Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota
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PAST ENVIRONMENTAL CHANGES: CHARACTERISTIC FEATURES OF QUATERNARY CLIMATE VARIATIONS

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INTRODUCTION

Climate varies, both temporally and spatially, and the focus of the body of palaeoclimatic research has been to characterize and explain this variation. What has emerged is a view of climate as a multi-component *system* that varies across a range of temporal and spatial scales. Imbedded in these variations are some characteristic features such as trends, abrupt changes, periodicities, and the formation of spatial mosaics of climatic changes; these features occur on many scales and are the subject of this paper.

Several approaches have been used to characterize the variability of climate at different temporal or spatial scales. These approaches include, for example:

1. the "powers-of-ten" presentation (Webb, 1989) wherein climatic time series of different duration (e.g., the past 100,000, the past 10,000, the past 1000 years) are plotted and examined;
2. portrayal of the variance spectrum of climatic time series, which reveals the relative importance of variations at different timescales (Mitchell, 1976; Shackleton and Imbrie, 1990); or
3. "scale diagrams" that indicate the characteristic temporal and spatial scales that the particular components of climate vary on (e.g., McDowell et al., 1990; Webb, 1995). Although these approaches indicate the general magnitude of climatic variations and the timescales that they occur on, the presentations tend to obscure the *particular* characteristics of the climatic changes that may have evoked spatial or evolutionary responses from terrestrial biota.

The plan of this paper is first to describe the hierarchy of controls and responses of components of the climate system, and then discuss some of the characteristic features of temporal and spatial variations of climate that recur on different scales. This discussion draws heavily on earlier papers by Barnosky (1987), Bartlein (1988), Bartlein and Prentice (1989), McDowell et al. (1990), Webb and Bartlein (1992), and Webb (1995).

THE HIERARCHY OF CLIMATE-SYSTEM CONTROLS AND RESPONSES

Climatic variations over time at a particular place are governed by a hierarchy of controls and responses (Table 1); these begin with the external controls of the climate system and end with the responses of a number of local climate components at a place. The responses at any one level of the hierarchy become the controls of the components at lower levels. For example, on timescales of 10^4 to 10^6 years, ice sheets are dependent variables in the climate system, governed by orbitally controlled variations in insolation. At shorter timescales (10^4 to 10^3 years), ice sheets act as independent variables that have an important influence on global temperatures and atmospheric circulation.

In general, the more slowly varying components of the climate system (e.g., ice volume, long-term trends in atmospheric composition) operate at higher levels of the hierarchy, while the more rapidly varying components (e.g., storm tracks, precipitation fields) operate at lower levels. The spatial and temporal scale of the potential impacts of the characteristic features can be gauged by considering which levels in the hierarchy control the climatic variations described below, and

Table 1. Hierarchy of climate system controls and responses

External Controls	astronomic solar (output, orbital variations) tectonic (continental distributions, mountain barriers, ocean gateways and barriers) atmospheric composition
Global-Scale Responses/Controls	latitudinal and seasonal distributions of insolation ice volume atmospheric composition zonal energy balance
Hemispheric-Scale Responses/Controls	atmospheric general circulation (e.g., westerlies) ocean general circulation ocean thermohaline circulation
Continental-Scale Responses/Controls	atmospheric circulation features (e.g., Aleutian low, E. Pacific STH) land-surface cover sea-surface temperature patterns
Regional-Scale Responses/Controls	storm track locations airmass distributions (heat and moisture fluxes) clouds
Mesoscale Responses/Controls	temperature, precipitation, and wind fields as modified by orography
Local-Scale Responses	precipitation, air temperature, incident shortwave radiation, net radiation, water vapor pressure, wind speed, soil moisture, atmospheric deposition, lightning

which are involved in the response.

The existence of this hierarchy also has implications for attempts to explain the variations at a particular place. For example, although the variations at a place are ultimately governed by global-scale controls, a specific palaeoclimatic record is generally not necessarily representative of the general state of the global system; this situation arises because the intermediate controls and responses have the potential of reinforcing, canceling, or even reversing the global trend. Gradual changes in large-scale controls may sometimes produce abrupt local changes when atmospheric circulation is reorganized. Conversely, abrupt changes in the large-scale circulation may produce warming in some regions and cooling or no change in others, as can be seen in the spatial anomaly patterns of year-to-year variations of climate. Consequently, it may be difficult or even impossible to ascribe a particular climate variation at a place to a specific set of higher-level controls.

ILLUSTRATING THE CHARACTERISTIC FEATURES OF TEMPORAL AND SPATIAL VARIATIONS OF PAST CLIMATE

The characteristic features of temporal variations of climate can be discussed using a selection of representative time series, in the style of the powers-of-ten diagrams; however, I will concentrate more on the kinds of variations that are evident than on the amplitude or timescale of the variations. The characteristic features of the spatial variations of climate are harder to describe, because, with the exception of the present, the requisite dense networks of sites exist only in a few regions. Consequently, these features will be described using the results of some palaeoclimatic simulations, supplemented by some contemporary observations.

Representative Time Series

A selection of representative time series illustrates the kinds of features that occur in palaeoclimatic variations (Figure 1). Series A in Figure 1 shows a composite record of oxygen isotope variations over the Cenozoic (Miller et al., 1987). The variations reflect both the average temperature of the oceans as well as the global ice volume. Series B is a 5 Myr-long record of oxygen isotope variations from an ocean core located off the coast of West Africa (Tiedemann et al., 1994). The short-term isotopic variations displayed in the record reflect mainly the growth and decay of ice sheets, while the trend in this series reflects the development and increase in size of Northern Hemisphere ice sheets. Series C is the “SPECMAP stacked-and-smoothed” oxygen isotopic record (Imbrie et al., 1984). In this series, short-term and local variations have been removed by the data analysis, and the record can be viewed as an index of the general level of global ice volume over the past 800 kyr. Series D displays the oxygen-isotopic variations contained in the Greenland Ice Core Project (GRIP) Summit core (Dansgaard et al., 1993). This record provides

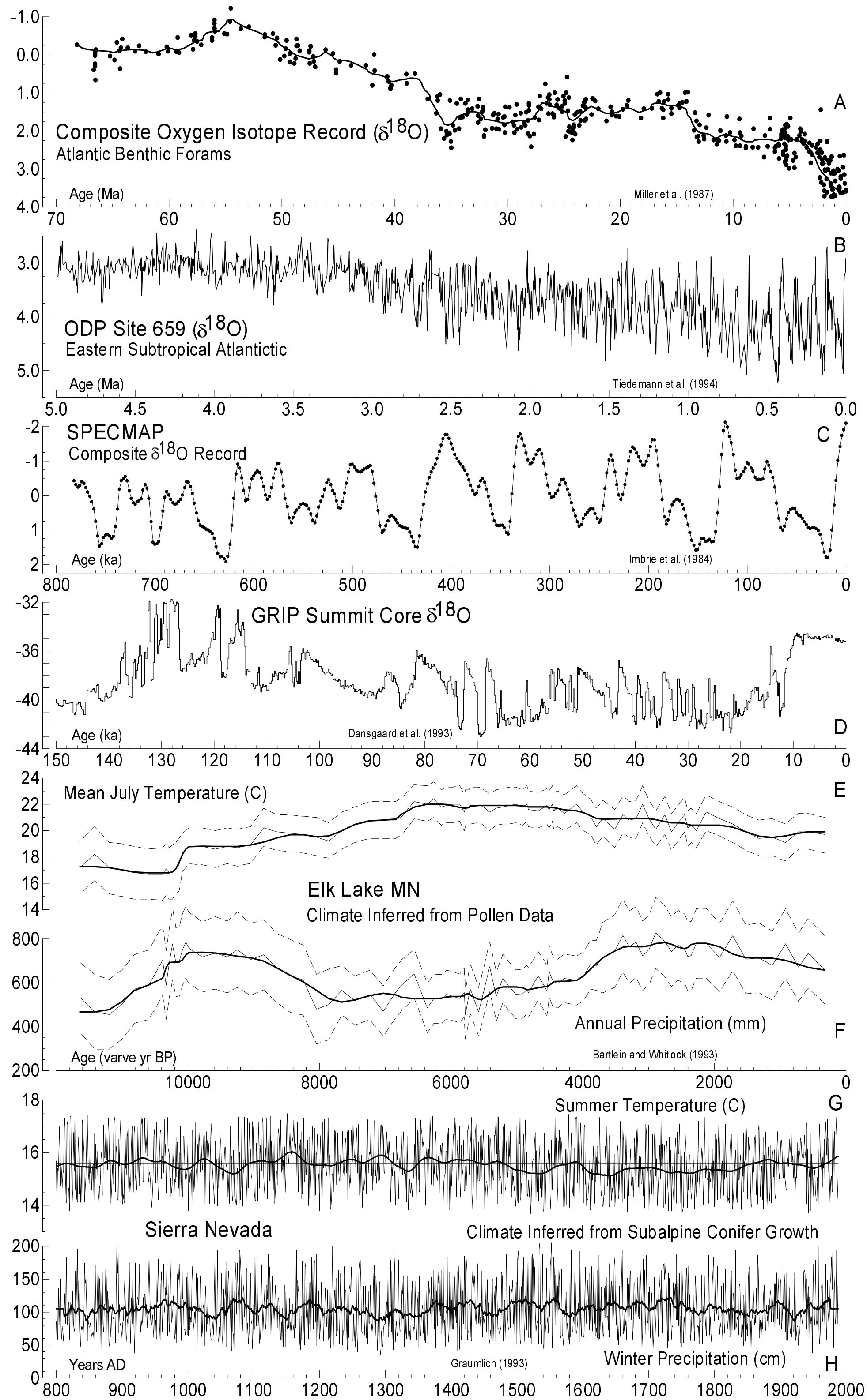

Figure 1: Representative time series that illustrate some characteristic features of palaeoclimatic variations (see text for discussion). Each series is plotted so that warm or wet conditions appear at the top of each graph, and cool or dry at the bottom.

a general indication of climatic conditions over the North Atlantic and adjacent regions for the last glacial-interglacial cycle, and comparison of this record with the SPECMAP record (Series C) suggests that these variations generally reflect global-scale variations. However, in detail, the isotopic variations in Series D probably also represent local variations in air temperature and, in part, variations in the moisture sources of precipitation over Greenland, both of which are controlled by atmospheric circulation variations (Charles et al., 1994).

The next sets of representative time series reflect regional- and local-scale variations more than they do global-scale ones. Series E and F display reconstructions of mean July temperature and annual precipitation based on pollen data in a varved core from Elk Lake, Minnesota (Bartlein and Whitlock, 1993). The effective sampling interval is about 100 yrs in this core. The prediction error intervals (dashed lines), and smoothed values of the reconstructions are also shown on the figure. Series G and H are annual reconstructions of summer temperature and winter precipitation, based on the growth of subalpine conifers in the Sierra Nevada (Graumlich, 1993). The thick solid lines superimposed on each series are smoothed values of the reconstructions, plotted to reveal the principal timescales of variability in each records, and the thin horizontal lines indicate the long-term mean of each series (Graumlich, 1993).

Spatial Patterns of Past Climatic Variations

Only few regions, such as eastern North America (e.g., Webb et al., 1993), or western Europe (e.g., Huntley and Prentice, 1988, 1993), have dense-enough networks of palaeoclimatic observations to allow reconstruction of the spatial patterns of past climate at the regional or smaller scale. Consequently, I used the results of a set of palaeoclimatic simulations done with the National Center for Atmospheric Research (NCAR) Community Climate Model (CCM 1) to illustrate the continental-scale pattern of past climates for North America (Kutzbach et al., in prep). The simulations were completed for 21, 16, 14, 11 and 6 ka (calendar years) and present, and I interpolated the simulated anomalies onto a 25-km grid of modern climate values over North America (Bartlein et al., in prep.), adding the anomalies to the modern values. Maps of these data display the changing patterns of climate since the last glacial maximum (Fig. 2). Although based on simulations that are likely inaccurate, such maps do illustrate the types of patterns of climatic change that arise over a continental-size region.

To further illustrate some of the features of the spatial variations of climate that occur, I determined the uniqueness of the simulated climate for each point and time (Fig. 3), by finding the minimum dissimilarity (Euclidean distance) between the climate at that point, and the climates at the other grid points and times. These dissimilarities reveal those points without good analogues at other times, i.e., those with unique climates. Although the simulated climates are inaccurate, the result-

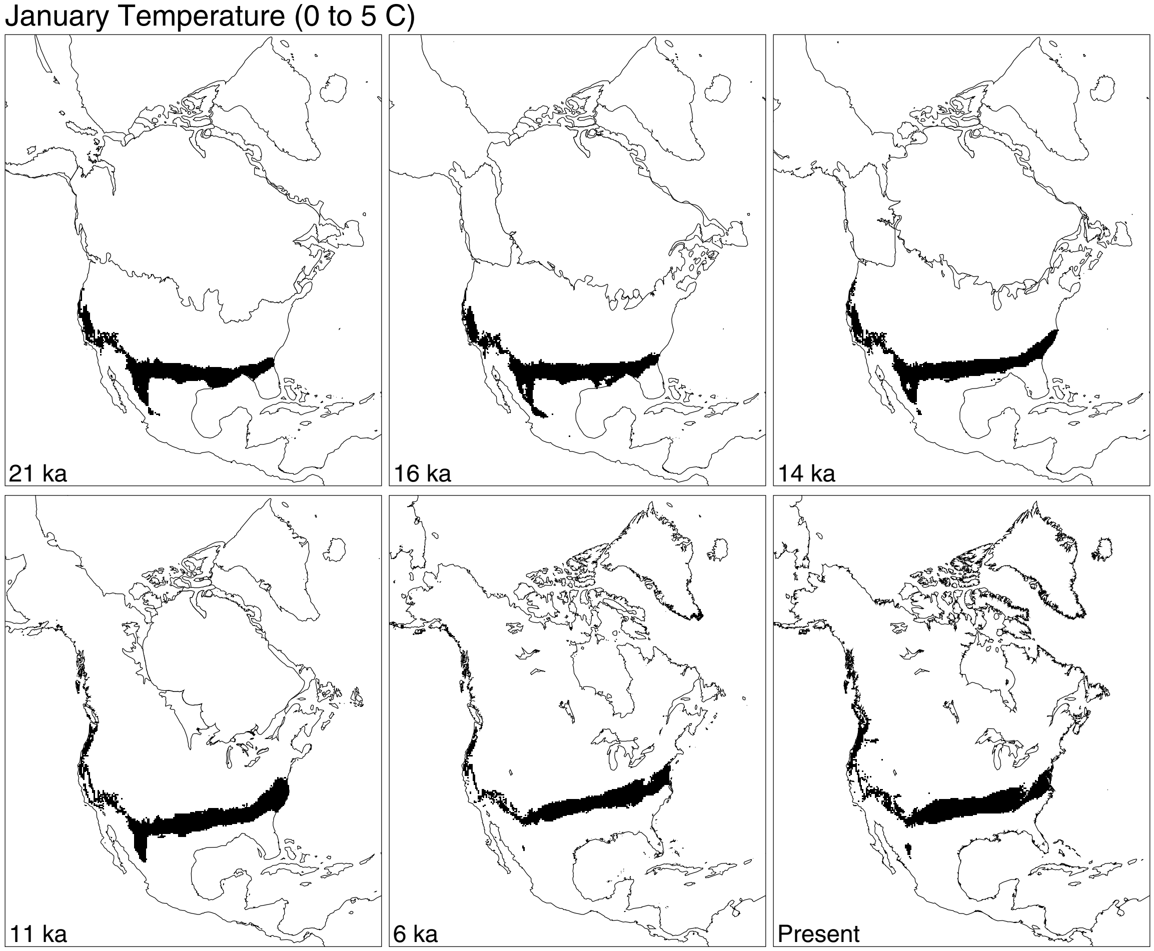

Figure 2: The changing location of the regions with mean January temperature between 0 and 5°C. In eastern North America, this region appears as a well-defined band that translates northward from 21 ka to present, while in the mountainous western North America, this region is discontinuous, with many outlying islands and inliers of different climates.

ing patterns of the uniqueness of the climate at each point and time nevertheless illustrate the kinds of patterns that likely occurred in the real climate.

Another perspective on spatial variations of climate can be gained by examining the pattern of precipitation seasonality using long-term average monthly precipitation (Mock, 1966). A map of the season of occurrence of the precipitation maximum for climate stations in western North America appears as Figure 4, and this display reveals broad-scale patterns of precipitation seasonality as well as more local-scale patterns of heterogeneity (see also Whitlock and Bartlein, 1993).

CHARACTERISTIC FEATURES OF CLIMATIC VARIATIONS

Several distinctive features or patterns of climatic variations occur at a number of spatial and temporal scales. Depending on the temporal and spatial scales they occur at, these features can have

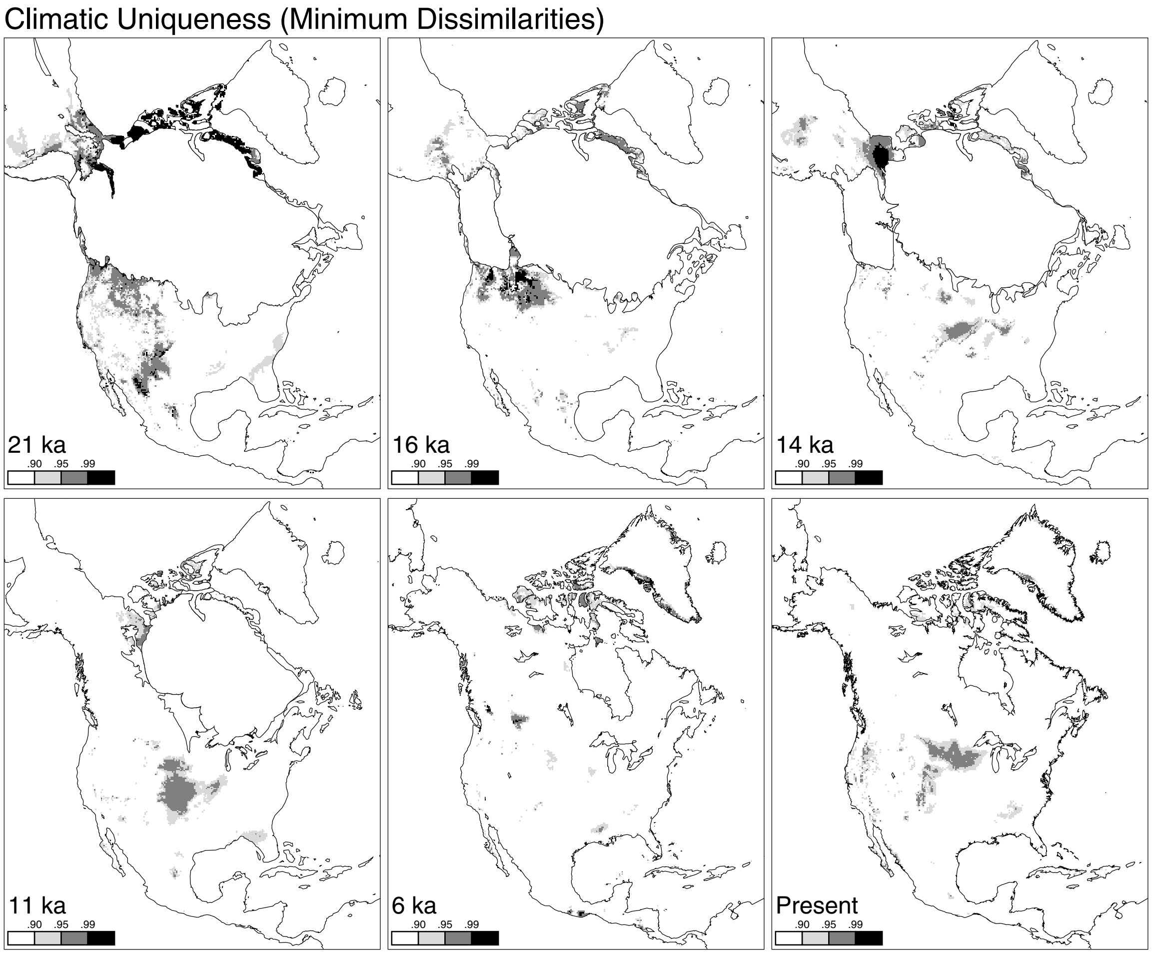

Figure 3: Uniqueness of simulated (21 - 6 ka) and observed present climate at individual 25-km grid points. For each grid point and time, the minimum dissimilarity between the climate of the point and the climates of all of the other points at the other times was determined. The shading indicates those points with climates that are relatively unusual (i.e., those with minimum dissimilarity values that exceed the 90th-percentile of the 1.6 x 10^5 minimum dissimilarities). Note the discontinuous patterns of unusual climates, or ones without analogous climates at other times.

pervasive influences on the terrestrial biota (as in the case of the larger-spatial, longer-temporal scale variations at higher levels in the hierarchy), or they may produce more localized responses (as in the case of the smaller-spatial, shorter-temporal scale variations of lower-level components) (see Barnosky, 1987; Bartlein and Prentice, 1989; and Webb and Bartlein, 1992 for further discussion). Table 2 lists and gives examples of the characteristic features, the levels in the climate system hierarchy that contain the controls of the feature, and those that are involved in the response. Table 2 also indicates the *predictability* and *reversibility* of the individual features. Features are a) *predictable* (P), if the timing and amplitude of the variations can be specified; b) *expectable* (E), if either the timing or amplitude can be specified, but not both; or c) *unpredictable* (U), if neither the timing nor amplitude of the feature can be specified. Features are *reversible* (R), if the climate returns to a previous general mean state following the occurrence of the feature, or *not reversible* (N), if the climate does not return. The table also shows for time series, the relative importance of trend,

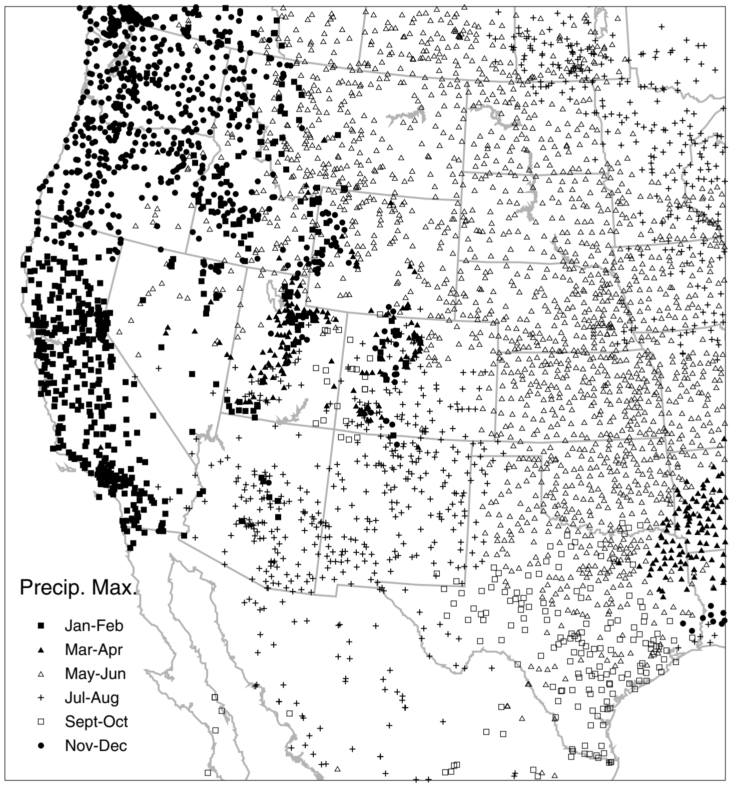

Figure 4: Seasonality of the precipitation maximum in western North America (Mock, 1966). The broadscale pattern of the winter maximum of precipitation along the west coast and summer maximum in the interior is evident, but there is also considerable spatial heterogeneity in the precipitation regime in topographically diverse portions of Colorado, Utah, Wyoming, Montana and Idaho. This pattern of spatial heterogeneity has probably been stable during the Holocene, leading to heterogeneity in the response of vegetation to large-scale climatic changes (Whitlock and Bartlein, 1993; Whitlock et al., 1995).

systematic (or periodic), and irregular components, and for spatial data, the relative importance of large-scale or small-scale patterns.

Trends, i.e., progressive increases or decreases in the levels of a particular climate variable, appear in palaeoclimatic variations on all timescales, but are particularly evident at certain scales. At the longest of timescales that are displayed in Figure 1 (Series A), cooling during the Cenozoic is evident in the general course of change in oxygen isotopic ratios toward heavier values (i.e., toward cooler oceans, more ice). This trend is likely driven by the external controls of the climate system, with all of the lower levels in the hierarchy responding. The general trend is broken, of course, by local increases in global temperature (as in the Eocene), and by locally more rapid decreases, but the overall impression one gets when viewing this series is of a progressive movement toward cooler conditions. The cooling trend is therefore expectable once underway (but its particular amplitude is not predictable), non-reversing overall, and dominated by the long-term changes (Table 2). Series B, oxygen-isotope data for the past 5 Myrs, also shows a generalized trend, which is the same climatic change as the more rapid decrease in global temperatures that is evident in

Table 2. Characteristic Features of Temporal and Spatial Variations of Climate

		Levels in Hierarchy *		Predictability/ Reversibility †		Components of Temporal Variations ‡		
Features	**Characteristic examples**	**Control**	**Response**	**Predict.**	**Reverse**	**Trend**	**System.**	**Irreg.**
Trends								
era-long	Cenozoic global cooling and glacierization	E	G-L	E	N	H	L	L
glacial/ interglacial	last deglaciation	E,G	H-L	P	R	H	L	L
multi-millennial	late-Holocene summer cooling in northern midlatitudes	G-C	R-L	E	R	L	L	H
century-long	20th century warming	G-C	R-L	E	R	L	L	H
Steps								
inter-epoch	onset of N. Hemisphere glaciation (ca. 2.65 Ma)	E	G-L	U	N	H	L	L
climate reversals	Younger Dryas climate reversal (ca. 13 - 11.5 ka)	G-C	R-L	E	R	H	L	L
Oscillations								
periodic (orbital)	ice sheet growth and decay, monsoon strengthen/weaken	E	G-L	P	R	L	H	L
changing-periodic (orbital)	strengthening of 100-kyr cycle in past million years	E	G-L	U	N	L	H	L
quasi-periodic (sub-orbital)	Dansgaard-Oeschger “cycles” /Heinrich events (75 - 10 ka)	E,G	H-L	E	R	L	M	H
interannual (10^0 - 10^1 yrs)	ENSO variations, decadal-scale climate anomalies	H,C	R-L	E	R	L	M	M
Fluctuations								
Holocene (10^3 - 10^4 yrs)	Holocene temperature and precipitation variations	G,H	C-L	E	R	M	L	H
sub-millennial (10^3 - 10^4 yrs)	Medieval Warm Period/ Little Ice Age variations	G-C	R-L	E	R	L	L	H
interannual (10^0 - 10^1 yrs)	aperiodic interannual climate variations	H,C	R-L	E	R	L	L	H
						Components of Spatial Variations ‡		
Translations						**Large**		**Small**
hemispheric (> 10^6 yrs)	high-latitude cooling, increase in N-S temperature gradients	E	G-L	U	N	H		L
continental (< 10^6 yrs)	latitudinal shifts of temperature zones, LGM-to-present	E-H	C-L	P	R	H		L
local	elevational shifts of temperature zones, LGM-to-present	E-R	M,L	P	R	L		H
Mosaics								
continental (> 10^6 yrs)	rainshadows; other continental-scale patterns	E	G-L	U	N	H		L
continental (< 10^6 yrs)	individualistic changes in climate variables since LGM	E-H	C-L	E	R	H		L
regional (> 10^2 yrs)	regional contrasts (e.g., PNW/ SW-US contrasts since LGM)	H,C	R-L	E	R	H		L
regional (10^1 - 10^2 yrs)	interannual variations (e.g., 1993 Mississippi R. floods)	H,C	R-L	E	R	H		L
mesoscale (> 10^1 yrs)	spatial heterogeneity of precipitation regimes	E-R	M,L	P	R	L		H
mesoscale (10^0 - 10^1 yrs)	synoptic-scale climate anomalies	E-R	M,L	P	R	L		H

* Levels in climate system hierarchy (see Table 1: E = external, G = global, H = hemispheric, C = continental, R = regional, M = mesoscale, L = local) controlling (Control) characteristic features of climatic variation or responding (Response) to them. † Predictability (Predict.) and reversibility (Reverse) of characteristic features of climatic variations: P = feature is predictable at the temporal or spatial scale indicated; E = feature is expectable, but not specifically predictable; U = feature is unpredictable. ‡ Relative amplitude (H = high, M = medium, L = low) of components of temporal (Trend, Systematic (Periodic), Irregular) or spatial (Large-scale, Small-scale) variations.

the last part of Series A. On a shorter timescale, the transition between the last glacial maximum (about 21,000 yrs ago) and present (Series C and D), can be viewed as a trend (predictable and reversible), although the higher temporal-resolution record from the GRIP Summit core (Series D) shows it broken by the Younger Dryas climate reversal (about 11.5 ka). During the latter half of the Holocene, many locations in the northern mid-latitudes experienced a cooling trend in summer; this is evident in the July temperature record at Elk Lake (Series E). Finally, during the last century, the global mean temperature, as well as that at individual stations has generally increased, and this trend is apparent in the summer temperature series from the Sierra Nevada (Series G). The climatic changes evident in Series E and G are expectable, but not predictable, and are dominated by the irregular component of variability.

Steps, i.e., abrupt (relative to the timescale of variations under consideration) transitions from one level to another, also appear on many different timescales. Notable examples of steps in the representative series include the unpredictable and non-reversing inter-epoch decreases in global temperature during the Cenozoic (as during the Eocene-Oligocene and Pliocene-Pleistocene transitions, Series A). Similarly, abrupt steps occur at the beginning and end of theYounger-Dryas climate reversal (around 11 ka) and at the terminations of the "Dansgaard-Oeschger" cycles (see Bond et al., 1993; Bond and Lotti, 1995) during the interval between 60 and 20 ka; these are evident in the Greenland ice core data (Series D). These steps are expectable, but not predictable, and have little irregular variation superimposed on the transition from one level to another.

Oscillations, i.e., either periodic or quasi-periodic variations about a stationary or slowly changing level, are one of the more prominent features of palaeoclimatic time series. Oscillations dominate the glacial-interglacial variations in global temperature, and the variations in the continent/ocean temperature contrast that govern the monsoons, each generated by the periodic variations of the earth's orbital elements (Series B and C) (Imbrie et al., 1984; Prell and Kutzbach, 1992). Consequently, these variations are highly predictable and systematic. One important characteristic of the oxygen-isotope variations apparent in the ODP Site 659 data (Series B) is the change in the relative importance of the different periodic components: prior to 1 Ma, the 41-kyr cycle is relatively more important, whereas afterward, the 100-kyr cycle becomes more prominent. These changes in periodicity seem inherently unpredictable, and non-reversing. Quasi-periodic variations (i.e., variations that are less-regular than the strictly periodic ones of the SPECMAP data (Series C)) appear at "sub-orbital" timescales, as in the aforementioned "Dansgaard-Oeschger" cycles. Interannual climate variations, such as those constituting the El Niño/Southern Oscillation (ENSO) variations (Diaz and Markgraf, 1992) also have been described as quasi-periodic. Although systematic variation is apparent in these series, they are only expectable, owing to the absence of strict periodicity.

Fluctuations, i.e., aperiodic variations of climate, appear at all timescales (unless they have been specifically suppressed, as in Series C), but tend to be more evident at shorter timescales. Variations in temperature and precipitation at Elk Lake (Series E and F), and in the Sierra Nevada (Series G and H), apart from the trends described above, can be described as fluctuations. Fluctuations are expectable, but not specifically predictable features in individual time series, and are distinguished from steps by their inherent reversibility.

Translations, i.e., lateral or elevational movements of climate zones, are apparent in sequences of palaeoclimatic simulations (e.g., Kutzbach et al., 1993; Webb et al., 1993) and may also be inferred from individual or global-scale palaeoclimatic records. For example, the movements toward cooler conditions apparent in Series A-D, like those observable in maps of the simulated climate of the Last Glacial Maximum, all involve greater cooling at high latitudes than at low, with a consequent equatorward displacement and latitudinal compression of individual isotherms, as in Figure 2 for eastern North America. In mountainous regions, these geographical shifts are expressed as vertical (downward in the case of cooling) movements of the elevations at which particular temperatures occur. The predictability and reversibility of translations depends on the timescale at which the changes occur.

Mosaics, i.e., heterogeneous patterns of climate or climatic changes, also develop on a variety of temporal and spatial scales. On the longer timescales, tectonism, and the changes in atmospheric circulation it induces, results in the development of rainshadows and belts of orographic precipitation (Ruddiman and Kutzbach, 1989). These fundamental changes in the patterns of climate variables are inherently unpredictable and non-reversing. On the decadal or interannual timescales, variations in the configuration of the large-scale circulation of the atmosphere create alternating patterns of positive and negative anomalies of temperature and precipitation (Namias, 1970). In regions of complex topography, even simple changes of a single climate variable will have a spatially heterogeneous expression (Fig. 2, western North America). Moreover, in such regions, the influence of hemispheric- and continental-scale circulation changes may be registered in a systematic fashion on the regional or mesoscale patterns of individual climate variables (Fig. 4), which may impart further spatial heterogeneity in the local response to changes in larger-scale controls (Whitlock and Bartlein, 1993; Whitlock et al., 1995; Mock, in press; Mock and Bartlein, 1995).

The variations of the simulated climate over North America since the Last Glacial Maximum also illustrate how the simultaneous changes of several individual climate variables can produce changing regional-scale patterns of unique climates--climates that do not have analogues at other times and other locations. The patterns suggest that the relatively simple translations of individual climate variables at the continental scale can produce regional-scale patterns of unusual climates.

For example, there is an area of unusual climate in the continental interior of North America at 11 ka (Fig. 3), where the values of individual climate variables are not particularly unusual (relative either to present or to earlier times), but the *combinations* of the values of the variables are (in this case, the seasonality of temperature is relatively high). Figure 3 also indicates that our conception of the present as "normal" or not unusual is mistaken. In overall terms, the climate of 6 ka is more representative of the climates at the other times during the past 21 kyr than is the present climate (the area of unique climates is smaller at 6 ka than at other times).

The unusualness of the present climate can be further illustrated by considering the variations in the combinations over the past 800,000 years of the July insolation anomaly at 65°N and global ice volume, two indices of the general state of the climate system (Fig. 5). One point stands out on this figure, the present. For nearly all of the time (allowing for some uncertainty in the oxygen-isotopic record), more ice has been present in the climate system than now, while about 70 percent of the time July insolation has been greater than present. The point in time that we know the most about is therefore quite unusual when viewed relative to the range of conditions that prevailed during the Quaternary. The last glacial maximum (LGM), which is often regarded as having a climate "opposite" to that of the present is also quite unusual; most of the time, the climate system has been in a state intermediate between the present and LGM. The tendency for the climate system to vary continuously, not dwelling in any particular state for long is also evident in the figure. Most of the time, the climate system is in the process of moving from one state to another, and only rarely do two of the points separated by 1 kyr overlap one another. Therefore, our understanding of how the biosphere responds to climatic variations is predicated on observations of relatively unusual situations.

DISCUSSION AND CONCLUSIONS

The characteristic features of climatic variations described above represent potential sources of environmental change that may evoke in the terrestrial biota the kinds of spatial and evolutionary responses discussed in other chapters of this volume. At any given time or place, the prevailing climate is the product of the superimposition of all of these features and their operation across all of the different timescales. The efficacy of a particular feature in producing a response probably depends on the amplitude of the associated climatic variation and its duration, the number of features superimposed, the tendency for a particular variation to be predictable or reversible, and also on the existence of intrinsic thresholds, which when exceeded, produce a response.

When the predictability, reversibility, and relative importance of the components of temporal and spatial variations (Table 2) are considered in light of the kinds of spatial and evolutionary

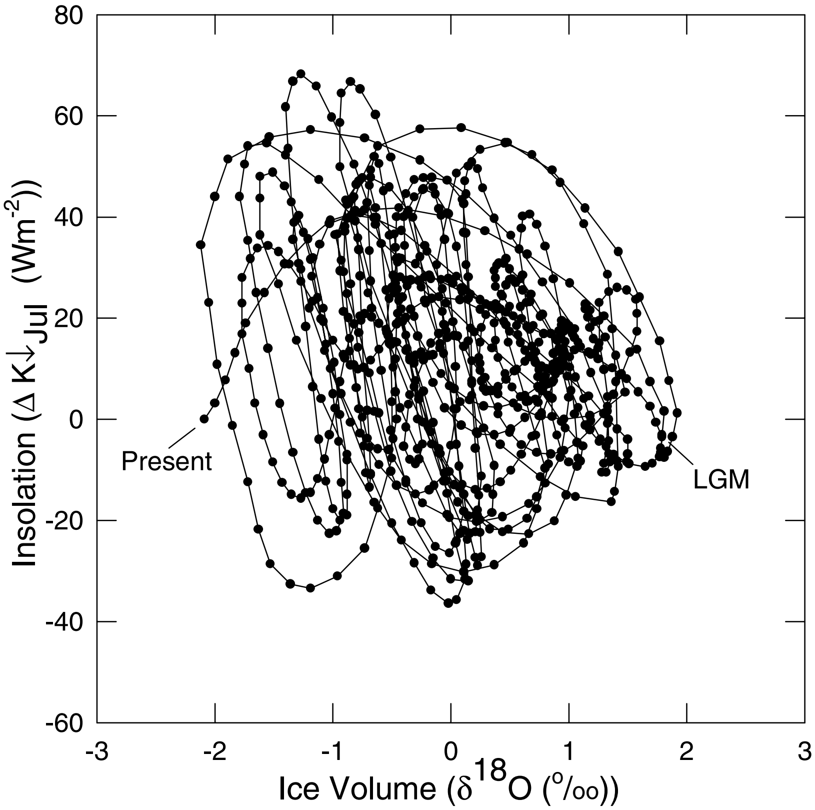

Figure 5: The trajectory of the climate system in a phase space defined by the July insolation anomaly (difference from present) at 65°N (Berger, 1978), and global ice volume as represented by the "SPECMAP" oxygen-isotope record (Imbrie et al., 1984). Points are plotted and 1-kyr intervals, and adjacent points are connected. The present and the last glacial maximum (LGM) are indicated.

responses described in this volume, the following picture emerges: Those climatic variations that are unpredictable and non-reversing, as well as those that are dominated by long-term or large-scale changes, are those that are more likely to evoke an evolutionary response, because they confront species with new and unfamiliar environments. Those variations that are predictable or expectable, or are dominated by short-term or small-scale variability, instead promote mainly spatial adjustments, such as migration (Huntley and Webb, 1989), because they present to species environments that have been experienced before and have been adapted to.

How species will likely respond to the potentially great future changes of climate will therefore depend on how large, rapid, and unfamiliar those changes are. The persistence of species across many large (as in the glacial-interglacial oscillations), and sometimes rapid (as in the case of the step-like climate reversals and quasi-periodic, sub-orbital oscillations) past climate changes, argues for a primarily spatial response at first. As the future climate grows increasingly more unfamiliar, however, evolutionary (extinction and speciation) responses should begin to emerge.

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REFERENCES

Barnosky CW (1987) Response of vegetation to climatic changes of different duration in the late Neogene. Trends in Ecology and Evolution 2:247-250.

Bartlein PJ (1988) Late-Tertiary and Quaternary palaeoenvironments. B. Huntley and T. Webb, III, (eds) Vegetation History Vol. 7, Kluwer Academic Publishers Amsterdam pp. 113-152.

Bartlein PJ and Prentice IC (1989) Orbital variations, climate and palaeoecology. Trends in Ecology and Evolution 4:195-199.

Bartlein PJ and Whitlock C (1993) Palaeoclimatic interpretation of the Elk Lake pollen record. J.P. Bradbury and W.E. Dean, (eds) Elk Lake, Minnesota: Evidence for Rapid Climate Change in the North-Central United States, Geological Society of America Boulder pp. 275-293.

Berger A (1978) Long-term variations of caloric insolation resulting from the Earth's orbital elements. Quaternary Research 9:139-167.

Bond G, Broecker W, Johnsen S, McManus J, Labeyrie L, Jouzel J and Bonani G (1993) Correlations between climate records from North Atlantic sediments and Greenland ice. Nature 365:143-147.

Bond G and Lotti R (1995) Iceberg discharges into the North Atlantic on millennial time scales during the Last Glaciation. Science 267:1005-1010

Charles CD, Rind D, Jouzel J, Koster RD and Fairbanks RG (1994) Glacial-interglacial changes in moisture sources for Greenland: influences on the ice core record of climate. Science 263:508-511

Dansgaard W, Johnson SJ, Clausen HB, Dahl-Jenson D, Gundestrup NS, Hammer CU, Hvidberg CS, Steffensen JP, Sveinbjörnsdottir AE, Jouzel J and Bond G (1993) Evidence for general instability of past climate from a 250-kyr ice-core record. Nature 364:218-220

Diaz HF and Markgraf V (1992) El Niño: historical and palaeoclimatic aspects of the southern oscillation. Cambridge: Cambridge Univ. Press, 476 p.

Graumlich LJ (1993) A 1000-year record of temperature and precipitation in the Sierra Nevada. Quaternary Research 39:249-255

Huntley B and Prentice IC (1988) July temperatures in Europe from pollen data, 6000 years before present. Science 241:687-690.

Huntley B and Prentice IC (1993) Holocene vegetation and climates of Europe. H.E. Wright, Jr., J.E. Kutzbach, T. Webb, III, W.F. Ruddiman, F.A. Street-Perrott and P.J. Bartlein, (eds) Global Climates since the Last Glacial Maximum, pp. 136-168.

Huntley B and Webb T, III (1989) Migration: species' response to climatic variations caused by changes in the earth's orbit. Journal of Biogeography 16:5-19.

Imbrie J, Hays JD, Martinson DG, McIntyre A, Mix AC, Morley JJ, Pisias NG, Prell WL and Shackleton NJ (1984) The orbital theory of Pleistocene climate: support from a revised chronology of the marine $\delta^{18}O$ record. A. Berger, J. Imbrie, J. Hays, G. Kukla and B. Saltzman, (eds) Milankovitch and Climate, Reidel Dordrecht, Netherlands pp. 269-305.

Kutzbach JE, Guetter PJ, Behling PJ and Selin R (1993) Simulated climatic changes: results of the COHMAP climate-model experiments. H.E. Wright Jr., J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott and P.J. Bartlein, (eds) Global Climates since the Last Glacial Maximum, University of Minnesota Press Minneapolis pp. 24-93.

McDowell PF, Webb T, III and Bartlein PJ (1990) Long-term environmental change. 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: Global and Regional Changes in the Biosphere over the Past 300 Years, Cambridge University Press Cambridge pp. 143-162.

Miller KG, Fairbanks RG and Mountain GS (1987) Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. Palaeoceanography 2:1-19.

Mitchell JM, Jr. (1976) An overview of climatic variability and its causal mechanisms. Quaternary Research 6:481-493.

Mock CJ (1996) Climatic controls and spatial variations of precipitation in the western United States. Journal of Climate 9:1111-1125.

Mock CJ and Bartlein PJ (1995 Spatial variability of Late-Quaternary palaeoclimates in the western United States. Quaternary Research 44:425-433.

Namias J (1970) Climate anomaly over the United States during the 1960's. Science 170:741-743.

Prell WL and Kutzbach JE (1992) Sensitivity of the Indian monsoon to forcing parameters and implications for its evolution. Nature 360:647-652.

Ruddiman WF and Kutzbach JE (1989) Forcing of Late Cenozoic northern hemisphere climate by plateau uplift in southern Asia and the American West. Journal of Geophysical Research 94:18409-18427.

Shackleton NJ and Imbrie J (1990) The $\delta^{18}O$ spectrum of oceanic deep water over a five-decade band. Climatic Change 16:217-230.

Tiedemann R, Sarnthein M and Shackleton NJ (1994) Astronomic timescale for the Pliocene Atlantic $\delta^{18}O$ and dust flux records of Ocean Drilling Program site 659. Palaeoceanography 4:619-639

Webb T, III (1989) The spectrum of temporal climatic variability: current estimates and the need for global and regional time series. R.S. Bradley, (ed) Global Changes of the Past, UCAR/ Office for Interdisciplinary Earth Studies Boulder, CO

Webb, T, III (1995) Pollen records of Late Quaternary vegetation change: plant community rearrangements and evolutionary implications. Board on Earth Sciences and Resources, Commission on Geosciences, Environment, and Resources, National Research Council, Effects of Past Global Change on Life, pp 221-232.

Webb T, III and Bartlein PJ (1992) Global changes during the last 3 Million years: climatic controls and biotic responses. Annual Reviews of Ecology and Systematics 23:141-173.

Webb T, III, Bartlein PJ, Harrison SP and Anderson KH (1993) Vegetation, lake levels, and climate in eastern North America for the past 18,000 years. H.E. Wright Jr., J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott and P.J. Bartlein, (eds) Global Climates since the Last Glacial Maximum, University of Minnesota Press Minneapolis pp. 415-467.

Whitlock C and Bartlein PJ (1993) Spatial variations of Holocene climatic change in the Yellowstone region. Quaternary Research 39:231-238.

Whitlock C, Bartlein PJ and Van Norman, KJ (1995) Stability of Holocene climate regimes in the Yellowstone Region. Quaternary Research 43:433-436.