Chapter 17

The Influence of Climate Variability and Change on the Science and Practice of Restoration Ecology

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Theory and Application

- Species, ecological communities, and ecosystems have been exposed to climate variation over ecological and evolutionary time scales, but future climate change may exceed past variability, making some reference conditions potentially less relevant to guide future restoration efforts.
- Ecological responses to climate change may include altered species ranges, disassembly of contemporary multispecies communities, and biome shifts driven by elevated mortality.
- Restoration ecology may need to focus on adaptive capacity and resilience by anticipating future species distributions, assisting migration into new areas, and conducting experiments to identify persistent assemblages under future conditions.

Variation in Earth's climate system has always been a primary driver of ecosystem processes and biological evolution. In recent decades, however, the prospect of anthropogenically driven change to the climate system has become an increasingly dominant concern for scientists and conservation biologists. Understanding how ecosystems may adapt to rapid contemporary and future change benefits from our knowledge of how they have responded to natural climatic variation across prehistoric time, especially during periods when Earth system conditions and ecosystems correspond to those of the modern era (e.g., Quaternary, the past 2.5 million years). Despite the dominant and pervasive influence of both climate variability and climate change, the restoration field is still learning how to accommodate these emerging influences. In this chapter we explore the consequences of climate variability and change for the science of restoration ecology and the practice of ecological restoration.

Earth's Climate System: A Paleoclimatology Primer

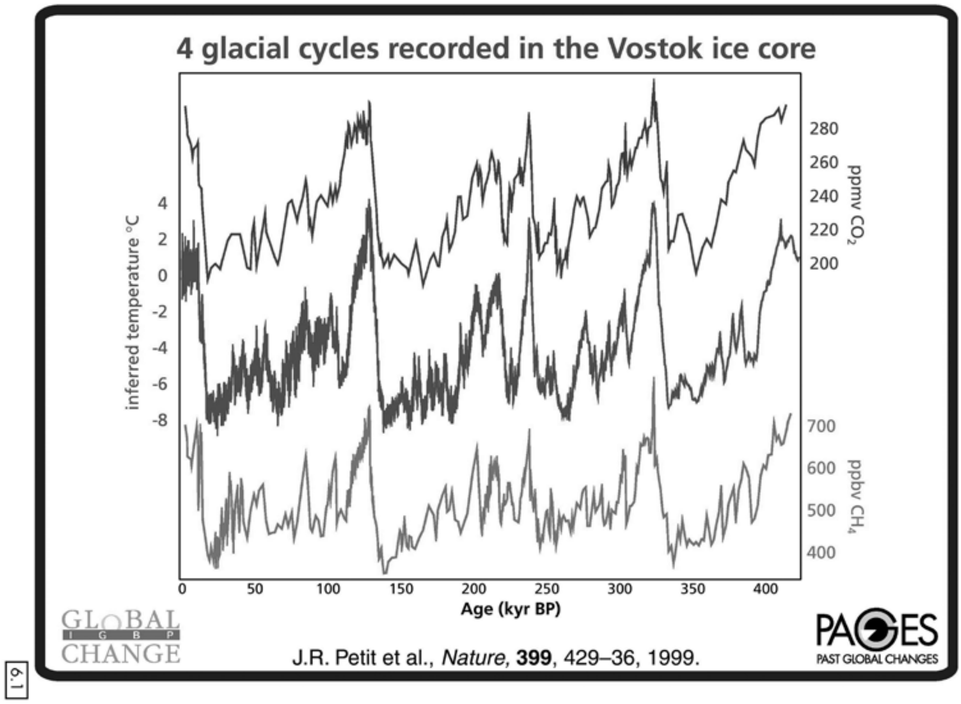
Climate variability in space and time has been a characteristic of the evolutionary and biogeographic context for life on Earth since its inception. All forms of life are influenced by this variability in where and how they live, including how they tolerate episodes of adverse weather effects through conditioned responses and evolved adaptations. The climate envelope of each species at various life stages is a fundamental property of its evolved ecological niche (Colwell and Rangel 2009). The species, communities, and systems that we attempt to conserve and restore are all thus preadapted through evolutionary experience to varying degrees of climate variation, from gradual and directional to abrupt and chaotic.

In recent decades, new tools with high precision and resolution, new models reliant on high-speed computing capacity, and a critical mass of empirical research have revolutionized understanding of Quaternary climate.

The deepest time proxies are derived from deep ocean sediment cores and ice cores retrieved in polar ice caps (Andersen et al. 2004; Barker et al. 2011; Bradley 2015). Cores drilled to the bottom of continental ice sheets (e.g., Greenland and Antarctica) have yielded highly resolved information on more than forty climate variables over the past 800,000 years (Jouzel et al. 2007; Bazin et al. 2013). Analysis of these and other climate-related isotopes are now extracted routinely from other environmental contexts where undisturbed deposition occurs, such as varved lake beds, coral reefs, and sea floor sediments. Other climatologically important indicators retrievable from ice and sediment cores that include greenhouse gas (CO_2, CH_4) concentrations, deuterium, atmospheric aerosols that indicate dust and volcanic ash, and species composition of past marine plankton rain.

Multimillennial Climate Cycles

These long, highly resolved records collectively document the repeating, cyclic nature of climate over the past 2.5 million years (fig. 17-1) (Bradley 1999; Wright 1989; Raymo and Ruddiman 1992). Oxygen-isotope records show a repeating pattern of more than forty glacial/interglacial cycles. A primary mechanism for these periodic climatic oscillations was proposed by Serbian mathematician Milatun Milankovitch (1941) long before detailed paleoclimate variability had been documented. From the many oxygen-isotope curves now available around the world, it is clear that major warm-cold oscillations of glacial/interglacial phases have been



4 glacial cycles recorded in the Vostok ice core

J.R. Petit et al., *Nature*, **399**, 429–36, 1999.

Figure 17-1. Primary fluctuations in temperature, CO_2, and CH_4 between glacial and interglacial periods for the past 400,000 years, derived from oxygen-isotope analysis of ice cores from the Vostok station in Antarctica. Our current interglacial period (Holocene) is at the *far left*, from 0 to 10,000 years ago. Pages International Project Office—modified from Petit et al. 1999.

expressed more or less synchronously on global scales (Mayewski et al. 2004). Global temperature differences between glacial and interglacial periods averaged 12°C–17°C (Petit et al. 1999; Bintanja et al. 2005).

Century- To Millennial-Scale Climate Variation

Analyses of oxygen-isotope variation, tree rings, and other proxies reveal that century- to millennial-scale variability has been common through the Quaternary. Multimillennial climate variation is driven by oscillations in solar input to Earth's atmosphere, greenhouse gas (GHG) concentrations, thermohaline ocean circulation, and other forcing factors that operate on scales of 1,000–2,000 years, within the life span of some long-lived organisms such as temperate trees (fig. 17-2) (Mann et al. 2008). Climate intervals exemplifying multicentury to millennial cycles during the recent Holocene include the Little Ice Age (LIA), a minor ice advance and global cold period from AD 1450 to 1920 (Grove 1988; Overpeck et

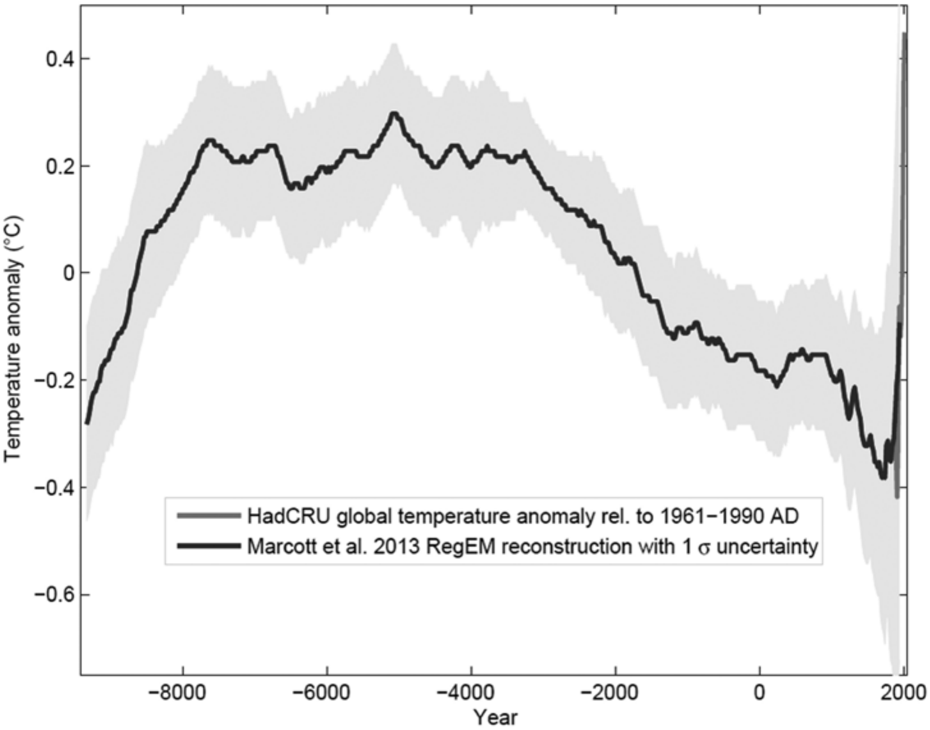


Figure 17-2. Holocene (past 10,000 years) mean global temperature variation. The rapid rise in global temperatures at the end of the last Ice Age was followed by a ~5,000 year period of relative stability with variation on centennial to millennial scales. Temperatures declined ~0.5°C over the following 5,000 years until the recent abrupt rise due to anthropogenic warming. Graphic from www.realclimate.org , modified from Marcott et al. 2013.

al. 1997; Mann 2002) and the Medieval Climate Anomaly, a warm, dry interval in some regions from AD 900 to 1350.

Interannual to Decadal-Scale Climate Variation

Climatologists have identified many climate modes operating on scales from a few years to several decades, using proxy information derived from tree rings, corals, layered ocean sediments, and other sources, as well as instrumental data for the past century. The best known of these is the El Niño pattern, called the El Niño-Southern Oscillation (ENSO) for its interhemispheric, atmospheric, and oceanographic expression and concentration in the tropical and subtropical Pacific Ocean (Sarachik and Cane 2010; fig. 17-3). ENSO brings opposing seasonal weather conditions to different parts of the world, referred to as *teleconnections* from oceans to terrestrial weather. For instance, El Niño events portend unusu-

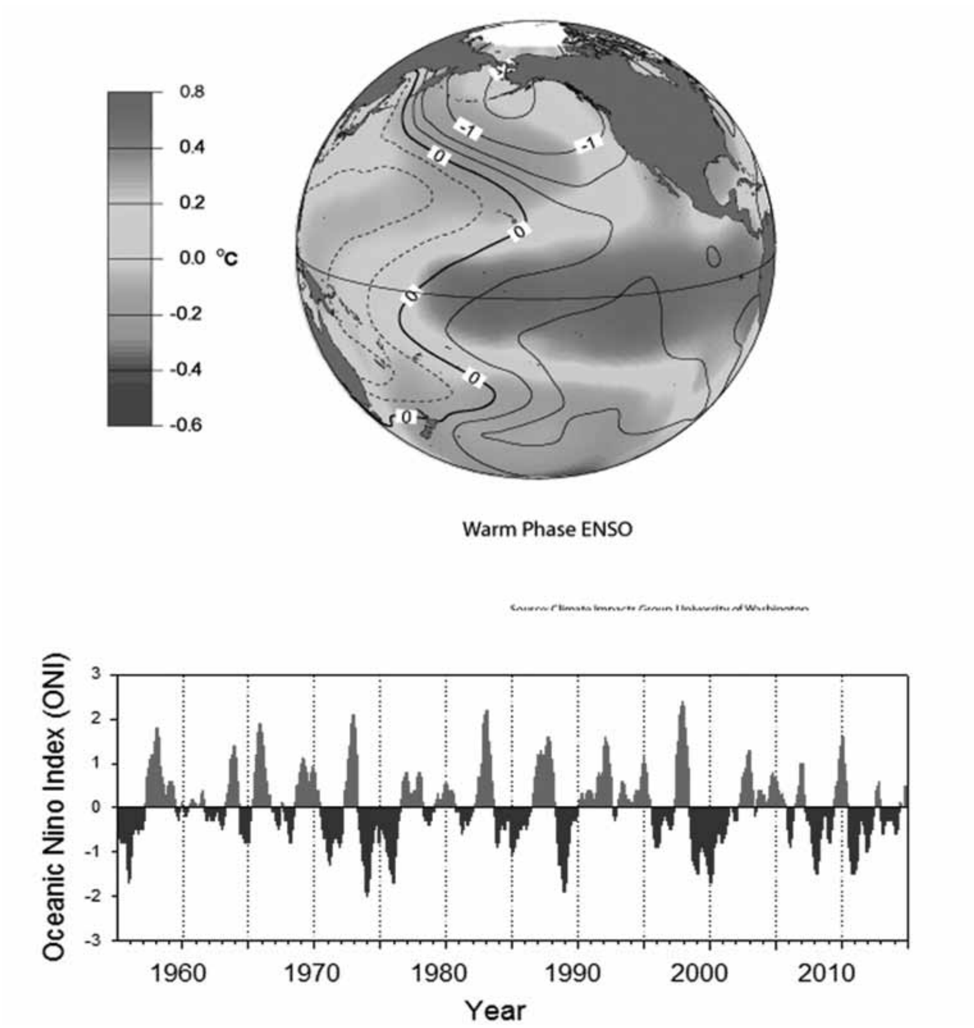


Figure 17-3. The El Niño/Southern Oscillation is an internally regulated, ocean-atmospheric dynamic process that affects global climate on interannual and decadal scales. Warm phase ENSO figure from Mantua et al. 1997; (©American Meteorological Society. Used with permission). Ocean Niño index from: NOAA Fisheries (*lower* panel).

ally warm and wet autumns and winters in the southwestern United States, and unusually cool and dry weather in the Pacific Northwest, with reversed expression during La Niña events.

Multidecadal (twenty-year to sixty-year) periodicities in the climate system have also been identified but remain poorly understood mechanistically in part because the instrumental record captures at most a few complete cycles. The Pacific Decadal Oscillation (PDO) is a multidecadal cycle of northern Pacific sea surface temperatures (SSTs) that affects the climate of northwestern North America. The

PDO reflects 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 ENSO (Mantua et al. 1997; Zhang et al. 1997).

Climate Variability as an Ecosystem Architect

Abundant evidence worldwide shows that life on Earth has responded to climate variability at all of these scales of space and time documented by pollen and plant remains deposited in sediment cores extracted from meadows, bogs, lakes, and ocean bottoms. In dry environments, packrat middens preserve macrofossils, while in temperate forests, tree-ring records archive annual tree growth.

Changes in Species and Communities over Millennial to Multimillennial Time

At multimillennial scales, paleoecological records document changes in regional floristic composition multiple times in correspondence with major climate phases. For instance, in the northeastern United States, eastern Canada, parts of Scandinavia, and northern Asia, species shifted latitudinally hundreds of kilometers in the late Pleistocene and early Holocene as regional climate warmed (fig. 17-4) (Davis 1981; Jackson et al. 1987). In more mountainous regions, species responded primarily by changes in elevation and aspect, illustrated by conifers of the Great Basin and southwestern desert region, which shifted as much as 1,500 m (Thompson 1988, 1990; Grayson 2011). Where habitats were highly patchy, such as areas with steep and discontinuous gradients, species responded by fluctuations in population size and smaller geographic shifts, as exemplified by oaks in California (Adam and Robinson 1988; Heusser 1995). Areas occupied by continental ice caps were often revegetated via rapid colonizations from refugia (Brubaker and McLachlan 1996).

Paleorecords in areas where abundant information exists can be used as a test of ecosystem stability or flux over time (case study box 17-1). Millar and Woolfenden (2016) found that at subregional scales within the Sierra Nevada, individual species ranges and population abundances shifted, often substantially. Vegetation assemblages have also changed over time and/or shifted locations as individual species followed separate climate envelopes (Woolfenden 1996). In the Great Basin of North America, major changes in population size and extent of single-leaf piñon (*Pinus monophylla*), and changes in floristic diversity, correspond to century-long climate fluctuations (Tausch et al. 2004). Most species responses are individualistic, time lags are common, and nonanalog patterns frequent, so that population geographic shifts may appear to lag behind climate variation, es-

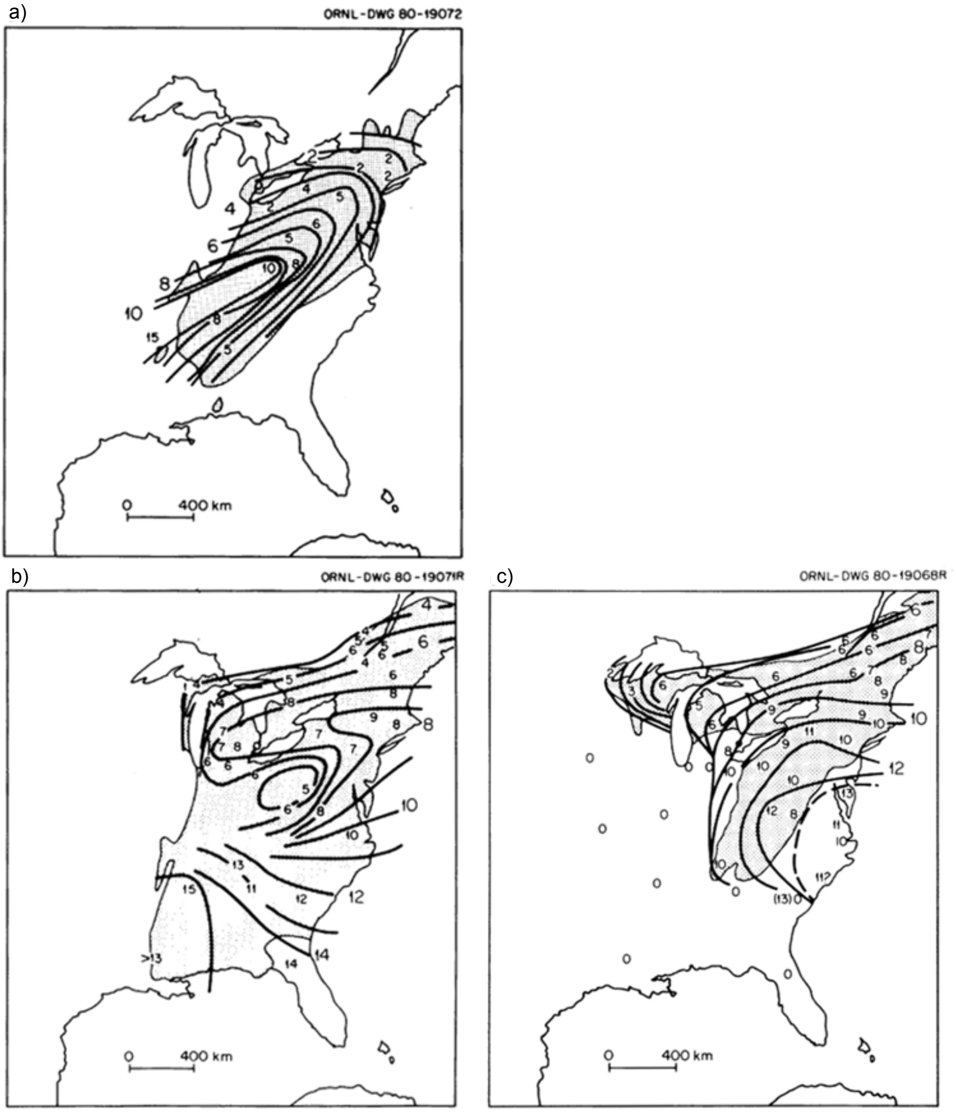


Figure 17-4. Shifts in ranges of (a) American chestnut (*Castanea dentata*), (b) American beech (*Fagus grandifolia*) and (c) eastern hemlock (*Tsuga canadensis*) in eastern North America as they tracked changing temperatures following the Last Glacial Maximum. Modified from Davis 1981.

pecially when changes are extreme and abrupt (Davis 1986; Webb 1986; Jackson and Overpeck 2000).

In addition to species ranges, ecosystem processes are also influenced profoundly by the prevailing climate regime. Fire regimes reconstructed from paleorecords in lake and bog sediment charcoal (Power et al. 2008; Marlon et al. 2009) and tree rings (Falk et al. 2011) reveal evidence of significant change in fire

Case Study Box 17-1
Species Range Shifts in Response to Past Climate Variation

Studies of paleoclimate and paleoecology allow us to put current species distributions in a longer-term context. Using records derived from tree rings, pollen analysis, packrat middens, and other sources, changes in space and time of many species distributions can be mapped in considerable detail.

Giant sequoia (*Sequoiadendron giganteum*) is one of the most iconic trees of North America. 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), and locations in the western Sierra Nevada that are both well above (2,863 m) and below (1,000 m in current chaparral shrubland; and 54 m at Tulare Lake in the California Central Valley) 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.

In the American Great Basin, singleleaf piñon (*Pinus monophylla*) radiated latitudinally following the last glacial cycle. Pollen and woodrat-midden records document that singleleaf piñon distribution was widespread in the late Pleistocene at the southern end of its current range, in the distribution of the current Mojave and Sonoran Deserts. As climates warmed during the early Holocene, the species migrated gradually northward and upslope in the Great Basin, reaching western Nevada 300 years ago (fig. 17-9). A similar well-documented example of species range shifts in response to century-scale climate variation is two-needle piñon (*Pinus edulis* Engelm.) in the western US. *P. edulis* is primarily a species of the Colorado Plateau, but new populations in northern Utah near the Wyoming border became established in the 1200s, as shown by pollen, tree ring, and packrat midden analyses. Piñon largely replaced Utah juniper (*Juniperus osteosperma*) as the dominant species in the 1300s. In the southern portion of its range, piñon has been experiencing significant dieback, especially at lower elevations. These coupled processes of mortality and recruitment lead to the emergent property of species range shifts.

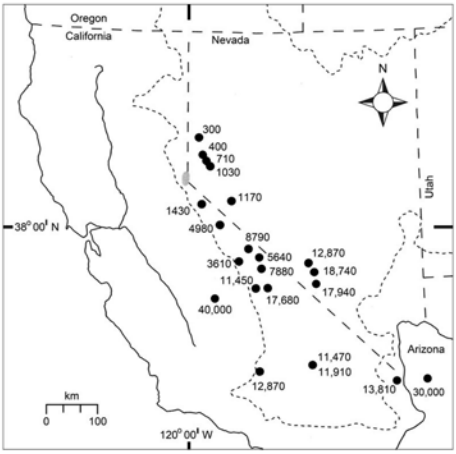


Figure 17-9. Arrival (years before present) of single-leaf piñon (*Pinus monophylla*) along the western Great Basin and in southern California and western Arizona from refugial regions in the current Mojave and Sonoran Desert regions as temperatures warmed from the last glacial maximum, to its current distribution limit north of Reno near Pyramid Lake. Dotted line shows the boundary of the hydrologic Great Basin. Sites from the central and eastern Great Basin are not shown. Note the arrival of the species in west central Nevada just 300 years ago. Modified, with permission, from DK Grayson (2011), *The Great Basin: A Natural Prehistory*.

References: Anderson and Smith 1994; Heusser 1995; Heusser and Sirocko 1997; Davis and Shaw 2001; Gray et al. 2006; Grayson 2011; Macalady and Bugmann 2014.

frequency and extent over time at multiple spatial scales. At mid elevations of the western Sierra Nevada beginning about 4,000 years ago, charcoal records indicate increased local fires and effect on regional vegetation (Anderson 1990; Anderson and Smith 1994). In giant sequoia forests, fire regimes shifted from frequent, light, and localized fires to infrequent, intense, and widespread fires in the last 1,000 years, tracking climate variation (Swetnam 1993). Fire frequency (as detected by sediment charcoal) in what is now Yellowstone National Park increased significantly 11,000 years BP as the region warmed and less flammable tundra gave way to forest, as reflected in the pollen record (Millspaugh et al. 2000).

Ecological Responses to Interannual, Decadal, and Centennial Variability

Decadal and centennial climate and vegetation fluctuations are well documented in the tree ring record, such as recurring variation in precipitation over the past 2,000 years in New Mexico (fig. 17-5) (Grissino-Mayer 1996), persistent droughts in the Colorado River Basin (Meko et al. 2007), and episodes of widespread and persistent drought in the western United States, especially the period AD 900–1300 (Cook et al. 2004). Recurring patterns of tree growth 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) are correlated with the PDO for up to 400 years. Vegetation type conversions from meadow to forest, changes in species growth rates and crown morphology, and changes in forest density have been associated with PDO cycles in conifer forests of the Sierra Nevada, California (Millar et al. 2004).

Climate variability drives interannual to multicentury changes in fire regimes by regulating plant productivity and fuel conditions in areas where teleconnections are strongest. Fire occurrence in western North America was higher during some periods of extended drought, and lower in some areas during the LIA (Pierce et al. 2004; Whitlock et al. 2010). These oscillations also govern fire regimes in regions where El Niño and La Niña influences on winter precipitation regulate fuel loads and snowpack development and persistence, which govern the length of fire season (Westerling et al. 2006). ENSO and other ocean-atmosphere processes force fire regimes at interannual to decadal time scales (Swetnam and Betancourt 1998; Kitzberger et al. 2001; Littell et al. 2009).

Current and Impending Changes to Earth's Climate System

This brief review of past variation in Earth's climate, and some of the processes that drive natural variability, establishes the principle that species and ecosystems have been exposed to variation in climate throughout their histories. If so, then

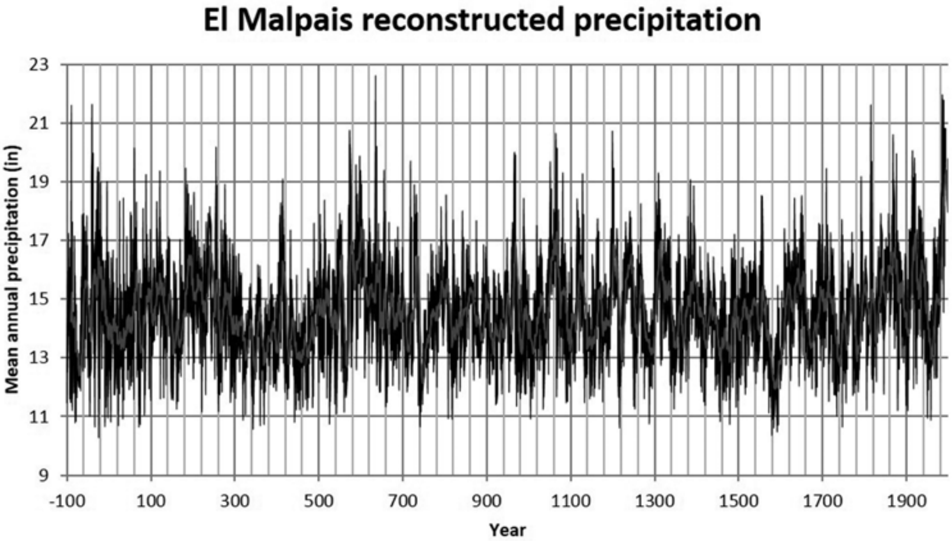


Figure 17-5. Decadal and centennial precipitation variability for the past 2,115 years based on tree-ring reconstruction of annual rainfall from western New Mexico, US. Gray line is a ten-year moving average. From this perspective a major recent drought in the 1950s was not exceptional in magnitude or duration compared to the historical record. Data from Grissino-Mayer (1996).

how is our current period different, and what implications do these differences have for sustainable ecological restoration and management?

An Overview of Global Change

Significant warming of the Earth's surface in the past century is now established unequivocally (Mann et al. 2002). Warming since the late 1800s has been ca. 0.85°C globally with much of the increase occurring due to increases in minimum temperature (Hansen et al. 2010; IPCC 2014b). Similar changes have affected other properties of the Earth's climate system, including spatial and temporal patterns of precipitation, sea ice extent, mean sea level, frequency of extreme events (droughts, severe storms), and others.

Most of the continued warming since mid-twentieth century can be explained only by the effects of recent anthropogenic-induced greenhouse gases (GHGs; Meehl et al. 2004; fig. 1.10 in IPCC 2014b), many of which are now at their highest level in 650,000 years (Karl et al. 2009; Montzka et al. 2011). In contrast, natural forcing factors that might contribute to global warming (solar irradiance, volcanic emissions) contribute essentially 0% of changes in surface temperature since 1950, compared to GHGs, which account for nearly all of the 0.85°C global mean increase. Roughly half of all GHG emissions since 1750 have occurred since 1970, of which ~40% of these emissions remain in the atmosphere; the remainder is taken up by vegetation, soils, oceans, and other "sinks." Effects on the global climate system from just the GHGs that are already in the atmosphere are projected to persist for centuries, due to their long residence time in the atmosphere (O'Neill et al. 2010).

The future trajectory of Earth's climate system depends primarily on how much, and how soon, human societies reduce CO_2 and other GHG emissions to the atmosphere. IPCC quantifies these using "representative concentration pathways" (RCPs), which estimate the total change in Earth land-surface temperature as a function of future emissions. Current RCPs range from 2.6 to 8.5, reflecting potential global mean temperature increases of 1.5°C–4.5°C by the end of the current century (Karl et al. 2009). These increases will likely not be uniform: under RCP 8.5, some parts of the globe (particularly boreal and polar regions) could experience temperature increases of up to 11°C, and mean temperature in many regions of the northern hemisphere could increase 5°C–9°C (IPCC 2014b).

Ecological Manifestations of Global Change

The ecological consequences of these changes to Earth's climate are already unfolding (table 17-1) (Walther et al. 2002). Short-term ecological responses to climate change can be difficult to separate from the inherent noise in ecological data, such as population sizes, reproductive and mortality rates, local species distributions, disease outbreaks, and disturbance events. Over decadal time, however, certain ecological properties are projected to have the clearest ecological signal, based on both empirical and modeling studies.

Shifts in Species Ranges and Phenology

Among the most immediate and visible expressions of ecological response to changing climate are shifts in species ranges (Parmesan 2006; Thomas 2010; Chen et al. 2011). For example, Hill et al. (2011) found that the ranges of many insect species have shifted to higher elevations and latitudes, with population loss at lower elevation species boundaries, during the twentieth century warming. Root et al. (2003) surveyed 143 studies globally and found consistent temperature-driven changes in 82% of species surveyed: invertebrates, amphibians, birds, and many plant taxa.

Range shifts are often predicted using bioclimatic envelope (BCE) models that project the future geography of suitable climate for a species, given where it occurs presently or in the recent past (Pearson and Dawson 2003; Rehfeldt et al.

Table 17-1.

Summary of primary ecological effects of climate change with relevance to the science and practice of restoration ecology. Adapted from IPCC 2014a (table 2.3) and other sources.

Reduction in terrestrial carbon sinks	Carbon stored in terrestrial ecosystems is vulnerable to loss back into the atmosphere, resulting from increased fire frequency due to climate change and the sensitivity of ecosystem respiration to rising temperatures.
Increased tree dieback and mortality	Persistent seasonal drought and elevated temperatures lead to reduced soil moisture and increased vapor pressure deficit. Larger trees in moisture-limited forests are already showing signs of increased mortality and replacement by drought-tolerant trees and shrubs.
Boreal tipping point	Arctic ecosystems are vulnerable to abrupt change related to the thawing of permafrost, spread of shrubs in tundra, and increase in pests and fires in boreal forests.
Amazon tipping point	Moist Amazon forests could change abruptly to less-carbon-dense, drought-and fire-adapted ecosystems.
Increased risk of species extinction	Species with an intrinsically low dispersal rates, especially those occupying flat landscapes where the projected climate velocity is high, and species in isolated habitats such as mountaintops, islands, or small protected areas are especially at risk.
Displacement of species populations from current range and habitat	Species populations may not persist in their current locations due to geographic shifts in suitable climate. Dispersal barriers and the rate of climate movement will prevent some species from migrating or being able to reach suitable habitat.
Altered disturbance regimes compound the direct effects of climate change	Major ecological disturbances, such as wildland fire, insect and disease outbreaks, and other processes are regulated directly and indirectly by climate and are likely to cause additional stresses to terrestrial ecosystems and species populations.
Increased abundance and competitiveness of nonnative invasive species	Warmer temperatures and altered rainfall patterns may favor invasive nonnative species at the expense of native species. Once established, nonnative species can displace native populations, contribute to altered fire regimes, and cause cascading ecological effects such as reductions in native pollinators.
Changes to hydrologic regimes and biogeochemical processes	Streamflow regimes, stream chemistry and water temperature, groundwater and aquifer replenishment, and cycling of essential nutrients (N, P, K) are altered by local and regional patterns of precipitation and temperature, influencing terrestrial and aquatic communities.

2006). While BCEs have limitations, especially at finer spatial scales, they suggest a likely null model for how species may respond to climate change over multiple decades. For example, Notaro and colleagues (2012) projected current and future ranges of trees and shrubs from the southwestern United States under current and potential future climate in the late twenty-first century. While there are both winners and losers, more species were reduced in range and displaced from their current locations, with especially large losses of area in species characteristic of cooler and high elevation forests (fig. 17-6).

Climate also influences the *phenology* (seasonal timing and progression) of species life cycles (Cleland et al. 2007; Schwartz et al. 2012). When phenology is altered (e.g., earlier flowering due to warmer spring temperatures), species interactions can be affected adversely by "phenological decoupling" (Walther 2010). For example, if insects arrive early to forage on host plants that have not yet flowered, the temporal mismatch may lead to pollination failure (Inouye 2008; Rafferty et al. 2015).

Elevated Tree Mortality

Persistent drought stress, especially when accompanied by elevated temperatures, is likely to lead to widespread forest dieback in many regions (Allen et al. 2010; Allen et al. 2015); indeed, this is likely occurring already. While the mechanisms of tree mortality are complex, combinations of reduced soil moisture and higher temperatures (leading to increased evaporative demand in the canopy) can initiate tree death more quickly than either factor acting in isolation (Adams et al. 2009). Mortality can be induced either by hydraulic failure (insufficient water in the xylem to maintain water transport from roots to canopy), or by "carbon starvation," which occurs when leaves close stomata to reduce transpiration water loss, which also closes off their essential source of carbon for metabolism (McDowell et al. 2011). Expressed over large geographic regions, these physiological responses to persistently warmer and drier climate are projected to lead to reduced tree growth and, ultimately, widespread tree mortality and replacement of current forests by more drought tolerant life forms (Williams et al. 2010; Williams et al. 2013).

The Emergence of Megadisturbances

Altered climate will inevitably produce disturbance regimes that are novel in some respects. In some cases, the properties of these new regimes may exceed the life history adaptation of species to cope with conditions outside of their evolutionary envelope. While disturbance processes such as fire, insect outbreaks, drought, and nonnative species, can be studied individually, it is their interactions that are

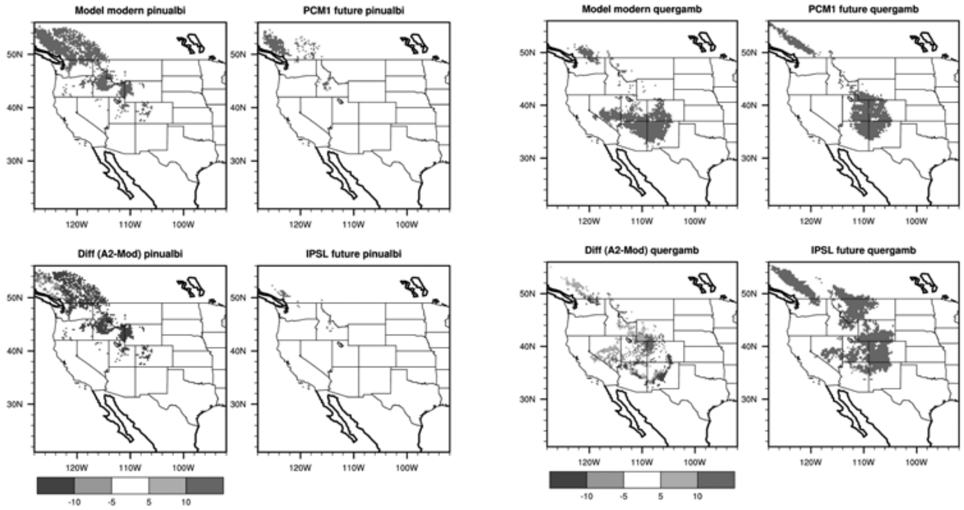


Figure 17-6. Current and projected (2100) ranges of (*left*) whitebark pine (*Pinus albicaulis*) and (*right*) Gambel oak (*Quercus gambellii*) under a consensus of 17 CMIP3 GCM projections based on IPCC A2 and B1 emissions scenarios, modeled contemporary distribution (*upper left*), future distribution under moderate climate (*upper right*) and more extreme change scenarios (*lower right*), and the percent change in each pixel (*lower left*). Full details in Notaro et al. (2012); figure courtesy of MA Notaro, University of Wisconsin (http://faculty.nelson.wisc.edu/notaro/maxent.html).

likely to lead to *megadisturbance* regimes and trigger rapid ecosystem degradation (Zedler 2009; Millar and Stephenson 2015).

Wildland fire regimes respond both directly (through direct climatic influences on combustion, such as short-term fuel moisture, air temperature and humidity, lightning ignition, and other factors) and indirectly (through influences on live vegetation mass and distribution, seasonal soil moisture, and snowpack) (Crimmins 2011; Hostetler et al. 2006). As a consequence, climate change is likely to be expressed strongly in changes to wildland fire regimes (Flannigan et al. 2009; Krawchuk et al. 2009; Littell et al. 2010; Moritz et al. 2012).

Evidence suggests that fire behavior, area burned, and fire severity (effects of fire on ecosystem attributes such as tree survivorship and soil integrity) are already increasing due to the combined effects of accumulated fuels, more extreme fire weather, and longer fire seasons. For example, Westerling and colleagues (2011) found that warming temperatures through the twenty-first century could increase the rate at which the landscape experiences fire by a factor of 3x–10x in the Greater Yellowstone Ecosystem. Fires that occur during extreme or anomalous climate episodes (for example, unusually warm droughts) can have persistent ecological effects and lead to *tipping point* abrupt change into new ecosystem states (Falk

2013). Wildfires are also a significant source of interannual variability in terrestrial emissions of carbon to the atmosphere, creating a feedback to the climate system (van der Werf et al. 2006).

Increased Abundance and Distribution of Invasive Nonnative Species

Nonnative species have been increasing in abundance and distribution worldwide in recent decades (chap. 8). Nonnative species can outcompete native species and drive them to local extirpation; alter nutrient pools and carbon dynamics; change ground cover and surface erosional processes; and alter fire regimes by increasing the mass, spatial distribution, and continuity of fine fuels (Brooks et al. 2004; Didham et al. 2005; Stevens and Falk 2009). As a consequence, many nonnative species, once established, create or reinforce conditions favorable to their continued dominance, thus creating a positive feedback or tipping point response in the local ecosystem (Ehrenfeld 2010).

Rapid increases in nonnative species are also associated with climate change and are thus predicted to become even more widespread in coming decades (Hellmann et al. 2008). Rahel and Olden (2008) found that nonnative species would expand in aquatic communities due to altered thermal and streamflow regimes, altered water chemistry, dispersal into currently nonsuitable habitat, and decline of competing native species. Thus, the progression of climate change may alter the relative competitive abilities of native and nonnative species in site- and species-specific ways (Bradley et al. 2009; Bradley et al. 2010).

Implications for Restoration Ecology

The role of the climate system as a pervasive driver of ecological change and species evolution is a fundamental element in any meaningful theory of restoration ecology. The resulting awareness of the dominant effect of climate variation in space and time in driving ecological change, and of the dynamic relationship of climate, vegetation, and disturbance, prompts us to evaluate assumptions about future species ranges, ecosystem processes, and restoration objectives.

Ecological Responses to Climate 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 (Botkin 1990; Millar and Stephenson 2015). In turn, restoration ecology and practice have also matured from emphasis on nature preservation to maintaining variability and natural function (Falk et al. 2006; Choi 2007; Perring et al. 2015). As a result, dynamic processes such as prescribed fires and managed floods have become important restoration tools, and recovery of ecosystem function, composition, and structure has been added to restoration goals.

Important as these changes have been, static views of nature still sometimes implicitly constrain restoration objectives (Harris et al. 2006). As we have shown, the climate system is a central physical force on Earth and significant agent of physical, ecological, and cultural change at micro- to macroscales. From this perspective, climate is a cross-scale disturbance element, the background stage of change on which evolutionary and successional dynamics play out (Jackson 1997). Such dynamism has been incorporated into evolutionary and ecological theory, but 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, need to become more fully informed by a more dynamic understanding of Earth systems. If there is one lesson from the study of paleoclimate and paleoecology, it is that change is a constant property of life on Earth.

Population and Species Distribution Responses

Declines (or increases) in population size and abundance—observed through monitoring or other measures—and reductions (or increases) in overall range are often the "front lines" of species responses to local conditions. Although such changes are often assumed to be anthropogenic (e.g., in response to suppression of the natural fire regime, altered stream flow regimes, elimination of top predators), population change may also be natural species' responses to climate variability. For instance, Utah juniper and single leaf piñon expanding in Great Basin rangelands have been treated as exotic invasives, and measures have been taken to remove thousands of trees, even though these species have been present in the region throughout at least the past million years. Such population changes in native species can also be viewed as adaptive responses to changes in disturbance regimes and climate (Nowak et al. 1994).

Although changes in population size and distribution may be natural responses to climate change, causes are often difficult to untangle 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 variation, especially during periods when rapid climate changes occur over short periods of time (Jackson and Overpeck 2000; Overpeck and Cole 2006). Because individual plants, unlike animals, cannot "pick up and move" (intragenerational), they migrate and shift their range by dying in some areas while expanding in others (intergenerational). These processes may be messy on the landscape—with patchiness and irregularity characteristic, making the effects difficult to evaluate while they are happening (Schwartz 1993).

The range of a species is typically the basis for monitoring its condition, identifying favorable habitat, diagnosing threats and risks, determining restoration targets, and indicting some competing species as "exotic" (Jackson 1997). Viewed against historic changes in distribution and natural flux, however, the native range of a species must be considered a transient and dynamic property, capable of moving in space as climate shifts over the landscape (Falk et al. 1996). Recognizing that nonequilibrium conditions exist and vegetation lags climate variation means that, like Lewis Carroll's Red Queen, vegetation chases a target (climate) that is itself changing (van Valen 1977). 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; Williams et al. 2001). In these cases, shifts in climate may be tracked with relatively minor overall geographic changes. By contrast, in landscapes with less topographic diversity, even small shifts in climate may bring large changes in local population abundance. In coming decades, we can expect population demographics and ranges of many species to be highly unstable, including the dissolution and reassembly of multispecies communities, as species respond individualistically as well as interactively (Gleason 1926; Temperton et al. 2004) (chap. 9).

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, and indeed constitute a foundational principle (Egan and Howell 2001). This assumes, however, that the climate template is unchanged between the benchmark target time and the present, and that human influence has not confounded historic conditions. These assumptions are tenuous, and the likelihood of their validity decreases with time between the historic target and present. For example, many contemporary forests originated during what is now identified as the Little Ice Age in parts of the Northern Hemisphere, and thus may provide problematic models for restoration (Fulé 2008; Millar 2014).

This does not mean that all aspects of climate or ecosystems of the past 500 years are irrelevant to restoration. The legacy of past ecosystems is extremely powerful, expressed in the form of dominant vegetation, regional species pools, community associations with major soil formations, broad-scale disturbance regimes, and general ecological genetic adaptations to regional climate (chap. 5). Indeed, throughout western North America there are large numbers of individual trees over 700 years old (and individuals of bristle cone pine, *Pinus longaeva*, that are approaching 5,000 years old), meaning that in their lifetimes they have persisted through multiple major episodes of drought, cold, and other climate extremes. Even as climate changes in coming decades, it is likely to do so progressively, working with the materials at hand and using adaptive processes that are millions of years old.

Restoration or Reorganization?

These considerations prompt reevaluation of some basic restoration assumptions and goals. As ecological resilience emerges as a new guiding concept in restoration ecology, its primary application may be to focus on sustaining future options for flexibility and adaptation to changing conditions, rather than attempting to maintain static composition or structure based on past distributions (Millar and Stephenson 2015). In practice, rather than emphasizing only time-specific historical ranges or predisturbance species assemblages, compositions, structures, and landscape patterns, a resilience approach to restoration embraces landscape macrodynamics that have characterized populations and species over long timeframes. These include the ability of species to shift locations significantly, fragment into refugia, expand or contract in range, coalesce with formerly disjunct populations, foster nonequilibrium genetic diversities, form novel plant associations, and accommodate population extirpations and colonizations—all in response to changing regional conditions. The question for restoration ecology thus becomes not if these changes will occur, but whether the restoration response will be to resist, stand back and watch, or facilitate such change (fig. 17-7).

Assisted migration (AM) exemplifies new, strategic responses that have been proposed to maintain biological diversity through a period of climate change (Stone 2010). As the literature summarized earlier demonstrates, all species move in space and time throughout their ecological and evolutionary history, often in response to shifting climate. However, several factors raise concerns that the ability of many species to migrate in response to changing climate may be constrained under contemporary conditions. The first of these is the sheer pace of climatic change (IPCC 2014a). Depending on the rate of change (and recalling that mean temperature is only one of many climate dimensions), many species may not be able to migrate quickly enough on their own (fig. 17-8). Many other factors complicate this equation, especially landscape barriers to species movement (large multilane highways), natural and anthropogenic habitat fragmentation and degradation, absence of biotic dispersal vectors, and increased competition from nonnative species (Wilcove 2008; Vitt et al. 2010).

An intense debate surrounds the AM option, also referred to as assisted colonization and managed relocation (McLachlan et al. 2007). Objections to its use as "ecological gambling" (Ricciardi and Simberloff 2009) include concerns for inadvertently introducing species that could become locally invasive, displacing native biota, as has occurred multiple times with introductions to islands; lack of essential symbionts (such as pollinators or food plants) in the new location; contamination of locally-adapted gene pools; and the sheer number of species that may require assistance on a global scale, not to mention the high probability of failure. More conservative variations on AM include *facilitated migration*, in which habitat and migratory pathways are protected and restored to allow species populations to adjust on their own, a "build it and they will come" approach (Pearson and Dawson 2005; McLachlan et al. 2007). AM is being used as a forestry option, with extensive provenance adaptation trials in Canada and elsewhere (Pedlar et al. 2012).

Closing Remarks

The reality of global warming has raised much concern in the restoration and conservation communities. As we now understand, this is not something coming in the future, but something ecosystems are already experiencing. Abrupt climate change and vegetation response have been common in Earth's history, but it is an open question whether the pace and magnitude of change expected in the climate system in the next century exceed those of the ecologically relevant past. 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 appear catastrophic but may also be expressions of landscape-scale resilience and realignment to changing external forces.

Accommodating the realities of climate change will require rethinking our concepts about what and where native habitat is, what "healthy" communities are, and when changes in species ranges are acceptable and appropriate. These are unfamiliar and even uncomfortable questions for restoration ecology. Society may choose not to accept such consequences and manage instead for conditions based on past climates. In such cases we will have to consider that our management and conservation efforts may run counter to natural process, and thus restoration efforts may require continuing manipulative input to maintain desired conditions and the potential for sustainability (chap. 1, table 1-1) (Palmer and Ruhl 2015). For example, society (through land managers) may choose to maintain iconic species such as giant sequoia even where its climate envelope is shifting away from the current population location. The lessons implied from paleoclimatology and paleoecology suggest that making peace with physical and ecological change is

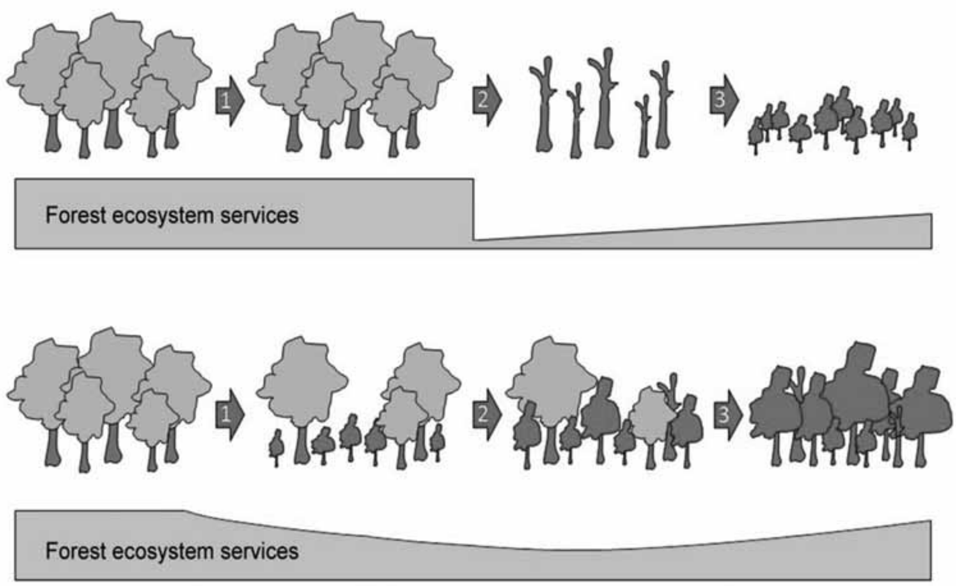


Figure 17-7. Management practices can influence the nature of transitions between forest types. Numbers represent forest transitions through time. *Top panel*: (1) Despite rapid directional environmental changes, managers strive to maintain forests within historical ranges of conditions and may initially succeed. (2) The forest may be more vulnerable to drought or wildfire in the new climate regime; once a threshold is exceeded, substantial mortality occurs, with an abrupt loss of ecosystem services. (3) After dieback, recovery of forest ecosystem is slow, and predisturbance forest structure may not be achieved. *Bottom panel*: (1) Managers anticipate and facilitate an impending forest transition by reducing the probability of sudden dieback (e.g., thinning to reduce competition for water and mitigate fire behavior) and by assisting establishment of species or genotypes better adapted to future conditions. (2) The transition is gradual rather than abrupt, and ecosystem services are maintained. (3) Forest ecosystem services are maintained closer to original levels, although species composition has shifted. Although some services are eventually lost in both cases, active management facilitates a gradual rather than abrupt transition. Modified from Millar and Stephenson (2015).

an important prerequisite to effective stewardship. Incorporating these ideas into new restoration ecology science and practice will require considerable difficult thought, discussion, experimentation, and research in coming years.

Such conclusions suggest that a rethinking of traditional concepts of sustainability and restoration targets is essential. We are challenged now to 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 (Foley et al. 2005; Hobbs and Suding 2009). The capacity for populations to grow, decline, migrate, and colonize has determined species survival during past periods of rapid change. Holding species and communities hostage to

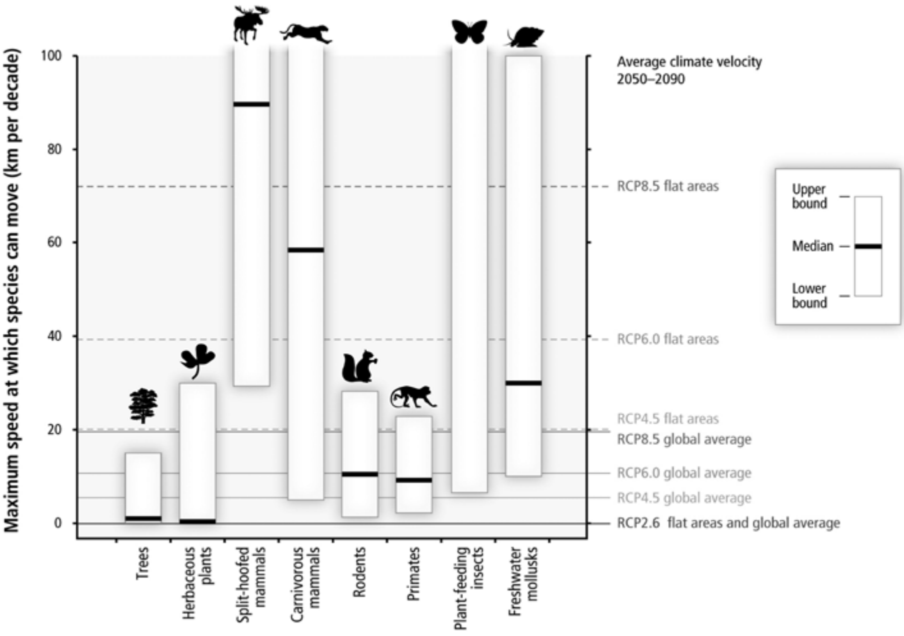


Figure 17-8. The average "climate velocity" in the late twenty-first century may exceed the maximum documented rate at which species can migrate across landscapes by natural processes. Climate velocity is higher in flat terrain than in more complex topography due to the lack of elevational diversity, which can absorb some of the poleward movement of climate envelopes. Some organism groups, such as large mammals, flighted insects, and freshwater mollusks may have sufficient migratory potential to match climate velocity, whereas others (most plants, smaller mammals) may not be able to keep up. Figure from IPCC (2014a).

specific locations and conditions may be both challenging and unproductive in a rapidly changing world. In some cases, it may be necessary to make the difficult choice to step away from a traditional restoration paradigm and find new models (Hobbs et al. 2015). Understanding that species have coped with change in the past suggests that restoration sciences have more important opportunities to help species cope with the dynamics of the current world.

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