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

Stephen T. Jackson and Jonathan T. Overpeck

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.

Stephen T. Jackson. Department of Botany, Aven Nelson Building, University of Wyoming, Laramie, Wyoming 82071. E-mail: jackson@uwyo.edu
Jonathan T. Overpeck. Institute for the Study of Planet Earth and Department of Geosciences, University of Arizona, Tucson, Arizona 85721. E-mail: jto@u.arizona.edu

Accepted: 15 June 2000

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 $10^1$–$10^2$ 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 independent 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-
Ecologists and resource managers are recognizing that environmental variability at timescales of $10^5$–$10^4$ 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 factors 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).
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 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., $[\text{Ni}]$ 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-
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 colonization 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.
199

LATE QUATERNARY ENVIRONMENTAL CHANGE

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.

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.

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 variation 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
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 Loutre 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...
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
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 glacial 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 CO$_2$ 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 10^3–10^4 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 bottlenecking 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 organ 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-
Late Quaternary Environmental 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; Hessl 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
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 paleoecological 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 Heström 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 re-treating 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 conception 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 = 14 Ka), early Holocene (9 rka = 11 Ka), mid-Holocene (6 rka = 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), hop hornbeam (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). 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-
receivably 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 Gleasonian?3

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 submerged 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 $10^3–10^5$ 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).

The niche-based conceptual scheme in this paper was originally presented by S. T. Jackson at the 1990 Ecological Society of America meeting, and subsequently in several seminars and workshops. He thanks the many colleagues who pestered him over the years to publish it. Discussions with T. Webb III played an important role in development of these ideas, and we appreciate his thoughtful and thorough critique of the paper. We also thank S. L. Wing, J. S. Clark, W. A. DiMichele, S. T.
Gray, and J. Norris for comments, and P. J. Bartlein and J. W. Williams for providing climate and paleoclimate data. This research was supported by the National Science Foundation (Ecology and Climate Dynamics Programs) and the National Oceanic and Atmospheric Administration (Paleoclimate Program). We are indebted to S. Stewart, K. H. Anderson, and S. T. Gray for creation of many of the illustrations, J. Keltner and J. W. Williams for help in climate data manipulation, and W. Gross for development of the interactive, three-dimensional web version of Figure 7.

Literature Cited


Clark, J. S., P. D. Royall, and C. Chumbley. 1996. The role of fire...


Gray, A. 1858. Diagnostic characters of new species of phengogamous 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 Northem Temperate Zone. Memoirs of the American Academy of Arts and Sciences 6:377–452.


C. D. Hewitt, D. Jolly, J. W. Kim, A. Kislav, A. Kitoh, M. F. Lou- 
tre, V. Masson, B. McAvaney, N. McFarlane, N. de Noblet, W. 
E. Schlesinger, J. Syktus, S. Thompson, P. Valdes, G. Vettoletti, 
years ago: results of 18 simulations from the Paleoclimate 
Modeling Intercomparison Project (PMIP). Geophysical Re-
search 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-Ho-
locene Northern Hemisphere climatic change. Paleocenoge-

rates objectively determined from fossil pollen data. Pp. 91– 

Kullman, L. 1995. Holocene tree-limit and climate change from 

———. 1996. Norway spruce present in the Scandes Mountains, 
Sweden at 8000 BP: new light on Holocene tree spread. Global 

———. 1998a. Non-analogous tree flora in the Scandes Moun-
tains, Sweden, during the early Holocene—macrofossil evi-
dence of rapid geographic spread and response to paleocli-

———. 1998b. Palaeoecological, biogeographical and paleoclim-
matological implications of early Holocene immigration of 
Larix sibirica Ledeb. into the Scandes Mountains, Sweden. Glob-
al 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 Ecol-
yogy 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. Cush-
ing, eds. Quaternary landscapes. University of Minnesota 
Press, Minneapolis.

———. 1993. Conceptual basis for understanding Late-Quater-
nary 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. Bar-
tlein, eds. Global climates since the last glacial maxi-
um. University of Minnesota Press, Minneapolis.

Simulated climatic changes: results of the CCM/MAP climate-
model experiments. Pp. 224–253 in H. E. Wright Jr., J. E. Kutz-
bach, 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. Lanzl. 1998. Climate and biome simulations for the past 
21,000 years. Quaternary Science Reviews 17:473–506.

Century-scale paleoclimatic reconstruction from Moon Lake, 
a closed-basin lake in the northern Great Plains. Limnology 
and Oceanography 41:890–902.

of pinyon pines in the American Southwest. Pp. 171–182 in D. 
M. Richardson, ed. Ecology and biogeography of Pini-n. Cam-
bridge University Press, Cambridge.

Leibold, M. A. 1996. The niche concept revisited: mechanistic 

472 in P. Goldberg, ed. Biological relationships between Af-
rica and South America. Yale University Press, New Haven, 
Conn.


don.

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 

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 Natu-

Hemisphere temperatures during the past millennium: infer-
ces, uncertainties, and limitations. Geophysical Research 

Mann, M. E., E. Gille, R. S. Bradley, M. K. Hughes, J. Overpeck, 
in past centuries: an interactive presentation. Earth Interac-
tions (in press).

Martin, P. S., and R. G. Klein, eds. 1984. Quaternary extinctions: 

Martinson, D. G., R. S. Bradley, 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.

within a pine/grassland ecotone: an approach with historic 
aerial photography and GIS modeling. Forest Ecology and 

and climatic influences on age structure of ponderosa pine at 
the pine/grassland ecotone, Colorado Front Range. Journal of 

environmental change. Pp. 143–162 in B. L. Turner II, W. C. 
Clark, R. W. Gates, J. F. Richards, J. T. Mathews, and W. B. Mey-
er, eds. The earth as transformed by human action. Cam-

Millsap, S. H., C. Whitlock, and P. J. Bartlein. 2000. Varia-
tions in fire frequency and climate over the past 17 000 yr in 

Mitton, J. B. 1997. Selection in natural populations. Oxford Uni-
versity Press, Oxford.

of limber pine (Pinus flexilis James) inferred from the popu-
ation structure of mitochondrial DNA. Molecular Ecology (in 
press).

A 30 000 year record of vegetation dynamics at a semi-arid 
590.

———. 1994b. Tree and shrub dynamics in northwestern Great 
Basin woodland and shrub steppe during the Late-Pleisto-

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.


Webb, S. L. 1987. Beech range extension and vegetation history:
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).