

Responses of plant populations and communities to environmental changes of the late Quaternary

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Abstract.—The environmental and biotic history of the late Quaternary represents a critical junction between ecology, global change studies, and pre-Quaternary paleobiology. Late Quaternary records indicate the modes and mechanisms of environmental variation and biotic responses at timescales of 10^1 – 10^4 years. Climatic changes of the late Quaternary have occurred continuously across a wide range of temporal scales, with the magnitude of change generally increasing with time span. Responses of terrestrial plant populations have ranged from tolerance in situ to moderate shifts in habitat to migration and/or extinction, depending on magnitudes and rates of environmental change. Species assemblages have been disaggregated and recombined, forming a changing array of vegetation patterns on the landscape. These patterns of change are characteristic of terrestrial plants and animals but may not be representative of all other life-forms or habitats. Complexity of response, particularly extent of species recombination, depends in part on the nature of the underlying environmental gradients and how they change through time. Environmental gradients in certain habitats may change in relatively simple fashion, allowing long-term persistence of species associations and spatial patterns. Consideration of late Quaternary climatic changes indicates that both the rate and magnitude of climatic changes anticipated for the coming century are unprecedented, presenting unique challenges to the biota of the planet.

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Introduction

The environmental history of the late Quaternary represents a critical bridge between ecology and pre-Quaternary paleobiology. Sites with records of past biota and climate spanning the last 25,000 years are distributed across the globe, and those records can be dated with high precision (10^0 – 10^3 years) using ^{14}C , U/Th, dendrochronology, varve chronology, and other methods. Thus, local to global patterns can be observed at timescales of 10^1 – 10^3 years. No other period in geological history permits observation of contemporaneous events and spatial patterns of temporal change at such timescales across such a wide range of spatial scales. Late Quaternary pollen and macrofossil assemblages have been studied from thousands of sites worldwide, and ecological knowledge of the species represented in the fossil record and taphonomic knowledge of relationships between modern and fossil assemblages underpin their interpretation. Records of past biota can be dated independently and compared with indepen-

dent records of environmental change from ice cores, marine sediments, tree rings, and many other sources.

Environmental changes of the past 25,000 years are superimposed upon longer-term and higher-magnitude changes during the entire Quaternary (Bartlein 1997; Bradley 1999), which are in turn embedded in trends of even higher magnitude spanning the Cenozoic (McDowell et al. 1990; Crowley and North 1991; Parrish 1998). The late Quaternary record does not encompass all of the dynamics of the earth's climatic or biotic systems. Nonetheless, the spatial and temporal detail of the record, together with the ability to connect past phenomena with ongoing, observable environmental processes and biological patterns, renders the late Quaternary a rich source of models, hypotheses, and exemplars for pre-Quaternary paleobiologists (Valentine and Jablonski 1993; Jablonski and Sepkoski 1996; Roy et al. 1996).

Modern ecological patterns and processes are superimposed on late Quaternary dynam-

ics. Ecologists and resource managers are recognizing that environmental variability at timescales of 10^1 – 10^4 years plays a major role in governing spatial patterns and temporal dynamics of populations, communities, and ecosystems (Swetnam and Betancourt 1998; Parsons et al. 1999). Furthermore, the magnitude of climatic change during the past 25,000 years matches the magnitude of predicted climate change over the next few centuries (Overpeck et al. 1991; Wright et al. 1993; Houghton et al. 1996), so late Quaternary records provide contexts for assessing biotic response to global change and for developing ecological management strategies in the face of environmental change, whether natural or anthropogenic (Hunter et al. 1988; Davis 1990; Huntley 1990d, 1999; Overpeck et al. 1991; Webb 1992; Overpeck 1993; Huntley et al. 1997).

In this paper, we discuss responses of terrestrial plant populations and communities to environmental changes of the late Quaternary. First, we present a conceptual scheme showing expected responses of plant species and communities to environmental changes. Our conceptual model, based on ecological niche theory, builds on some ideas presented by Good (1931) and Webb (1987, 1988), and parallels recent conceptual schemes of Huntley (1996, 1999). Second, we discuss the multivariate nature of climatic change, using insights from climate modeling and paleoclimate studies. Third, we review the broad spectrum of population responses and the narrow spectrum of community responses to environmental changes of the late Quaternary. In that review, we emphasize examples from North America and Europe, which are the best-studied parts of the globe. We then discuss whether the patterns observed in terrestrial plant populations and communities can be generalized to other organisms and habitats, speculate on evolutionary responses of niches, and briefly note implications for ongoing and future climate changes.

A Conceptual Model of Biotic Response to Environmental Variation

Ecological Niche Theory and the Nature of Environmental Space

Ecological niche theory is central to understanding how environmental change affects

species abundance patterns. However, modern niche theory is inadequate for understanding the responses of plant populations and communities to environmental changes characteristic of the late Quaternary. Hutchinson (1958, 1978) conceived of the niche as a multidimensional conceptual space whose n dimensions are defined by the environmental factors¹ that influence fitness of individuals of a species (Appendix). Most discussions of niche theory implicitly assume that sites exist in the natural world that correspond to all possible combinations of niche variables (but see Austin 1990, 1992). Hutchinson (1958) noted possible exceptions but did not explore their implications. As Griesemer (1992) has observed, Hutchinson's conception of the niche is static and overlooks temporal changes in environment and population response. Environmental change, however, involves emergence and disappearance of combinations of niche variables.

The *fundamental niche* of a species comprises a subset of the *environmental space* defined by the n dimensions, consisting of the suite of combinations of variables that permit survival and reproduction of individuals (Hutchinson 1978). Maguire (1973) noted that the fundamental niche could be envisioned as a fitness response-surface, with an outer boundary delineating the absolute limit of population viability, and inner contours representing increasing fitness. In classical niche theory, the actual niche space occupied by a species comprises a subset of the fundamental niche. This subset, the *realized niche*, is constrained by biotic factors, which may prevent individuals of a species from occupying part of its fundamental niche. The realized niche can be portrayed as a response-surface of population density or biomass (Bartlein et al. 1986; Austin et al. 1990, 1997).

Large portions of environmental space are

¹ These factors include resources consumed by individuals and nonresource factors that affect individuals. We focus on nonresource factors, defining the niche similar to the *requirement niche* of Leibold (1996), and roughly equivalent to the *habitat hyperspace* (Whittaker et al. 1973), the *scenopoetic niche* (Hutchinson 1978), the *Grinnellian niche* (James et al. 1984), and the *environmental niche* (Austin et al. 1990, 1997).

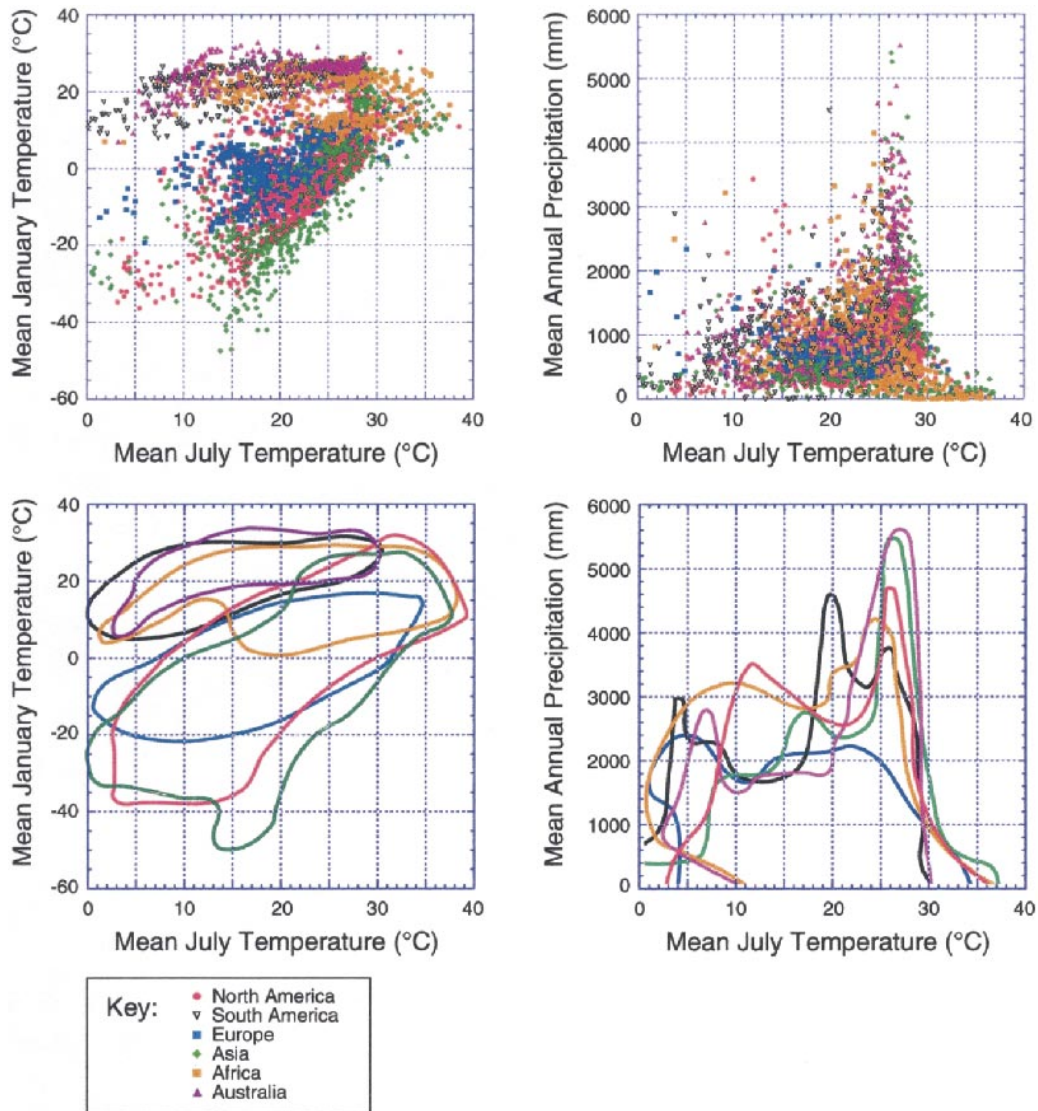


FIGURE 1. Summary climate space for Earth's major vegetated continents. The point clouds (upper graphs) represent the particular observed combinations of mean July temperature, mean January temperature, and mean annual precipitation that were realized at 8516 climate stations (Vose et al. 1992) on six continents in the late twentieth century (averaged for the period 1951 to 1980). The station counts for each continent are: North America (3364), South America (776), Europe (864), Asia (1010), Africa (1665), and Australia (837). Lower graphs show generalized outlines of the climate space for each continent as defined by the point clouds.

empty (i.e., unrepresented in the realized world) at any given time, and temporal environmental change inevitably leads to portions of environmental space alternating between empty and full. Empty environmental space arises for two reasons. First, many niche variables covary. For example, summer and winter temperatures are positively correlated for each continent (Fig. 1 top left). Summer temperature and annual precipitation do not occur

in all possible combinations (Fig. 1 top right). Second, spatial heterogeneities imposed by geology, topography, and other factors dictate that not all combinations of variables can occur. For example, serpentine outcrops do not occur in midcontinental North America, and therefore much of the environmental space defined by three variables—soil [Ni], summer temperature, and annual precipitation—does not exist in North America.

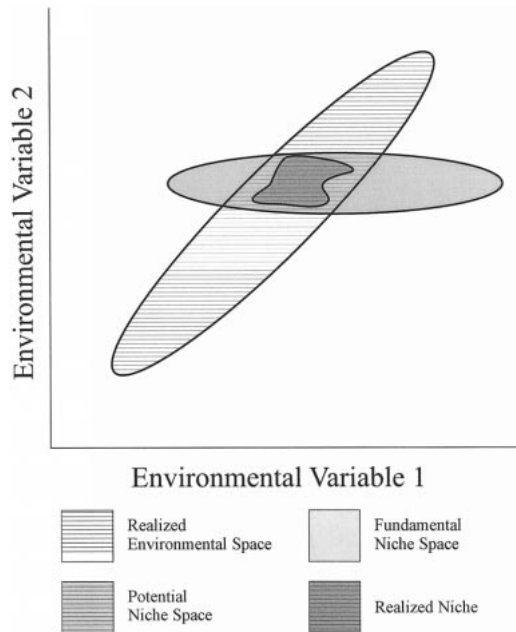


FIGURE 2. Fundamental, potential, and realized niches of a species in response to two environmental variables. The realized environmental space comprises the particular combinations of the two environmental variables that exist at a particular time. The fundamental niche space is the tolerance or survival envelope for a species within the entire environmental space defined by the two variables. Some portion of the fundamental niche space may lie outside the realized environmental space at a particular time. The intersection between the fundamental niche space and the realized environmental space defines the potential niche space, which comprises the portion of the realized environmental space within which the species can survive and reproduce. The potential niche depends on the position of the realized environmental space at a given time. The realized niche, the portion of environmental space in which populations of the species actually occur, is a subset of the potential niche, constrained by biotic and other factors.

The existence of empty environmental space constrains niche shape and size (Fig. 2). A finite set of combinations of the n variables relevant to a species will exist at any given time. The particular realization of environmental conditions that occur in nature at a particular time is the *realized environmental space*. We term the intersection of the fundamental niche with the realized environmental space at a particular time the *potential niche* for that time (Fig. 2).

To summarize, the fundamental niche represents the response of a species to all possible combinations of all environmental variables.

The potential niche is a subset of the fundamental niche, comprising the portion of the fundamental niche that corresponds to realized combinations of the environmental variables at a given time. If those realizations change as a consequence of environmental change, the potential niche will change in shape, size, and/or position in environmental space. Finally, the realized niche comprises a subset of the potential niche, owing to constraints imposed by biotic processes, which include not only competition, consumption, and mutualism, but also dispersal and colonization.

Environmental Change and the Nomadic Niche

Some niche variables, especially those controlled by bedrock composition, are spatially constrained—i.e., particular values occur at fixed locations that are not likely to change at timescales less than 10^4 – 10^6 years. However, other variables, especially those influenced or controlled by atmospheric conditions, can shift spatially. This, of course, occurs seasonally as temperature isotherms are displaced latitudinally and temperature gradients are steepened or expanded. Such displacements and gradient alterations are characteristic of climatic change at interannual and greater temporal scales.

The realized environmental space can change in a variety of ways, depending on the relationships between environmental variables and how those variables change (Fig. 3). For two uncorrelated variables, one variable might change while the other remained constant (Fig. 3A) (e.g., [Ni] and summer temperature). Two positively correlated variables might change in concert—for example, summer and winter temperatures might both increase by the same amount at all sites (Fig. 3B). Alternatively, one variable might change while the other remained constant, resulting in a lateral shift in the point cloud (Fig. 3C). Positively correlated environmental variables might also change in opposite directions (Fig. 3D). For example, summer temperatures might increase while winter temperatures decreased. At any given time, these variables are positively correlated along latitudinal and ele-

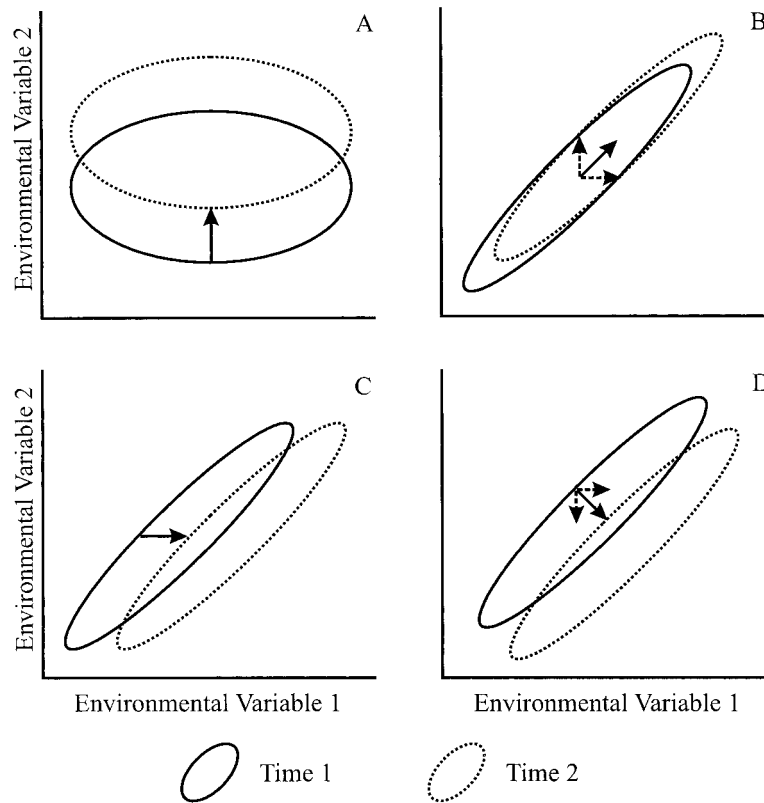


FIGURE 3. How realized environmental space can change through time. For uncorrelated variables, one variable may change while the other remains constant (A), or both variables may change independently. Correlated variables (B–D) can change in a variety of ways. Both variables can change in the same direction (B), one variable can change while the other remains constant (C), or one variable can increase in value while the other decreases (D).

vational gradients. However, they are under different controls (summer and winter insolation) that do not necessarily operate in concert; summer insolation can increase while winter insolation decreases, and vice versa (Berger and Loutre 1991).

Changes in position of the realized environmental space result from changes in the values of the environmental variables at specific locations in geographic space. Individual organisms are faced with one of two potential qualitative responses. First, at sites where the environmental change stays within the fundamental niche, individuals can persist at the site (*a* in Fig. 4), though they may change in abundance. Second, at sites where the change goes beyond the species' environmental tolerance, the population will undergo local extinction (*b* in Fig. 4). However, environmental change may also create opportunities for col-

onization of previously unsuitable sites (*c* in Fig. 4). Those new sites may be 10^1 – 10^2 m from previously occupied sites (e.g., along local soil-moisture or elevational gradients), or many kilometers away.

Necessary conditions for survival of a species in the face of environmental change are that (1) it continues to have a potential niche in the realized world (i.e., an intersection between the realized environmental space and its fundamental niche) and (2) it is capable of dispersing propagules at a sufficient rate and over sufficient distances to occupy suitable sites during times of environmental change. The first condition will depend on the magnitude of environmental change as well as the size and shape of the fundamental niche, while the second will depend on the rate of environmental change and the reproductive and dispersal capacity of the species.

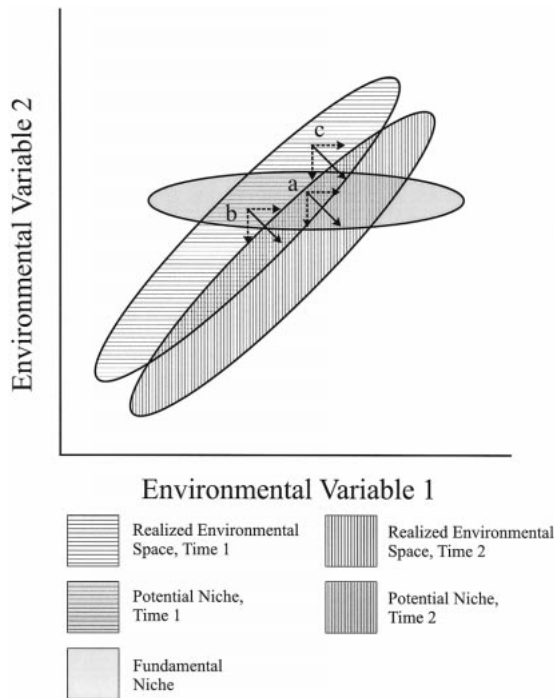


FIGURE 4. How environmental change can affect a species population at a site. Vectors represent the direction and magnitude of change at individual sites within the environmental space. In all cases, Environmental Variable 1 increases while Environmental Variable 2 decreases; solid vector shows net change in both variables at the site. If the environment changes, but a particular site remains within the potential niche space of a species, the population can remain in place (a). However, if a site moves out of the potential niche of a species, the population at that site will undergo extinction (b). New sites may move into the potential niche space of the species (c), creating opportunities for colonization.

Nomadic Niches and Contingent Communities

Species differ in their fundamental niches, and different species respond to different environmental variables. Consequently, particular species combinations may appear and disappear as the environment changes (Fig. 5). A particular ecological community can exist only in that portion of environmental space where fundamental niches of all its constituent species overlap. In general, a particular species association will occupy a smaller portion of realized environmental space than any of its constituent species. Put another way, the amplitude of environmental change that will allow survival of a particular species will tend to be much greater than the amplitude of var-

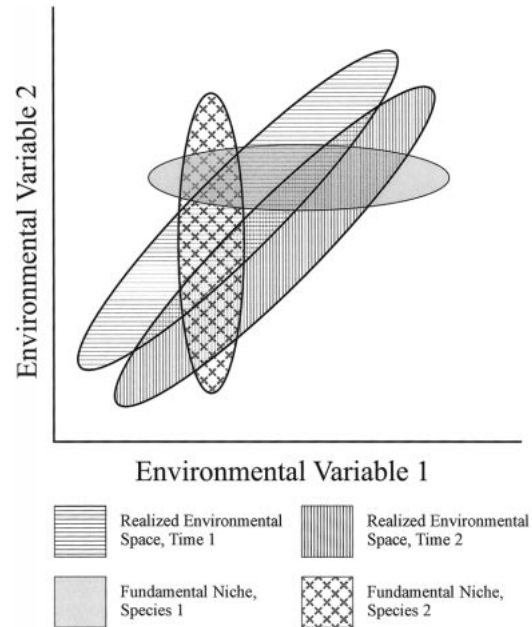


FIGURE 5. How environmental change can affect species associations. At Time 1, the potential niches of species 1 and 2 overlap, and hence the species can potentially coexist at sites within that intersection. At Time 2, the potential niches of the two species do not overlap, and hence the species will not coexist in the realized world.

iation that will allow continued realization of a particular collection of species (Fig. 5).

This model predicts not only that environmental change will alter composition of ecological communities, but also that it can alter the sequence of species arrayed along spatial gradients (Fig. 6). Different species combinations may arise along a spatial gradient, and species may even reverse positions along the gradient as the environment changes (Fig. 6).

The Nature of Environmental Change

Climate Change: A Redundant Expression

Recent advances in paleoclimatology have demonstrated that climate changes continually on all timescales (Overpeck 1995; Parrish 1998; Bradley 1999), and hence the term "climate change" is redundant—climate is always changing. High-resolution studies indicate significant shifts in atmospheric circulation patterns at annual to decadal scales during the last two centuries (Martinson et al. 1995; Diaz and Markgraf 2000), and changes in climate are recognized at progressively expanding

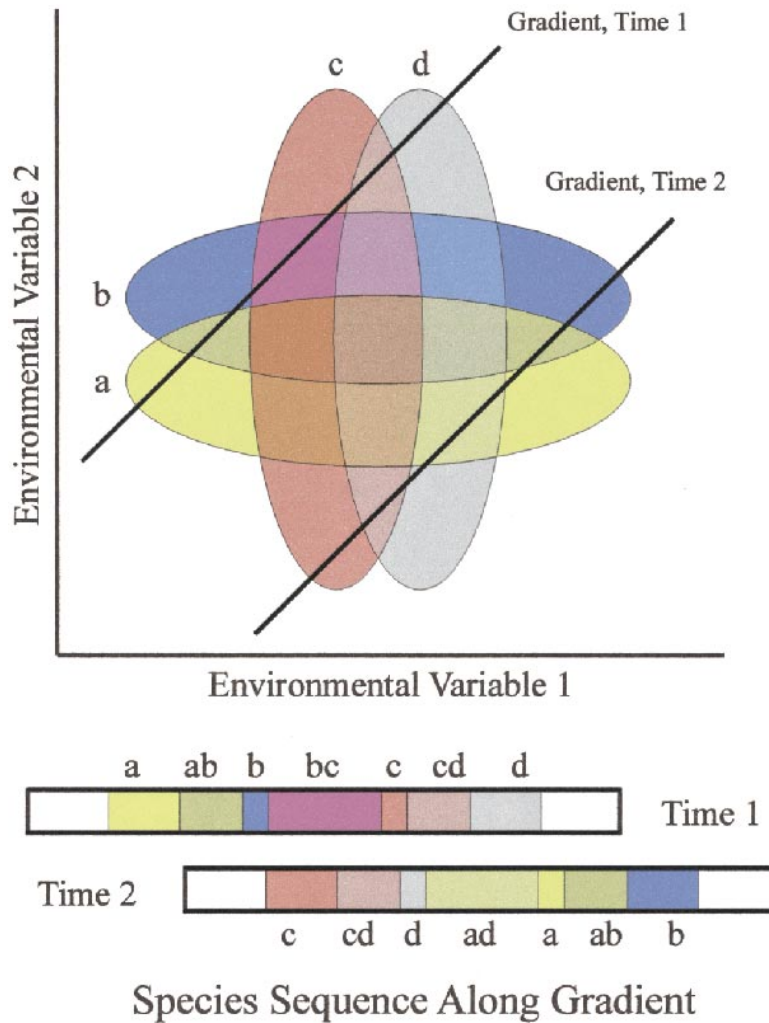


FIGURE 6. How environmental change can influence patterns of species and communities along environmental gradients. Ovals represent fundamental niches of four species (*a-d*). The diagonal lines represent a spatial gradient at two different times. For example, the gradient might be an elevational or latitudinal transect, with Environmental Variables 1 and 2 respectively representing summer and winter temperatures. Lower part of figure shows species sequence projected along the gradients. Vegetational transects along the spatial gradient would yield a different array of species associations (e.g., *b* and *c* co-occur at Time 1 but not at Time 2, whereas *a* and *d* co-occur only at Time 2). Furthermore, the sequence of species encountered along the gradient might shift. For example, in a latitudinal gradient, species *a* would be north of species *d* at Time 1, while species *d* would be north of species *a* at Time 2.

timescales, from centuries (Bradley and Jones 1992; Woodhouse and Overpeck 1998) to millennia (Wright et al. 1993) and beyond (Crowley and North 1991; Parrish 1998). In general, the magnitude of change increases with the timescale considered (e.g., Bradley 1999: Fig. 2.14). The regional climates represented by instrumental observations are just a snapshot of an ever-changing continuum, and also just a

subset of the possible range of future climate change. The shape of Earth's realized environmental space is continually changing.

Climate Forcing and the Ever-Changing Shape of the Realized Climate Hyperspace

Paleoclimatology was revolutionized by the demonstration that climate variability at glacial-interglacial scales (10^4 – 10^5 years) is paced

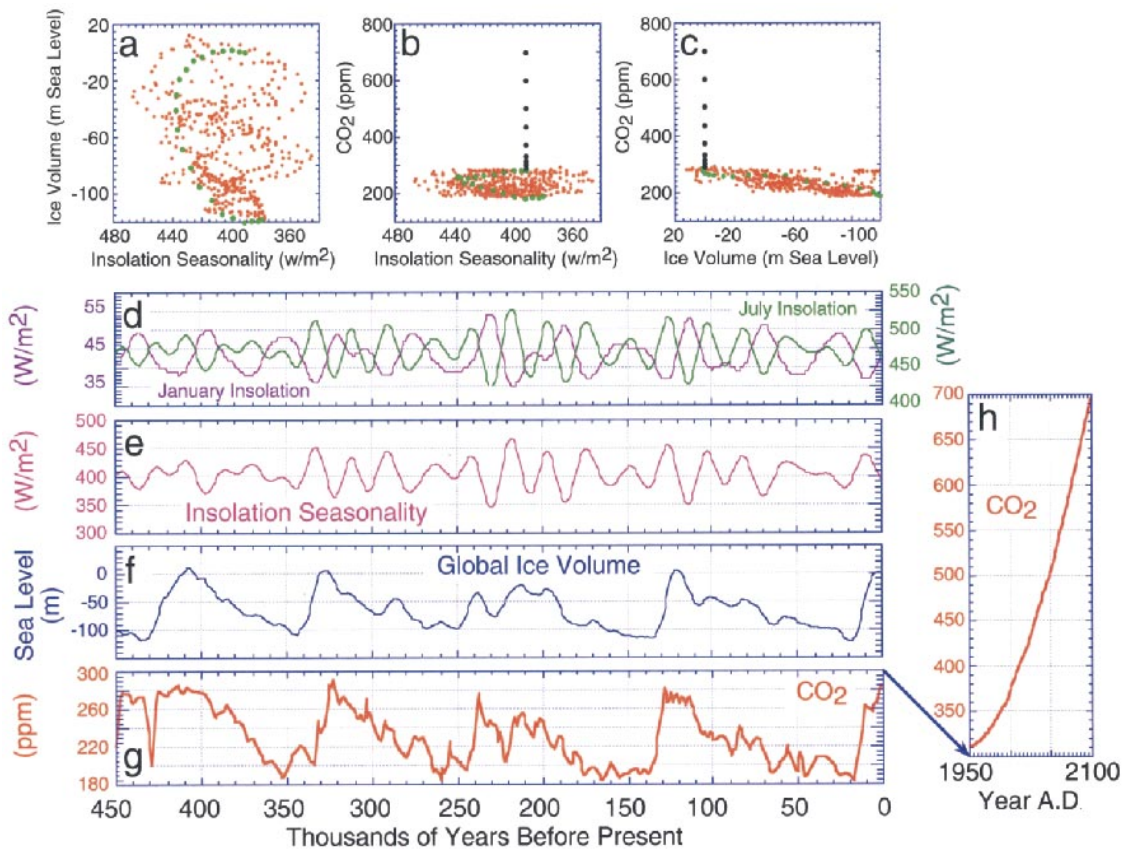


FIGURE 7. Major climate forcing for the last 450,000 years (observed at 1000-year intervals to 1950), and for the period 1850 to 2100 (observed and projected at 25-year intervals). Scatter plots (A–C) and time series (D–H) of glacial ice volume (in meters of sea-level equivalent, see below), insolation at the top of the atmosphere (January, July, and July minus January [“seasonality”], all calculated for 60°N [Berger and Loutre 1991]), and atmospheric CO₂ concentration (Etheridge et al. 1996; Houghton et al. 1996; Petit et al. 1999; Robertson et al. 2000). Note that CO₂ levels projected for the next century (red line in H, and black dots in A–C) (Houghton et al. 1996) are plotted versus years A.D. rather than B.P. Glacial ice volumes were obtained using the global-average deep-water (“benthic”) $\delta^{18}\text{O}$ (Imbrie et al. 1992) scaled to a 20,000 years B.P. (glacial) to present (interglacial) sea-level amplitude equal to the observed value of 120 m (Fairbanks 1989). The trajectory (sensu Bartlein 1997) of climate forcing over the last 21,000 years is displayed as green dots (A–C). Whereas atmospheric trace gas (e.g., CO₂) levels are expected to increase dramatically to unprecedented levels in the next century (A–C, H), both insolation and global sea level are not likely to change much relative to recent geologic variations. An interactive 3-D view of climate forcing over the period 450,000 years ago to A.D. 2100 can be viewed on the worldwide web at: <http://www.ngdc.noaa.gov/paleo/class/javatest/solidtest/SolidTest.html>

by variations in Earth’s orbital geometry (Hays et al. 1976; Imbrie et al. 1992, 1993). Gravitational influences of other planets in the solar system cause long-term variations in eccentricity of Earth’s orbit, precession of the equinoxes, and tilt of Earth’s rotational axis. These Milankovitch variations have been calculated for the past several million years, and can be quantified in terms of insolation at the top of the atmosphere as a function of year, season, and latitude (Fig. 7) (Berger and Lou-

tre 1991). Their net effect is to alter the seasonal and latitudinal distribution of insolation, which in turn causes changes in atmospheric circulation patterns, including changes in seasonal and geographic patterns of temperature, precipitation, and other climate variables (Fig. 8) (Kutzbach and Webb 1991, 1993; Kutzbach et al. 1993, 1998; Bartlein et al. 1998).

The COHMAP (Cooperative Holocene Mapping Project) Group provided another

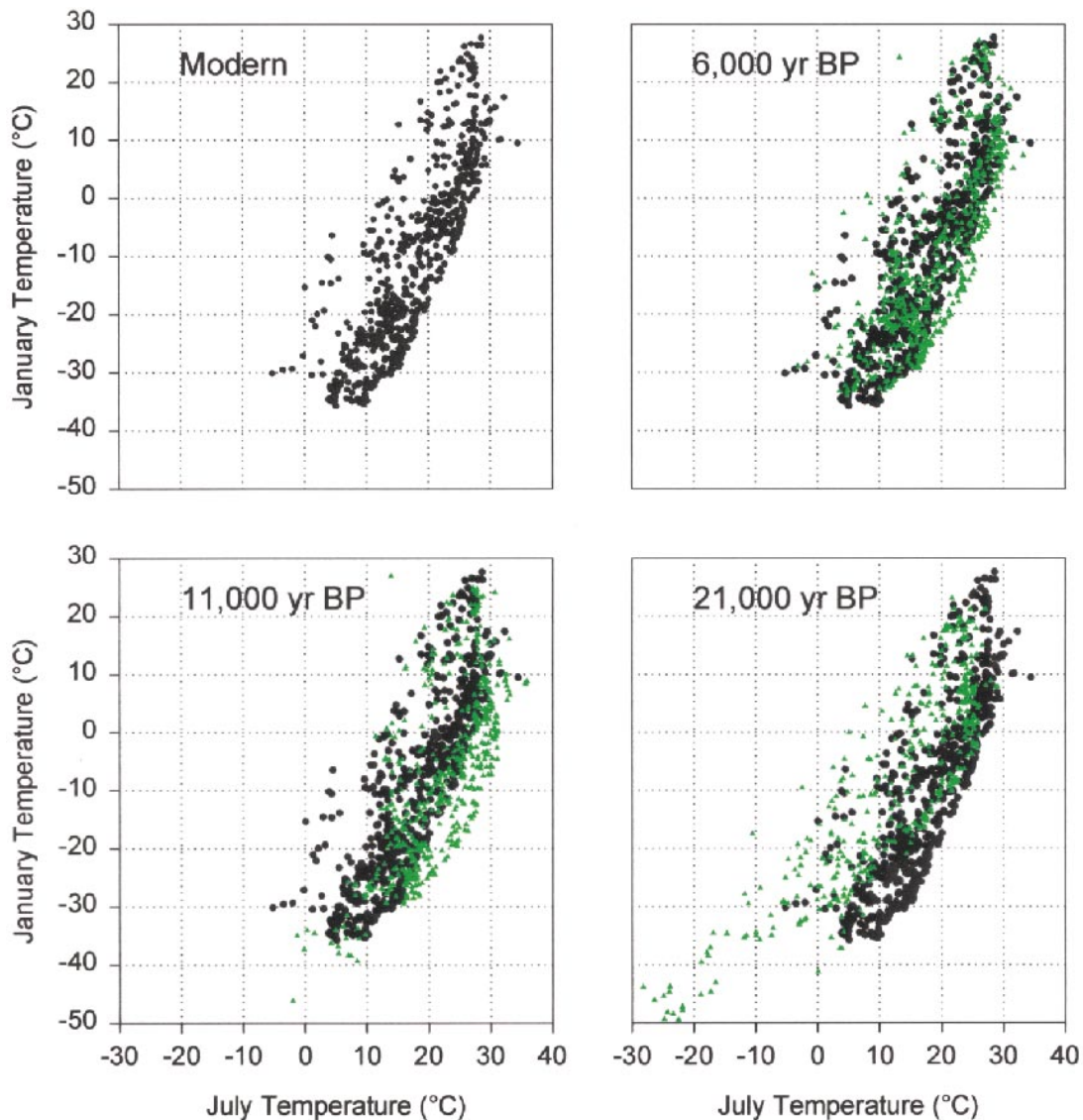


FIGURE 8. Simulated changes in the realized environmental space of North America (Canada, United States, Mexico) since the Last Glacial Maximum. Modern January and July temperatures (black circles) are from a 25-km equal-area grid based on >8000 modern climate stations (Thompson et al. 1999). Simulated January and July temperatures for 6000, 11,000, and 21,000 years B.P. (green triangles) are from NCAR CCM1 simulations (Kutzbach et al. 1998). We used the data of Bartlein et al. (1998), in which anomalies (paleoclimate simulation minus modern control simulation) were applied to the 25-km grid of modern climate data. Because of the size of the data sets (22,690 to 23,839 points), we plotted 2% of the values for each time period, selected at random, to give a representation of the scatter patterns. The contrasting scatter patterns indicate the extent of simulated change in the shape, position, and orientation of the realized environmental space as defined by these two variables under different forcings of the last 21,000 years. The time periods differ in orbital forcing, ice-sheet extent, and atmospheric CO_2 concentration (Kutzbach et al. 1998).

key advance, detailing how the earth's climate system (broadly defined to include the atmosphere, oceans, biosphere, and cryosphere) evolved through the last glacial cycle in response to Milankovitch forcing and changes

in continental ice sheets (COHMAP 1988; Wright et al. 1993). Key lessons of the COHMAP effort and modern climate theory are that climate is multivariate and that biologically relevant climate variables may change

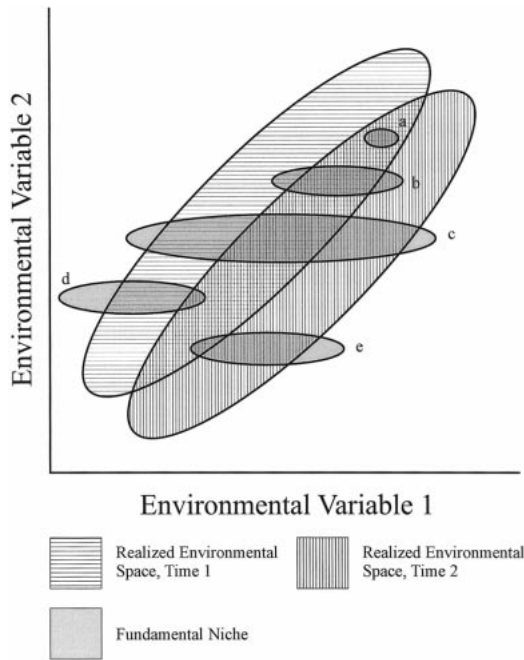


FIGURE 9. Modes of population response to environmental change. Species a: Mode 1 (populations stay in place). Species b: Modes 1 and 2 (populations shift along local habitat gradients). Species c: Modes 1, 2, and 3 (populations migrate to distant, newly suitable sites and disappear from some former sites). Species d: Modes 1 and 4 (widespread extirpation without colonization of new territory). In this case a formerly widespread species becomes restricted in geographic range and habitat. Species e: Inverse of species d: A formerly rare species colonizes extensive new territory.

independently. For instance, summer and winter insolation vary independently in response to orbital forcing (Fig. 7) (Berger and Loutre 1991). From 14,000 to 6000 years ago², high-latitude Northern Hemisphere summer insolation was up to 9% higher than today, while winter insolation was up to 15% lower (Fig. 7) (see also COHMAP 1988: Fig. 2). Thus, summer and winter temperatures, although positively correlated along geographic gradients, changed in opposite directions in many

² Late Quaternary timescales are complicated by long-term variations in atmospheric ¹⁴C concentrations; ¹⁴C-based age estimates do not correspond precisely to calendar years. Calibrations between ¹⁴C chronologies and calendar-year chronologies have been developed based on dendrochronology, annually laminated sediments, and U/Th dating (Hughen et al. 1998; Bradley 1999). For example, the Last Glacial Maximum, dated at 18,000 ¹⁴C years B.P., is closer to 21,500 calendar years B.P. We use calendar-year ages except where noted.

regions during the Holocene (Fig. 8; cf. Fig. 3D). The mean values, variability, and seasonal patterns of the many biologically influential climatic variables have changed in complex ways, leading to continual changes in the realized environmental space.

In summary, climate is a dynamic system, the global climate system is always on its way elsewhere, and the particular realization of the climate hyperspace at any given time rarely repeats any previous realization (Fig. 7). For example, climates from one glacial or interglacial period do not represent analogues for previous or succeeding glacials and interglacials (Watts 1988; Imbrie et al. 1992, 1993; Webb et al 1993). The major forcing elements were different in each case (Fig. 7), and hence each interglacial, glacial, stadial, and interstadial period has differed in important respects from others. Each point in time represents a unique set of climate gradients and combinations of gradients. Atmospheric CO₂ concentration, which not only influences climate but is an environmental variable directly affecting plant ecophysiology, has also varied substantially at these timescales (Fig. 7), as have other climatically influential variables (other trace gases, stratospheric [volcanic] aerosols, tropospheric aerosols [e.g., dust]).

Case Studies from the Late Quaternary

Modes of Biotic Response to Environmental Change

Environmental change exerts its influence directly on individual organisms at the sites where they live. As noted earlier, the environment of a site may remain within the fundamental niche of a species, so individuals can continue to live and reproduce there. The local environment may pass out of the fundamental niche, leading to extirpation via mortality or lack of recruitment. And other sites may pass into the fundamental niche, so individuals can colonize if propagules reach the sites. Depending on the nature, magnitude, and rate of the environmental changes, these site-specific processes are manifested at coarser spatial scales as a spectrum of patterns. We have, somewhat arbitrarily, classified this spectrum into four distinct response modes (Fig. 9).

Mode 1: Populations continue to occupy the same sites as before the change. *Mode 2:* Populations shift locally along habitat gradients (e.g., elevation, soil texture). *Mode 3:* Populations undergo migration, colonizing suitable territory 10^1 – 10^3 km from the origin, often disappearing from formerly occupied territory. *Mode 4:* Populations undergo local extinction while failing to colonize new territory, resulting in range contraction.

Each of these response modes has ecological, geographic, and evolutionary consequences for the species as a whole. The particular geographic range occupied by a species is a realization of local colonization and extinction processes and biotic interactions in the context of the spatial distribution of the species' potential niche. As a species migrates in response to spatial shifts in its potential niche, it may encounter new species (competitors, facilitators, consumers) and lose contact with others as it colonizes new and abandons old territory. Such properties as the total area occupied by a species, the total population size of the species, spatial structure (e.g., continuity versus patchiness), and genetic structure (e.g., diversity, gene flow, clinal variation, hybridization) will be governed or constrained by the outcome of the individual population responses. If population extinctions are unaccompanied by migrations, the species may undergo genetic bottlenecks or extinction. Evolutionary changes resulting from selection and genetic drift will accompany all of these response modes, although magnitude and rate will vary widely.

Each of these response modes can be applied to species associations as well. Conceivably, associations can remain intact in situ, they can shift position along local habitat gradients, they can migrate, or they can simply vanish entirely. We describe each of these responses in turn, noting examples (or lack thereof) from the Quaternary record for each.

Mode 1: Remaining in Place

Species Populations.—Individual plants, particularly long-lived perennials, often tolerate environmental variation at timescales of 10^0 – 10^3 years. Net photosynthesis, resource allocation, seed production, growth form, and or-

gan morphology may change, but the plants remain literally rooted in place unless the environmental change exceeds their capacity to adapt physiologically and morphologically. Such persistence of individuals is well known in the case of long-lived woody plants, but genets of some herbaceous and graminoid species may persist for hundreds to thousands of years (e.g., Steinger et al. 1996). Similarly, populations of a species may persist at a site for many generations. Populations may change in density, age structure, size structure, and growth form as the environment changes, and they may undergo recruitment or mortality pulses in response to decade- and century-scale environmental variation (Swetnam and Betancourt 1998; Swetnam et al. 1999). They may also undergo evolutionary changes resulting from selection and from immigration of genotypes better suited to the local environment (Rehfeldt et al. 1999).

Some populations have occupied single sites over several millennia. *Choisya dumosa*, *Juniperus osteosperma*, and other species have grown at some sites in the southwestern United States since the Last Glacial Maximum (Thompson 1988; Nowak et al. 1994a; Betancourt et al. 2000). Several temperate tree species grew in the lower Mississippi Valley during the Last Glacial Maximum (Delcourt et al. 1980; Givens and Givens 1987; Jackson and Givens 1994) and still grow there today. However, these populations have experienced different climatic regimes and species associations and have likely changed in density, age structure, and genetic structure.

Even though these and other populations have persisted at some sites through entire glacial/interglacial cycles, geographic ranges have changed. For example, *Juniperus osteosperma* populations in western Nevada during the Last Glacial Maximum were at the northern limit of the species range (Nowak et al. 1994b). Populations at the site are now at the southwestern end of the range, which extends >1000 km to the northeast. Most plant species well documented in the fossil record have undergone geographic range shifts during the past 25,000 years.

Species Associations.—Modes of community response to decade- and century-scale envi-

ronmental change are poorly known. Ecological studies are based on permanent-plot monitoring, repeat photography, age-structure studies, and repeated floristic surveys, and interpretation is confounded by impacts of human activity and secondary succession. Studies in relatively undisturbed areas often show community stasis in a coarse sense (e.g., no species invasion or extirpation). However, many studies show changes in relative abundance of species, and wholesale conversion of vegetation physiognomy (e.g., grassland to woodland) has been documented. Several of these cases are attributable at least in part to climatic change (e.g., Weaver and Albertson 1936, 1944; Weaver 1954; Hastings and Turner 1965; Archer 1989).

Paleoecological studies of sites with relatively high spatial and/or temporal resolution provide records of vegetation dynamics at decade to century timescales before extensive human disturbance (Bernabo 1981; Campbell and McAndrews 1993; Foster and Zebryk 1993; Davis et al. 1994; Björkman and Bradshaw 1996; Clark et al. 1996; Laird et al. 1996). Interpretation can be hampered by coarse taxonomic resolution, spatial smoothing, and absence of independent records of climatic change at similar timescales. However, in cases where independent paleoclimate data are available, changes in vegetation correspond well to climatic changes. A singular exception is the mid-Holocene *Tsuga* decline in eastern North America, which is attributable to a pathogen outbreak (Davis 1981a; Allison et al. 1986; Bhiry and Filion 1996).

Persistence of particular species assemblages at individual sites for more than a few thousand years is rare. Pollen sequences typically show turnover in assemblage composition over periods greater than 2000–5000 years (Jacobson and Grimm 1986; Overpeck 1987; Overpeck et al. 1991, 1992; Foster and Zebryk 1993). Macrofossil data show that this turnover consists of not only changes in the relative abundance of plant taxa at the site but also invasion and extirpation of species (Thompson 1988, 1990; Nowak et al. 1994a; Baker et al. 1996; Jackson et al. 1997; Weng and Jackson 1999), even at sites where some species have persisted for longer periods.

The best examples of apparent community stasis are from montane forests dominated by a single species. For example, Ponderosa pine (*Pinus ponderosa*) forests have persisted for 10,000 years on the Kaibab Plateau of northern Arizona (Weng and Jackson 1999). Lodgepole pine (*P. contorta*) forests have occupied the Yellowstone Plateau of northwestern Wyoming for a similar period (Whitlock 1993). However, Holocene climate changes have forced changes in fire frequency and intensity within the lodgepole pine forests (Millspaugh et al. 2000), undoubtedly causing changes in emergent attributes such as stand density, standing crop, and understory composition. Subalpine forests in New York and New Hampshire have been dominated by balsam fir (*Abies balsamea*) throughout the Holocene, but disturbance regime and stand structure appear to have varied (Jackson 1989; Spear et al. 1994). In all these cases the forests were established in the early Holocene, replacing late-glacial tundra or spruce woodland.

Mode 2: Shifts along Local Habitat Gradients

Species Populations.—Species populations can respond to environmental changes by fine-scale adjustments in their site or habitat occupation within a region. Such shifts are documented at decade to century scales for woody species based on tree-ring demographic studies. Tree invasions of open areas are documented from demography of living populations (e.g., Archer 1989; Graumlich 1994; Hessler and Baker 1997; Mast et al. 1998), and tree-ring studies of dead wood in open areas reveal extirpation patterns (Szeicz and MacDonald 1995; Lloyd and Graumlich 1997). Comparison of aerial or ground photographs taken at different times document twentieth-century dynamics of tree lines (Mast et al. 1997) and other ecotones (Allen and Breshears 1998). Spatial shifts in individual species distributions can be very rapid (<5 yr) when climate episodes lead directly to adult mortality (Allen and Breshears 1998).

Holocene shifts of populations along local habitat gradients have been documented by paleoecological studies in many regions. Examples of shifts along elevational gradients are legion, and come from radiocarbon-dating

of dead wood above tree line (Luckman et al. 1993; Kullman 1995) and from elevational transects of lake cores (Gaudreau et al. 1989; Jackson 1989; Spear et al. 1994; Anderson 1996; Weng and Jackson 1999) and packrat-midden series (Betancourt 1990; Cole 1990; Thompson 1990; Nowak et al. 1994b). In general, the magnitude of elevational displacement increases with the time span considered. Studies along other environmental gradients (soil texture, soil chemistry, bedrock type) are fewer. In a now-classic study, Brubaker (1975) showed that mesic tree species colonized coarse-textured outwash soils during moist periods but were restricted to fine-textured soils during dry periods.

Species Associations.—Shifts of species associations along habitat gradients at decade to century timescales are not as well known as population shifts, especially for nonwoody species. Movement of woody species is individualistic, but invasion or retreat of woody plants (e.g., upper or lower tree line) may induce secondary environmental changes (e.g., ground-level insolation, soil temperature and moisture, soil chemistry) important to other plants. For example, twentieth-century expansion of juniper woodlands from thin, rocky soils onto deep-soiled slopes in Wyoming is accompanied by extirpation of many steppe/grassland species and invasion of forb and graminoid species better suited to the micro-environment created by the junipers (Wight and Fisser 1968; S. T. Jackson et al. unpublished data). In a sense, the juniper woodland association is moving in toto along the edaphic gradient, but the movement is driven by invasion of the dominant species.

Holocene shifts along habitat gradients have been generally nonzonal: the shifts do not involve displacement of vegetation zones but instead lead to recombined associations and new zonation patterns. For example, the current elevational zonation of montane forests in New York and New England runs from subalpine *Abies* forest downward through *Picea/Abies* forest into mixed conifer/hardwood forests (*Acer*, *Betula*, *Fagus*, *Tsuga*, *Pinus*). In the warmer mid-Holocene (8000–4000 years B.P.), several low-elevation species (*Betula allegheniensis*, *Pinus strobus*, *Tsuga canadensis*) grew as

much as 300 m higher than today (Jackson 1989; Spear et al. 1994). However, they graded upward directly into subalpine *Abies* forest; no intervening *Picea*-dominated forest existed before 3000 years B.P. (Jackson and Whitehead 1991; Spear et al. 1994). Elevational gradients in western North America show similar zonal reorganization (Thompson 1988; Betancourt 1990; Van Devender 1990).

Mode 3: Migration

Species Populations.—Late Quaternary shifts in geographic distributions of species have been discussed since the recognition of a “Glacial Epoch” and accompanying climatic changes (Lyell 1832; Forbes 1846; Gray 1858; Darwin 1859), and postglacial migration patterns and pathways were proposed long ago from phytogeographic patterns (e.g., Peattie 1922; Gleason 1923; Clements 1934). Pollen and macrofossil records now allow mapping of migration patterns at scales ranging from regional (Davis and Jacobson 1985; Gaudreau 1988; Woods and Davis 1989) to continental (Davis 1976; Huntley and Birks 1983; Webb 1988; Jackson et al. 1997).

Shifts in species distributions can involve two processes, colonization of previously unoccupied territory and extirpation in formerly occupied territory. Most discussions of migration have focused on patterns and dynamics at the advancing end (Gleason 1917, 1923; Davis 1976; Huntley and Webb 1989; Clark et al. 1998).

Colonization is a slow process, at least by human timescales. It proceeds by ecological processes (dispersal, establishment, population growth, reproduction) that can be studied directly, but the aggregate consequences of these processes for migration may take decades to centuries or more to be manifested. Mapping of pollen and macrofossil data indicates that spread of many species has been far more rapid than can be accounted for by mean seed-dispersal distances, so infrequent long-distance dispersal and colonization events must play critical roles (Clark 1998; Clark et al. 1998). Such events are rarely observed directly. Although some recent “alien” plant invasions are well documented, (e.g., Mack 1981, 1986), most of our knowledge of

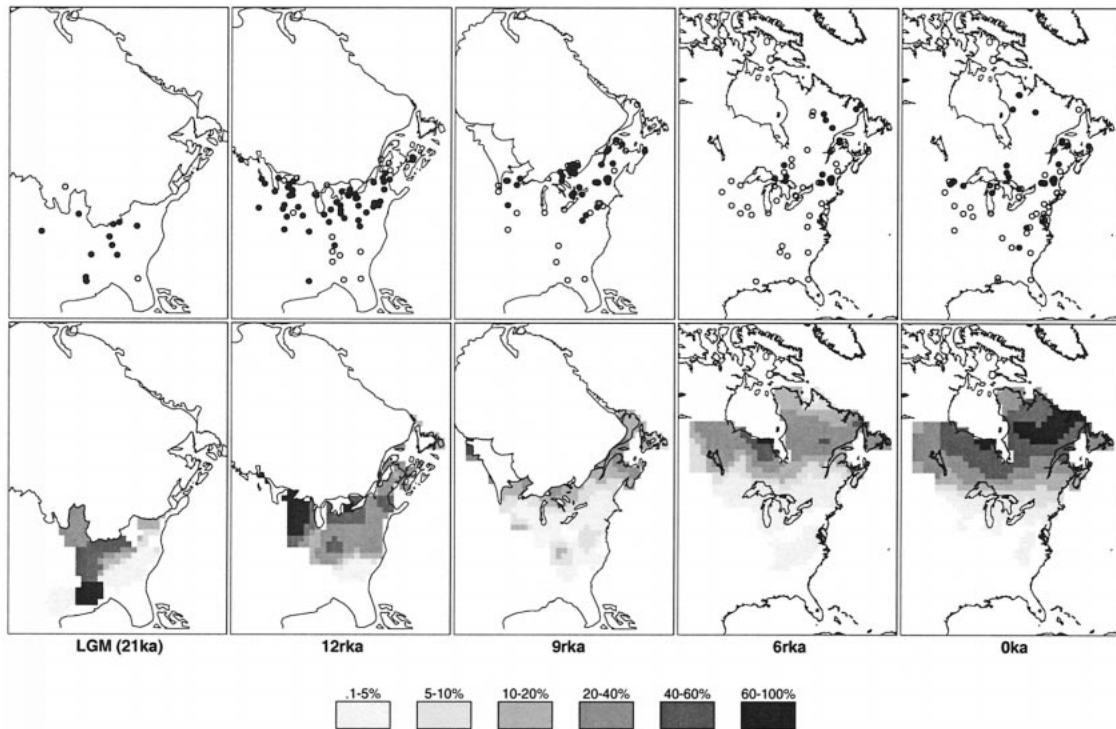


FIGURE 10. Changes in the geographic distribution and abundance of spruce (*Picea* spp.) in eastern North America since the Last Glacial Maximum (21,500 calendar years B.P., approximately 18,000 ^{14}C years B.P.), as shown by maps of macrofossil presence/absence (upper) and isopolls (lower). Closed circles in macrofossil maps denote sites where *Picea* macrofossils occurred at the specified time interval; open circles represent absence of *Picea* macrofossils. "rka" denotes 1000 ^{14}C years B.P. (6 rka \cong 6 Ka; 9rka \cong 11 Ka; 12 rka \cong 14 Ka). Modified from Jackson et al. 1997, 2000.

natural plant invasions comes from the paleoecological record.

Unfortunately, paleoecological data are ineffective at recording colonizing events and populations (Bennett 1985; Davis et al. 1991). Pollen data provide a distance-weighted integration of populations within 10–50 km of a basin and are better at showing approach and expansion of population masses than establishment and growth of individual populations. Macrofossil studies indicate that scattered populations of tree species can go unrecorded by pollen data for thousands of years (Kullman 1996, 1998a,b,c). Macrofossils constitute a finer-scale sensor but are spatially biased (toward lake margins for lake sediments and rock outcrops for packrat middens). Macrofossil data networks are usually not dense enough to record colonization patterns, with a few exceptions (Gear and Huntley 1991; Lyford et al. 2000).

Despite these limitations, the paleoecologi-

cal record provides some general lessons. Migrations spanning hundreds to thousands of kilometers have occurred throughout the last 25,000 years. Rare, long-distance dispersal events have played a key role (Betancourt et al. 1991; Clark et al. 1998). Dispersal across geographic barriers of ca. 100 km has occurred frequently (e.g., S. L. Webb 1987; Betancourt et al. 1991; Kullman 1996, 1998a,b,c). Migration rates vary in space and time (King and Herstrom 1997) and in some cases have been limited more by rate of climatic change than by biotic factors such as dispersal and establishment (Johnson and Webb 1989). Postglacial migration of *Picea* and other taxa onto deglaciated terrain in North America was limited only by the rate of ice retreat (Webb 1988; Jackson et al. 1997) (Fig. 10). The migrations not only consisted of range extensions but also involved shifts in population mass and density, and probably changes in genetic structure as well. Rapid migrations may have been accom-

panied at least temporarily by selection for more effective seed dispersal (Cwynar and MacDonald 1987), decrease in genetic diversity owing to multiple founder effects (Premoli et al. 1994), and escape from pathogens and herbivores.

Population declines or extirpations at the retreating end of a species migration, although little studied, are undoubtedly diverse in pattern, rate, and mechanism. Unfavorable environmental changes may be manifested in adult mortality, which can be gradual or episodic, or in recruitment decline via lowered seed production, germination, or survival. Climatic effects may be amplified by biotic factors (e.g., competition from indigenous or newly arrived species, increased susceptibility to pathogens or herbivores). Disturbances (fire, windthrow) can induce mortality and provide recruitment opportunities for other species (Clark et al. 1996; Weng and Jackson 1999). Population extirpation is likely to be patchy. Population susceptibility will track landscape-scale heterogeneity in environment, disturbance, and population size. Relict populations may persist in locally suitable habitats.

Paleoecological studies of population retreat face many of the same challenges of scale, lag, and resolution as for colonization. Pollen sequences record regional population declines effectively, but population fragmentation and disappearance are harder to document owing to spatial imprecision of the record. Scattered remnant populations, like scattered colonizing populations, may go undetected. Nevertheless, opportunities exist for "model-system" studies in regions where suitably dense site networks with sufficient temporal resolution can be developed. Such studies, in tandem with ecological and demographic studies of extant populations and documentation of disturbance events, could greatly advance understanding of population retreat.

Plant Associations.—Early discussions of postglacial migrations (Adams 1902; Transeau 1903; Clements 1904; Gleason 1923) conceived of them as zonal, consisting of latitudinal, longitudinal, and elevational shifts in the same species associations that can be recognized today. Clements formalized this in his concep-

tion of the *clisere*, which he defined as a temporal series of associations corresponding to those found along a spatial transect (Clements 1916: Fig. 37).

Paleoecologists have long argued, on the basis of both past pollen assemblages that have no modern counterparts and independent rates and routes of migration for different species, that the *clisere* concept is untenable (West 1964; Davis 1976, 1981b). Jacobson et al. (1987) showed how pollen assemblages formed new and unique combinations in eastern North America during the last deglaciation, and Webb (1988) noted that most of the major vegetation associations of the region cannot be traced before the early Holocene. Overpeck et al. (1992) demonstrated this formally via application of distance metrics between modern and fossil pollen assemblages (Fig. 11). The European record shows similar patterns (Huntley 1990a,b,c). At various times, spatially extensive plant associations unlike any existing today have been established. A particularly striking example is the late-glacial and early Holocene mixed forest of *Picea* and hardwoods (*Ulmus*, *Ostrya/Carpinus*, *Fraxinus*, *Quercus*) in midcontinental North America (Jacobson et al. 1987; Baker et al. 1996). These floristically unique assemblages represent extensive, dense populations of several taxa (*Ulmus*, *Ostrya*, *Fraxinus nigra*) now restricted to small and scattered populations in disturbed or wet habitats.

The inference that species migrate independently does not imply that correlated migration patterns among associated species do not occur. The fundamental niches of many coexisting species are probably similar on some environmental dimensions, and hence an environmental change may induce migration by two or more species in the same general direction. Furthermore, some niche variables may be correlated with vegetation physiognomy. For example, many forest understory species require cool, moist microclimates with low insolation. Thus it is unsurprising to observe, for instance, replacement of forest by prairie accompanied by extirpation of forest-floor herbs and establishment of prairie herbs, shrubs, and graminoids (e.g., Baker et al. 1996).

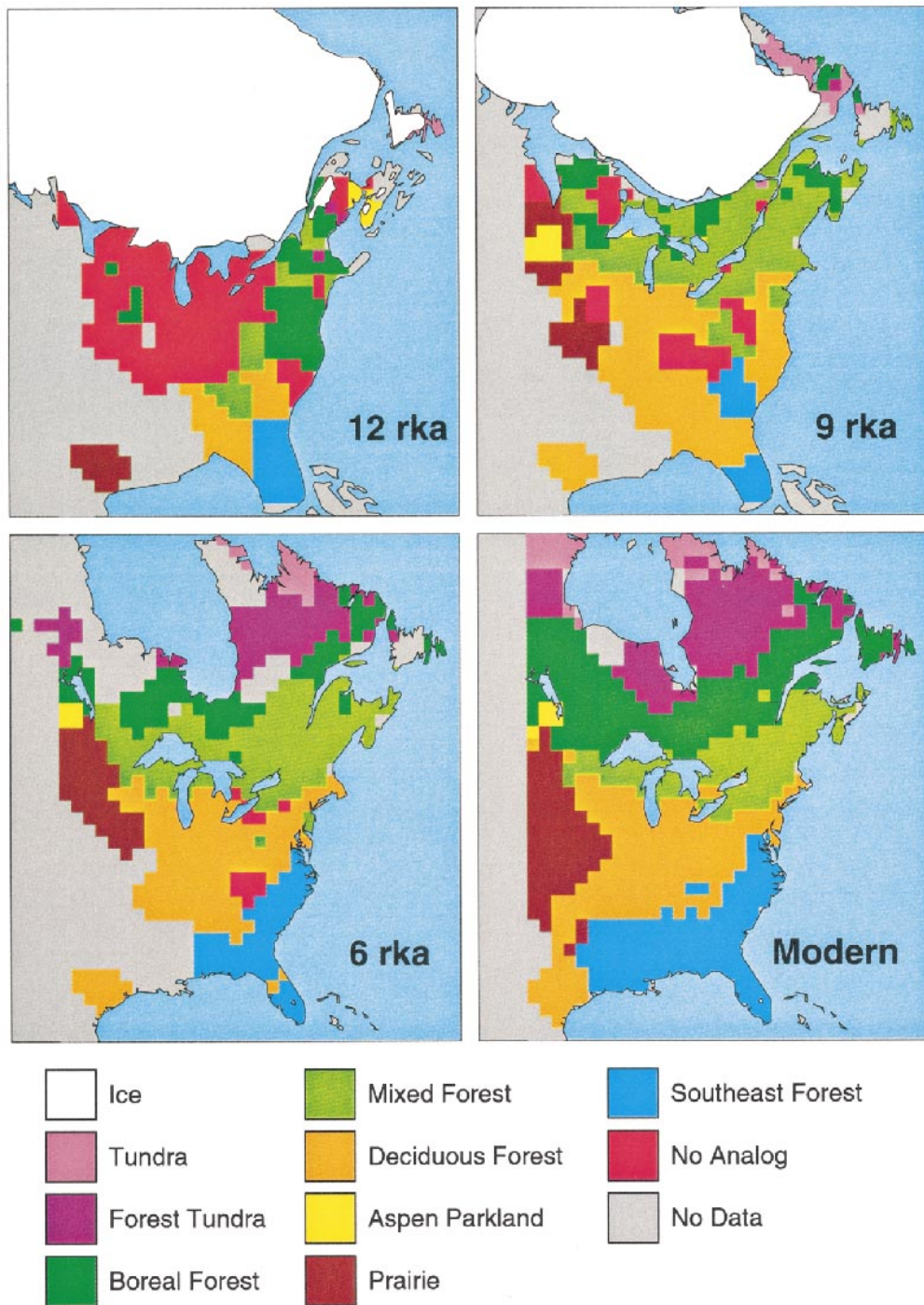


FIGURE 11. Paleovegetation maps of eastern North America during the late-glacial (12 rka \approx 14 Ka), early Holocene (9 rka \approx 11 Ka), mid-Holocene (6 rka \approx 6 Ka), and modern times, based on application of multivariate distance metrics to modern and fossil pollen data. Modified from Overpeck et al. 1992.

Mode 4: Extinction/Contraction

Species Populations.—Environmental change that reduces the overall size of a species' potential niche may result in widespread extirpation of populations unaccompanied by colonization of new sites. Thus, the geographic range of the species may shrink substantially, and the species may become relegated to scattered populations in isolated habitats. Depending on the nature of environmental change relative to size and shape of the fundamental niche, species may alternate between being widespread and abundant at certain times and being scattered or isolated at others.

Numerous examples are documented in the Quaternary fossil record. Papershell pinyon (*Pinus remota*) is currently restricted to a few scattered populations in mountain ranges along the Texas/Chihuahua border. During the Last Glacial Maximum, it formed extensive woodlands on valley floors and extended 300 km to the north (Lanner and Van Devender 1998). During the glacial/interglacial transition, elm (*Ulmus*), hophornbeam (*Ostrya*), and black ash (*Fraxinus nigra*) were extensive and abundant in midcontinental North America, but they have since contracted their ranges and habitat distributions (Jacobson et al. 1987; Webb 1988).

Some species display an inverse pattern, going from rarity to abundance. Ponderosa pine (*P. ponderosa*), now widespread and abundant in the western United States, occurred as small, scattered populations during the Last Glacial Maximum (Betancourt et al. 1990). Many of the important temperate tree taxa of eastern North America occurred as small, isolated populations as recently as the early Holocene (Webb 1988; Jackson et al. 1997, 2000). Interglacial populations of many temperate species in northern Europe evidently did not migrate south during transition to glacial conditions, but underwent extinction. Residual populations in southern Europe survived the glacial periods and provided seed sources for recolonization of northern Europe during subsequent deglaciations (Bennett et al. 1991; Willis 1994; Bennett 1997).

Species undergoing widespread range con-

traction during periods of environmental change face some risk of extinction. One late Quaternary plant extinction has been reported to date (Jackson and Weng 1999). *Picea critchfieldii* had a widespread range (>240,000 km²) and was a dominant component of forests in the Lower Mississippi Valley during the Last Glacial Maximum. It was probably extinct by 10,000 years B.P. (Jackson and Weng 1999). Like many vertebrates in North America, it disappeared during the last deglaciation (Martin and Klein 1984; Stuart 1991; MacPhee 1999). Unlike the vertebrates, however, its demise cannot be attributed to direct human activities. The last deglaciation was characterized by rapid and often abrupt climatic changes of high magnitude (Overpeck et al. 1991; Taylor et al. 1993; Broecker 1997), so *P. critchfieldii* may have encountered a brief period of "bad luck" in which its potential niche contracted or vanished.

Differentiation of *P. critchfieldii* from extant *Picea* species, which was required to recognize the extinction, was made possible only by detailed anatomical and morphological studies of ovulate cones and needles. The demise of *P. critchfieldii* may have been a unique event. However, the last deglaciation may have been accompanied by other species extinctions masked by the coarse taxonomic resolution of pollen data and the paucity of detailed studies of pre-Holocene floras in North America.

Species Associations.—Earlier we presented evidence that late Quaternary plant associations have not persisted in situ, nor have they shifted zonally along habitat gradients, nor have they migrated across the landscape as cliseres. In the face of late Quaternary environmental changes, plant associations were transformed into other associations different in composition, structure, and dynamics. These associations can (and usually do) share species with those existing at other time periods but are sufficiently different to warrant recognition as different entities. Webb (1988: p. 406) suggested that "plant assemblages are to the biosphere what clouds, fronts, and storms are to the atmosphere. . . . They are features that come and go."

Although plant associations are not conserved through time, an association could con-

ceivably disappear and reappear later if environmental conditions conducive to it were repeated. For example, associations might be similar between different interglacial periods or glacial maxima. This is difficult to evaluate in view of the paucity of pre-Wisconsinan pollen and macrofossil assemblages. However, periodic reappearance of associations over glacial/interglacial timescales is probably not routine. Pollen studies spanning the past 100,000–250,000 years show continual transformation of community composition, with no repeating patterns (e.g., Whitlock and Bartlein 1997; Allen et al. 1999). Comparative floristic studies of successive interglacial periods show that no two interglacial floras are alike (West 1980), although Watts (1988) suggests some climatic and vegetational parallels between portions of successive interglacials. The global climate system follows a complex, multidimensional trajectory, never returning precisely to a preexisting state (Fig. 7), and so plant associations are unlikely to be duplicated precisely through time.

Is All the World Gleasonian³?

The biotic response patterns we described in the previous section can be explained as direct consequences of multivariate environmental changes. If fundamental niches vary among species in shape, orientation, and position within environmental space, then temporal changes in realized environmental space should result in predictably individualistic behavior, including disaggregation of species associations and emergence of new ones. As the magnitude of environmental change increases,

population responses should go from tolerance to habitat shift to migration and extinction. Larger environmental changes should lead to larger shifts in realized environmental space and to greater reorganization of species assemblages.

Our discussion has focused on terrestrial plant populations and communities at mid- to high latitudes and underscores the conclusion of many other authors that terrestrial plant species have behaved individualistically (e.g., Davis 1976; Webb 1987, 1988; Huntley 1988, 1991, 1996; Betancourt et al. 1990). Vegetation history of low-latitude regions has been less intensively studied, but data emerging from the Tropics shows substantial late Quaternary change in vegetation composition and species associations (e.g., Bush et al. 1990; Livingstone 1993; Colinvaux et al. 1996). Late Quaternary records of terrestrial fauna show a similar array of population responses and recombinations of species assemblages (Coope 1995; FAUNMAP 1996; Ashworth 1997; Preece 1997), which can also be explained by changes in realized environmental space. Figure 6, for example, provides an explanatory model for mammalian range reversals along latitudinal gradients during the late Quaternary (FAUNMAP 1994, 1996).

To what extent are the individualistic patterns of change observed in terrestrial plants, vertebrates, coleopterans, and gastropods representative of other environments and biotic groups? The answer for any specific group or environment will depend on the nature of the primary environmental factors that influence individuals and populations and, in particular, on how those factors and gradients change through time. Establishment, growth, and reproduction of terrestrial plants are strongly influenced by climate, a dynamic, multivariate entity. The high magnitude and complex nature of late Quaternary climate changes account for the dramatic changes in distribution and abundance of individual plant species, as well as the consequent reorganizations of terrestrial plant communities. Terrestrial animals responded not only to these climate changes but also to consequent changes in vegetation composition and structure.

In contrast, coral reef communities appear

³ We define "Gleasonian" as individualistic behavior of species responding primarily to environmental variables, with stochastic factors of colonization and establishment playing restricted roles in space and time. Gleasonian communities are often confounded with random assemblages of species, evidently stemming from Gleason's (1926) hypothetical examples of identical environments reaching alternative stable communities owing to stochastic differences in colonization. Our definition here is closer to Gleason's own environmentally deterministic view at broader spatial and temporal scales, as indicated by his emphasis on physiological tolerances as constraints to community composition in the 1926 paper, and by his explicit statements in a companion paper (Gleason 1927) that has been largely overlooked.

to have maintained their overall structure through glacial/interglacial cycles, at least in terms of the dominant coral species (Jackson 1992; Pandolfi 1996). Modern coral species array themselves mainly along gradients of water depth and disturbance, and changes at millennial scales have consisted of local spatial shifts in response to sea-level changes, with water-depth zonation patterns conserved (Jackson 1992). The nature of environmental change in these habitats may be similar to that depicted in Figure 2A. The gradient in water depth (x-axis) has remained constant, while other variables (water temperature, salinity) may have increased or decreased. Thus, the realized environmental space has changed relatively little, and the essential community patterns have remained the same.

The coral reef pattern may have terrestrial counterparts. Arrays of species along certain soil-nutrient or hydrological gradients are likely to show similar patterns along those gradients under contrasting climatic regimes. Throughout the late Quaternary, lake-margin gradients in cool-temperate eastern North America have consisted of deep-water submersed aquatics (*Potamogeton*, *Najas*), shallow-water emergents (*Scirpus*, *Carex*), and lakeshore trees (*Picea*), whether they were in mixed pine/spruce/oak forest in northern Georgia 21,000 years ago (Watts 1970), in spruce/elm/ash/hornbeam forest in south-central Minnesota 11,000 years ago (Watts and Winter 1966), or in hemlock/hardwood forest in northern Wisconsin today (Curtis 1959). The realized environmental space for variables controlling upland vegetation along latitudinal and elevational gradients has behaved like that depicted in Figures 2C and 2D, while changes in the variables controlling vegetation along lakeshore gradients have been more like Figure 2A.

Some communities that are structured strongly by biotic interactions (e.g., host-specific herbivores, parasites, parasitoids, and mutualists) may be conserved in the face of environmental change. Host-specific organisms are probably under strong selection to develop environmental tolerances similar to those of their host, and in many cases the host's tissues will provide buffering from the

climatic environment (except during interhost dispersal). In such cases, the associations may be highly stable through long periods of time, although examples from the Quaternary fossil record are scarce. Also, the short generation times of many host-specific consumers and mutualists may permit rapid evolutionary responses to environmental changes.

The Fundamental Niche in Time

Phylogeographic studies are revealing the impact of Quaternary history on genetic structure of species (Hewitt 1999; Sinclair et al. 1999; Mitton et al. 2000; Terry et al. 2000). We focus on the specific question of evolutionary change in the fundamental niche. To what extent do the shape, size, and position of fundamental niches change at timescales of 10^1 – 10^5 years?

If a species is to avoid extinction, either it must maintain a fundamental niche sufficiently broad that the fundamental niche and realized environmental space always overlap, or it must be capable of evolutionary changes sufficiently large and rapid to allow the fundamental niche to track the realized environmental space. The latter strategy will work if the evolutionary response time is short compared with the rate of environmental change. Species with relatively long evolutionary response times must track environmental change through spatial displacement rather than evolution (Good 1931; Webb 1987, 1997; Huntley and Webb 1989). Populations of such species will be subject to different selection regimes as the realized environmental space changes, but this selection is likely to be interrupted or redirected by subsequent environmental changes. However, genetic variations lost to drift or to strong selection under an environmental regime will not necessarily reappear even if favorable under a new regime.

At timescales of 10^3 – 10^4 years, the population mass of a species might be envisioned as sloshing from one portion of the fundamental niche to another as populations track the realized environmental space, with the fundamental niche boundaries remaining stable overall. T. Webb (1987) and Bennett (1990, 1997) have argued that millennial-scale cli-

matic changes obliterate adaptation to local environments at shorter timescales.

Assessment of long-term evolutionary change in niches is difficult. A comparative study of *Fagus* in Europe and North America indicates little divergence in climatic tolerances since the Tertiary (Huntley et al. 1989), suggesting that the fundamental niche for *Fagus* along several climatic axes is constrained phylogenetically (by physiological and developmental pathways, leaf architecture, wood anatomy, etc.). Similar comparative studies are needed for other taxa.

Species that track the environment by spatial displacement must have fundamental niches broad enough to ensure that sites always exist in the realized world where they can establish and maintain populations. Niche breadth can be governed by phenotypic plasticity within genotypes and/or genetic variation among genotypes. A species with a narrow fundamental niche relative to the magnitude of environmental change it experiences is at high risk of eventual extinction. Many species have restricted realized niches (Austin et al. 1990; Thompson et al. 1999), which may result from currently restricted potential niches (masking broader fundamental niches) but may also represent narrow fundamental niches. Narrow fundamental niches may represent low genetic diversity resulting from genetic drift (e.g., Waters and Schaal 1991).

Broad niches may be maintained in some cases because suites of traits adaptive in one environmental setting may be useful in others. For example, many conifers have morphological and physiological traits that impart high carbon-use efficiency, which is advantageous where growing seasons are short and cool (Smith and Brewer 1994; Smith et al. 1997; Eckstein et al. 1999). These same traits may have been advantageous in the low-CO₂ environment of the Last Glacial Maximum (Jackson et al. 2000), which is nowhere replicated on Earth today.

Environmental variability across a range of timescales may also help maintain broad fundamental niches. Genetic diversity within a population can be maintained by environmental heterogeneity, and temporal variation can

have similar effects (Gillespie 1991; Mitton 1997).

Environmental Changes of the Future in the Context of the Past

History is better suited to providing cautionary tales rather than specific images of future climate and vegetation change. Past climate change does not provide strict analogues for future conditions (Webb and Wigley 1985; Crowley 1990; Webb et al. 1993). For example, the total amount, seasonal pattern, and latitudinal distribution of solar energy reaching Earth are expected to remain constant for the foreseeable future. In contrast, concentrations of atmospheric greenhouse gases are likely to rise within the next century beyond any documented in recent Earth history (Fig. 7) (Petit et al. 1999). Thus, the planet is entering a domain of the climate-forcing space that it has never experienced before.

Recent efforts at simulating observed late Quaternary climate changes indicate that, although many aspects of regional climate change (e.g., moisture-related variables) are difficult to simulate accurately, the current generation of predictive climate models are effective in estimating the mean global and hemispheric sensitivity to altered climate forcing (Webb 1998; Joussaume et al. 1999). The paleoclimate data/model comparisons lend confidence to model-based estimates of future sensitivity to altered trace-gas (e.g., CO₂) forcing, which indicate that future global warming will be significant (i.e., 1.5 to 4.5°C by the end of the twenty-first century) (Houghton et al. 1996). Regional climatic shifts could match or exceed the magnitude of those associated with the past 21,000 years (Fig. 12) (Wright et al. 1993; Cuffey and Clow 1997). In many regions, the largest changes occurred over hundreds to thousands of years (e.g., Overpeck et al. 1991), in sharp contrast to the speed at which regional climates could change in the next 100 years.

Future shifts in the realized environmental space are likely to be unprecedented both in terms of climate forcing (i.e., atmospheric greenhouse-gas levels) and in terms of the possible rates and magnitudes of climate change. A comparison of potential future tem-

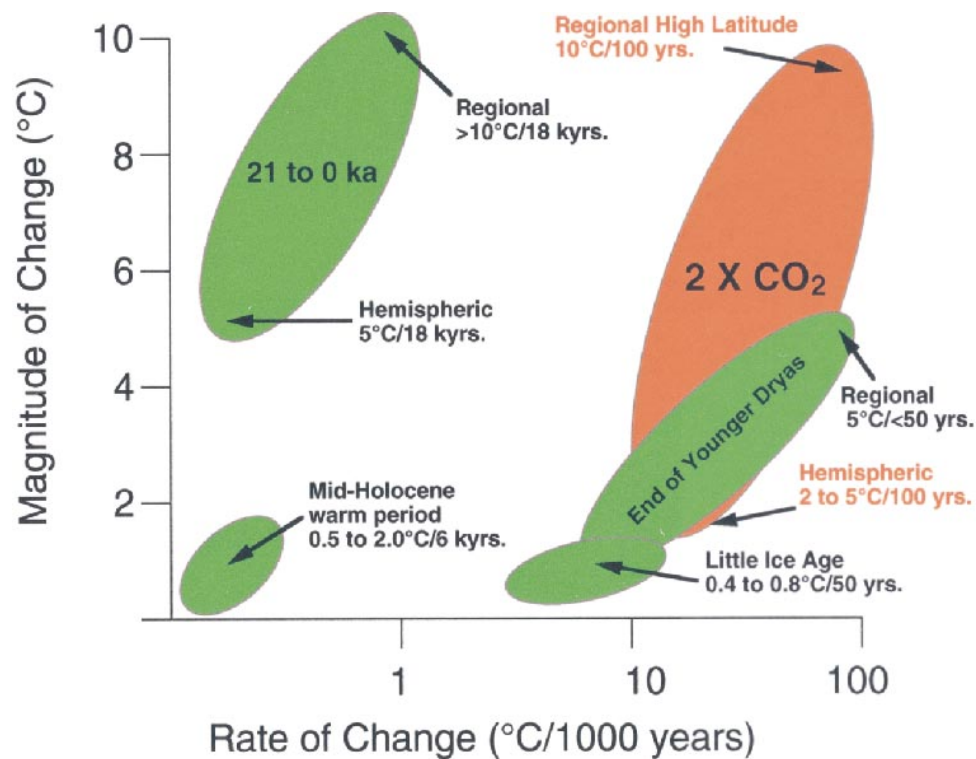


FIGURE 12. Summary comparison of the rates and magnitudes of possible future climate change (estimated in terms of mean annual temperature) with those associated with several well-known periods of past change in regions that were vegetated. Rates of future regional temperature change could far exceed any widespread change in the late Quaternary. See text for sources, and note that the estimated warming associated with the end of the "Little Ice Age" is currently estimated to be about half of the warming observed over the last 150 years (Overpeck et al. 1997; Mann et al. 1999, 2000).

perature change with changes during well-known periods in the past (Fig. 12) indicates that biota of many regions will be faced with high-magnitude environmental changes more rapid than any experienced in a pre-industrial natural world. Although some past changes (e.g., the warming associated with the end of the Younger Dryas ca. 11,500 years ago) were both rapid and large, they were restricted to small portions of the earth (Rind et al. 1998; Hughen et al. 1996; Fawcett et al. 1997). The time-transgressive mid-Holocene warm period (Wright et al. 1993; Kerwin et al. 1999) was characterized by slow rates of change, and the late Holocene "Little Ice Age" (Overpeck et al. 1997; Mann et al. 1999, 2000) was of relatively small magnitude. Moreover, once biologically important factors other than temperature are considered (e.g., drought variability), it becomes increasingly likely that many of the earth's species will encounter changes sub-

stantially different from any they have faced in the course of their evolution. Disruption and fragmentation of the natural landscape by human activities pose additional challenges. Will the mechanisms by which plants and animals have responded to environmental changes of the past be sufficient to ensure their survival in the coming centuries?

Acknowledgments

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Literature Cited

- Adams, C. C. 1902. Postglacial origin and migrations of the life of the northeastern United States. *Journal of Geography* 1: 303–310, 355–357.
- Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences USA* 95:14839–14842.
- Allen, J. R. M., U. Brandt, A. Brauer, H.-W. Hubberten, B. Huntley, J. Keller, M. Kraml, A. Mackensen, J. Mingram, J. F. W. Negendank, N. R. Nowaczyk, H. Oberhänsli, W. A. Watts, S. Wulf, and B. Zolitschka. 1999. Rapid environmental changes in southern Europe during the last glacial period. *Nature* 400: 740–743.
- Allison, T. D., R. K. Moeller, and M. B. Davis. 1986. Pollen in laminated sediments provides evidence for a mid-Holocene forest pathogen outbreak. *Ecology* 67:1101–1105.
- Anderson, R. S. 1996. Postglacial biogeography of Sierra lodgepole pine (*Pinus contorta* var. *murrayana*) in California. *Écoscience* 3:343–351.
- Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134:545–561.
- Ashworth, A. C. 1997. The response of beetles to Quaternary climate changes. Pp. 119–127 in Huntley et al. 1997.
- Austin, M. P. 1990. Community theory and competition in vegetation. Pp. 215–238 in J. B. Grace and D. Tilman, eds. *Perspectives on plant competition*. Academic Press, San Diego.
- . 1992. Modelling the environmental niche of plants: implications for plant community response to elevated CO₂ levels. *Australian Journal of Botany* 40:615–630.
- Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized quantitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs* 60: 161–177.
- Austin, M. P., J. G. Pausas, and I. R. Noble. 1997. Modelling environmental and temporal niches of eucalypts. Pp. 129–150 in J. E. Williams and J. C. Z. Woinarski, eds. *Eucalypt ecology: individuals to ecosystems*. Cambridge University Press, Cambridge.
- Baker, R. G., E. A. Bettis III, D. P. Schwert, D. G. Horton, C. A. Chumbley, L. A. Gonzalez, and M. K. Reagan. 1996. Holocene paleoenvironments of northeast Iowa. *Ecological Monographs* 66:203–234.
- Bartlein, P. J. 1997. Past environmental changes: characteristic features of Quaternary climate variations. Pp. 11–29 in Huntley et al. 1997.
- Bartlein, P. J., I. C. Prentice, and T. Webb III. 1986. Climatic response surfaces from pollen data for some eastern North American taxa. *Journal of Biogeography* 13:35–57.
- Bartlein, P. J., K. H. Anderson, P. M. Anderson, M. E. Edwards, C. J. Mock, R. S. Thompson, R. S. Webb, T. Webb III, and C. Whitlock. 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. *Quaternary Science Reviews* 17:549–585.
- Bennett, K. D. 1985. The spread of *Fagus grandifolia* across eastern North America during the last 18 000 years. *Journal of Biogeography* 12:147–164.
- . 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* 16:11–21.
- . 1997. *Evolution and ecology: the pace of life*. Cambridge University Press, Cambridge.
- Bennett, K. D., P. C. Tzedakis, and K. J. Willis. 1991. Quaternary refugia of north European trees. *Journal of Biogeography* 18: 103–115.
- Berger, A., and M. F. Loutre. 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10:297–317.
- Bernabo, J. C. 1981. Quantitative estimates of temperature changes over the last 2700 years in Michigan based on pollen data. *Quaternary Research* 15:143–159.
- Betancourt, J. L. 1990. Late Quaternary biogeography of the Colorado Plateau. Pp. 259–292 in Betancourt et al. 1990.
- Betancourt, J. L., T. R. Van Devender, and P. S. Martin. 1990a. Synthesis and prospectus. Pp. 435–447 in Betancourt et al. 1990b.
- Betancourt, J. L., T. R. Van Devender, and P. S. Martin, eds. 1990b. *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson.
- Betancourt, J. L., W. S. Schuster, J. B. Mitton, and R. S. Anderson. 1991. Fossil and genetic history of a pinyon pine (*Pinus edulis*) isolate. *Ecology* 72:1685–1697.
- Betancourt, J. L., K. A. Rylander, C. Peñalba, and J. L. McVickar. 2000. Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* (in press).
- Bhiry, N., and L. Filion. 1996. Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quaternary Research* 45:312–320.
- Björkman, L., and R. Bradshaw. 1996. The immigration of *Fagus sylvatica* L. and *Picea abies* (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. *Journal of Biogeography* 23:235–244.
- Bradley, R. S. 1999. *Paleoclimatology: reconstructing climates of the Quaternary*, 2d ed. Academic Press, San Diego.
- Bradley, R. S., and P. D. Jones. 1992. *Climate since A.D. 1500*. Routledge, London.
- Broecker, W. S. 1997. Thermohaline circulation, the Achilles heel of our climate system: will man-made CO₂ upset the current balance? *Science* 278:1582–1588.
- Brubaker, L. B. 1975. Postglacial forest patterns associated with till and outwash in north-central upper Michigan. *Quaternary Research* 5:499–527.
- Bush, M. B., P. A. Colinvaux, M. C. Wiemann, D. R. Piperno, and K.-B. Liu. 1990. Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quaternary Research* 34:330–345.
- Campbell, I. D., and J. H. McAndrews. 1993. Forest disequilibrium caused by rapid Little Ice Age cooling. *Nature* 366:336–338.
- Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204–224.
- Clark, J. S., P. D. Royall, and C. Chumbley. 1996. The role of fire

- during climate change in an eastern deciduous forest at Devil's Bathub, New York. *Ecology* 77:2148–2166.
- Clark, J. S., C. L. Fastie, G. Hurtt, S. T. Jackson, W. C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, I. C. Prentice, G. Schupp, T. Webb III, and P. Wyckoff. 1998. Dispersal theory offers solutions to Reid's paradox of rapid plant migration. *BioScience* 48:13–24.
- Clements, F. E. 1904. The development and structure of vegetation. Contributions from the Botanical Survey of Nebraska, No. 7. University of Nebraska, Lincoln.
- . 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington Publication No. 242.
- . 1934. The relict method in dynamic ecology. *Journal of Ecology* 22:39–68.
- COHMAP. 1988. Climatic changes of the last 18,000 years: observations and model simulations. *Science* 241:1043–1052.
- Cole, K. L. 1990. Late Quaternary vegetation gradients through the Grand Canyon. Pp. 240–258 in Betancourt et al. 1990.
- Colinvaux, P. A., P. E. De Oliveira, J. E. Moreno, M. C. Miller, and M. B. Bush. 1996. A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* 274:85–88.
- Coope, G. R. 1995. Insect faunas in ice age environments: why so little extinction? Pp. 55–74 in J. H. Lawton and R. M. May, eds. *Extinction rates*. Oxford University Press, Oxford.
- Crowley, T. J. 1990. Are there any satisfactory geologic analogs for a future greenhouse warming? *Journal of Climate* 3:1282–1292.
- Crowley, T. J., and G. R. North. 1991. *Paleoclimatology*. Oxford University Press, New York.
- Cuffey, K. M., and G. D. Clow. 1997. Temperature, accumulation, and ice sheet elevation in central Greenland through the last deglacial cycle. *Journal of Geophysical Research* 102:26, 383–26, 396.
- Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison.
- Cwynar, L. C., and G. M. MacDonald. 1987. Geographical variation in lodgepole pine in relation to population history. *American Naturalist* 134:668–673.
- Darwin, C. 1859. On the origin of species by means of natural selection: or the preservation of favoured races in the struggle for life. John Murray, London.
- Davis, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. *Geoscience and Man* 13:13–26.
- . 1981a. Outbreaks of forest pathogens in Quaternary history. Fourth international conference on palynology, Lucknow (1976–1977) 3:216–228.
- . 1981b. Quaternary history and the stability of forest communities. Pp. 132–154 in D. C. West, H. H. Shugart, and D. B. Botkin, eds. *Forest succession: concepts and applications*. Springer, New York.
- . 1990. Climatic change and the survival of forest species. Pp. 99–110 in G. M. Woodwell, ed. *The earth in transition: patterns and processes of biotic impoverishment*. Cambridge University Press, Cambridge.
- Davis, M. B., M. W. Schwartz, and K. Woods. 1991. Detecting a species limit from pollen in sediments. *Journal of Biogeography* 18:653–668.
- Davis, M. B., S. Sugita, R. R. Calcote, J. B. Ferrari, and L. E. Frelich. 1994. Historical development of alternate communities in a hemlock-hardwood forest in northern Michigan, USA. Pp. 19–39 in P. J. Edwards, R. May, and N. R. Webb, eds. *Large-scale ecology and conservation biology*. Blackwell Scientific, Oxford.
- Davis, R. B., and G. L. Jacobson Jr. 1985. Late glacial and early Holocene landscapes in northern New England and adjacent areas of Canada. *Quaternary Research* 23:341–368.
- Delcourt, P. A., H. R. Delcourt, R. C. Brister, and L. E. Lackey. 1980. Quaternary vegetation history of the Mississippi Embayment. *Quaternary Research* 13:111–132.
- Diaz, H. F., and V. Markgraf, eds. 2000. *El Niño and the Southern Oscillation: multiscale variability and global and regional impacts*. Cambridge University Press, Cambridge.
- Eckstein, R. L., P. S. Karlsson, and M. Weih. 1999. Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist* 143:177–189.
- Etheridge, D. M., L. P. Steele, R. L. Langenfelds, R. J. Francey, J.-M. Barnola, and V. I. Morgan. 1996. Natural and anthropogenic changes in atmospheric CO₂ over the last 1000 years from air in Antarctic ice and firn. *Journal of Geophysical Research* 101(D2):4115–4128.
- Fairbanks, R. G. 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger-Dryas event and deep-ocean circulation. *Nature* 342:637–617.
- FAUNMAP Working Group. 1994. FAUNMAP: a database documenting Late Quaternary distributions of mammal species in the United States. *Illinois State Museum Scientific Papers* 25.
- . 1996. Spatial responses of mammals to Late Quaternary environmental fluctuations. *Science* 272:1601–1606.
- Fawcett, P. J., A. M. Agustsdottir, R. B. Alley, and C. A. Shuman. 1997. The Younger Dryas termination and North Atlantic deep water formation: insights from climate model simulations and Greenland ice cores. *Paleoceanography* 12:23–28.
- Forbes, E. 1846. On the connexion between the distribution of the existing fauna and flora of the British Isles, and the geological changes which have affected their area, especially during the epoch of the northern drift. *Memoirs of the Geological Survey of Great Britain* 1:336–432.
- Foster, D. R., and T. M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology* 74:982–998.
- Gaudreau, D. C. 1988. Paleoecological interpretation of geographic patterns in pollen data: spruce and birch in north-eastern North America. *Bulletin of the Buffalo Society of Natural Sciences* 33:15–29.
- Gaudreau, D. C., S. T. Jackson, and T. Webb III. 1989. Spatial scale and sampling strategy in paleoecological studies of vegetation patterns in mountainous terrain. *Acta Botanica Neerlandica* 38:369–390.
- Gear, A. J., and B. Huntley. 1991. Rapid changes in the range limits of Scots pine 4000 years ago. *Science* 251:544–547.
- Gillespie, J. H. 1991. *The causes of molecular evolution*. Oxford University Press, Oxford.
- Givens, C. R., and F. M. Givens. 1987. Age and significance of fossil white spruce (*Picea glauca*), Tunica Hills, Louisiana–Mississippi. *Quaternary Research* 27:283–296.
- Gleason, H. A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club* 43:463–481.
- . 1923. The vegetational history of the Middle West. *Annals of the Association of American Geographers* 12:39–85.
- . 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.
- . 1927. Further views on the succession-concept. *Ecology* 8:299–326.
- Good, R. O' D. 1931. A theory of plant geography. *New Phytologist* 30:149–171.
- Graumlich, L. J. 1994. Long-term vegetation change in mountain environments: paleoecological insights into modern vegetation dynamics. Pp. 167–179 in M. Beniston, ed. *Mountain environments in changing climates*. Routledge, London.
- Gray, A. 1858. Diagnostic characters of new species of phenogamous plants, collected in Japan by Charles Wright, Botanist of the U.S. North Pacific Exploring Expedition (Published by

- request of Captain John Rodgers, Commander of the Expedition). With observations upon the relations of the Japanese flora to that of North America, and of other parts of the Northern Temperate Zone. *Memoirs of the American Academy of Arts and Sciences* 6:377–452.
- Griesemer, J. R. 1992. Niche: historical perspectives. Pp. 231–240 in E. Fox-Keller and E. A. Lloyd, eds. *Keywords in evolutionary biology*. Harvard University Press, Cambridge.
- Hastings, J. R., and R. M. Turner. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semiarid region. University of Arizona Press, Tucson.
- Hays, J. D., J. Imbrie, and N. J. Shackleton. 1976. Variations in the Earth's orbit: pacemaker of the ice ages. *Science* 194:1121–1132.
- Hessl, A. E., and W. L. Baker. 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. *Arctic and Alpine Research* 29:173–183.
- Hewitt, G. M. 1999. Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68:87–112.
- Houghton, J. T., L. G. Meira-Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell, eds. 1996. *Climate change 1995: the science of climate change*. Cambridge University Press, Cambridge.
- Hughen, K. A., J. T. Overpeck, L. C. Peterson, and S. Trumbore. 1996. Abrupt deglacial climatic change in the tropical Atlantic. *Nature* 380:51–54.
- Hughen, K. A., J. T. Overpeck, S. J. Lehman, M. Kashgarian, L. C. Peterson, and R. Alley. 1998. Deglacial ^{14}C calibration, activity and climate from a marine varve record. *Nature* 391:65–68.
- Hunter, M. L., Jr., G. L. Jacobson Jr., and T. Webb III. 1988. Paleocology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* 2:375–385.
- Huntley, B. 1988. Glacial and Holocene vegetation history: Europe. Pp. 341–383 in Huntley and Webb 1988.
- . 1990a. Dissimilarity mapping between fossil and contemporary pollen spectra in Europe for the past 13,000 years. *Quaternary Research* 33:360–376.
- . 1990b. European post-glacial forests: compositional changes in response to climatic change. *Journal of Vegetation Science* 1:507–518.
- . 1990c. European vegetation history: palaeovegetation maps from pollen data—13 000 yr BP to present. *Journal of Quaternary Science* 5:103–122.
- . 1990d. Lessons from climates of the past. Pp. 133–148 in J. Leggett, ed. *Global warming: the Greenpeace report*. Oxford University Press, Oxford.
- . 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany* 67(Suppl. 1):15–22.
- . 1996. Quaternary palaeoecology and ecology. *Quaternary Science Reviews* 15:591–606.
- . 1999. The dynamic response of plants to environmental change and the resulting risks of extinction. Pp. 69–85 in G. M. Mace, A. Balmford, and J. R. Ginsberg, eds. *Conservation in a changing world*. Cambridge University Press, Cambridge.
- Huntley, B., and H. J. B. Birks. 1983. *An atlas of past and present pollen maps for Europe: 0–13000 years ago*. Cambridge University Press, Cambridge.
- Huntley, B., and T. Webb III, eds. 1988. *Vegetation history*. Kluwer Academic, Dordrecht.
- . 1989. Migration: species' response to climatic variations caused by changes in the earth's orbit. *Journal of Biogeography* 16:5–19.
- Huntley, B., P. J. Bartlein, and I. C. Prentice. 1989. Climatic control of the distribution and abundance of beech (*Fagus L.*) in Europe and North America. *Journal of Biogeography* 16:551–560.
- Huntley, B., W. Cramer, A. V. Morgan, H. C. Prentice, and J. R. M. Allen, eds. 1997. *Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota*. Springer, New York.
- Hutchinson, G. E. 1958. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:425–427.
- . 1978. *An introduction to population ecology*. Yale University Press, New Haven, Conn.
- Imbrie, J., E. A. Boyle, S. C. Clemens, A. Duffy, W. R. Howard, G. Kukla, J. Kutzbach, D. G. Martinson, A. McIntyre, A. C. Mix, B. Molino, J. J. Morley, L. C. Peterson, N. G. Pisias, W. L. Prell, M. E. Raymo, N. J. Shackleton, and J. R. Toggweiler. 1992. On the structure and origin of major glaciation cycles. 1. Linear responses to Milankovitch forcing. *Paleoceanography* 7:701–738.
- Imbrie, J., A. Berger, E. A. Boyle, S. C. Clemens, A. Duffy, W. R. Howard, G. Kukla, J. Kutzbach, D. G. Martinson, A. McIntyre, A. C. Mix, B. Molino, J. J. Morley, L. C. Peterson, N. G. Pisias, W. L. Prell, M. E. Raymo, N. J. Shackleton, and J. R. Toggweiler. 1993. On the structure and origin of major glaciation cycles. 2. The 100,000-year cycle. *Paleoceanography* 8:699–735.
- Jablonski, D., and J. J. Sepkoski Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–1378.
- Jackson, J. C. B. 1992. Pleistocene perspectives on coral reef community structure. *American Zoologist* 32:719–731.
- Jackson, S. T. 1989. Postglacial vegetational changes along an elevational gradient in the Adirondack Mountains (New York): a study of plant macrofossils. *New York State Museum Bulletin* 465.
- Jackson, S. T., and C. R. Givens. 1994. Late Wisconsinan vegetation and environment of the Tunica Hills region, Louisiana/Mississippi. *Quaternary Research* 41:316–325.
- Jackson, S. T., and C. Weng. 1999. Late Quaternary extinction of a tree species in eastern North America. *Proceedings of the National Academy of Sciences USA* 96:13847–13852.
- Jackson, S. T., and D. R. Whitehead. 1991. Holocene vegetation patterns in the Adirondack Mountains. *Ecology* 72:641–653.
- Jackson, S. T., J. T. Overpeck, T. Webb III, S. E. Keatts, and K. H. Anderson. 1997. Mapped plant macrofossil and pollen records of Late Quaternary vegetation change in eastern North America. *Quaternary Science Reviews* 16:1–70.
- Jackson, S. T., R. S. Webb, K. H. Anderson, J. T. Overpeck, T. Webb III, J. W. Williams, and B. C. S. Hansen. 2000. Vegetation and environment in eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews* 19:489–508.
- Jacobson, G. L., Jr., and E. C. Grimm. 1986. A numerical analysis of Holocene forest and prairie vegetation in central Minnesota. *Ecology* 76:958–966.
- Jacobson, G. L., Jr., T. Webb III, and E. C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. Pp. 277–288 in W. F. Ruddiman and H. E. Wright Jr., eds. *North America and adjacent oceans during the last deglaciation*. *Geology of North America*, Vol. K-3. Geological Society of America, Boulder, Colo.
- James, F. C., R. F. Johnston, N. O. Wamer, G. J. Niemi, and W. J. Boecklen. 1984. The Grinnellian niche of the wood thrush. *American Naturalist* 124:17–47.
- Johnson, W. C., and T. Webb III. 1989. The role of blue jays (*Cyanocitta cristata L.*) in the postglacial dispersal of fagaceous trees in eastern North America. *Journal of Biogeography* 16:561–571.
- Joussaume, S., K. E. Taylor, P. Braconnot, J. F. B. Mitchell, J. E. Kutzbach, S. P. Harrison, I. C. Prentice, A. J. Broccoli, A. Abe-Ouchi, P. J. Bartlein, C. Bonfils, B. Dong, J. Guiot, K. Herterich,

- C. D. Hewitt, D. Jolly, J. W. Kim, A. Kislov, A. Kitoh, M. F. Loure, V. Masson, B. McAvaney, N. McFarlane, N. de Noblet, W. R. Peltier, J. Y. Peterschmitt, D. Pollard, D. Rind, J. F. Royer, M. E. Schlesinger, J. Syktus, S. Thompson, P. Valdes, G. Vettoretti, R. S. Webb, and U. Wyputta. 1999. Monsoon changes for 6000 years ago: results of 18 simulations from the Paleoclimate Modeling Intercomparison Project (PMIP). *Geophysical Research Letters* 26:859–862.
- Kerwin, M., J. T. Overpeck, R. S. Webb, A. DeVernal, D. H. Rind, and R. J. Healy. 1999. The role of oceanic forcing in mid-Holocene Northern Hemisphere climatic change. *Paleoceanography* 14:200–210.
- King, G. A., and A. A. Herstrom. 1997. Holocene tree migration rates objectively determined from fossil pollen data. Pp. 91–101 in Huntley et al. 1997.
- Kullman, L. 1995. Holocene tree-limit and climate history from the Scandes Mountains, Sweden. *Ecology* 76:2490–2502.
- . 1996. Norway spruce present in the Scandes Mountains, Sweden at 8000 BP: new light on Holocene tree spread. *Global Ecology and Biogeography Letters* 5:94–101.
- . 1998a. Non-analogous tree flora in the Scandes Mountains, Sweden, during the early Holocene—macrofossil evidence of rapid geographic spread and response to paleoclimate. *Boreas* 27:153–161.
- . 1998b. Palaeoecological, biogeographical and palaeoclimatological implications of early Holocene immigration of *Larix sibirica* Ledeb. into the Scandes Mountains, Sweden. *Global Ecology and Biogeography Letters* 7:181–188.
- . 1998c. The occurrence of thermophilous trees in the Scandes Mountains during the early Holocene: evidence for a diverse tree flora from macroscopic remains. *Journal of Ecology* 86:421–428.
- Kutzbach, J. E., and T. Webb III. 1991. Late Quaternary climatic and vegetational change in eastern North America: concepts, models, and data. Pp. 175–217 in L. C. K. Shane and E. J. Cushing, eds. *Quaternary landscapes*. University of Minnesota Press, Minneapolis.
- . 1993. Conceptual basis for understanding Late-Quaternary climates. Pp. 5–11 in H. E. Wright Jr., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein, eds. 1993. *Global climates since the last glacial maximum*. University of Minnesota Press, Minneapolis.
- Kutzbach, J. E., P. J. Guetter, P. J. Behling, and R. Selin. 1993. Simulated climatic changes: results of the COHMAP climate-model experiments. Pp. 24–93 in H. E. Wright Jr., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein, eds. 1993. *Global climates since the last glacial maximum*. University of Minnesota Press, Minneapolis.
- Kutzbach, J. E., R. Gallimore, S. Harrison, P. Behling, R. Selin, and F. Laarif. 1998. Climate and biome simulations for the past 21,000 years. *Quaternary Science Reviews* 17:473–506.
- Laird, K. R., S. C. Fritz, E. C. Grimm, and P. G. Mueller. 1996. Century-scale paleoclimatic reconstruction from Moon Lake, a closed-basin lake in the northern Great Plains. *Limnology and Oceanography* 41:890–902.
- Lanner, R. M., and T. R. Van Devender. 1998. The recent history of pinyon pines in the American Southwest. Pp. 171–182 in D. M. Richardson, ed. *Ecology and biogeography of Pinus*. Cambridge University Press, Cambridge.
- Leibold, M. A. 1996. The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371–1382.
- Livingstone, D. A. 1993. Evolution of African climate. Pp. 455–472 in P. Goldblatt, ed. *Biological relationships between Africa and South America*. Yale University Press, New Haven, Conn.
- Lloyd, A. H., and L. J. Graumlich. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology* 78:1199–1210.
- Luckman, B. H., G. Holdsworth, and G. D. Osborn. 1993. Neoglacial glacier fluctuations in the Canadian Rockies. *Quaternary Research* 39:144–153.
- Lyell, C. 1832. *Principles of geology*, Vol. 2. John Murray, London.
- Lyford, M. E., J. L. Betancourt, and S. T. Jackson. 2000. Holocene vegetation and climate history of the northern Big Horn Basin, Montana. *Quaternary Research*, in review.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145–165.
- . 1986. Alien plant invasion into the Intermountain West: a case history. Pp. 191–213 in H. A. Mooney and J. A. Drake, eds. *Ecology of biological invasions of North America and Hawaii*. Springer, New York.
- MacPhee, R. D. E., ed. 1999. *Extinctions in near time: causes, contexts, and consequences*. Plenum, New York.
- Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. *American Naturalist* 107:213–246.
- Mann, M. E., R. S. Bradley, and M. K. Hughes. 1999. Northern Hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. *Geophysical Research Letters* 26:759–762.
- Mann, M. E., E. Gille, R. S. Bradley, M. K. Hughes, J. Overpeck, F. T. Keimig, and W. Gross. 2000. Global temperature patterns in past centuries: an interactive presentation. *Earth Interactions* (in press).
- Martin, P. S., and R. G. Klein, eds. 1984. *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press, Tucson.
- Martinson, D. G., K. Bryan, M. Ghil, M. M. Hall, T. R. Karl, E. S. Sarachik, S. Sorooshian, and L. D. Talley, eds. 1995. *Natural climate variability on decade-to-century time scales*. National Academy Press, Washington, D.C.
- Mast, J. N., T. T. Veblen, and M. E. Hodgson. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *Forest Ecology and Management* 93:181–194.
- Mast, J. N., T. T. Veblen, and Y. B. Linhart. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *Journal of Biogeography* 25:743–755.
- McDowell, P. F., T. Webb III, and P. J. Bartlein. 1990. Long-term environmental change. Pp. 143–162 in B. L. Turner II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, eds. *The earth as transformed by human action*. Cambridge University Press, Cambridge.
- Millsaugh, S. H., C. Whitlock, and P. J. Bartlein. 2000. Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone National Park. *Geology* 28:211–214.
- Mitton, J. B. 1997. *Selection in natural populations*. Oxford University Press, Oxford.
- Mitton, J. B., B. R. Kreiser, and R. G. Latta. 2000. Glacial refugia of limber pine (*Pinus flexilis* James) inferred from the population structure of mitochondrial DNA. *Molecular Ecology* (in press).
- Nowak, C. L., R. S. Nowak, R. J. Tausch, and P. E. Wigand. 1994a. A 30 000 year record of vegetation dynamics at a semi-arid locale in the Great Basin. *Journal of Vegetation Science* 5:579–590.
- . 1994b. Tree and shrub dynamics in northwestern Great Basin woodland and shrub steppe during the Late-Pleistocene and Holocene. *American Journal of Botany* 81:265–277.
- Overpeck, J. T. 1987. Pollen time series and Holocene climate variability of the midwest United States. Pp. 137–143 in W. H. Berger and L. D. Labeyrie, eds. *Abrupt climatic change*. D. Reidel, Dordrecht.
- . 1993. The role and response of continental vegetation in the global climate system. Pp. 221–238 in J. A. Eddy and H.

- Oeschger, eds. Global changes in the perspective of the past. Wiley, New York.
- . 1995. Paleoclimatology and climate system dynamics. *Reviews of Geophysics* 33:863–871.
- Overpeck, J. T., P. J. Bartlein, and T. Webb III. 1991. Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science* 254:692–695.
- Overpeck, J. T., R. S. Webb, and T. Webb III. 1992. Mapping eastern North American vegetation changes of the past 18 ka: no-analogs and the future. *Geology* 20:1071–1074.
- Overpeck, J., K. Hughen, D. Hardy, R. Bradley, R. Case, M. Douglas, B. Finney, K. Gajewski, G. Jacoby, A. Jennings, S. Lamoureux, A. Lasca, G. MacDonald, J. Moore, M. Retelle, S. Smith, A. Wolfe, and G. Zielinski. 1997. Arctic environmental change of the last four centuries. *Science* 278:1251–1256.
- Pandolfi, J. M. 1996. Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. *Paleobiology* 22: 152–176.
- Parrish, J. T. 1998. Interpreting pre-Quaternary climate from the geologic record. Columbia University Press, New York.
- Parsons, D. J., T. W. Swetnam, and N. L. Christensen, eds. 1999. Historical variability concepts in ecosystem management. *Ecological Applications* 9:1177–1277.
- Peattie, D. C. 1922. The Atlantic Coastal Plain element in the flora of the Great Lakes. *Rhodora* 24:57–88.
- Petit, J. R., J.-M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V. M. Kotlyakov, M. LeGrand, V. Y. Lipenkov, C. Lorius, L. Pepin, C. Ritz, E. Saltzman, M. Stievenard, J. Jouzel, D. Raynaud, and N. I. Barkov. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–436.
- Preece, R. C. 1997. The spatial response of non-marine Mollusca to past climate changes. Pp. 163–177 in Huntley et al. 1997.
- Premoli, A., S. Chischilly, and J. B. Mitton. 1994. Genetic variation and the establishment of new populations of pinyon pine. *Biodiversity and Conservation* 3:331–340.
- Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton Jr. 1999. Genetic responses to climate for *Pinus contorta* in British Columbia: niche breadth, climate change, and reforestation. *Ecological Monographs* 69:375–407.
- Rind, D., D. Peteet, W. S. Broecker, A. McIntyre, and W. F. Ruddiman. 1986. Impact of cold North Atlantic sea surface temperatures on climate: implications for the Younger Dryas cooling (11–10k). *Climate Dynamics* 1:1–33.
- Robertson, A. D., J. T. Overpeck, D. Rind, E. Mosley-Thompson, G. A. Zielinski, J. L. Lean, D. Koch, J. E. Penner, I. Tegen, and R. Healy. 2000. Hypothesized climate forcing time series for the last 500 years. *Journal of Geophysical Research* (in press).
- Roy, K., J. W. Valentine, D. Jablonski, and S. M. Kidwell. 1996. Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology and Evolution* 11:458–463.
- Sinclair, W. T., J. D. Morman, and R. A. Ennos. 1999. The post-glacial history of Scots pine (*Pinus sylvestris*) in western Europe: evidence from mitochondrial DNA variation. *Molecular Ecology* 8:83–88.
- Smith, W. K., and C. A. Brewer. 1994. The adaptive importance of shoot and crown architecture in conifer trees. *American Naturalist* 143:165–169.
- Smith, W. K., T. C. Vogelmann, E. H. DeLucia, D. T. Bell, and K. A. Shepherd. 1997. Leaf form and photosynthesis. *BioScience* 47:785–793.
- Spear, R. W., M. B. Davis, and L. C. K. Shane. 1994. Late Quaternary history of low- and mid-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* 64:85–109.
- Steinger, T., C. Körner, and B. Schmid. 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia* 105:94–99.
- Stuart, A. J. 1991. Mammalian extinctions in the Late Pleistocene of Northern Eurasia and North America. *Biological Reviews* 66:453–562.
- Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128–3147.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189–1206.
- Szeicz, J. M., and G. M. MacDonald. 1995. Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *Journal of Ecology* 83:873–885.
- Taylor, K. C., G. W. Lamorey, G. A. Doyle, R. B. Alley, P. M. Grootes, P. A. Mayewski, J. W. C. White, and L. K. Barlow. 1993. The “flickering switch” of late Pleistocene climate change. *Nature* 361:432–436.
- Terry, R. G., R. S. Nowak, and R. J. Tausch. 2000. Variation in chloroplast and nuclear ribosomal DNA in Utah juniper (*Juniperus osteosperma*, Cupressaceae): Evidence for interspecific gene flow. *American Journal of Botany* 87:250–258.
- Thompson, R. S. 1988. Western North America. Vegetation dynamics in the western United States: modes of response to climatic fluctuations. Pp. 415–458 in Huntley and Webb 1988.
- . 1990. Late Quaternary vegetation and climate in the Great Basin. Pp. 200–239 in Betancourt et al. 1990.
- Thompson, R. S., K. H. Anderson, and P. J. Bartlein. 1999. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. United States Geological Survey Professional Paper 1650.
- Transeau, E. N. 1903. On the geographic distribution and ecological relations of the bog plant societies of North America. *Botanical Gazette* 36:401–420.
- Valentine, J. W., and D. Jablonski. 1993. Fossil communities: compositional variation at many time scales. Pp. 341–349 in R. E. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.
- Van Devender, T. R. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. Pp. 134–163 in Betancourt et al. 1990.
- Vose, R. S., R. L. Schmoyer, P. M. Steurer, T. C. Peterson, R. Heim, T. R. Karl, and J. K. Eischeid. 1992. The global historical climatology network: long-term monthly temperature, precipitation, sea level pressure, and station pressure data. Data Set NDP-041, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Waters, E. R., and B. A. Schaal. 1991. No variation is detected in the chloroplast genome of *Pinus torreyana*. *Canadian Journal of Forest Research* 21:1832–1835.
- Watts, W. A. 1970. The full-glacial vegetation of northwestern Georgia. *Ecology* 51:17–33.
- . 1988. Europe. Pp. 155–192 in Huntley and Webb 1988.
- Watts, W. A., and T. C. Winter. 1966. Plant macrofossils from Kirchner Marsh, Minnesota—a paleoecological study. *Geological Society of America Bulletin* 77:1339–1360.
- Weaver, J. E. 1954. North American prairie. Johnsen, Lincoln, Nebr.
- Weaver, J. E., and F. W. Albertson. 1936. Effects of the great drought on the prairies of Iowa, Nebraska, and Kansas. *Ecology* 17:567–639.
- . 1944. Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecological Monographs* 14: 393–479.
- Webb, S. L. 1987. Beech range extension and vegetation history:

- pollen stratigraphy of two Wisconsin lakes. *Ecology* 68:1993–2005.
- Webb, T., III. 1987. The appearance and disappearance of major vegetational assemblages: long-term vegetational dynamics in eastern North America. *Vegetatio* 69:177–187.
- . 1988. Eastern North America. Pp. 385–414 in Huntley and Webb 1988.
- . 1992. Past changes in vegetation and climate: lessons for the future. Pp. 59–75 in R. L. Peters and T. E. Lovejoy, eds. *Global warming and biological diversity*. Yale University Press, New Haven, Conn.
- . 1997. Spatial response of plant taxa to climate change: a palaeoecological perspective. Pp. 55–71 in Huntley et al. 1997.
- , ed. 1998. Late Quaternary climates: data synthesis and model experiments. *Quaternary Science Reviews* 17:463–688.
- Webb, T., III, and T. M. L. Wigley. 1985. What past climate climates can indicate about a warmer world. Pp. 237–258 in M. C. MacCracken and F. M. Luther, eds. *Projecting the climatic effects of increasing carbon dioxide*. U.S. Department of Energy Report DOE/ER-0237. Washington, D.C.
- Webb, T., III, T. J. Crowley, B. Frenzel, A.-K. Gliemeroth, J. Jouzel, L. Labeyrie, I. C. Prentice, D. Rind, W. F. Ruddiman, M. Sarntheim, and A. Zwick. 1993. Group report: use of paleoclimatic data as analogs for understanding future global changes. Pp. 51–71 in J. A. Eddy and H. Oeschger, eds. *Global changes in the perspective of the past*. Wiley, Chichester, England.
- Weng, C., and S. T. Jackson. 1999. Late Glacial and Holocene vegetation history and paleoclimate of the Kaibab Plateau, Arizona. *Palaeogeography, Palaeoclimatology, Palaeoecology* 153:179–201.
- West, R. G. 1964. Inter-relations of ecology and Quaternary paleobotany. *Journal of Ecology* 52(Suppl.):47–57.
- . 1980. Pleistocene forest history in East Anglia. *New Phytologist* 85:571–622.
- Whitlock, C. 1993. Postglacial vegetation and climate of Grand Teton and Yellowstone National Parks. *Ecological Monographs* 63:173–198.
- Whitlock, C., and P. J. Bartlein. 1997. Vegetation and climate change in northwest America during the past 125 kyr. *Nature* 388:57–61.
- Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat, and ecotope. *American Naturalist* 107:321–338.
- Wight, J. R., and H. J. Fisser. 1968. *Juniperus osteosperma* in northwestern Wyoming: their distribution and ecology. *Science Monograph* 6:1–31. Agricultural Experiment Station, University of Wyoming, Laramie.
- Willis, K. J. 1994. The vegetational history of the Balkans. *Quaternary Science Reviews* 13:769–788.
- Woodhouse, C. A., and J. T. Overpeck. 1998. 2000 years of drought variability in the central United States. *Bulletin of the American Meteorological Society* 79:2693–2714.
- Woods, K. D., and M. B. Davis. 1989. Paleocology of range limits: beech in the Upper Peninsula of Michigan. *Ecology* 70:681–696.
- Wright, H. E., Jr., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein, eds. 1993. *Global climates since the last glacial maximum*. University of Minnesota Press, Minneapolis.

Appendix

Glossary of Terms Used in Conceptual Model of Biotic Response to Environmental Change

Environmental Space: An n -dimensional hyperspace delimited by the n environmental variables that are relevant to establishment, growth, survival, and reproduction of individuals of a species. Two-dimensional views of this space are shown in Figures 1 and 2.

Realized Environmental Space: The portion of the total n -dimensional environmental space that is actually represented on Earth (or within a specified region, such as eastern North America) at a given time t (Figs. 1, 2). The realized environmental space can be envisioned as a cloud of points within the boundaries of the environmental space, with each point representing the joint values of the n variables at some point in geographic space at time t . In a two-dimensional environmental space (e.g., Fig. 2), the cloud may appear as an ellipse, circle, blob, or some other planar shape. The point cloud may change shape and position through time as the environment changes at each point in geographic space (Figs. 3, 8).

Empty Environmental Space: The portion of the total environmental space that is not represented by any points on Earth (or within a specified region) at time t . Some portions of environmental space are permanently empty, representing combinations of variables that are physically impossible at Earth's surface (Fig. 1). Other parts of environmental space will alternate between realized and empty environmental space (Figs. 3, 8).

Fundamental Niche: The portion of n -dimensional environmental space that is capable of sustaining populations of a species. This can be visualized as a uniform solid within the n -dimensional environmental space, representing all possible combinations of the n environmental variables that permit establishment, survival, and reproduction of individuals of the species (Fig. 2 provides a two-dimensional representation). Alternatively, it can be perceived as a variable-density solid, with density corresponding to fitness or potential population density. The shape, orientation, and position of the solid are determined by the species' environmental tolerances and requirements, as governed by the genetic attributes of the species (diversity, structure, phenotypic plasticity, etc.), and hence is subject to evolutionary change.

Potential Niche: The portion of environmental space that is capable of supporting populations of a species at time t , defined as the intersection of the fundamental niche for the species with the realized environmental space for time t (Fig. 2). The potential niche will change shape, size, and position within the environmental space as the realized environmental space changes through time (Fig. 4), and as the fundamental niche changes through evolution.

Realized Niche: The portion of n -dimensional environmental space that is actually occupied by populations of a species. The realized niche can be modeled empirically given suitable information on geographic occurrences of the species and associated environmental factors. The realized niche is a subset of the potential niche and may not fill the entire potential niche space owing to dispersal limitations and biotic interactions (Fig. 2).