

# Climatically forced vegetation dynamics in eastern North America during the Late Quaternary Period

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## Introduction

Vegetation dynamics span multiple spatial and temporal scales, and the changes involved manifest themselves in a variety of ways depending upon the ecological unit (from individuals to biomes) and/or taxonomic level (e.g. species, genera, families and orders) of description. Many biotic phenomena contribute to vegetation change including: (1) the establishment, growth, and death of individual plants within stands; (2) changes in the frequency, size, and genetic make-up of populations within landscapes; (3) changes in the distribution of species, genera, and plant functional types across regions and continents; and (4) the evolution and extinction of species. These biotic phenomena cause the vegetation to change in structure, density, extent, and composition, and they lead to and result from a variety of biospheric dynamics (such as variations in net primary production and carbon sequestration). Depending on scale, vegetation changes are caused by some combination of external (i.e. environmental) forcing and the biotic phenomena themselves. The multiple competing forcings (at work at different scales) and many nonlinear linkages (including feedbacks) can make the cause-and-effect explanations difficult to sort out at certain temporal and spatial scales. Across long-time spans, however, such as the late Quaternary, environmental variations are large and well known and their effect on vegetation history is relatively easy to recognize.

In this chapter, we consider vegetation dynamics at regional to continental scales and across millennia, scales at which vegetation change is primarily forced by centennial to orbital scales of climate change. The vegetation changes show up as the changing abundance, geographic extent, location, and association of plant taxon populations, which we record as changing pollen percentages. Only by linking the forces and induced responses can we convert the study of vegetation change and history into an analysis of vegetation dynamics, because to do so we must relate the apparent “motion” in these taxon populations to underlying forces, which is the very definition of dynamics. Motion by definition is temporal change in location, which requires temporal sequences of maps, difference maps, and/or isochrone maps to illustrate. Mapping temporal change in the vegetation is therefore central to studies of climatically forced vegetation dynamics. Here, we map fossil pollen data, as a proxy for vegetation data, from eastern and northern North America and compare both continental-scale and local records of the pollen-recorded vegetation change to maps and time series of independently observed or estimated

paleoclimate data. These comparisons are key to our empirical understanding of late-Quaternary vegetation dynamics. We admit that the “motion” of taxon populations shown on our maps is an epiphenomenon of the differential carbon sequestration in the different taxa in different locations, but we focus here on the motion apparent in the time series of pollen maps and use it and other pollen-recorded changes to represent how the vegetation changed. Many studies show how well pollen data from surficial sediments represent plant taxon abundances today and thus underpin our interpretative step here (Bradshaw & Webb, 1985; Jackson, 1994; Webb, 1995, 1974).

Datasets of lake-level variations, chironomid-inferred temperatures, and stable isotope ratios, as well as climate model output, help us to show the “forces” behind vegetation changes and to identify dynamics. We therefore take advantage of advances in paleoclimate data, analysis, and modeling that are providing an increasingly detailed picture of late-Quaternary climate changes. Just as radiocarbon dating freed pollen data from a correlation-based time frame, newly developed paleoclimate datasets now allow pollen data to be interpreted within an independently derived climate framework. We can therefore describe how the vegetation responded to multivariate changes in climate involving temperature, moisture, and seasonality.

We use both time series and maps of pollen data and climate estimates: (1) to illustrate a strong connection between climate and vegetation change; (2) to document continental- and regional-scale vegetation dynamics that result from millennial- and orbital-scale climate forcing; and (3) to demonstrate that the conditions held for dynamic equilibrium between vegetation and climate at orbital time scales and possibly at millennial scales. By mapping both individual taxa and assemblages of taxa, we describe vegetation responses to independently documented climatic forcing at several levels of ecological organization from taxon movements to shifts in biome position, extent, and composition. Our chapter focuses on examples from North American vegetation history that illustrate key climatically forced vegetation dynamics. In doing so, we aim to complement the discussion of vegetation history by Grimm & Jacobson (this volume), Thompson *et al.* (this volume), and Anderson *et al.* (this volume), and build on the critical reviews written by Cushing (1965), Davis (1965), and Whitehead (1965) that Grimm & Jacobson (this volume) so ably review in their introduction. Too few pollen diagrams with radiocarbon dates existed for mapping the data on an independent time frame in 1965. Since then palynologists

have published over 500 pollen diagrams with radiocarbon dates in eastern and northern North America. Other researchers have generated data independent of pollen data for estimating past changes in climate, and climate modeling has yielded valuable simulations of late Quaternary climates and climate change (Webb, 1998; Wright *et al.*, 1993). These developments allow a fresh understanding of vegetation dynamics and testing of many of the hypotheses posed by Cushing (1965), Davis (1965), and Whitehead (1965).

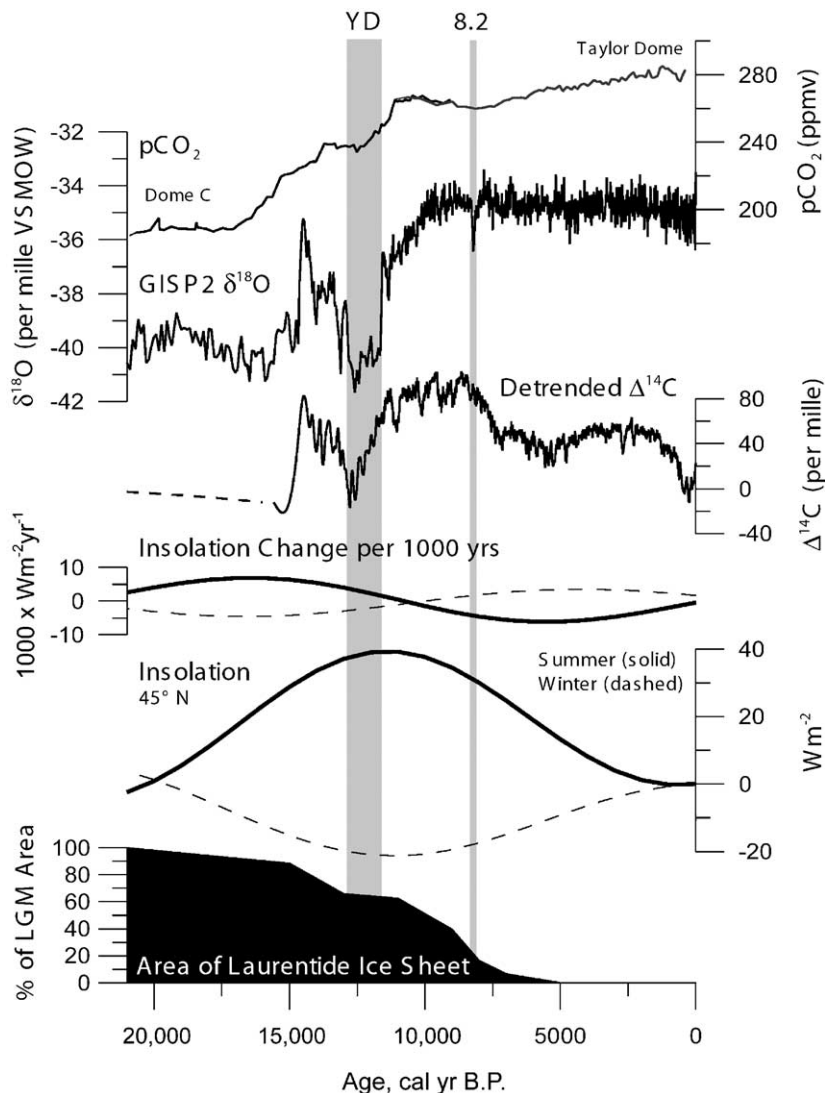
**Data and Methods**

*Records of Pollen, Lake Levels, and Vegetation Change*

We apply the zoom-lens concept (i.e. linking maps and time-series data in order to span spatial and temporal scales, Figs 1–11, Webb, 1995, 2001) to describe vegetation dynamics across several levels of ecological organization. We zoom from individual sites up to continental patterns and

from centuries up to several millennia in order to incorporate local changes for taxon populations up to continental scale rearrangements of taxa, tree-cover groups, and biomes. We use time sequences of continental-scale maps to show long-term spatial trends (e.g. range shifts and changing abundances) that most likely result from macroclimatic patterns (Figs 1–3) and subsume all of the short-term, small-scale vegetation dynamics most often studied by ecologists, such as succession. Contouring the pollen data (via locally weighted spatial smoothing) emphasizes the broad-scale patterns. Uncertainties in: (a) radiocarbon dates; (b) their calibration into calendar years (Stuiver *et al.*, 1998); and (c) the interpolation of time between dates limit the temporal resolution of maps to ~500–1000 yr, but much higher temporal resolution can be obtained in individual pollen diagrams. By combining maps and time series, we can zoom in spatially to individual sites and gain temporal resolution that is not possible when correlating data between sites at the broader map scale (Webb, 2000, 2001). Pairing time series of pollen data with independent climate records from the same site allows focused

*Fig. 1. Controls on North American climates and climate changes over the past 21,000 years. Atmospheric carbon dioxide concentration (pCO<sub>2</sub>) is shown from Antarctic ice core records (Taylor Dome, Indermühle *et al.*, 1999; Dome C, Monnin *et al.*, 2001). Oxygen isotope ratios from a Greenland ice core (GISP2) record abrupt temperature changes in the North Atlantic region (Stuiver *et al.*, 1995). The linearly detrended record of change in atmospheric radiocarbon concentration (Stuiver *et al.*, 1998) records long-term changes in radiocarbon production, but also rapid changes in oceanic ventilation and North Atlantic thermohaline circulation (Clark *et al.*, 2001; Stuiver *et al.*, 1995). Long-term changes in summer and winter insolation at 45°N latitude are shown as calculated by Berger (1978). The area of the Laurentide ice sheet was estimated from maps by Dyke & Prest (1987) and shifted in calendar years in accordance with Barber *et al.* (1999).*



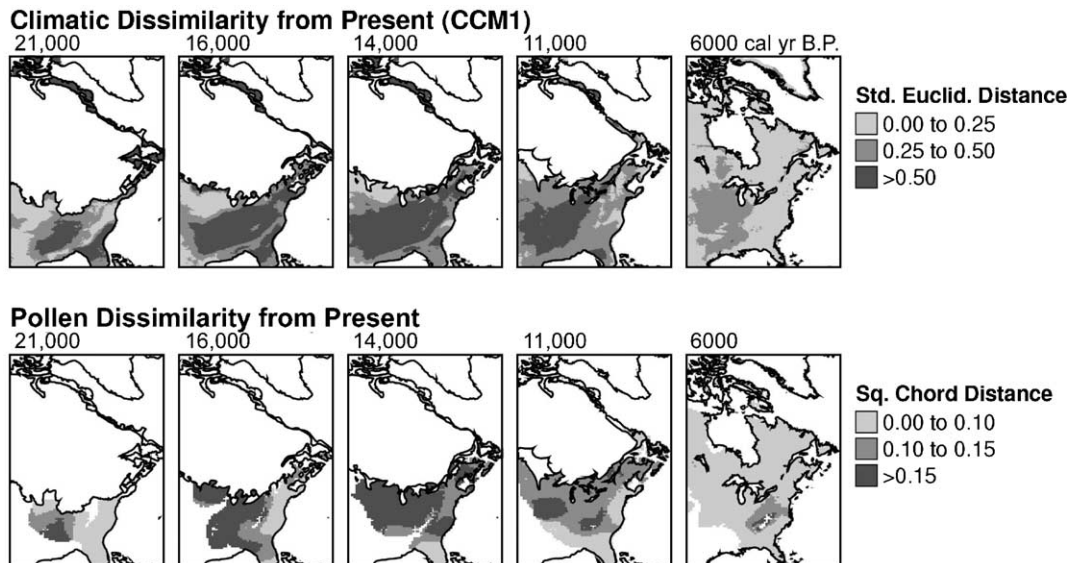


Fig. 2. Dissimilarity values for the fossil pollen data and CCM1 climate simulations for different times. The rows of maps indicate the dissimilarity of the simulated climates (top) and fossil pollen assemblages (bottom) from their best modern counterpart. (See Williams *et al.*, 2001, for explanation of the dissimilarity measures used.)

study of the nature and rates of vegetation change associated with millennial- and finer-scale changes in climate. These temporal changes are the local and regional manifestations of continental-scale phenomena shown on the maps.

The contoured maps of pollen percentages show changes in range and abundance for individual taxa and associations of taxa (Figs 3 and 4). Biome maps (Fig. 4) derived from a pollen-to-biome classification method (Prentice *et al.*, 1996; Prentice & Webb, 1998; Williams *et al.*, 1998) and tree cover maps (Fig. 5) characterize vegetation physiognomy and structure (Williams, 2003; Williams & Jackson, 2003). We also assess the changes in vegetation between time intervals by mapping: (1) the difference in the percent abundance of individual pollen types (Fig. 6); (2) biome distribution changes (Fig. 6); and (3) dissimilarity measures for assemblage changes at each grid point (Figs 2 and 7). To highlight long-term changes, we focus on the changes that took place between both 21,000 and 6000 cal yr B.P. and presettlement time (500 cal yr B.P.) (Fig. 6). Squared-chord distances (Overpeck *et al.*, 1985) provide a multivariate measure of the difference between pollen samples, either between fossil and modern samples (Fig. 2) or between consecutive time intervals spaced apart by 1000, 3000, and 5000 years (Fig. 7). These latter maps provide an update to the histograms of chord distances between samples at 100-yr intervals from selected sites in Jacobson *et al.* (1987) and between 500-, 1000-, and 3000-year intervals at all sites in Overpeck *et al.* (1991).

Our maps of the pollen and lake-level data update those of Bernabo & Webb (1977), Webb *et al.* (1983), Jacobson *et al.* (1987), Webb (1988), Harrison (1989), R.S. Webb (1990), R.S. Webb *et al.* (1993), T. Webb *et al.* (1993), and Jackson *et al.* (1997) by showing the data after their radiocarbon dates are calibrated to calendar years. We also map paleoge-

graphic features like ice-sheet extent, shorelines, and glacial lakes. Shuman (2001) and Shuman *et al.* (2002b) describe the lake-level data and their mapping, and T. Webb *et al.* (1993), Shuman (2001), and Williams *et al.* (2000, 2001) list the pollen sites and dating choices. The pollen data are available from (<http://www.ngdc.noaa.gov/paleo/napd.html>).

#### Independent Climate Estimates

A multi-proxy paleoclimate framework for the past 21,000 calendar years is emerging from recent studies that is suitable for comparison with the maps of fossil pollen data at millennial and longer time-scales and with selected individual pollen records at shorter time-scales. Each type of paleoclimate data is sensitive to different aspects of climate, and together they provide a rich source of information about past climatic variations. Many aspects of past climates can be deduced, independently of the fossil pollen record, using paleolimnological data to infer past lake levels (e.g. Digerfeldt, 1986), to obtain stable isotopes ratios (e.g. Fritz *et al.*, 2000; Stuiver, 1968; Yu *et al.*, 1997), and to yield assemblages of aquatic biota such as diatoms, ostracodes, chironomids, and testate amoebae (e.g. Booth & Jackson, 2003; Fritz *et al.*, 2000; Smith, 1993; Walker *et al.*, 1991). Pairing such records with fossil pollen assemblages enables the study of ecological responses to environmental change, particularly when all records are collected from the same site (Ammann *et al.*, 2000; Bradbury & Dean, 1993; Shuman *et al.*, in press; Williams *et al.*, 2002; Yu *et al.*, 1997).

We compare the fossil pollen data to local and regional temperature trends inferred from hydrogen isotope ratios (Fig. 8) (Huang *et al.*, 2002) and from chironomid

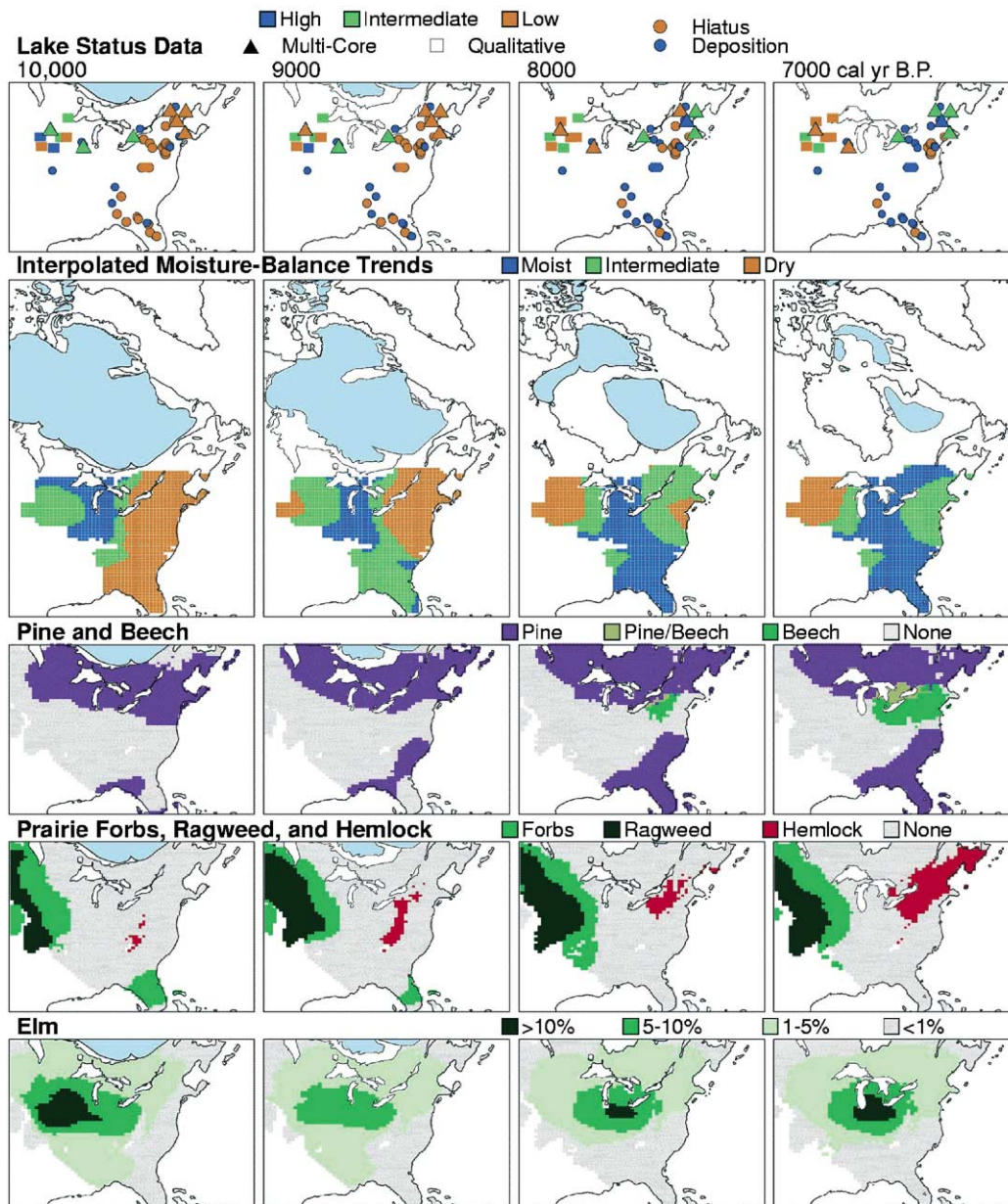


Fig. 3. Maps from 10,000 to 7000 cal yr B.P. illustrate changing moisture-balance patterns and vegetation distributions as the Laurentide ice sheet collapsed. The uppermost panel shows three types of lake-level data: multi-core, multi-proxy studies like *Digerfeldt (1986)*, qualitative assessments of lake-level indicators following *Harrison (1989)*, and hiatuses in published pollen stratigraphies. The second panel shows the general trends in moisture balance according to a locally weighted interpolation of the lake-level data. Two lower panels show parallel changes in the extent of regions with >25% pine (*Pinus*), 5% beech (*Fagus*), 15% prairie forb (*Asteraceae*, *Chenopodiaceae*/*Amaranthaceae*, and *Artemisia*), 10% ragweed (*Ambrosia*), and 10% hemlock (*Tsuga*) pollen (from *Shuman et al., 2002b*).

assemblages (Fig. 9) (*Levesque et al., 1993; Walker et al., 1991; Williams et al., 2002*). Both types of data can be controlled by factors other than temperature, but in certain settings, such as those considered here, each can yield useful paleotemperature estimates. We also map past moisture balance trends derived from lake-level data (Fig. 3) (e.g. *Harrison, 1989; Shuman, 2001; Shuman et al., 2002b; R.S.*

*Webb et al., 1993*). Striking regional similarities among the lake-level histories of multiple lakes studied by the *Digerfeldt (1986)* method likely reflect long-term changes in regional moisture-balance (e.g. among New England and Quebec lakes studied by *Almquist et al., 2001; Lavoie & Richard, 2000; Newby et al., 2000; Shuman, 2001; Shuman et al., 2001*). The maps also include: (1) evidence for drier-than-modern

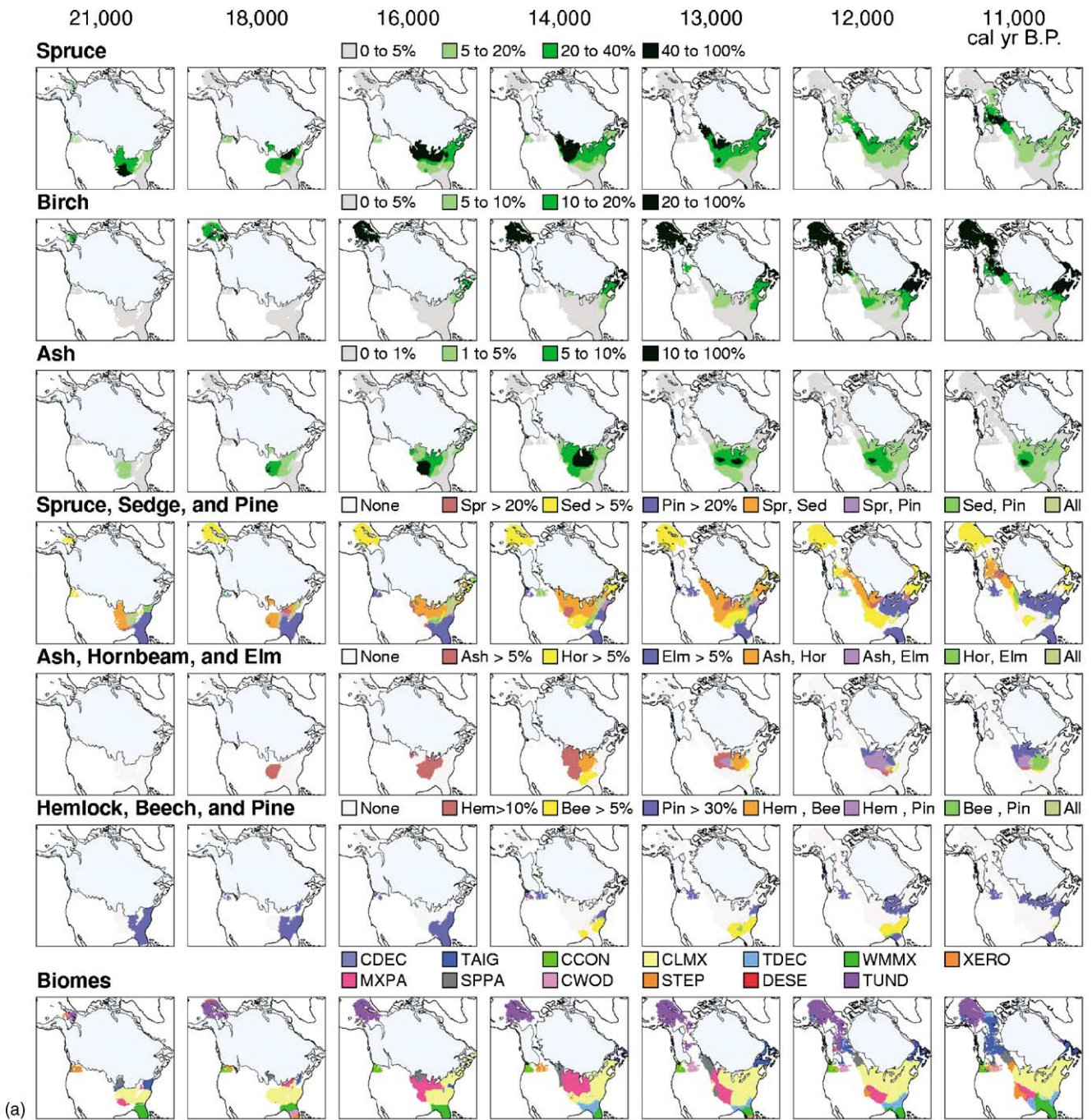


Fig. 4. Maps of individual taxa, combinations of three taxa, and biomes for selected dates during the past 21,000 years. Upper three rows show the distributions of individual taxa: spruce (*Picea*), birch (*Betula*), and ash (*Fraxinus*). Three progressively darker shades of green represent progressively higher relative abundance. Grey indicates the absence of the taxa at the mapped abundance level, and white indicates regions with no data. The fourth through sixth rows contain maps of three combinations of three taxa: spruce, sedge (*Cyperaceae*), and pine (*Pinus*); ash, hornbeam (*Ostrya*-type), and elm (*Ulmus*); pine, hemlock (*Tsuga*) and beech (*Fagus*). Individual taxa are plotted, where they grow alone, as either red, yellow, or blue, and combinations of the taxa are plotted as combinations of these primary colors. The bottom row shows maps of biome distribution. Biomes include cool deciduous forest (CDEC, light blue), taiga (TAIG, dark blue), cool conifer forest (CCON, light green), cool mixed forest (CLMX, yellow), temperate deciduous forest (TDEC, pale blue), warm mixed forest (WMMX, bright green), xerophytic woodland (XERO, orange), mixed parkland (MXPA, red), spruce parkland (SPPA, gray), conifer woodland (CEOD, pink), steppe (STEP, orange), desert (DESE, bright orange), and tundra (TUND, purple). Maps are accurate within an envelope of 500 years about the time assigned to them.

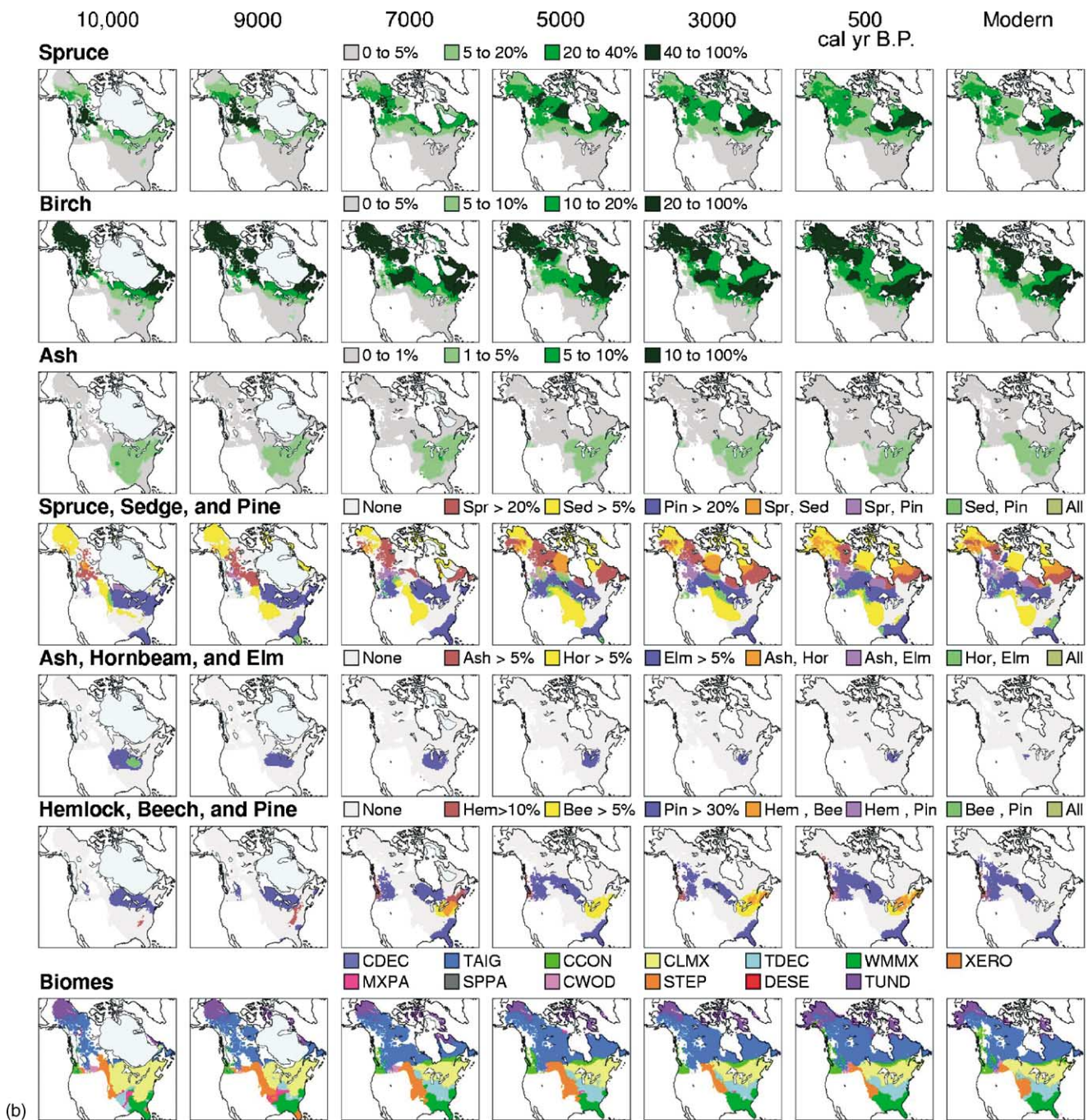


Fig. 4. (Continued)

conditions from sedimentary hiatuses in lake cores (Webb & Webb, 1988); and (2) qualitative estimates of lake-level change based upon sediment type, aquatic macrofossils, and other indicators (e.g. Harrison, 1989; Webb, 1990).

General circulation model experiments have provided another source of independently derived information about past climates at broad scales. The experiments show possible climate responses to known changes in climatic boundary conditions (Fig. 1), such as the long-term changes in inso-

lation (Berger, 1978), glacial extent (Dyke & Prest, 1987), and atmospheric carbon dioxide concentrations (Indermühle *et al.*, 1999; Monnin *et al.*, 2001). Model simulations may not be accurate at all scales or for each climatic variable, but previous data-model comparisons support the general simulation of glacial-to-interglacial climate change (Webb, 1998; Whitlock *et al.*, 2001; Wright *et al.*, 1993) and of certain millennial-scale climate changes (Rind *et al.*, 1986; Rutter *et al.*, 2000).

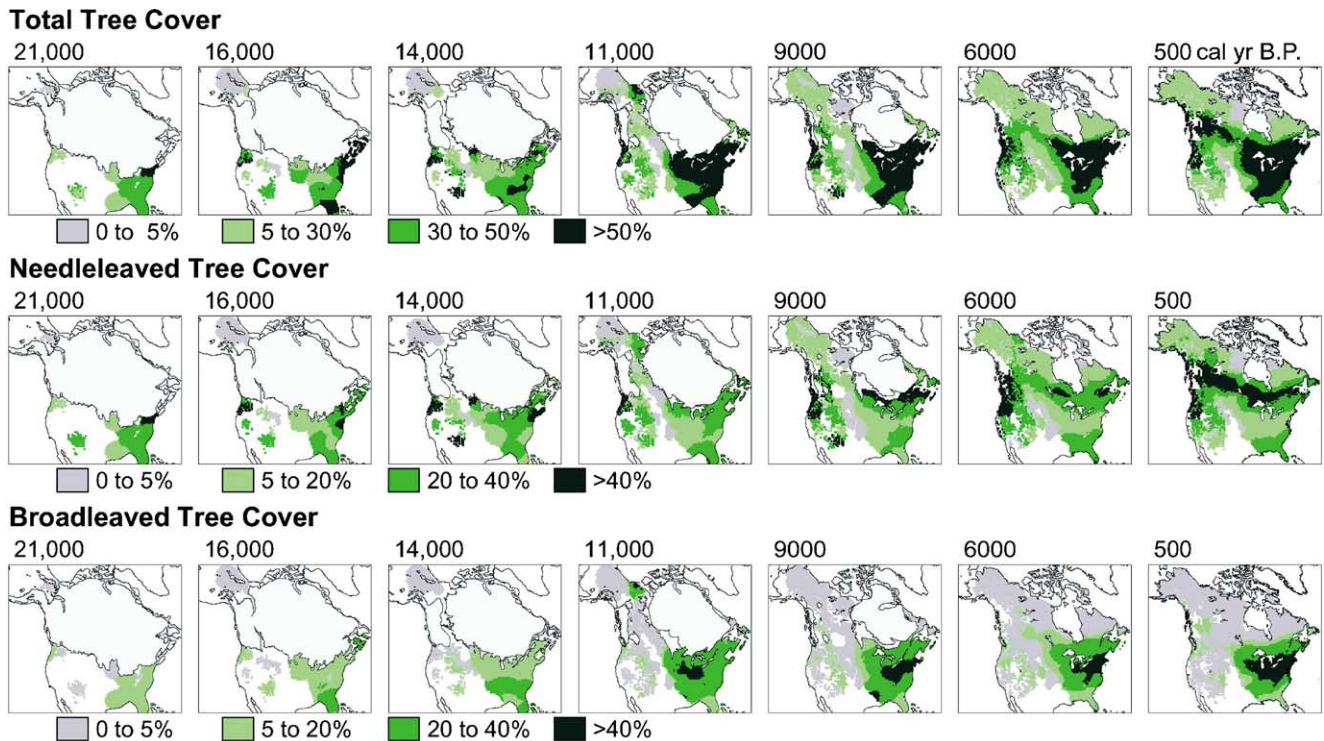


Fig. 5. Tree cover maps for all woody taxa, needle-leaved taxa, and broad-leaved taxa. Tree coverages are expressed as percentages of total area within each  $50 \times 50$  km grid cell (from Williams, 2003).

## Results

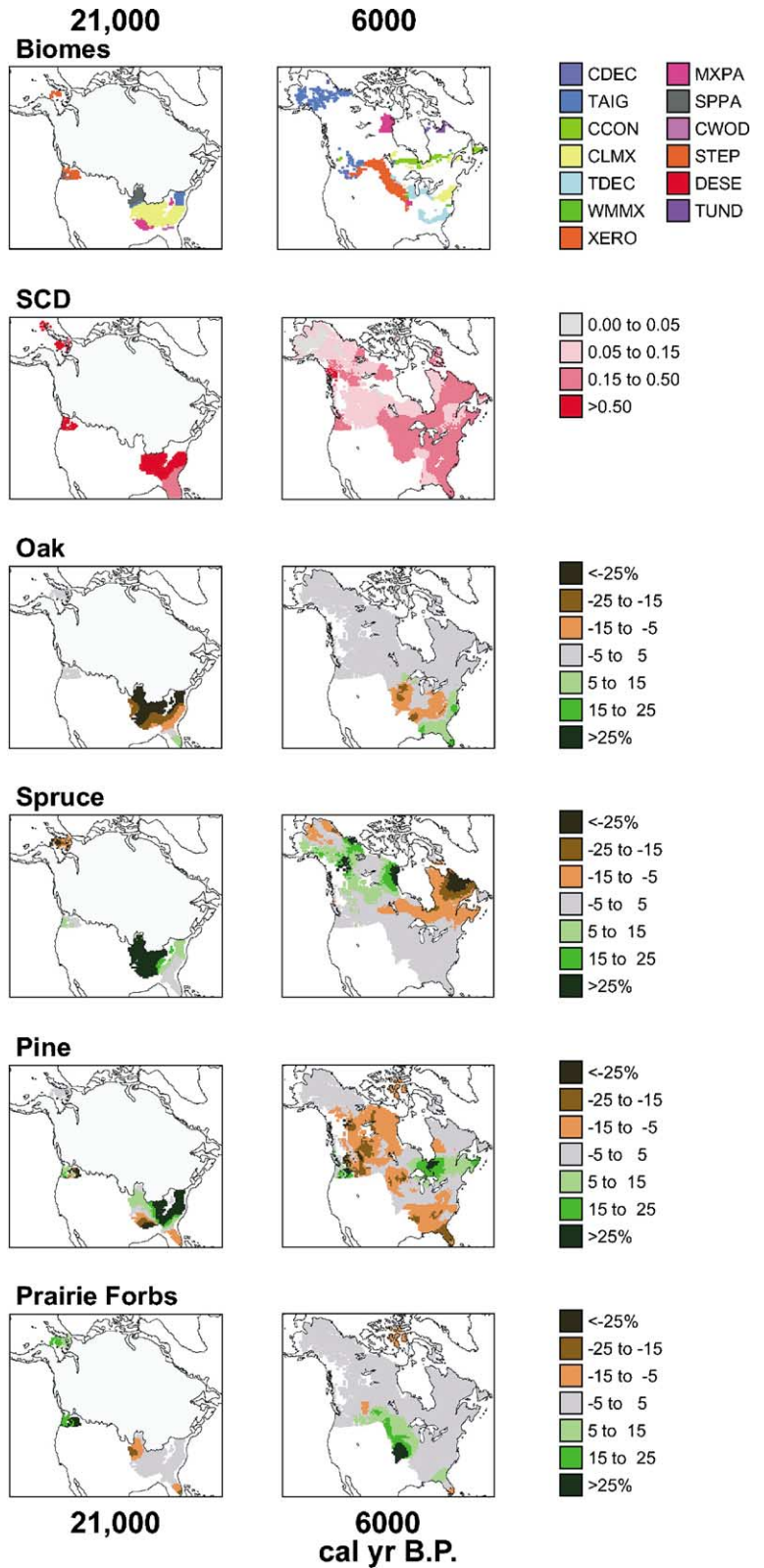
### North American Climates Over the Past 21,000 Years

In the time since the last glacial maximum (LGM), 21,000 years ago, North American climates have changed significantly at both orbital and millennial time scales. Between 21,000 and 6,000 years ago, climates warmed and full-glacial conditions gave way to interglacial conditions (Bartlein *et al.*, 1998; COHMAP, 1988). Changes in seasonal insolation, ice-sheet extent, and atmospheric carbon dioxide and dust concentration are the main controls for these orbital-scale changes (Kutzbach *et al.*, 1993, 1998) (Fig. 1). The glacial-interglacial transition was punctuated, however, by fast changes in global climate controls (Fig. 1), such as: (1) the reorganization of oceanic heat transport ca. 14,600, 12,900, and 11,600 cal yr B.P. at the beginning and end of the Bølling/Allerød and Younger Dryas chronozones (Broecker *et al.*, 1985; Clark *et al.*, 2002; Ruddiman & McIntyre, 1981; Rühlemann *et al.*, 1999), which is tracked by changes in atmospheric  $^{14}\text{C}$  concentration (Clark *et al.*, 2001; Stuiver *et al.*, 1995); (2) the rapid increases in atmospheric carbon dioxide concentration ca. 15,000 and 11,000 cal yr B.P. (Monnin *et al.*, 2001); and (3) the final collapse of the Laurentide ice sheet ca. 8200 cal yr B.P. (Barber *et al.*, 1999).

At orbital time scales, data and model syntheses by COHMAP (1988; Webb, 1998; Wright *et al.*, 1993) show how: (1) ice-sheet retreat; and (2) the shift from low to high to low seasonality in insolation (Fig. 1) created spatially

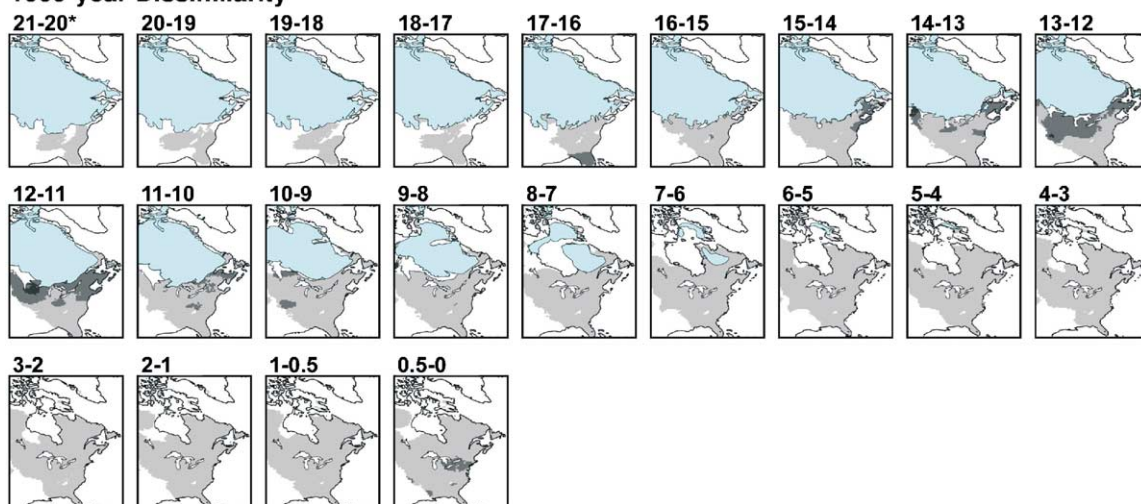
variable patterns of climate change across North America and the globe. In North America, the southern branch of the jet and winter storm track moved north, and the glacial anticyclone lessened and then disappeared as continental ice sheets retreated. From 16,000 to 9,000 cal yr B.P., the combination of ice sheet coverage,  $\text{CO}_2$  levels, and increased insolation seasonality (Fig. 1) was different enough from today to induce the NCAR CCM1 to simulate climates unlike any today in the North American mid-continent (Fig. 2). These simulated climates without modern analogs were characterized by warmer-than-present summers, colder-than-present winters, and low precipitation levels relative to present (Kutzbach *et al.*, 1998; Webb *et al.*, 1998). The timing of maximum warmth, cooling, dryness, or wetness varied geographically, however, in response to the spatial variations in: (a) forcing; and (b) atmospheric circulation changes, which differentially altered the advection of heat and moisture (Bartlein *et al.*, 1998). For example, during the early Holocene, higher-than-present seasonality of insolation and the retreating ice sheet altered radiation and temperature gradients. As a result, circulation patterns changed. The maps of lake-level variations (Fig. 3) in eastern North America illustrate the resulting spatial patterns of moisture-balance change by showing how the Midwest dried out while the Southeast and then the Northeast became wetter. Part of this gradual change was punctuated by an abrupt change in atmospheric circulation at 8200 cal yr B.P. induced by the final collapse of the Laurentide ice sheet (Shuman *et al.*, 2002b).

Fig. 6. Vegetation anomaly maps for the last glacial maximum and mid-Holocene, expressed in terms of biomes, oak, spruce, pine, and prairie forbs. All anomalies are expressed as differences between the past time period and pre-settlement vegetation (21,000–500 cal yr B.P.; 6000–500 cal yr B.P.). Blank areas in the biome maps indicate no data or no change in biome type. In the top panels, colored areas show the biome assignments for the past interval in grid cells that have changed between the present and past. Biome abbreviations same as in Fig. 4. Green colors in the individual taxon anomaly maps indicate that a taxon was locally more abundant in the past; browns indicate areas where a taxon is more abundant at present.

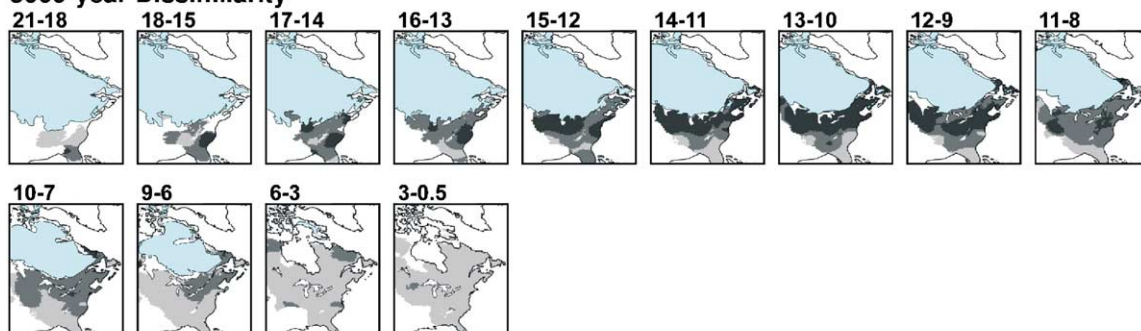


## Pollen Dissimilarities Across the Time Interval at Each Grid Cell

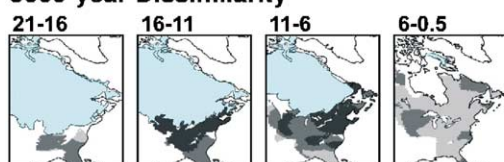
### 1000-year Dissimilarity



### 3000-year Dissimilarity



### 5000-year Dissimilarity



Squared Chord Distance  
 □ 0.00 to 0.20    ■ 0.20 to 0.40    ■ > 0.40    □ No Data  
 \*Age, x1000 cal yr B.P.

Fig. 7. Maps of square-chord distance between fossil pollen spectra at each mapped  $50 \times 50$  km grid point and pollen spectra at the same grid point 1000, 3000, and 5000 years later. The difference between modern (0 yr ago) and just before European settlement (500 yr ago) is also shown. Large differences between intervals are estimated by large square-chord distances, and plotted as dark gray or black. Distances greater than 0.20 are greater than the modern difference among biomes (see [Overpeck et al., 1985](#)). The contour intervals were chosen because they allow the maps to illustrate the contrast in the spatial patterns between the 1000-yr difference maps and the 3000-yr and 5000-yr difference maps.

Millennial-scale climate variability also resulted in distinct spatial patterns of change. Changes during the Younger Dryas chronozone (12,900–11,600 cal yr B.P.) provide an illustrative example. Sea-surface temperatures (SST's) in the North Atlantic were colder than during the previous two millennia ([Ruddiman & McIntyre, 1981](#)) and directly cooled proximate regions of North America ([Mott et al., 1986](#); [Peteet et al., 1990](#); [Walker et al., 1991](#)). These patterns of climate change during the Younger Dryas chronozone resulted from reorganized ocean and atmospheric heat transport, which

also led to seasonally warmer climates elsewhere in North America ([Kneller & Peteet, 1999](#); [Shuman et al., 2002a](#)) and in other regions of the world ([Bluiner et al., 1998](#); [Clark et al., 2002](#); [Rühlemann et al., 1999](#)). Globally, Younger Dryas climate patterns were unique within the past 21,000 years because the changes in ocean circulation were embedded within a context of radiation forcing, ice-sheet extent, and carbon dioxide concentrations that was strikingly different from other times ([Figs 1 and 4](#)) (see also figures in [Whitlock et al., 2001](#)).

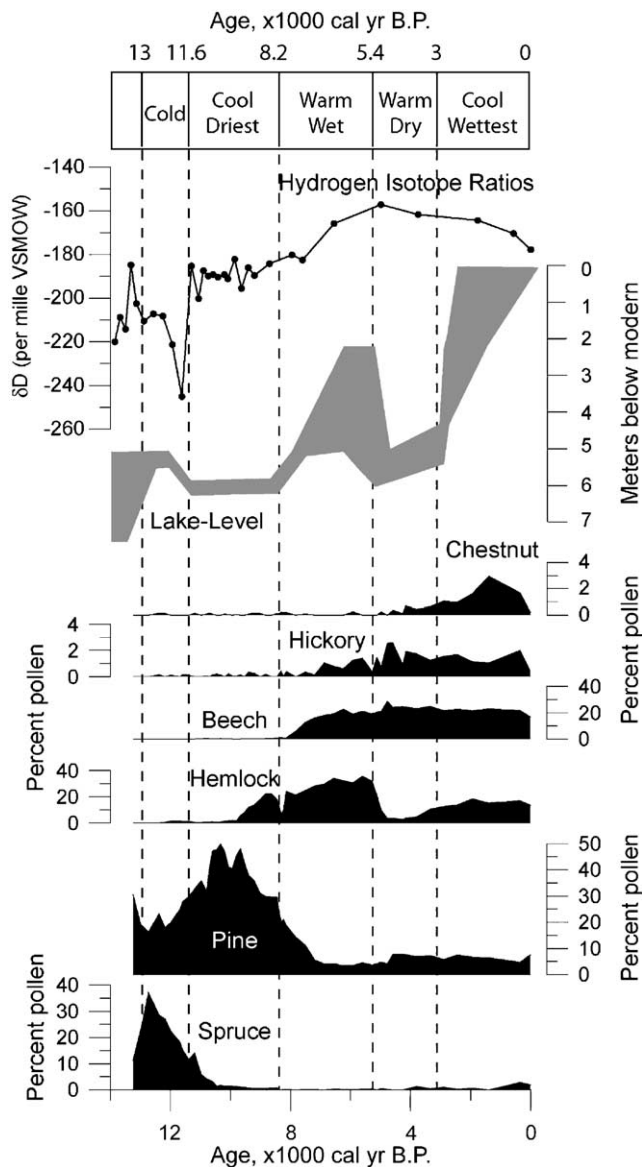


Fig. 8. Summary of New England climate and vegetation history. Hydrogen isotope ratios and lake-level estimates from Crooked Pond (Huang *et al.*, 2002; Shuman *et al.*, 2001) in southeastern MA are compared with pollen percentages from North Pond (Whitehead & Crisman, 1978) in western MA 206 km to the northwest of Crooked Pond. Inferred climate phases are given at top (from Shuman *et al.*, 2003).

#### Individualistic Responses by Taxa to Orbital-Scale Climate Change

Our maps match those of Jackson *et al.* (2000) in showing how much the vegetation patterns at the LGM differed from those today (Figs 4 and 6). Conifer parklands grew south of the ice sheet grading into pine woodlands along the southeast coast into Florida (Fig. 4). Deciduous trees and shrubs were not numerous, but grasses and sedges were relatively abundant implying an openness to the vegetation (Figs 4 and 5).

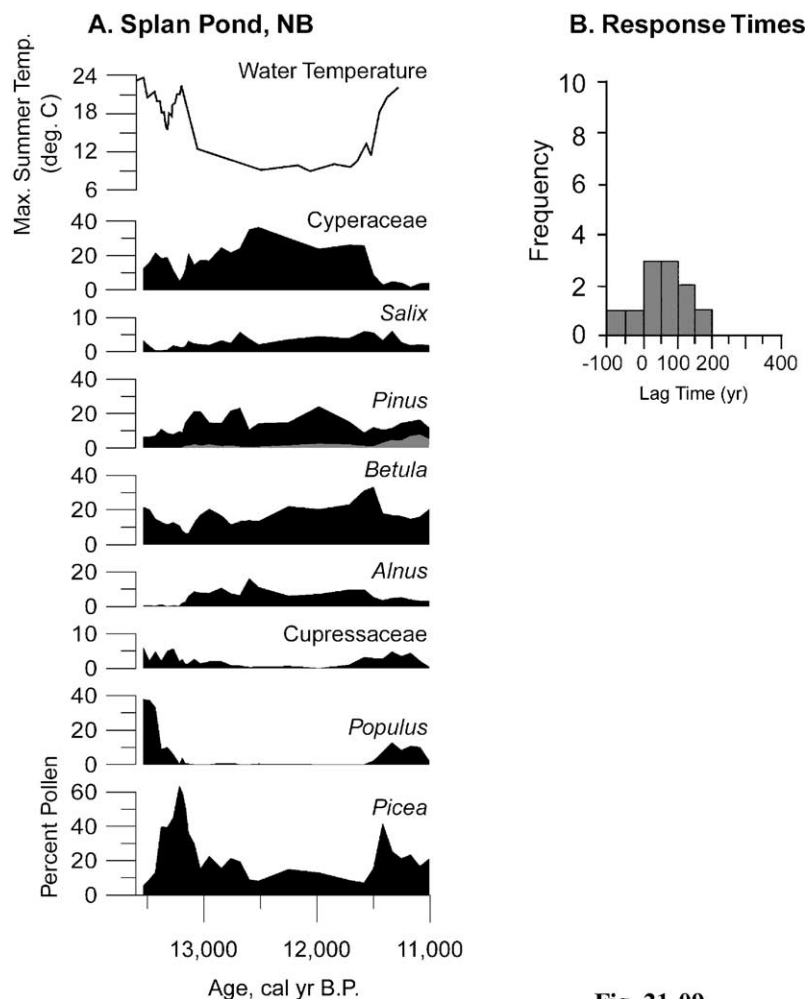
The full-glacial climatic conditions produced a distribution of biomes that differed markedly from today. Several modern biomes (e.g. taiga, cool conifer forest, and temperate deciduous forest) were not evident or were much restricted in range (Figs 4 and 6).

With the beginning of the long-term ice-sheet retreat and temperature increase (Fig. 1), both the range boundaries and the regions of peak abundance for many taxa shifted northward as well as east or west (Fig. 4). For example, spruce was abundant from 21,000 to 13,000 cal yr B.P. in the east and its area of high abundance then rapidly shifted into western Canada by 11,000 cal yr B.P. By the early Holocene, the range of spruce covered much of boreal Canada as it does today, but was restricted by the ice sheet. Following 7000 years of low abundance in the east, however, the peak of spruce abundance shifted eastward from western to eastern Canada after 6000 cal yr B.P. The maximum abundance of many taxa also increased as ranges shifted. Birch abundance began increasing in Beringia after 18,000 cal yr B.P. and south of the ice sheet only after 16,000 cal yr B.P. In eastern North America, hemlock only began increasing as it spread north through the Appalachians after 10,000 cal yr B.P. (Figs 3 and 4). Other taxa (e.g. ash and elm) reached greater-than-modern abundance and range extent during the late Pleistocene and early Holocene from 16,000 to 10,000 cal yr B.P. (Fig. 4). As a consequence of these varying independent movements among the taxa in terms of their geographic range and the location of their abundance maxima, new assemblages emerged and then disappeared. For example, spruce, sedge, and ash overlapped in their area of abundance from 16,000 to 12,000 cal yr B.P. to create a mixed parkland biome that does not exist today (Fig. 4). The mixed forest that contains both hemlock and beech today only formed after the ice sheet collapsed ca. 8000 cal yr B.P. (Figs 3 and 4).

The associations of plant taxa and functional types that were unlike any growing today in North America (i.e. no-analog vegetation) appear to have developed under climates that were also dissimilar from today (Fig. 2). From 16,000 to 11,000 cal yr B.P., the NCAR CCM1 simulated climates without modern analogs just where the pollen data indicate that plant assemblages without modern equivalents grew (Fig. 2) (Williams *et al.*, 2001). The observed match between the pollen data and model simulations supports earlier hypotheses that the no-analog plant associations formed as a consequence of plant taxa responding individually to multivariate changes in climate (Cushing, 1965; Overpeck *et al.*, 1992).

Besides changes in temperature and the seasonality of insolation, variations in moisture balance also played a large role in altering vegetation patterns. For example, within the early Holocene, lake-level maps show the Midwest becoming dry between 10,000 and 7000 cal yr B.P. and the vegetation responding with the eastward expansion of the prairie (Fig. 3). In the Northeast, conditions were dry at 10,000 cal yr B.P., and then became wetter as mesic taxa like birch, hemlock, maple, and beech replaced the white pine populations that had been dominant there (Fig. 3; Davis & Jacobson, 1985; Jackson *et al.*, 1997; Newby *et al.*, 2000; Shuman *et al.*, 2001, 2002b). The Southeast was

Fig. 9. (a) Summer temperatures at Splan Pond, New Brunswick, spanning the Younger Dryas chronozone, inferred from fossil chironomid evidence (Levesque *et al.*, 1993) and compared to pollen data from the same site (Mayle & Cwynar, 1995). Arboreal pollen types shown are spruce (*Picea*), aspen (*Populus*), cedars (*Cupressaceae*), alder (*Alnus*), birch (*Betula*), and total pines (*Pinus*) with white pine (*P. strobus*-type) shown in gray; nonarboreal pollen types are willow (*Salix*) and sedges (*Cyperaceae*). (b) A histogram of the time lags (positive if pollen data are lagging) associated with the most significant (i.e. lowest *p*-value) cross-correlations between the climate proxy record and pollen principal components done down-core for each of eleven sites in Maritime Canada and Europe (Williams *et al.*, 2002).



also drier than today before 10,000 cal yr B.P. and then its moisture balance became more positive as southern pines replaced oaks there after 8000 cal yr B.P. These maps show how closely the vegetation changes match those in moisture balance and how well taxa favoring wet or dry conditions respond to the appropriate changes in moisture (Fig. 3). The climate response surfaces for these pollen taxa support these interpretations (T. Webb *et al.*, 1993, 1998).

The adjustments of individual plant taxa to climate change also led to new arrangements of vegetation cover, density, and functional composition. Biome maps (Figs 4 and 6) show large changes in the position and area of biomes between the last glacial maximum and present, with a major reorganization between 14,000 and 9000 cal yr B.P. Compared to the individual taxa, the reconstructed biomes did not move much, however. Instead of migrating large distances as climate changed, biomes grew and shrank in places where novel associations of taxa and functional types appeared and disappeared (Fig. 4). Biomes characteristic of the Holocene (e.g. temperate deciduous forest, taiga) were absent or occurred only in limited areas during the late Pleistocene, whereas the mixed parkland biome largely disappeared after 11,000 cal yr B.P. (Fig. 4). In some cases, shifts in biome position and type can be traced

to the distribution of individual plant taxa – for example, the northward spread of spruce populations caused the end of its association with sedge, ash, and hornbeam (the end of the mixed parkland) and the beginning of an association with alder and birch (the rise of taiga) (Fig. 4). Here, not only range shifts but the increases in maximum abundances of alder and birch after 16,000 cal yr B.P. also played a key role in the development of the new biome. In other cases, variations in the distribution of individual taxa are subsumed as internal variations in biome composition (Williams *et al.*, in press). As categorical representations of the vegetation, the biome maps limit apparent vegetational change to ecotonal regions between biomes (see the 6000 cal yr B.P. to present differences in Fig. 6). Continuous measures of the vegetation variation such as shown on isopoll maps (Fig. 4) and difference maps (Fig. 6) demonstrate that this emphasis on ecotones is an artifact of the biome categories; actual change was far more widespread (Figs 4–7).

Describing the relative density of various plant life forms avoids limitations inherent to categorical classifications of the vegetation while still providing an estimate of vegetation structure (DeFries *et al.*, 2000). Reconstructions of % tree cover based on calibrating pollen records to AVHRR

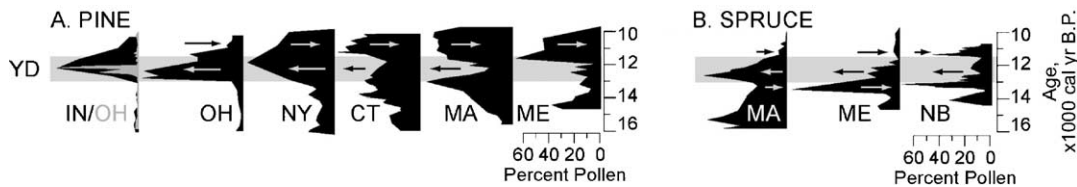


Fig. 10. Pine and spruce pollen percentages track abrupt range shifts during the Younger Dryas chronozone (12,900–11,600 cal yr B.P.) Records of pine (*Pinus*) (A) and spruce (*Picea*) (B) pollen percentages are plotted with time on a vertical axis to show changes in their geographic distributions. Arrows indicate the east-west range shifts of pine (A) and the north-south range shifts of spruce (B). Each site is labeled by state as in Shuman et al. (2002a). The Stotzel-Leis site in Ohio (Shane, 1987) is shown in gray in inset A, and superimposed upon the stratigraphy from Pretty Lake in Indiana (Williams, 1974) (from Shuman et al., 2002a).

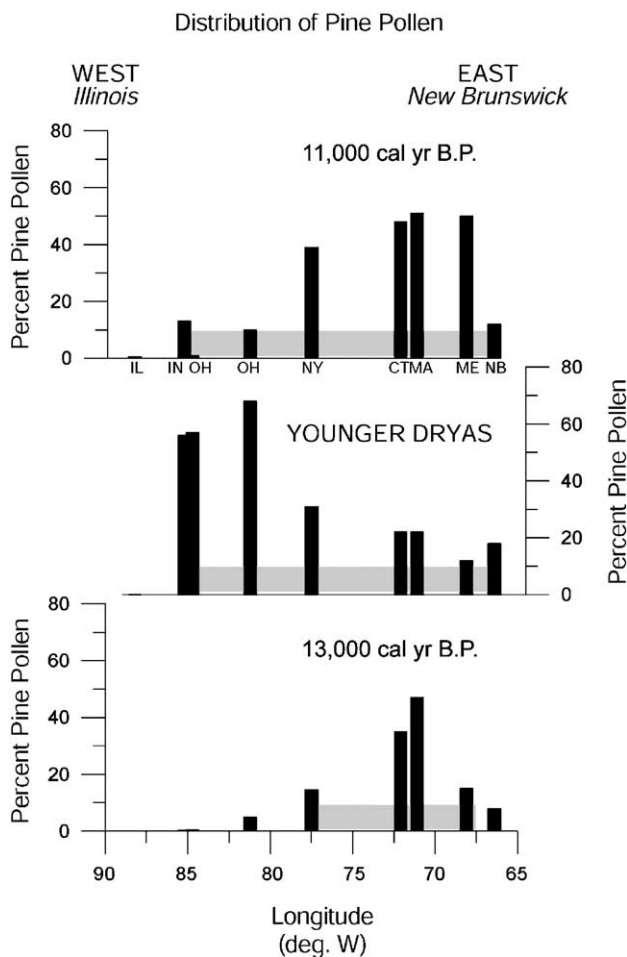


Fig. 11. The abundance of pine pollen across eastern North America before, during, and after the Younger Dryas chronozone. Histograms represent the % pine (*Pinus*) pollen at each of nine sites (Shuman et al., 2002a) at 13,000, 12,000 (middle of the Younger Dryas chronozone), and 11,000 cal yr B.P. The percentages are plotted with respect to longitude to show changes in abundance across the range of pine. Each site is labeled by state. Horizontal gray bars mark the range of sites where the presence of pine populations is indicated by pollen percentages of >10% (from Shuman et al., 2002a).

(Advanced Very High Resolution Radiometer) observations of the modern vegetation indicate that total tree cover has increased since the last glacial maximum (Fig. 5) (Williams, 2003; Williams & Jackson, 2003). Total tree cover in eastern North America at the last glacial maximum was generally <50%, and forests and parklands were dominated by needle-leaved tree taxa. Much of the subsequent increase in total tree cover is due to the rise in the abundances of broadleaved deciduous tree taxa as temperatures increased. Needle-leaved tree coverage, initially high across most of eastern North America, separated into northern and southern bands by 11,000 cal yr B.P. The tree cover maps are able to show subtler gradients and features in the vegetation than shown by biome maps (Figs 4 and 5). For example, the prevalence of cool mixed forest across much of eastern North America during the late Pleistocene does not hint at the increase in tree-cover densities or at the general shift from needle-leaved to broad-leaved taxa during this period (Figs 4 and 5).

*Zoomed-in View of Climate and Vegetation History in New England*

When we zoom in to specific time series in the Northeast (Shuman et al., 2003), stable isotope ratios and lake-level estimates show six phases of climate history in southern New England during the past 15,000 years, corresponding with six regional pollen zones (Fig. 8). The different arrival times of the dominant taxa match well with the development of favorable conditions for their growth and do not appear to be controlled by dispersal limitations (Johnson & Webb, 1989). The new climate records support Deevey’s (1939) original climatic interpretation of the sequence of pollen zones and add to the climate history in Davis et al. (1980).

Highly negative hydrogen isotope ratios and lower-than-modern lake levels (Huang et al., 2002; Newby et al., 2000; Shuman et al., 2001) indicate that New England climates were colder and drier than present before 13,000 cal yr B.P., when cold-tolerant spruce and pine populations were common. An expansion of spruce populations and a decline of pine populations during the Younger Dryas chronozone followed a cooling indicated by lowered stable isotope ratios (Huang et al., 2002; Shemesh & Peteet, 1998). After 11,600 cal yr B.P., a rapid positive shift in hydrogen isotope

ratios and a decrease in lake levels indicate a rapid shift to warmer- and drier-than-earlier conditions coincident with the decimation of spruce populations and expansion of white pines (Huang *et al.*, 2002; Lavoie & Richard, 2000; Newby *et al.*, 2000; Shuman *et al.*, 2001; R.S. Webb *et al.*, 1993). The pines remained abundant until the populations of mesic types like hemlock and beech expanded. This change coincided with a rise of lake levels ca. 8000 cal yr B.P. (Shuman *et al.*, 2002b). Hickory populations did not expand in New England until more than a thousand years later when the hydrogen isotope ratios indicate that conditions became at least as warm as modern. Chestnut populations, which prefer higher soil moisture levels, expanded after 3000 cal yr B.P. when lake-levels indicate that conditions became as wet as modern (Shuman *et al.*, in press). Warm and dry conditions from 5400 to 3000 cal yr B.P. likely contributed to the decline of hemlock populations at 5400 cal yr B.P. by contributing to moisture stress in the trees and making them more susceptible to disease (Bhiry & Filion, 1996; Davis, 1981a, b; Haas & McAndrews, 2000; Newby *et al.*, 2000; Shuman *et al.*, 2001, 2003; Yu *et al.*, 1997). The independent climate records clarify many of the issues that Davis (1965) critically evaluated.

#### *Individualistic Responses by Taxa to Millennial-Scale Climate Change*

Paired records of fossil pollen data and independent climate estimates at individual sites indicate rapid vegetation responses to the abrupt climate changes associated with the Younger Dryas chronozone (Fig. 9). Many North American sites show a shift to cold-tolerant vegetation between 12,900 and 11,600 cal yr B.P. (e.g. Mayle & Cwynar, 1995; Mott *et al.*, 1986; Peteet *et al.*, 1990; Shane, 1987; Shuman *et al.*, 2002a). High-resolution records reveal that such vegetation changes were nearly as fast as the climate changes that caused them. For example, cross-correlation analysis between pollen and chironomid data from Splan Pond, New Brunswick, shows that vegetation lagged climate by less than 100 years (Williams *et al.*, 2002) (Fig. 9). Similarly rapid responses (<100 years to ca. 200 years) to century-scale climate changes are observed for European lakes (Ammann *et al.*, 2000; Birks & Ammann, 2000; Tinner & Lotter, 2001), implying that abrupt climate change led to rapid widespread vegetation change in areas adjacent to the North Atlantic.

Rapid changes in taxon abundance associated with the Younger Dryas interval are equally evident across eastern North America (Shuman *et al.*, 2002a) (Figs 10 and 11), and changes within the ranges of most taxa (and within biomes) are qualitatively no slower than responses quantified near range limits and ecotones, such as in New Brunswick. The rapid decimation of spruce populations at Splan Pond, New Brunswick (Mayle & Cwynar, 1995; Williams *et al.*, 2002), occurred as conditions cooled and tree line shifted southward in the first century of the Younger Dryas chronozone (Figs 9 and 10). Simultaneously, spruce populations increased again to the south in southern New England (Peteet *et al.*, 1990; Shuman *et al.*, 2002a) (Fig. 10). Because peak spruce

abundance occurs only under a narrow, optimal range of climate conditions, intermediate levels of spruce abundance were maintained in Maine where conditions were neither too harsh nor optimal for spruce growth from 12,900 to 11,600 cal yr B.P. (Shuman *et al.*, 2002a) (Fig. 10).

A similar shift in the range and peak abundance of pine populations also occurred during the Younger Dryas chronozone and extended well inland (Fig. 10). Pine populations declined at the center of their former range (Fig. 11), but expanded their range into new sites in Ohio and Indiana (Figs 10 and 11). A unimodal distribution of pine abundance was maintained because, as the range of pine expanded westward, pine populations decreased in New England (where climates had become less favorable) and increased in western New York (Webb *et al.*, 2003) and the Midwest (where climates had become warm-enough for pine growth). As the climatic gradients shifted, the narrow range of optimal conditions for pine growth shifted westward in parallel with the range of tolerable conditions. Significant vegetational change, therefore, occurred not only at range boundaries or ecotones, but within the ranges of taxa (and within biomes) as well (Figs 10 and 11). Maps of plant assemblages show that the westward expansion of pine was part of a broad-scale reorganization of North American vegetation patterns between 13,000 and 12,000 cal yr B.P. (Shuman *et al.*, 2002a) (Figs 4 and 7). By classifying the vegetation into biomes, however, some of these abrupt vegetation changes can be hidden as within-biome changes in composition (compare maps of spruce, sedge, and pine assemblages with biome maps in Fig. 4), and mapped biomes changes are emphasized at ecotones, even though dramatic ecosystem changes were much more widespread (Fig. 6) (Williams *et al.*, in press).

The responses by spruce and pine were similar in that both taxa rapidly shifted their distribution during the Younger Dryas chronozone, but the responses represent distinct and individualistic plant responses (Figs 4 and 10). The change in the distribution of spruce reflects a north-to-south shift in abundance (Fig. 10b), largely within a region previously colonized by spruce, whereas the changes in pine distribution reflect an east-to-west shift in abundance (Fig. 10a) that included the colonization of many new sites, although rapid expansion from *in situ* midwestern populations cannot be ruled out. The difference between spruce and pine response appears to arise because pines require warmer summer temperatures than spruce, and mid-continent summers may have warmed at the onset of the Younger Dryas chronozone when summer conditions cooled in New England (see GISS GCM results of Rind *et al.*, 1986; Shuman *et al.*, 2002a).

#### *Linking Orbital and Millennial Scales of Vegetation Change*

In the last 21,000 years, the magnitude of vegetation changes has not been uniform in space or time (Fig. 7). Maps of the differences between subsequent millennia (i.e. 1000-year dissimilarity maps, Fig. 7) show the most widespread, large magnitude changes going into (13,000–12,000 cal yr B.P.)

and out of (12,000–11,000 cal yr B.P.) the Younger Dryas chronozone. This pattern of temporal changes agrees with the histograms of [Overpeck \*et al.\* \(1991\)](#). Mapping the same dissimilarity data with an alternative scale that highlights smaller magnitude changes agrees with the histograms of [Jacobson \*et al.\* \(1987\)](#) and shows that change was widespread near the ice sheet from 15,000 to 9000 cal yr B.P. (not shown). The differences from one millennium to the next are dwarfed, however, by those over 3000- and 5000-year intervals ([Fig. 7](#)). These latter maps show the cumulative impact of orbitally forced changes in climate. They also show that the 1000-year dissimilarity maps slice up the vegetation changes too finely for the slow, large-magnitude changes to become manifest.

Over 3000-year intervals, the largest areas were affected from 18,000 to 6000 cal yr B.P. with the largest magnitude changes from 15,000 to 9000 cal yr B.P. focused in the 500 km south of the retreating ice sheet ([Fig. 7](#)). Changes across 3000-year timesteps before (17,000–14,000; 16,000–13,000 cal yr B.P.) and after the Younger Dryas (11,000–8000; 10,000–7000 cal yr B.P.) exceed the millennial differences at the beginning and end of the Younger Dryas ([Fig. 7](#)). And even the 3000-year changes across the Younger Dryas chronozone (14,000–11,000; 13,000–10,000 cal yr B.P.), which entirely ignore any change into and out of the Younger Dryas chronozone, far exceed the magnitude of the more rapid changes. Here we see the prominence of the orbital-scale changes over the millennial-scale climate variability in overall impact. This dominance of the orbital-scale is also evident in the maps of individual taxa and biomes ([Fig. 4](#)), which show long-term migrations of taxa and reorganization of biomes more clearly than the rapid migrations of some taxa across hundreds of kilometers at the beginning and end of the Younger Dryas ([Figs 10 and 11](#)). But on the millennial scale maps, we also see how the changes going into and out of the Younger Dryas stand out as the largest differences between millennia.

### Summary of Results

The maps and diagrams have shown some of the patterns and processes active across time and space scales, as well as across different levels of ecological organization. Vegetation appears: (a) to track multivariate changes in climate (i.e. the combination of temperature, moisture, seasonality) ([Figs 2, 3 and 8](#)); and (b) to respond widely and rapidly to climate change ([Figs 6, 7 and 9–11](#)). Analyses of time-series of pollen data show that vegetation changed rapidly at times of century-scale climate change (i.e. beginning and end of the Younger Dryas chronozone) with a non-linear but continuous response across the region where climate changed ([Figs 9–11](#)). On a longer-time scale, the combination of temperature and moisture changes in New England is sufficient to explain the different arrival and expansion times of the key taxa that distinguish the classic sequence of pollen zones ([Fig. 8](#)). Seasonality is also a factor driving vegetation change given the parallel distributions of vegetation types and simulated climates without modern equivalent ([Fig. 2](#)).

Vegetation changed in structure and composition as dictated by the climate and by the differential response of individual taxa to climate. The changes yielded plant associations unlike those today when the combination of climate variables differed from those of today ([Figs 2–4](#)). Biomes are one way of summarizing vegetation structure but mapped time-series of biomes hide much of the variation evident in isopoll and plant-cover maps. Biomes, unlike individual taxa, do not shift large distances, but form and expand or contract in area as the result of changes in vegetation composition that result from individualistic changes in plant distributions ([Fig. 4](#)). Map patterns of pollen data are dominated by progressive vegetation responses to long-term orbitally forced climate changes ([Fig. 7](#)), but vegetation also rapidly reorganized in response to century- and millennial-scale climate variability ([Figs 9–11](#)). Such rapid responses show that rates of orbital-scale climate change were far slower than potential rates of vegetation change and that the impact of abrupt events is more pronounced at the local scale than at the continental scale (compare [Figs 9 and 10](#) with [Figs 4 and 7](#)).

### Discussion

The growing set of climate estimates constructed from sources other than pollen data has enabled new assessment of the degree to which climate controls vegetation dynamics. Changes in temperature, moisture-balance, and seasonality have all affected the vegetation of North America. As [Williams \*et al.\* \(2002\)](#) – building on the work of [Tinner & Lotter \(2001\)](#), and [Ammann \*et al.\* \(2000\)](#) – have shown, vegetation responds rapidly (within ~100 years) when climate changes rapidly on centennial time scales. The rapid responses are not just restricted to mountainous terrain but also occur in lowlands where dispersal distances can be large. These response times support the hypothesis that vegetation has been and is in a dynamic equilibrium with climate ([Webb, 1986](#)), particularly at the temporal and spatial scales of our 1000-year interval continental maps. For the conditions of dynamic equilibrium to be met, the vegetation response time must be short relative to the time scale of forcing. Orbitally forced climate variations set a beat throughout Earth history as certain as the diurnal and annual cycles (though perhaps more complex in their generation and hence more broad band). Therefore, plant taxa not only have had to evolve in the face of orbitally forced climate changes but have had to develop coping mechanisms that facilitate rapid-enough responses to changes in the position of their optimal climates ([Davis & Shaw, 2001](#); [Huntley & Webb, 1989](#)). Taxa maintain distinct climate preferences over long time periods ([Huntley \*et al.\*, 1989](#)), and to do so, they must have the ability to disperse long-distances while being flexible enough to adapt to other environmental changes (e.g. changes in day length as taxa migrate northward – see [Davis, 1965](#), and [Davis & Shaw, 2001](#), for a discussion of this requirement).

Plant taxa also had to develop mechanisms to cope with frequent millennial-scale climate variations. That so many pollen diagrams record big changes during the Younger Dryas

chronozone illustrates century-scale response times for most taxa (Shuman *et al.*, 2002a). We recognize, however, that range shifts for some taxa may significantly lag century-scale and even some millennial-scale climate oscillations. If so, our claim for dynamic equilibrium between the vegetation and climate at millennial scales involves just the Type A response (*sensu*, Webb, 1986) but not the full Type B response involving equilibrium range shifts and complete soil development. The vegetation changes significantly within centuries but its full response in remote areas can take longer.

The results of Shuman *et al.* (2002a) have further shown that the rapid responsiveness to climate change is widespread and not just limited to ecotones. In fact the perception of action being focused along ecotones presupposes the existence of biomes or communities, which the data show to be ephemeral because of individualistic taxon changes well beyond any ecotones (Figs 6, 7, 10 and 11). Here we can see how our human choice to classify the vegetation and pollen data affects what we conclude and perceive. Paleoecology is fraught with such traps. Because choices of how to analyze, summarize, and display the data can influence interpretation, multiple and sometimes conflicting conclusions can be and often have been drawn from the same data. We are keen for the focus on ecotones (as areas for high sensitivity of the vegetation to climate change) to disappear. The sensitivity of vegetation to climate is widespread, and the processes that enable rapid vegetation change at sites well away from ecotones (and range limits) need to be better understood. Greater climatic sensitivity at ecotones is not a feature of the data but rather a feature of how the data are summarized (Fig. 6). If the climate changes at a site, the vegetation will respond regardless of where the site is located within a biome or taxon's range (Figs 6–8, 10 and 11).

The equilibrium responses involve individualistic-type changes in range and abundance among taxa (Davis, 1981a, b; Gleason, 1926; Jacobson *et al.*, 1987; Jackson & Overpeck, 2000) that in turn lead to changes in association among taxa (Figs 2–4). Plant assemblages are never resilient to big changes in climate and either persist while undergoing large changes in the relative abundances of dominant taxa or emerge or disappear (Fig. 4). Some of the past climates were so different from those today that the contemporary plant-assemblages have no modern equivalents (Overpeck *et al.*, 1992), and the Williams *et al.* (2001) analysis of the climate model results helps to confirm this conclusion (Fig. 2). Williams *et al.* (2000) also showed that one advantage of the biome-classification method of Prentice *et al.* (1996) is that it allows biomes that do not exist today to be defined and identified in the past, and thus provides one way of classifying the no-analog vegetation in terms of biomes (Figs 4 and 6).

A major feature of our continental and regional maps is that they show vegetation at spatial and temporal scales where climate forcing is strong enough to drive the major vegetational dynamics. These maps contrast with pollen diagrams that have the time span of 10,000 to 15,000 years for major changes in climate but record vegetation changes over several spatial scales some of which are too small for climate to be controlling. Soil development, fires, disease,

and disturbance can locally dominate over climate in forcing changes in vegetation. When such is the case, changes in local pollen assemblages do not record climate. A zoom lens view that allows for both the map and diagram perspectives helps paleoecologists sort out the different factors controlling change. When local changes fit together as regional trends, then climate is likely the dominant control (as noted even by von Post, 1916). When local trends are anomalous or unique, then other factors prevail (Graumlich & Davis, 1993; Webb, 1974); and difference diagrams (Gaudreau *et al.*, 1989; Jacobson, 1979), charcoal records (Green, 1981; Patterson & Backman, 1988; Swain, 1973), and knowledge of human disturbance (Davis, 1965) can help identify the cause for the vegetation change. Furthermore, comparing vegetation and climate changes across temporal scales also requires spanning spatial scales. At the local scale, rapid climate changes alter the vegetation patterns as greatly as orbital-scale climate changes; whereas on continental scales, orbital-scale changes dwarf millennial-scale differences (Figs 4 and 7).

The warming at the end of the Younger Dryas Chronozone is large and results from both orbital and millennial-scale forcing. To argue that the 4–8 °C temperature increase is all millennial scale variation is to ignore the long-term impacts of orbital scale changes and ice-sheet retreat. There is no question that large millennial-scale differences going into and out of the Younger Dryas chronozone reflect the rapid climatic reorganization associated with changes in North Atlantic circulation (Fig. 1). But these abrupt changes are imbedded within the rapid part of glacial-interglacial transition, and occur on the scale of decades to a millennium, which are too short for the orbital-scale controls to cause significant differences. Even the large long-term differences measured between 11,000 and 6000 cal yr B.P. (3000- and 5000-yr distance maps in Fig. 7), which can be attributed to rapidly decreasing summer insolation and the rapid melting of the Laurentide ice sheet (Fig. 1), are not distinguishable on the square-chord distance maps when divided into 1000-year segments (Fig. 7). Progressive changes in insolation, ice volume, and atmospheric carbon dioxide concentration were also faster before the Younger Dryas than during it (Fig. 1), and yet, the large long-term differences between 16,000 and 11,000 cal yr B.P., evident across >3000 years, did not register as millennial-scale differences (Fig. 7). Likewise, slow orbitally forced climate changes probably contributed little to the large changes calculated for the beginning of the Younger Dryas chronozone (1000-yr distance maps in Fig. 7). Much of the difference from 13,000 to 12,000 and from even 12,000 to 11,000 cal yr B.P. resulted from century-scale changes in vegetation composition that were synchronous at many sites ca. 12,900 and 11,600 cal yr B.P. (Fig. 10) (Shuman *et al.*, 2002a).

The vegetation changes across 3000- and 5000-year intervals (Fig. 7) and across the past 21,000 years (Fig. 6), however, dwarfed even the large millennial-scale differences associated with the Younger Dryas climate changes. The glacial-to-interglacial climate warming was far larger than the reorganization of climate patterns during rapid climate changes caused by ocean and atmospheric circulation changes. Maps of the long-term changes in insolation (Berger,

1978; Whitlock *et al.*, 2001) and net radiation (Whitlock *et al.*, 2001) show that the mid-latitudes underwent a large long-term increase in summer radiative forcing between 21,000 and 11,000 cal yr B.P. (as well as between LGM and modern). Consequently, even a large reorganization of the thermohaline circulation and oceanic heat transport could not widely alter climatic patterns of ca. 12,000 cal yr B.P. to be like those of 21,000 cal yr B.P. In some regions, cooling was significant at the onset of the Younger Dryas (e.g. Greenland, Stuiver *et al.*, 1995) (Fig. 1) and local vegetation patterns changed significantly (Figs 9–11), but the continental-scale climate gradients (and vegetation patterns) immediately before, during, and after the Younger Dryas remained more like each other than those even 3000 years later (Figs 4–7). The long-term northward migration of taxa, such as spruce (Fig. 4), was altered only subtly because the latitudinal band where climate was appropriate for them remained north of their LGM positions and well south of their Holocene positions.

Comparison between pollen diagrams and maps shows that large local changes are not always indicative of large continental-scale changes. On local scales, orbital- to centennial-scale climate changes had a large impact on ecosystem composition (Figs 8–10), but only the larger magnitude, long-term changes appear important in continental-scale maps of individual taxa and assemblages (Fig. 4). The geographic displacement of vegetation types associated with century-scale climate changes (even when those that involved range shifts of hundreds of kilometers, Figs 10 and 11) resulted in large local changes in vegetation composition, but was small compared to the range shifts of thousands of kilometers from 17,000 to 6000 cal yr B.P. (Fig. 4). On the continental scale, rapid change is only evident (e.g. 13,000–12,000 and 12,000–11,000 cal yr B.P.) when many individual sites show rapid change simultaneously (Fig. 10). Many pollen diagrams show several rapid (century-scale) changes during the past 21,000 years, but most of these changes resulted from long-term time-transgressive changes that rapidly impacted individual sites while gradually shifting species' ranges (see spruce decline discussion in Bernabo & Webb, 1977). The inference that large local changes reflect global climate changes is "iffy" at best and can only be sustained when maps show how the local changes link to other changes over a large area.

## Conclusions

The emerging view from independently inferred paleoclimate estimates and patterns is allowing new assessment of climate-induced vegetation dynamics. Forcing factors at both orbital and millennial scales cause climate to change which in turn affects the pattern of major vegetation changes across the continent and at individual sites. The data show that the vegetation has changed when climate changed both at continental scales and at individual sites. The rates of migration, abundance change, and assemblage change have all varied at the recorded rate of climate change. Different recorders of the climate along with climate modeling results are allowing: (a) the influence of temperature changes to be separated from that

of moisture change (Huang *et al.*, 2002; Shuman *et al.*, 2002b, 2003); and (b) the impact of the changing seasonality to be assessed (Williams *et al.*, 2001). The multivariate nature of climate change combined with multivariate response surfaces that are unique for each plant taxon allow for widely varying responses among taxa to similar changes in climate (Bartlein *et al.*, 1986; T. Webb *et al.*, 1993). Differential migration paths and rates among taxa are expected as the result of such multivariate climate forcing and responsiveness (Prentice *et al.*, 1991), and taxa today that grow together should have in general arrived or at least expanded in abundance at different times (Shuman *et al.*, 2002a, b, 2003; Williams *et al.*, in press).

Individualistic plant behavior scales up to cause the emergence and disappearance of plant assemblages, of combinations of plant functional types, and hence of biomes. Changes at these higher levels of ecological organization ultimately result in feedbacks to the climate system (Kutzbach *et al.*, 1996; Street-Perrott *et al.*, 1990). The individual taxa move farther and more dramatically, however, than the biomes that they comprise. Changes by individual taxa combine and scale up to become differences in vegetation structure and composition not captured by biome classification (Williams, 2003; Williams *et al.*, in press). Multiple depictions and visualizations of vegetation change are therefore needed to portray its full diversity of changes. As new data sets and increasingly sophisticated vegetation and climate models come on-line to improve past climate estimates, we foresee many new insights into vegetation dynamics that will include how: (1) vegetation-climate feedbacks (Kutzbach *et al.*, 1996); (2) changing atmospheric concentrations of carbon dioxide (Cowling & Sykes, 1999; Davis, 1991); and (3) evolution and extinction of taxa (Davis & Shaw, 2001; Jackson & Weng, 1999) enhance or inhibit the shifting of taxon abundances and distributions as climate changes. A current fascination with understanding the impact of global warming on ecosystems, landscapes, and human livelihood has placed a premium on studying decade-to-millennial scale climate changes. We are hopeful that the reductionism of this approach will in time give way to a more holistic approach to understanding vegetation and climate dynamics. Such will be necessary if we are to understand the roles of millennial and orbital scale climate and vegetation dynamics in evolution and speciation. Studies of the genetic make-up of fossil plants are just beginning and should open many exciting lines of inquiry (Davis & Shaw, 2001). Such studies will allow us to understand how Hutchinson's (1965) evolutionary play unfolds in the continuously changing ecological theater (Webb, 1995).

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