes in forest density were associated with PDO cycles in conifer forests of the Sierra Nevada, California (Millar et al. 2004).

Summary of Climate Change and Vegetation Response

This brief overview yields several conclusions: First, climate has *oscillated* between warm and cold, wet and dry regimes over the last 2.5 million years rather than being dominantly directional or stochastic. In broad terms, our present warm period (Holocene) is 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 temporal scales*, including interan-

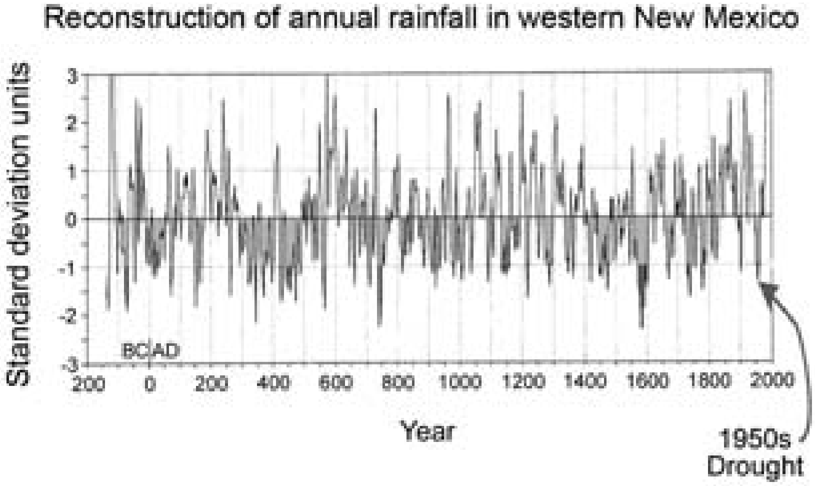


FIGURE 15.8 Decadal variability in precipitation for the past 2,200 years as indicated in ponderosa pine/Douglas-fir (*Pinus ponderosa/Pseudotsuga menziesii*) tree-ring reconstruction of annual rainfall from western New Mexico. The drought of the 1950s is shown, as well as droughts of equal and greater magnitude. Data from Grissino-Mayer 1996; graphic modified and first produced by Connie Woodhouse, NOAA National Geophysical Data Center Paleoclimatology Program.

nual, decadal, century, millennial, and multimillennial; 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 were mostly in productivity, abundance, and local shifts in community composition, whereas responses at century/millennial scales involved major and often recurring colonization and extirpation (migration and range shifts) events. Repetitive climate changes at each scale thus exert significant recurring evolutionary and ecological force on vegetation. Modern species have been exposed to fluctuating climates and rapid transitions for at least two million years, and they have likely been exposed to similar phases that punctuated the past 20 million years (Zachos et al. 2001).

A key characteristic of Quaternary paleoecology is that species respond individually to particular climate cues with unique rates and sensitivities to individual climate variables. Individual species follow their own ecological trajectories as climates cycle, leading to changes in community compositions that themselves form, dissolve, and may reform over time. Often non-analog communities form, that is, assemblages not observed in modern vegetation. From this perspective, plant communities exist as transient assemblages of species; species move individually through time and space following favorable climates and environments. The apparent recoalescence 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).

Implications for Restoration Ecology

Compelling evidence of climate variation across all timescales has implications for the theoretical bases and practice of restoration ecology. In particular, our awareness of the dominant effect that climate has in driving ecological change, and of the dynamic nature of climate and vegetation change, prompts us to evaluate assumptions about ecological sustainability, native species range, and restoration targets.

Concepts of Sustainability

Ecological sustainability is a dominant paradigm in restoration ecology. Variously defined, sustainability and related concepts of ecological heath and integrity, imply species, community, and ecosystem endurance and persistence over time, and they are often used as implicit or explicit restoration goals (e.g., Jordon et al. 1990; Lele and Norgaard 1996). In practice, sustainability has been difficult to describe or to recognize. Sustainability is generally accepted to pertain when natural species diversity is maintained, species are abundantly distributed throughout their recent historic native range, community associations are maintained, natural processes occur at reference intervals and conditions, and human disturbance is minimized (Lackey 1995; Hunter 1996).

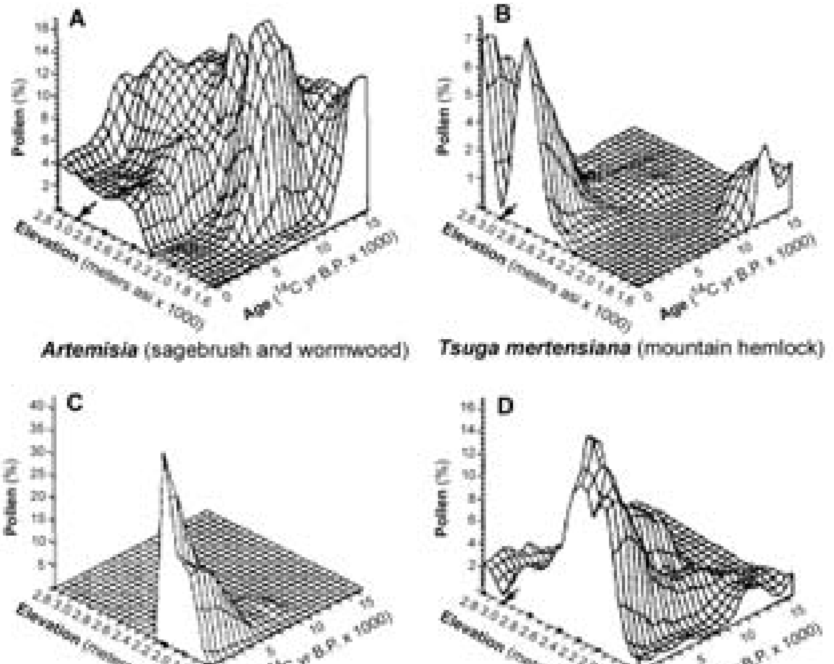
The complex and recurring cycles of ecological change in response to climate cycling challenge the conceptual bases of this interpretation of ecological sustainability. Species ranges have, and will—even in the absence of human influence—shift naturally and individualistically over small to large distances as species follow, and 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. A major conclusion from the paleorecord is that, at scales from years to millennia, ecological conditions are not in equilibrium, do not remain stable, nor are they sustained, but, by contrast, are in ongoing flux (Jackson and Overpeck 2000). The flux is not random, chaotic, or unlimited, but it is driven by regional climate and modified stochastically by local conditions.

It is important to note that the timescales under discussion are short relative to the lifespans of most extant plant species. Notwithstanding recently speciated taxa, many native North American plant species originated during the Tertiary or earlier, commonly 20 to 40 million years ago. Thus, many extant species have been subjected to the demands of shifting climates, in both large tempo and small, throughout their histories. This implies that adaptation to abrupt climate changes has had many opportunities to evolve. Resilience and sustainability, at least in terms of species persistence, appear to have been met through the capacity of plants to track favorable environments as they shift over time and through adjustment in range distribution, habitat, associates, and population characteristics.

Paleorecords in areas where abundant information exists can be used as a test of what has been sustained naturally over time. When Quaternary vegetation records from the Sierra Nevada were assessed in this way, Millar and Woolfenden (1999a) found that only a few conditions often associated with ecological sustainability concepts pertained. These included (1) relative stability of the Sierra Nevada ecoregion, that is, 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 associated with ecological sustainability did not occur. At subregional scales within the Sierra Nevada, species diversity changed at timescales of centuries to millennia. Similarly, individual species ranges and population abundances shifted, often drastically. An example is giant sequoia (*Sequoiadendron giganteum*). Currently limited to small and disjunct groves between 1,500 and 2,100 m in the southwestern Sierra Nevada, giant sequoia's range over the past 10,000 to 26,000 years included the eastern Sierra Nevada (Mono Lake; Davis 1999a), and locations in the western Sierra Nevada that are both well above (2,863 m, Power 1998) and below (1,000 m in current chaparral shrubland; Cole 1983, and 54 m at Tulare Lake in the California Central Valley, Davis 1999b) its current range. Giant sequoia did not appear in its current range until 4,500 years ago and did not reach modern abundance there until about 2,000 ago, that is, the age of the oldest living individuals (Figure 15.9) (Anderson and Smith 1994).

Several other conditions often considered elements of ecological sustainability did not pertain in the California paleorecord. Movement of individual species meant that vegetation assemblages 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 occurred transiently, such



Artemisia (sagebrush and wormwood) ***Tsuga mertensiana*** (mountain hemlock)

Sequoiadendron giganteum (giant sequoia) ***Abies*** (white and red fir)

FIGURE 15.9 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 2,000–3,000 years. From Anderson and Smith 1994.

as the co-occurrence 20,000 to 30,000 years ago in the southern Sierra Nevada of yucca (*Yucca brevifolia*) and Utah juniper (*Juniperus osteosperma*) with an understory of *Artemesia tridentata*, *Purshia tridentata*, and *Atriplex concertifolia* (Koehler 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 4,000 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 1,000 years following climate changes.

These and similar records challenge interpretations of ecological sustainability that have emphasized persistence of species and stability of communities within current ranges. As widely used, such concepts of sustainability do not adequately accommodate natural dynamics and promote misinterpretations about behavior of natural systems.

Population Size, Population Abundance, and Native Species Range

Declines (or increases) in population size and abundance—observed through monitoring or other measures—and reductions (or increases) in overall range often are assumed to be anthropogenic, whereas these may be instead natural species' responses to climate change. Two examples in California illustrate adaptation at millennial to decadal scales. Species of oak (*Quercus*) and juniper (*Juniperus*) expand and contract in complementary fashion: oak population abundances and total range distribution expanded repeatedly during warm climates and, as often, contracted during cool climates, while the opposite occurred for juniper species (Figure 15.10) (Adam and West 1983; Heusser 1995). Although oaks in general are widespread and common in California now, during repeated long glacial periods, they were rare in the region. Although these changes are most obvious between glacial and interglacial times, significant changes in abundance tracked climate at scales as short as a decade (Heusser and Sirocko 1997).

Coast redwood (*Sequoia sempervirens*) is another example. Currently rare, it has fluctuated in population extent and abundance following both long (millennial) and short (century-decadal) cold/warm cycles. Redwood was even more sparsely distributed than at present during climate periods when coastal fog did not develop and temperatures were hotter or cooler relative to present (Heusser 1998; Poore et al. 2000). Redwood expanded during mild, equable parts of interglacials when ocean temperature and circulation influenced development of coastal fog.

This perspective of Quaternary vegetation dynamics compels us to evaluate causes for changes in population size, abundance, and native range more carefully. Rather than interpreting changes as resulting from undesired anthropogenic threat, we might investigate instead whether these are natural species' adaptations. For instance, *Juniperus* expanding in Great Basin rangelands has been considered an exotic invasive, and measures have been taken to remove plants. These changes appear, rather, to be adaptive responses to climate change (Nowak et al.1994). Other things being equal, an ecologically informed conservation action would be to encourage, not thwart, juniper expansion.

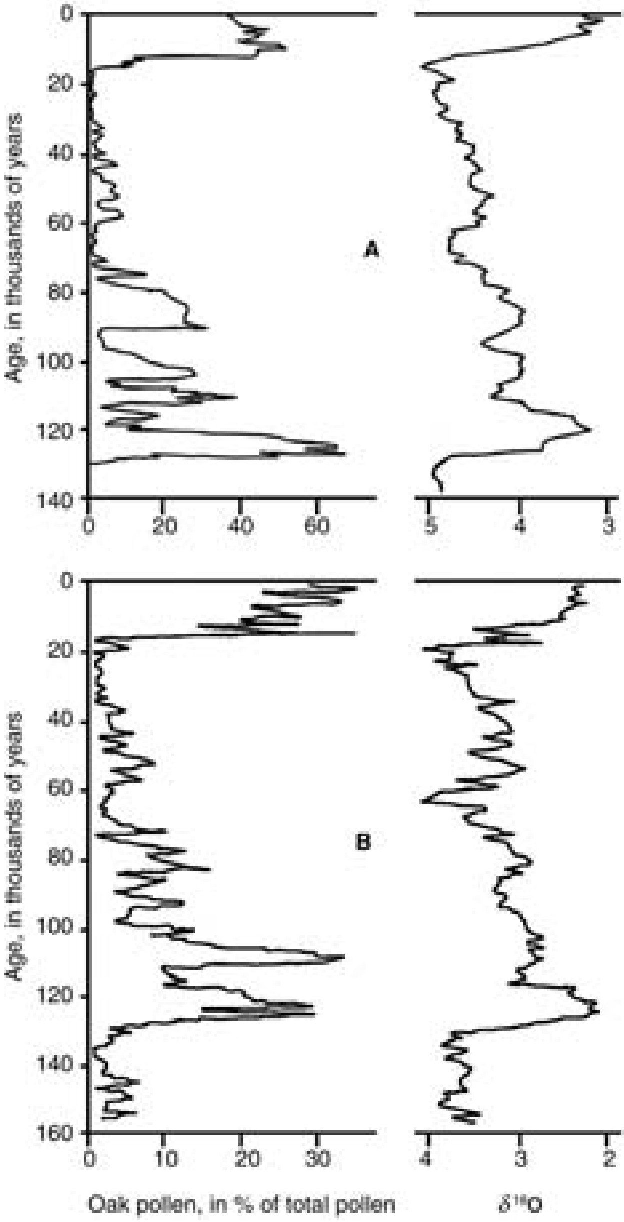


FIGURE 15.10 Correspondence of California oak (*Quercus*) abundance (pollen ‰) and temperature fluctuations recorded as variability in oxygen-isotope ratios indicating fluctuations between high and low abundance. Similar and synchronous patterns throughout the California oak ranges document species fluctuations 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).

Although changes in population size and distribution may be natural responses to climate change, causes are often difficult to discern in practice. Lags in adjustment and other disequilibria between population distributions and climate mean that population increases or decreases may not be synchronous with climate change, especially during periods when rapid climate changes occur over short periods, making difficult the search for mechanistic causes (Jackson and Overpeck 2000). Because individual plants, unlike animals, cannot "pick up and move" (intragenerational), they migrate and shift in distribution by dying in some areas while expanding in others (intergenerational). These may be messy on the landscape—with patchiness and irregularity characteristic—making the effects difficult to evaluate while they're happening. Causes may be attributed readily to other proximal factors, such as to insects and pathogens, or anthropogenic effects, such as fire suppression, even where climate is the ultimate underlying factor.

A challenging question for restoration ecology becomes, "what is the native range of a species?" To define the range of a species is the basis for monitoring its condition, understanding favorable habitat and ecological interactions, diagnosing threats and risks, 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 transient and dynamic process itself, readily capable of moving in space as climate shifts over the landscape. 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. Population abundances and species' distribution ranges may be relatively stable whenever climate is in a more stable phase and/or if the environment of a species offers considerable local heterogeneity (Thompson 1988; Jackson and Overpeck 2000; Williams et al. 2001). In these cases, shifts in climate may be tracked with relatively minor overall geographic changes. By contrast, in regions that are inelastic to change, for instance, landscapes with little topographic diversity, even small shifts in climate may bring large changes in population condition. "Given that the climate has been undergoing rapid changes with high variability during the twentieth and twenty-first centuries, we would expect population demographics and species ranges to also be highly unstable."

Genetics and Restoration in a Climate-Change Context

During the last 15 years, increasing attention has been given to the importance of genetics in restoration ecology (Millar and Libby 1989; Falk and Holsinger 1991; Lesica and Allendorf 1999; Rice and Emory 2004; Guerrant et al. 2004). Theory and guidelines have been developed regarding provenance (genetic origin); allelic and genotypic diversity; effective population size, gene flow, and genetic drift relevant to material for restoration; and long-term maintenance of reintroduction populations (Falk et al. 1996). These have been based on population-genetic assumptions that local populations are best adapted, that genetic contamination and inbreeding or drift decrease fitness and are to be avoided, and that safeguarding diverse local gene pools over time provides the best option for adaptedness in reintroduced populations.

New understanding of climate variability and its influence on plant population dynamics and biogeography raises questions about assumptions concerning local adaptation and genic diversity and suggests a need to rethink the role of genetics in restoration (Westfall and Millar 2004). Genetic theory on selection, drift, and genic diversity rests heavily on equilibrium conditions in regard to population size, gene flow, and drift. If, by contrast, rates of fragmentation, coalescence, population growth and mortality, and selection coefficients are changing within or between generations, then local populations will almost always remain in disequilibrium (Pease et al. 1989; García-Ramos and Rodríguez 2002; Bürger and Gimelfarb 2002). This leads to the likelihood that local populations are not necessarily best adapted, as has been found in common-garden experiments (Matyas 1996; Rehfeldt et al. 1999; Rehfeldt et al. 2001). Further, lags and persistent disequilibria could accumulate over time, creating a new kind of genetic load. Whenever climates are relatively stable, progress toward equilibrium may occur. In most species, especially perennial species, and during times of high climate variability, however, this is unlikely to be the case. Such theoretic possibilities suggest that restoration guidelines regarding appropriate germplasm collection zones, requirements for genic diversity in restoration, and germplasm transfer rules be reevaluated.

Reference Conditions and Restoration Targets

"Predisturbance" or "pre-Euro-American impact" conditions are used routinely as reference models and descriptions of desired targets for ecological restoration. This assumes, however, that climate hasn't changed between the historic target time and the present, and that human influence hasn't confounded historic conditions. These assumptions are tenuous, and the likelihood of their validity decreases with time between the historic target and present.

In western North America the disturbance period is regularly assumed to start at European/Asian contact with native peoples and their landscape, about 1840–1860, and the prior centuries are used as predisturbance reference conditions. As that period coincides with the coldest part of the Little Ice Age, however, it makes a poor model for twenty-first century restoration. Even in eastern North America, where European contact with the landscape was several centuries earlier, the dominant climate was Little Ice Age, with ecological conditions very different from present. Although "premodern contact" times differ around the world, the point remains: because of climate change, historic conditions are likely to be very different from present and are poor models for restoration.

The use of historic "predisturbance" landscapes is made further tenuous by confounding of human influence on environmental conditions. A bold new hypothesis offers an extreme example. Compiling several lines of evidence, Ruddiman (2003) suggests that humans have significantly altered world climates for over 8,000 years as a result of the spread of agriculture, thus radically changing the physical and ecological trajectory of Earth systems for millennia. Ruddiman's model postulates that cultural practices associated with agriculture triggered increases in wetlands and clearing and burning of forests, which in turn elevated carbon dioxide and methane far above natural levels. The cumulative effect is that global temperature is 1.5°C above what it would be without the anthropogenic input, and that Holocene climates are more stable than they would have been (W. Ruddiman, pers. comm.). Such long-term confounding of human with nonhuman influences challenges use of historic conditions as models for "pristine" or natural conditions in restoration.

Restoration or Realignment?

The discussions above prompt reevaluation of restoration assumptions and goals. If sustainability is to remain a guiding concept in restoration ecology, its interpretation would better focus on sustaining future options for flexibility and adaptation to changing conditions, rather than attempting to recreate stable conditions that resist change. In practice, rather than emphasizing historic ranges, or predisturbance species assemblages, compositions, structures, and landscape patterns, sustainability might instead embrace landscape macrodynamics that have characterized populations and species over long timeframes. These include, for instance, the ability to shift locations significantly, fragment into refugia, expand or contract in range, coalesce with formerly disjunct populations, alter dominance relations, foster non-equilibrium genetic diversities, and accommodate population extirpations and colonizations—all in response to changing regional and global conditions.

Biotas increasingly respond to more than change in climate at these scales. Although a fundamental goal of ecological restoration may be to remove direct manipulative effects of humans, in many cases this is impossible. Air pollution, alterations in landscapes surrounding the restoration site, presence of exotic invasives from distant continents, and changes in disturbance regimes all are imposed on restoration populations with little hope of mitigation. Sustainability in this context implies encouraging successful adaptation to conditions that cannot be turned back. Restoration ecology would better minimize the focus on restoring predisturbance historic structures and functions, and, instead promote efforts that foster natural macrodynamics as processes of adapting to inevitable change.

This does not imply, however, that "anything goes" in restoration. Adaptation is not chaotic, although stochastic processes play important roles. Populations and species respond and adapt to external forces of climate, invasives, and disturbance regimes with definable relationships and patterns; these can be better defined by restoration science, and mimicked in restoration practice. Rather than *restoring* past conditions, the challenge may be *realigning* systems to present and anticipated future conditions in such a way that they can respond adaptively to ongoing change (Millar and Woolfenden 1999b).

Realignment will require an understanding of relevant prehistories as well as changing influences on population dynamics over time in the restoration region. Modeling (quantitatively or qualitatively) these conditions as a trajectory forward into the present and future, including known or anticipated changes in climate as well as other environmental changes, allows target conditions for a realigned population to be developed. An example comes from the Mono Lake, California, ecosystem. A former pluvial lake at the western edge of the Great Basin, Mono Lake receives its water from four Sierra Nevada streams. It has been documented that surface elevation has naturally fluctuated with climate for the last 3,700 years (Stine 1990). In 1941, when the natural elevation of Mono Lake was 1,956 m, the city of Los Angeles began diverting water from Mono's tributaries for municipal use. This caused Mono Basin rivers to dry, aquatic communities and riparian forests to disappear, the lake level to drop, salinity to increase; diversion also triggered significant declines in floral and faunal populations. At the low point, Mono Lake stood 14 m below the 1941 elevation (Stine 1990, 1991). Rather than adopting the predisturbance lake elevation of 1,956 m as a restoration goal, scientists sought to determine a level based on current and anticipated future climate and water conditions. Using historic relationships of surface elevation, snowpack, stream flow, and climate, a water balance model was developed that allowed estimation of the current elevation level, if diversions didn't exist, incorporating antecedent climates (Vorster 1985). Then, estimates of future climate and water trends, extremes, and fluctuations were used to estimate input needed to keep the lake at or above a level considered adequate to sustain aquatic and riparian biota. The resulting lake level modeled was lower than the 1941 level, but this can be understood given that the lake was in rebound at the time from an extremely wet period in the early twentieth century. The court set the level at 1,948 m, incorporating the scientific approach in its decision. "A lawsuit involving restoration advocates and the City of Los Angeles resulted in a court decision that incorporated scientific realignment, and the level for Mono Lake was set at 1,948."

Another example of realignment comes from a conservation assessment of Monterey Pine (*Pinus radiata*), currently a rare species with three small California coastal populations and two Mexican island populations. Each population is suffering significant declines from human threats and conservation plans have been designed to restore these populations. All plans focus on improving conditions of the extant populations. Another approach to restoration derives from examining Quaternary dynamics of the species (Millar 1999). Analysis of Monterey pine paleorecords and paleoclimatologic data suggests that the species has a repeating metapopulation behavior that responds sensitively to fluctuations in climate. Under favorable climates, Monterey pine responds via colonization of many small, disjunct populations extensively along the California and Mexican coast, while during unfavorable climates, the species contracts to small networks of few populations. This process appears to have been repeated many times in Monterey pine's history.

Monterey pine occurred in the past in coastal northern California locations, as far as 600 km from the closest current native population. In this region, Monterey pine has been planted for landscaping, where it has naturalized widely, eventually spreading into parks and nature reserves. In these locations, the species is considered an unwanted exotic and is aggressively removed as part of restoration projects.

Based on analysis of Monterey pine's paleoecology, a realignment strategy was proposed as a supplemental restoration approach for the species (Millar 1998). The core of the idea is that Monterey pine would be encouraged to persist in certain areas on the north coast rather than being removed as an exotic pest. These locations are defined as areas where Monterey pine has naturalized, overlaps its historic range under similar climates at present, and includes floristic associates found in Monterey pine fossil assemblages. Such realignment locations are considered "neonative" sites for Monterey pine.

Opportunities for Climatological Research from Ecological Restoration

Whereas we have been describing implications from climate sciences to ecological restoration, there are opportunities for the reciprocal, that is, situations where ecological restoration research could advance climate science, as the following sections suggest.

Paleoclimate and Modern Climate Monitoring

Restoration projects that incorporate concepts of climate variability and realignment will, by design, include assessments of prehistory and paleoecological relationships of the restoration ecosystems. When this is done for the benefit of designing a restoration project, it will also contribute to paleoclimatology and paleoecology broadly. Restoration sites are often in locations that would not be selected for paleoclimatological research, and thus their addition to databases can be valuable. A similar benefit derives from archeology, where inferences about cultural sites and ancient human behavior depend on understanding the paleoenvironmental context of settlement sites. The need for this has motivated many excellent new paleoecological and paleoclimatic analyses that would not have been undertaken otherwise. The cumulative effect of such contributions is to saturate regions with local information, which in turn provides new understanding of well-resolved spatial relationships in paleoclimate and paleoecology.

Similarly, assessment of existing ecological conditions for a restoration project may provide information about modern climate relationships. In restoration ecology, causes for impacts are sought. Because many aspects of species biology are sensitive indicators of climate change, such analysis may bring to light important climate effects that would otherwise be unmonitored. For instance, investigation of conifer invasion into mountain meadows revealed that the primary correlations with invasions were not human disturbance (grazing or fire suppression) as had been suspected, but instead, multidecadal climate patterns related to the Pacific Decadal Oscillation (PDO) (Millar et al. 2004). Prior to this assessment, it had not been known whether PDO was expressed in that region or the nature of its effect. Similarly, restoration concerns throughout southwestern United States, where massive forest diebacks are occurring, provide an opportunity to understand spatial patterning of climate. Forest mortality is a sensitive indicator of persistent drought, and so it can be used to delineate resolved maps of the affected climate landscape. Local areas within a general drought zone where mortality is low may indicate microspatial patterns, such as anomalies in storm tracks that wouldn't be recognized otherwise. In this way, restoration projects can contribute to understanding the spatial and temporal influences of current climate and ongoing changes in climate.

Biotic Feedback to the Climate System

Global circulation models are the workhorses of modern climate change analysis. As models become more sophisticated, they are able to accommodate more information and thus become better estimators of future change. Model improvement focuses on greater spatial resolution of climate, incorporation of background climate variability (e.g., ENSO, PDO), and role of biota as feedback to climate. The latter is poorly understood and little integrated into climate change models. Biotic feedback occurs when changes in climate induce changes in biota, which in turn trigger further changes in climate. Examples include climate-mediated changes in vegetation life form (e.g., tree to shrub to grass), or changes in fire regimes or wetland extant, which initiate changes in albedo and carbon storage and eventually feedback to further climate changes. Ruddiman's (2003) Anthropocene is a millennial-scale hypothesis of biotic feedback to climate. Recent experiments in Rocky Mountain flora demonstrate carbon sequestration and feedbacks in meadow ecosystems (Saleska et al. 2002).

Restoration, when conducted with strategic experimental design, provides opportunities to investigate changes in variables related to climate feedback. For instance, introduction of restoration materials presents a chance to compare, at one location, the introduced system with the original, control condition. Monitoring changes in climate-responsive variables, such as carbon storage and albedo for specific environments, ecosystems, species, and climate zones, would contribute valuable input into the nature of biotic feedback and enable calculations of the significance of cumulative effects.

"Space-for-Time" Studies Versus Experimental Manipulation

A challenge in environmental sciences is how to study long-term processes in short, available (grant-determined) timescales. An option is to substitute space for time in research design. Experimental manipulation studies are also surrogates for time. Because studies about climate change implicitly invoke time-series analysis, these two approaches are often used—either one, or the other, or interchangeably, with the assumption that they yield similar results.

What is rarely studied is a comparison of methods and their value or appropriateness for different ecological or physical processes. Long-term studies by both space-for-time (gradient-analysis studies) versus experimental manipulation of Rocky Mountain plant communities to climate change document that, depending on trait, the two approaches can yield similar or different results. For some traits (e.g., flowering phenology) the two experimental approaches were comparable, while for others (e.g., carbon storage) they were discordant (Shaw and Harte 2001).

Because experimental manipulation is expensive, it is less often chosen in ecological or climatological research. Ecological restoration projects, by contrast, are almost always manipulative by design and provide an opportunity to do active experimentation. In such cases, opportunities exist to provide valuable information to climate and climate-related sciences about anticipated future responses to climate change under contrasting situations of experimentation, gradient analysis (e.g., contrasting elevations approximates space-for-time studying climate change), and *in situ* controls.

Global Warming and Restoration Ecology

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 something we already are experiencing. At one extreme, the "Anthropocene" era of human-induced climate began 8,000 years ago with the spread of agriculture and its cumulative biotic feedback effects. Nested within this background, warming observed in the last 120 years is partly rebound in the Bond cycling events, superimposed on the longer periods of internal and orbital cycling to which Earth is inextricably bound, and partly induced by modern human effects. Abrupt climate change and vegetation response have been common in Earth's history. On the one hand, this is comforting in that most species, whose roots extend into the Tertiary, must be at least somewhat adapted to the rates of change occurring now. Certain responses, such as massive landscape mortality events, range expansions, minor and major population extirpations, shifts in native ranges, or changes in community composition, may be expressions of landscape-scale resilience and realignment to changing external forces. Accommodating these factors—if we choose to accept them—will require rethinking our concepts about what and where native habitat is, what are "healthy" population sizes, what are causes of changes in population size, and when is change acceptable and appropriate. Society may choose not to accept such consequences and manage instead for other desired conditions. In such cases we will benefit by knowing that our management and conservation efforts may run counter to natural process, and thus restoration efforts may require continuing manipulative input to maintain the desired conditions. The lessons implied from paleoclimatology and paleoecology suggest that making friends with physical and ecological change is an important prerequisite to effective stewardship. Incorporating these ideas into new restoration ecology science and practice will require considerable thought, discussion, experimentation, and research in coming years.

Summary

New information from climate sciences and paleoecology increasingly challenges our ability to grasp dynamic nature. Key concepts for restoration include *natural* (without human influence) climate *oscillates* regularly, at *multiple* and *nested temporal scales*, including interannual, decadal, century, millennial, and multimillennial. *In addition, transitions between climate phases often occur abruptly*, and *vegetation responds to climate change*. Repetitive climate changes at each scale exert significant recurring evolutionary and ecological force on vegetation, and species have evolved mechanisms to adapt despite ongoing environmental change. These include changes in population size, abundance, and productivity, population migration, colonization, and extirpation. Plant communities exist as transient assemblages as species move individually through time and space following favorable climates and environments.

Such conclusions suggest a rethinking of concepts of sustainability and restoration targets. Rather than restoring historic, "pre-human-disturbance" conditions, we may better help species persist into the future by realigning populations with current and future anticipated conditions, and providing options to cope with uncertain futures with certain high variability. The capacity for populations to grow, decline, migrate, colonize, even extirpate, has determined species survival under past conditions of rapid change. Many situations thwart this capacity at present, including fragmentation, urbanization and development, static land-use policies (including conservation measures such as reserves, easements, etc.), and even rigid conservation philosophies that hold species hostage to specific locations and conditions. Understanding that species have coped with change in the past suggests that restoration sciences have opportunities to assist species cope with the dynamics of the current world.

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