Mapping eastern North American vegetation change of the past 18 ka: No-analogs and the future

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ABSTRACT
The method of modern analogs and an extensive data base of modern and fossil pollen data were used to generate a new series of paleovegetation maps for eastern North America spanning the past 18 ka. The maps illustrate the continuous nature of climate-induced vegetation change and the development, after about 10 ka, of modern regional vegetation patterns. Before the Holocene, vegetation biomes without modern analogs were widespread in response to climate conditions without modern analogs and, to a lesser extent, to the rapidity of climate change over the last glacial-interglacial transition. This geological perspective suggests that possible future climate changes could force similarly complex changes in natural vegetation, including the development of biomes without modern analogs.

BACKGROUND AND METHODS
An understanding of past and possible future ecological, biogeochemical, and climate changes will require a clear picture of how vegetation changed in the past and may change in the future (Overpeck, 1992). Records of past climate and vegetation change suggest that a future rapid 1.5 to 4.5 °C rise in the mean global temperature could induce vegetation change that is unprecedented in the context of the late Quaternary (Houghton et al., 1990; Overpeck et al., 1991). Anticipating the nature of this change is made more difficult by the likelihood that future tracegas-induced climate change will have no geologic analogs (Webb and Wigley, 1985; Crowley, 1990). Assessments of future change will thus have to rely on climate and vegetation models, and not on analogs from the past. The record of past environmental change, however, provides information needed to improve these models and to test how well they can simulate observed changes of the past (Webb et al., 1987, 1992; COHMAP Members, 1988; Overpeck et al., 1991).

Several approaches have been used to reconstruct past continental-scale vegetation change, including interpretations of fossil pollen data from many sites (e.g., Delcourt and Delcourt, 1987; Adams et al., 1990) and mapped pollen data for individual taxa (Davis, 1981, 1983; Webb, 1988, Jacobson et al., 1987). Herein we use pollen data and a quantitative method to map biome-scale patterns of past vegetation change in eastern North America, including regions without modern analogs. The maps produced by our method obscure to some extent the individualistic responses of plant taxa to climate change. We therefore illustrate the changing composition of biomes through time, thus revealing the continuous individualistic responses of different taxa. Although the sparse distribution of fossil pollen and plant macrofossil data may not be enough to produce global paleovegetation maps, regional maps such as ours will provide a crucial test of the model-based methods that can be used to simulate global maps of vegetation (e.g., Prentice and Fung, 1990; Prentice and Solomon, 1991).

We used the quantitative method of modern analogs (Overpeck et al., 1985) and the squared-chord distance dissimilarity coefficient (SCD), i.e.,

$$SCD_i = \sum_k (p_{ik}^M - p_{ik}^F)^2,$$

where $p_{ik}$ is the proportion of pollen type $k$ in sample $i$. On the basis of calibration comparisons among the modern pollen samples, we determined that a fossil sample had no modern analog if all of the comparisons with the 1744 modern samples yielded an SCD of $>0.15$ (Overpeck et al., 1985). "No-analog" fossil samples are thus defined as samples that are unlikely to have come from any modern-day biome. When the SCD between a fossil sample and at least one modern sample was $<0.15$, we concluded that the fossil sample had a modern analog that could be mapped. Our data and methods are detailed in R. Webb et al. (unpublished).

We specified a pollen sum to reflect the composition of the regional vegetation and to avoid biases that can be introduced by the inclusion of taxa now overrepresented due to local edaphic factors (R. Webb et al., unpublished). We found that the SCD dissimilarity coefficient is generally able to distinguish among all eight of the biomes we have mapped (R. Webb et al., unpublished).

RECONSTRUCTED VEGETATION CHANGE
A time sequence of paleovegetation maps illustrates the continuous patterns of change that have taken place over the past 18 ka in eastern North America (Fig. 1). Despite a limited sample coverage for 18 ka, the reconstruction suggests that a broad belt of spruce-dominated forest grew north of approximately lat 35°N (boreal forest and forest tundra), whereas pine-dominated mixed forests grew to the south (Fig. 1). Conifer-dominated pollen samples mapped at 18 ka all were found to have modern analogs, but they were somewhat different from average pollen samples from modern-day mixed and eastern boreal forests (Webb, 1998). Modern-day eastern boreal forests are generally characterized by significant amounts of birch, alder, and fir, whereas these taxa are not as abundant in the western boreal forest or in eastern North American fossil samples for 18 ka. Slightly higher sedge values in the fossil samples relative to modern ones also suggest that the early boreal forest was more open than the modern boreal forest. Open spruce-rich forests thus probably covered much of the region at 18 ka; areas of tundra and forest tundra were to the north, and
more closed forests were to the south (Jacobson et al., 1987). Samples from the two sites available in Florida were most analogous to those in the present-day deciduous forest (Watts and Stuiver, 1980).

Sample coverage increases steadily after 18 ka, and by 12 ka most of the region can be mapped. The most obvious feature on the 12 ka map (Fig. 1) is the large (about 26% of the total map area) region covered by vegetation without modern analogs. East of the Appalachian Mountains, a north-to-south zonation of vegetation regions had developed. Pine-dominated southeast forests were present in Florida, merging northward with the newly emerged oak-rich deciduous forest. Farther north, pine-dominated mixed forests and spruce-dominated boreal forests covered most of the Atlantic seaboard; the northernmost areas were populated by aspen parkland, tundra, and no-analog vegetation.

A biome more like the modern eastern closed boreal forest, with significant amounts of birch, alder, and fir, did not become widespread until after 12 ka (Fig. 2A; Webb, 1988). Tundra and forest tundra were not widespread prior to about 9 ka, and their composition before this time also reflected a scarcity of birch and alder (R. Webb et al., unpublished). Before 12 ka, the mixed forest was also more dominated by pine and was less rich in other tree taxa (e.g., birch, hemlock, elm, and beech) than its modern-day counterpart (Fig. 2B; Webb, 1988). Plant macrofossil data support the mapping of northern-pine-rich mixed forests in the southeast United States prior to 9 ka (Watts, 1983; S. T. Jackson and D. R. Whitehead, unpublished). Macrofossil data also suggest that southern pine species were restricted to Florida until about 9 ka, when southeast pine forests, similar to modern forests, spread northward (Watts, 1983; Webb, 1988). This expansion was coincident with the formation of a large prairie biome, similar to a modern prairie, in eastern North America, and it was preceded by the rapid development of the modern deciduous forest after about 12 ka.

Although much of the vegetation in eastern North America prior to 9 ka had modern analogs, there were large regions that did not. Several types of no-analog vegetation existed. The vegetation map for 12 ka depicts a large area of no-analog vegetation that was essentially a spruce-dominated woodland with high amounts of sedge in the southwest and significant amounts of sedge, ash, elm, and ironwood-hornbeam in the north and east (Wright et al., 1963; Overpeck et al., 1985; Webb, 1988). No-analog forests dominated by aspen and birch were also common along the southern margin of the Laurentide ice sheet between 11 and 8 ka.

By 9 ka, the modern-day vegetation patterns were well established, but there were important differences between this mapped vegetation and that of today (Fig. 1). Ice still covered about 18% of the region, and southern ice margins were bordered primarily by pine-rich mixed forests. Spruce-dominated boreal forest was less common. Tundra vegetation was located only to the east of the shrinking Laurentide ice sheet. The area covered by deciduous forest, however, looked much more modern than before 9 ka, with southeast forest to the south and prairie-aspen parkland to the west and northwest. Areas covered by no-analog vegetation were still present at 9 ka, but they were reduced to about 7% of the map area (10% of the ice-free area). The progression of maps for 9 ka to the present illustrates that vegetation change was continuous throughout the Holocene, even if the change was small and slow relative to the change that took place before 9 ka.

DISCUSSION
Past Vegetation Change

The record of vegetation change in eastern North America reveals that the patterns and
composition of biomes changed continuously during the past 18 ka as plant taxa responded individually to climate change (Webb, 1988; Huntley and Webb, 1989; Davis, 1991). Vegetation regions without modern analogs have appeared and disappeared since the last glacial maximum, and modern-looking biomes came into existence only after about 10 ka (Webb, 1988). Our method of vegetation reconstruction illustrates these changes and is particularly well suited for identifying samples of fossil pollen without modern analogs. Although our method identified a small number of modern analogs for the 18 ka spruce- and pine-rich samples, we have already documented that these samples were different from typical samples from the modern-day eastern boreal forest. This example illustrates that, although good at identifying distinctly nonanalogous fossil pollen samples, our method can be crude at times when reconstructing the composition of past vegetation (Baker et al., 1989).

Our analysis indicates that the area of no-analog vegetation was proportionally greatest (>40%) between 16 and 11 ka (Fig. 3). By 9 ka, the area of no-analog vegetation was reduced to 10%, and by 7 ka it was insignificant. Climate conditions unlike modern-day conditions (e.g., different combinations of seasonal temperatures and precipitation) are the most likely cause for the large areas of no-analog vegetation (Webb et al., 1987; Huntley, 1990a). Between 16 and 11 ka, the seasonal distribution of insolation reaching the Northern Hemisphere was significantly different from today, and the Laurentide ice sheet covered much of North America. These two factors probably contributed to climatic conditions in eastern North America unlike those today (COHMAP Members, 1988). Unsuccessful efforts to quantify the exact nature of these no-analog climate conditions using modern-day climate-pollen relations highlight the need for further work on paleoclimatic reconstruction methods (Prentice et al., 1991).

An alternative interpretation for the widespread no-analog fossil pollen assemblages could be that climate change was too rapid over the last deglaciation for individual plant taxa to keep up with their favored environments (Davis, 1981; Delcourt and Delcourt, 1985; Baker et al., 1989). The response of individual taxa may have lagged climate change by different amounts of time. Rapid climate change may thus have contributed to the formation of plant assemblages with mixtures of taxa unlike any of today, but this mechanism was probably less important than no-analog climate conditions. The maximum rate of vegetation change in eastern North America occurred between 12 and 9 ka (Jacobson et al., 1987; Overpeck, 1987; Overpeck et al., 1991), after the peak in the areal extent of no-analog vegetation (Fig. 3). Rates of vegetation change were low at 15 and 14 ka, whereas no-analog vegetation was widespread at these times. The simplest interpretation of our results (Fig. 3) is that the large areas of no-analog fossil pollen samples and no-analog vegetation coincided temporally with environmental conditions different from those prevailing anywhere in eastern North America today. This conclusion is consistent with evidence from Europe, where high rates of vegetation change also coincided with minimal extent of no-analog vegetation at 10 ka (Huntley, 1990a).

**Implications for the Future**

Greenhouse-gas forcing of future climate will be distinct from climate forcing of the past 18 ka, and the climate response to this forcing may not always have modern or past analogs (Webb and Wigley, 1985; Crowley, 1990). As plant taxa respond individualistically to this future environmental change, the patterns and composi-
tions of some future biomes may be different from today or from any of the past 18 ka. No-analog vegetation regions are likely to occur. Rates of climatic change in the future could also exceed rates during the past 18 ka, including those over the most rapid shift from glacial to interglacial conditions (Jacobson et al., 1987; Overpeck et al., 1991). Thus, even though high rates of climate change played a secondary role in the past occurrence of no-analog vegetation regions, the potential for future disequilibrium between climate and vegetation may be larger than at any time during the past 18 ka (Davis, 1989; Overpeck et al., 1991; Huntley, 1990b; Solomon, 1986). The probability of no-analog vegetation in the future may be even greater than it was in the past because of extensive anthropogenic disturbance of natural landscapes (Davis, 1989; Huntley, 1990b).

Realistic assessments of future ecosystem, atmospheric trace gas, and climate change will require vegetation models that are capable of simulating global subcontinental-scale patterns of vegetation change. Before confidence can be placed in simulations of future change, however, vegetation models must first be shown able to simulate the observed change of the past. This model validation effort will be most straightforward in regions where there is detailed paleovegetation information (i.e., parts of North America and Eurasia), but efforts in other regions (e.g., low latitudes) may be hampered by the lack of data. Attempts must be made to improve the coverage of paleovegetation data for these regions and for time periods with limited data coverage (e.g., 18 ka). The record of the past not only offers key insights for building vegetation models, but it also enables us to test how well the models simulate realistic patterns and rates of vegetation change.

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