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Climatic impacts on the vegetation of eastern North America during the past 2000 years

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Abstract

Pollen diagrams from seven lakes with annually laminated sediments sampled at 40-year intervals are analyzed to isolate the climatic effects from other effects on the long-term dynamics of vegetation during the past 1000–2000 years along a transect from Maine to Minnesota. Principal components analysis is used to reduce the dimensionality of the pollen data. The pollen records from all lakes show long-term trends, medium frequency oscillations, and higher frequency fluctuations. The long-term trend is associated with the neoglacial expansion of the boreal forest. The mechanism causing this replacement is a change in frequency of air masses in the area. The medium-frequency oscillations are also associated with climate changes, the most recent of which is the 'Little Ice Age'. The climate-related mechanism causing the medium-frequency changes may be changes in disturbance frequency. The higher frequency fluctuations may also be related to disturbance.

This analysis of pollen diagrams into time scales of variation has enabled the separation of climate from other factors affecting vegetation dynamics. By comparing the principal components across a transect of sites it proved possible to interpret the climatic effects on vegetation at most sites and not only at range boundaries and 'sensitive' sites.

Introduction

Ecologists have analyzed sediment cores sampled at close intervals (50 yr or less) to interpret the processes by which plant populations and the environment interact on timescales of decades to centuries (Green, 1983). These analyses, and more recently model simulations, have identified a number of factors that affect vegetation at the scale of centuries (Walker, 1982; Prentice, 1983; Davis & Botkin, 1985): fire frequency, soil type, biotic factors, and climatic change.

The influence of fire on vegetation can be seen

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at two different scales (Swain, 1978). Succession after an individual fire has been identified in high resolution pollen diagrams (Swain, 1978; Green, 1981), and changes in fire frequency have affected vegetation composition (Swain, 1978; Grimm, 1983). In other cases, the regional vegetation has been shown to persist for centuries in the presence of repeated fires (Swain, 1973; Cwynar, 1978). Bernabo (1981) suggested that vegetation in areas of sandy soil is less sensitive to changes in climate than vegetation on more mesic soils. The state of the vegetation and the topographic location of the site influence the susceptibility of the vegetation to changes in the fire frequency or climate (Swain, 1978; Green, 1981; Grimm, 1983).

A number of studies have presented evidence of a rapid response of vegetation to century-scale climate changes (Swain, 1978; Bernabo, 1981; Gajewski, 1983; Grimm, 1983; Dean *et al.*, 1984; Gajewski *et al.*, 1985). These studies have suggested the importance of climatic change in causing the vegetation changes, and also demonstrated the difficulty in interpreting high frequency pollen changes. Although these authors have attributed changes in the vegetation to changes in climate (directly or indirectly), there is some question as to whether vegetation responds to climate at this scale.

Davis (1982) and Woods & Davis (1982) suggest that climate changes affect vegetation only at certain times (e.g., the Little Ice Age) or at certain locations (e.g., the range boundary of *Fagus* in Michigan, Davis, 1978). Model simulations of Davis & Botkin (1985) suggest that brief (200 year) climatic changes influence vegetation composition only in the absence of disturbance and on poor soils.

In this paper, seven Late-Holocene pollen diagrams from eastern North America (Fig. 1) are analyzed to demonstrate the influence of century-scale climate changes on the vegetation of the region. This analysis is based on the observation that climate anomalies and changes are large-scale in nature, and therefore that the effects of climatic changes on ecosystems should be traceable from place to place. Unlike previous studies (e.g. Swain, 1978; Bernabo, 1981), this paper analyzes the region as a whole rather than providing a detailed analysis and interpretation of an individual site. This approach follows, in general, that of Bernabo & Webb (1977) in using large-scale spatial patterns of pollen change to document the impact of climatic change on plant communities. Bernabo & Webb (1977) used 62 sites in eastern North America to analyze patterns of pollen taxon change. Data such as these are not available for the temporal scale of this study. Seven pollen diagrams (Swain, 1973, 1978; Gajewski *et al.*, 1985, subm.), with sample intervals of 20–80 yr (typically 40) on a transect from Maine to Minnesota provide a means to analyze the large scale quantitative changes (in time and space) in pollen (and therefore vegetation; Bradshaw & Webb, 1985) during the past 2000 years. Mapping of the spatial patterns of pollen abundance is more difficult for this study, as the changes in pollen percentages are smaller in the past 2000 years than in the early and middle Holocene (Bernabo & Webb, 1977; Davis, 1981) and the changes are of a different scale (within rather than between biomes). Principal components of the pollen diagrams enable the analysis of community level changes across the region, and thus permit the identification of spatial changes of forest communities and climate.

Methods

A description of field and laboratory methods, complete pollen diagrams and a discussion of the local vegetation histories are contained in Swain (1973, 1978), and Gajewski *et al.* (1985, subm.). All of the lakes are in the Hemlock-White Pine-Northern Hardwoods Region of the Eastern Deciduous Forest Formation (Fig. 1; Braun, 1950). Each sample includes 10 yr (or in some cases, 20 yr) accumulation of sediment.

Principal components analysis (PCA) was done on the correlation matrix of pollen percentages from each core (see Prentice, 1980 for a review of the application of PCA to palynology). Only those pollen types with a mean percentage in the core greater than or equal to 1% (2% in Ely Lake) were used in the PCA. Because the purpose of the analysis was to analyze the trends in the pollen diagram, only samples at even intervals in the core (80 yr at Ely Lake, 20 yr at Lake of the Clouds, 40 yr at the remaining lakes) were included in this analysis even though some cores were sampled at finer intervals over parts of the core. Samples from the uppermost 100 yr (pollen showing disturbance due to European settlement) were also not included in the analy-

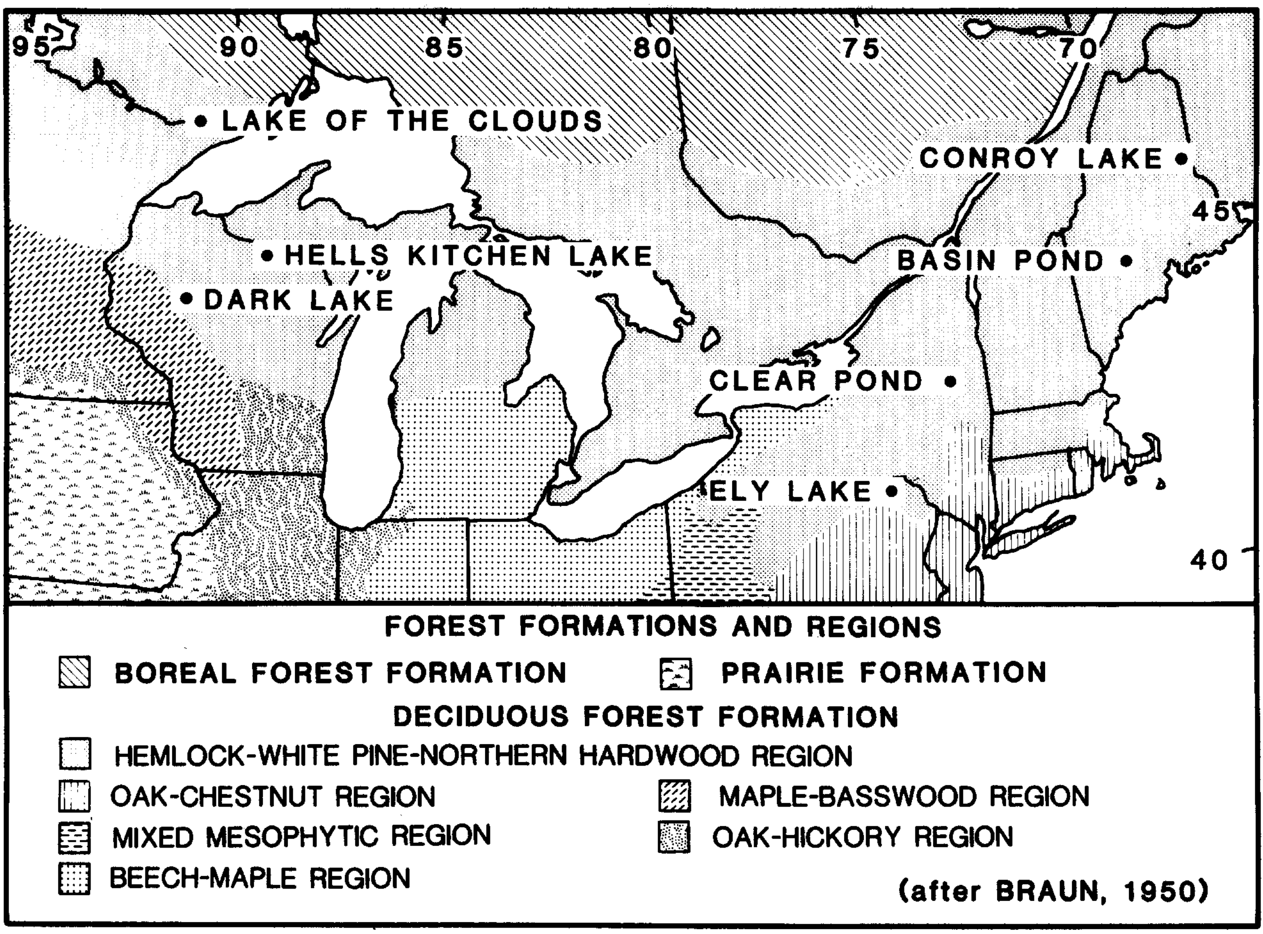


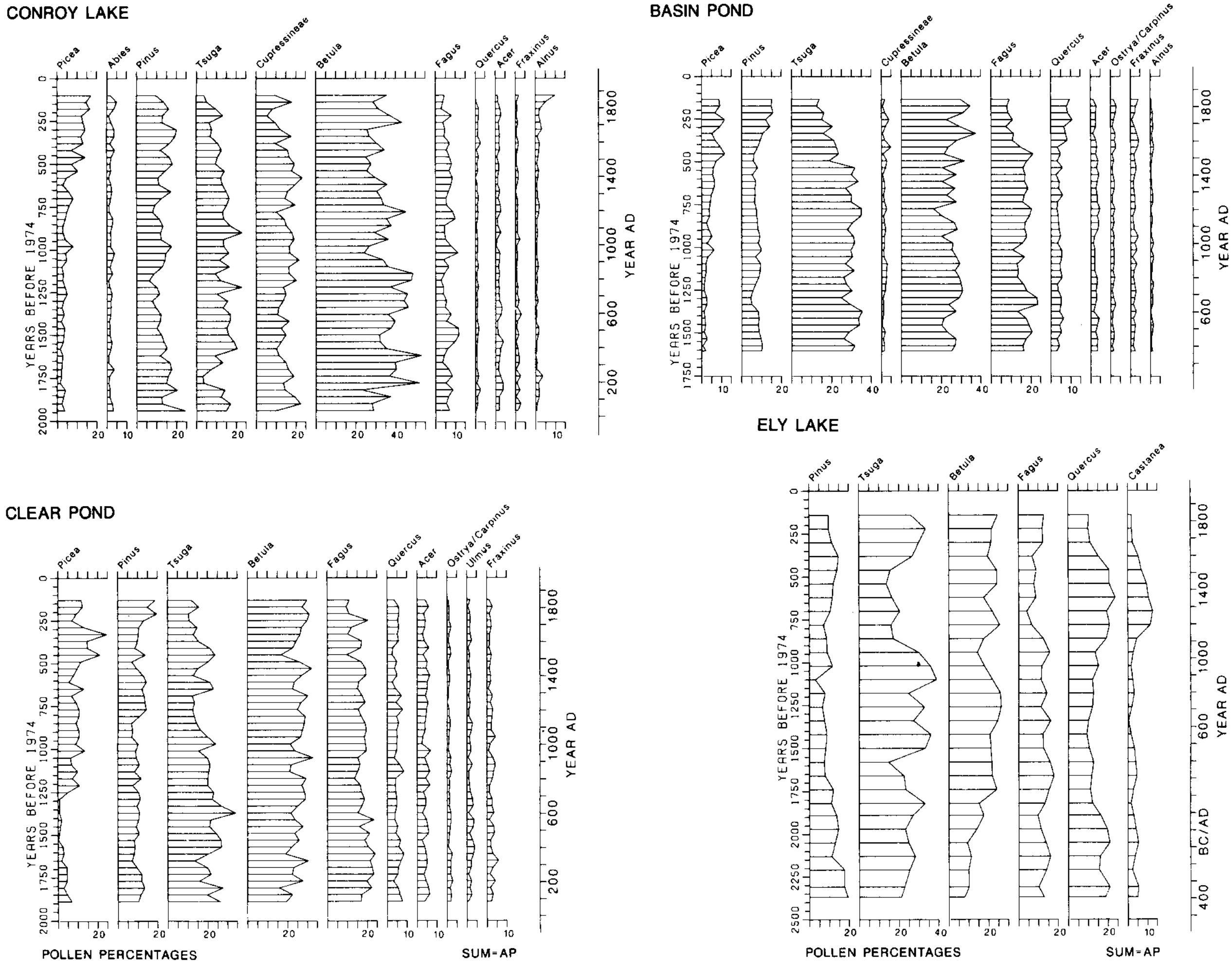
Fig. 1. Location of pollen core sites in northeastern United States. Vegetation zones are adapted from Braun (1950).

sis. When analysis was done using all levels, the results were usually similar to those presented here.

Results

PCA allows the comparison of the pollen analyses (Figs 2, 3) between lakes, and all show a long-term trend, medium frequency oscillations, and high frequency changes (Fig. 4). Except for Lake of the Clouds and Dark Lake, these high frequency changes are not shown or described.

The first component at Conroy Lake and Clear Pond and the first and second components at Basin Pond (Fig. 4) record a long term increase in boreal forest taxa (e.g., some combination of *Picea, Abies, Alnus*) at the expense of taxa of the northern hardwoods forest (e.g., *Tsuga, Fagus, Acer*). Taxa such as *Betula* or *Pinus* can be correlated with either boreal forest or northern hardwoods taxa depending on the particular species that is dominant at the site. For example, the correlation of *Betula* with *Tsuga* in the first component of Conroy Lake suggests that this component records primarily *Betula lutea,* a species characteristic of mesic hemlock-hardwoods forests, while at Clear Pond *Betula* is correlated with *Picea* and *Pinus,* and may be primarily *Betula papyrifera* (Table 1). The major difference in the first component between Clear Pond and Conroy Lake or Basin Pond occurs between 900 to 500 years ago (Fig. 2). At this time, the trend in the first component reverses at Basin Pond and Conroy Lake, while it does not at Clear Pond (Fig. 2). The first major increase in *Picea* pol-


CONROY LAKE

BASIN POND

CLEAR POND

ELY LAKE

Fig. 2. Percentage pollen diagrams for Conroy Lake, Basin Pond, Clear Pond, and Ely Lake. Only pollen types used in the principal components analysis are shown. Dates are determined from varve counts.

len percentages occurred at 1300 years ago at Clear Pond, but not until 1000 years ago at Conroy Lake and Basin Pond.

The second component at Ely Lake (Fig. 4) shows a long-term trend of increasing *Betula* and decreasing *Pinus* (Fig. 2). The first component of the pollen diagram of Hells Kitchen Lake is highly correlated with *Pinus, Alnus* (positive), *Betula* and *Tsuga* (negative) and indicates a long-term increase of mesic tree types (Curtis, 1959) in the area. The time sequence of the scores closely resembles that of Clear Pond. The first component of Dark Lake is positively correlated with mesic types that are not fire tolerant, for example, *Betula, Acer, Ulmus,* and *Ostrya/Carpinus* (McAndrews, 1968; Kline & Cottam, 1979; Curtis, 1959). The first component of Lake of the Clouds is negatively correlated with *Pinus* and positively correlated with *Picea, Betula,* and *Quercus* and, as in the sites in northeastern United States, shows an increase of the boreal forest at the expense of the conifer-hardwood forest.

Higher order components record medium frequency changes in the pollen assemblages, which are typically on the order of centuries. For example, the scores of the second component at Conroy Lake show century scale fluctuations (Fig. 4) of *Pinus* (mostly *strobus* type), *Fagus* and *Betula* especially in the lower (earlier) part of the record. In ad-

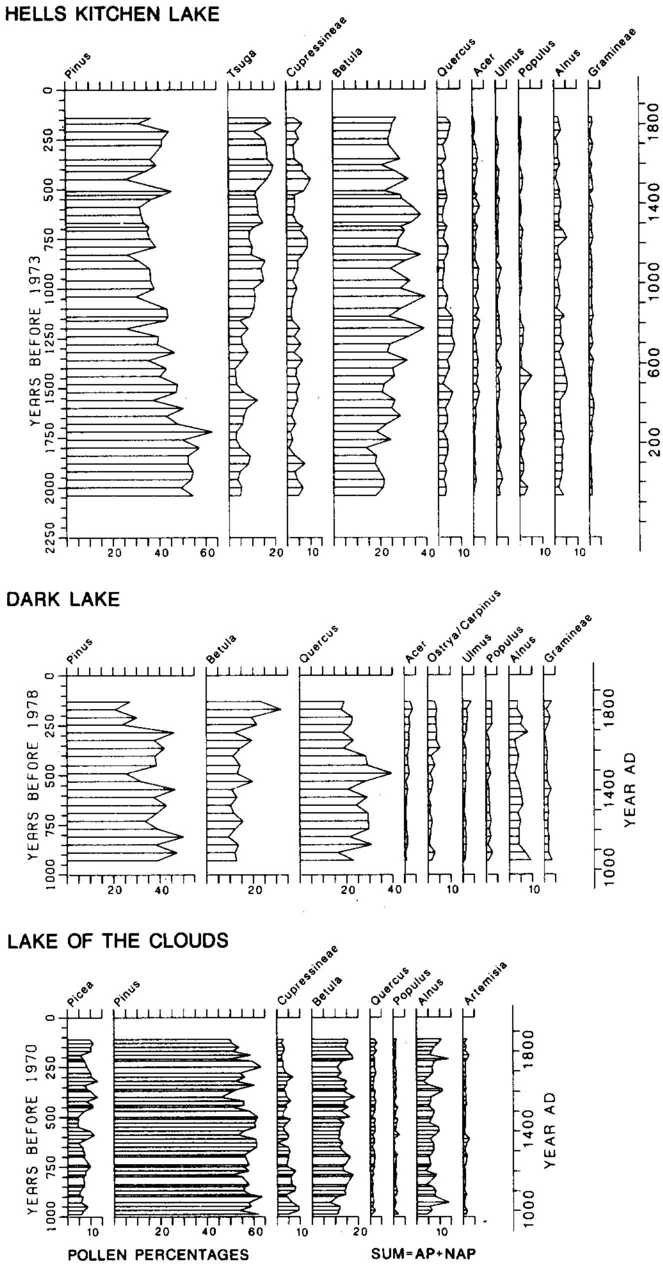


Fig. 3. As in Fig. 2 for Hells Kitchen Lake, Dark Lake, and Lake of the Clouds.

dition, the first component of Conroy Lake and Basin Pond can be divided into four periods, separated by times of more rapid transition at 1700–1600, 1150–950 and 600–500 years ago. The first component of Basin Pond separates the core into relatively wet and dry periods, with *Tsuga, Fagus,* and *Acer* (*saccharum*?) characterizing older mesic forests, and the other types drier conditions. The first component at Ely Lake is highly correlated with *Quercus, Pinus, Castanea,* (positive), *Tsuga* and *Fagus* (negative) and the time series of the scores (Fig. 4) shows a pronounced oscillation

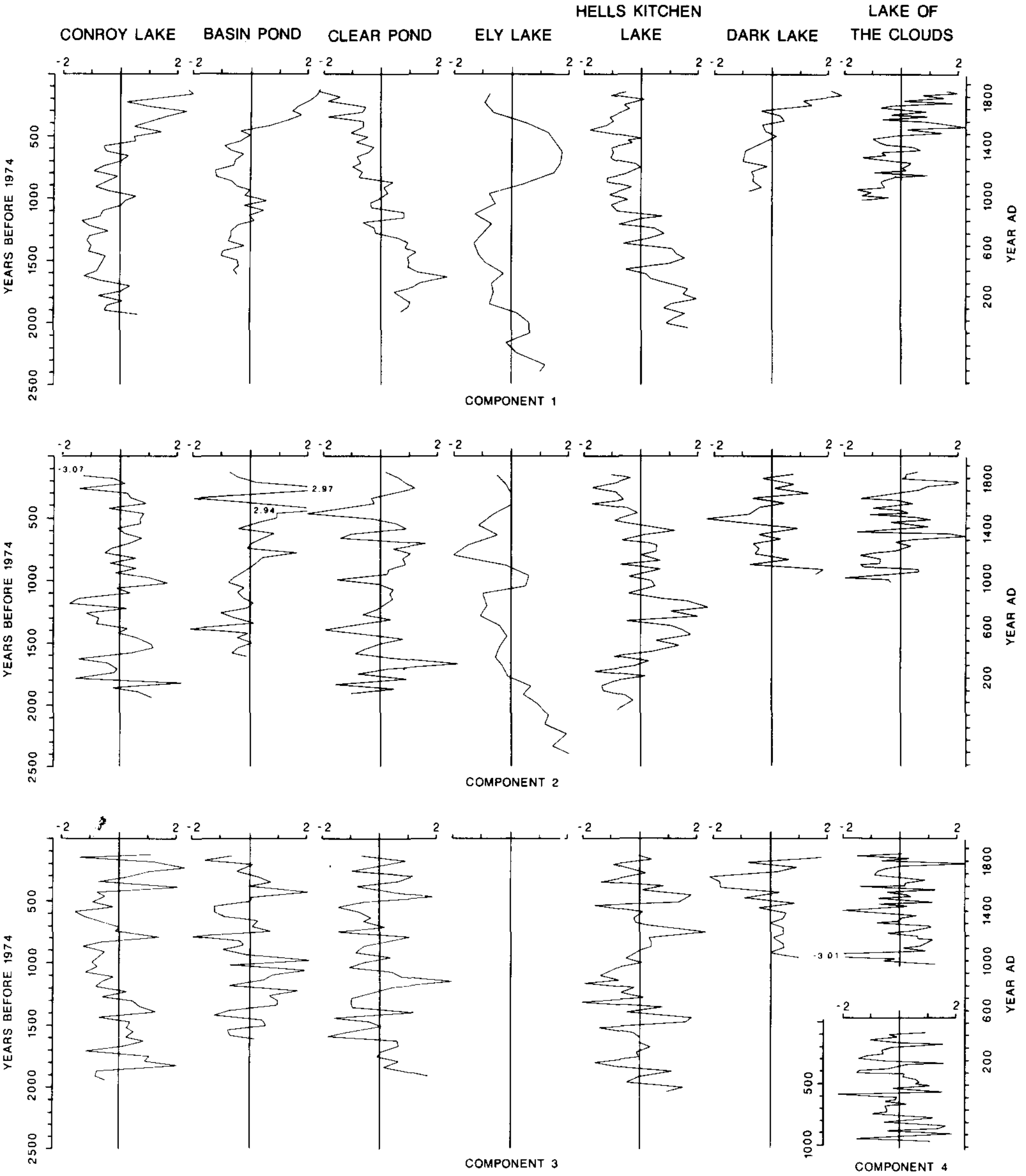


Fig. 4. Principal component scores of the pollen assemblages for the seven lakes shown in Figs 2 and 3.

which is out of phase with that of Basin Pond.

The second component of Hells Kitchen Lake is positively correlated with *Quercus* and *Acer,* and negatively correlated with *Pinus* and *Tsuga* (Table 1), and divides the pollen diagram (Fig. 3) into periods that correspond roughly to the zones determined by Swain (1978). High negative values of this component correspond to Swain's (1978) 'moist' periods and positive values correspond to his 'dry' periods. The third component at Hells Kitchen Lake shows fluctuations in pollen types that are characteristic of disturbance – *Populus,* Gramineae, and Cupressineae.

The third and fourth components of Lake of the Clouds are positively correlated with pioneer species. Time series plots of the third and fourth components show high frequency oscillations. Many of the changes in the higher order components of the three sites in the midwest are high frequency, probably because fires are an important factor in the forests of this region (Heinselmann, 1973; Swain, 1973).

Table 1. Principal component loadings of the pollen assemblages shown in Figs 2 and 3. The communality (comm), percentage of the original data explained by the principal component (fract expl var) and cumulative percentage of the principal components (cum var expl) are listed for each component.

Taxon	Conroy Lake				Basin Pond				Clear Pond				Ely Lake		
	1	2	3	comm	1	2	3	comm	1	2	3	comm	1	2	comm
Pinus	0.53	0.53	0.02	0.56	0.81	-0.05	-0.23	0.71	-0.55	-0.03	0.09	0.31	0.52	0.72	0.80
Picea	0.87	-0.13	0.21	0.82	0.61	0.52	-0.14	0.66	-0.74	-0.15	0.25	0.63			
Abies	0.60	0.10	-0.39	0.52											
Betula	-0.54	-0.72	0.18	0.84	0.54	-0.48	0.22	0.57	-0.40	0.69	-0.29	0.72	-0.26	-0.91	0.89
Alnus	0.60	-0.43	0.26	0.61	0.05	0.22	0.87	0.81							
Quercus	0.08	0.49	0.56	0.56	0.78	0.05	-0.15	0.63	0.36	0.41	0.31	0.40	0.94	0.12	0.90
Acer	-0.26	0.08	0.53	0.35	-0.52	0.39	-0.43	0.61	0.11	0.27	0.03	0.08			
Fraxinus	-0.19	-0.01	0.34	0.15	0.42	-0.29	0.02	0.26	0.50	0.46	0.50	0.71			
Ostrya/Carpinus					0.45	0.19	0.07	0.24	0.56	0.03	0.57	0.64			
Tsuga	-0.55	0.53	-0.08	0.59	-0.87	-0.15	-0.05	0.78	0.55	-0.74	0.05	0.85	-0.76	0.17	0.61
Fagus	-0.12	0.63	0.13	0.43	-0.85	0.11	0.14	0.75	0.71	0.11	-0.45	0.72	-0.67	0.40	0.61
Cupressineae	-0.15	0.08	-0.75	0.59	0.21	0.67	0.18	0.53							
Ulmus									0.53	0.10	-0.50	0.54			
Castanea													0.87	-0.38	0.91
Eigenvalue	2.51	1.95	1.60		4.11	1.32	1.14		2.80	1.52	1.28		3.03	1.68	
fract expl var	0.23	0.18	0.15		0.37	0.12	0.10		0.28	0.15	0.13		0.51	0.28	
cum var expl	0.23	0.41	0.56		0.37	0.49	0.59		0.28	0.43	0.56		0.51	0.79	

Taxon	Hells Kitchen Lake				Dark Lake				Lake of the Clouds				
	1	2	3	comm	1	2	3	comm	1	2	3	4	comm
Pinus	0.86	-0.41	-0.14	0.93	-0.74	0.48	-0.24	0.84	-0.90	0.30	-0.01	-0.07	0.91
Picea									0.68	-0.40	-0.09	-0.42	0.81
Betula	-0.73	0.47	-0.05	0.76	0.89	-0.13	-0.08	0.83	0.59	0.06	0.61	0.12	0.75
Alnus	0.65	0.41	0.24	0.65	-0.27	0.74	0.08	0.63	0.28	0.32	-0.54	0.60	0.83
Quercus	0.15	0.51	-0.47	0.50	-0.37	-0.83	0.30	0.92	0.55	0.25	-0.50	-0.35	0.74
Acer	-0.35	0.57	-0.25	0.51	0.86	-0.11	-0.20	0.80					
Ostrya/Carpinus					0.66	0.31	-0.60	0.89					
Tsuga	-0.82	-0.37	0.00	0.81									
Populus	0.41	0.29	0.59	0.60	0.61	0.12	0.40	0.54	0.27	-0.31	0.22	0.61	0.59
Cupressineae	-0.34	0.05	0.68	0.58					-0.37	-0.75	0.02	-0.09	0.71
Ulmus	0.43	0.40	-0.07	0.35	0.69	0.20	0.38	0.66					
Gramineae	-0.14	0.18	0.43	0.24	0.11	0.41	0.83	0.86					
Artemisia									0.14	0.66	0.48	-0.20	0.72
Eigenvalue	3.00	1.55	1.37		3.60	1.82	1.55		2.25	1.51	1.21	1.10	
fract expl var	0.30	0.16	0.14		0.40	0.20	0.17		0.28	0.19	0.15	0.14	
cum var expl	0.30	0.46	0.60		0.40	0.60	0.77		0.28	0.47	0.62	0.76	

Discussion*

Late-Holocene vegetation and climate changes in eastern North America

At Conroy Lake, Basin Pond, and Clear Pond, the long-term trend is associated with an increase in *Picea, Abies,* and *Pinus* and a decrease in *Tsuga* and northern hardwood species. In the Lake of the Clouds pollen diagram, the long-term is also an expansion of the boreal forest species at the expense of more southerly species. This southward expansion of the boreal forest has been identified by Bernabo & Webb (1977), Wright (1971), Davis (1983) and others, from numerous local studies.

Bryson (1966) has shown that the major vegetation zones of eastern North America are associated with characteristic seasonal patterns of dominance by different air masses. For example, the boreal forest is dominated by continental polar or arctic air masses in winter and spring and by Pacific or tropical air masses in summer. Conroy Lake, Basin Pond and Clear Pond are located along the modal winter position of the arctic front. The long-term trend records an increase in the frequency of arctic air masses during the past 2000 years.

At Ely Lake the changes in the first two components reflect changes in the abundances of taxa of the conifer-hardwood forest and the southern deciduous forest. The dominant airmasses that cause vegetation changes in northern Pennsylvania are the moist maritime tropical and the drier Pacific air (Bryson, 1966). Periods of time with enhanced westerlies, for example, would be drier at Ely Lake, as may have occurred from 900 to 500 years ago.

At Hells Kitchen Lake, an increase in *Tsuga* and *Betula* (yellow birch; Swain, 1978), and a decrease in *Pinus* and *Alnus,* are the local manifestations of the long term increase of arctic airmasses which is seen as an increase in boreal forest at Lake of the Clouds and at the northeastern sites. Davis (1978) has shown that *Fagus* expanded its westward extent 350 years ago at the same time as the increase of *Tsuga* and *Betula* at Hells Kitchen Lake. At Dark Lake, there was an increase in mesic tree types at this time. Changes in pollen accumulation in southern Minnesota (Grimm, 1983) are also coherent with those at Dark Lake (Gajewski *et al.,* 1985).

The medium frequency changes are more difficult to interpret, as the climate forcing is not always as easily identified. However, these also show coherent changes between lakes. All of the lakes show changes at similar times: 1700–1500, 1200–1000, 600–500 and 200 years ago. These times coincide with climate episodes identified in other regions: the Medieval Warm Period from AD 1000–1200 and the Little Ice Age from AD 1450–1850 (Lamb, 1977). In some cases, a climate signal was evident, as in the interpretation of relatively moist and dry periods in the first components of Basin Pond and Ely Lake and the second component at Hells Kitchen Lake. In other cases, these periods are defined by a more rapid change in the long-term trend.

The interpretation of European impact on North American vegetation

MacIntosh (1972), Siccama (1974) and Bormann *et al.* (1970) have noted that the presettlement forest in the northeast differed from that of the present day, based on the analysis of land survey vegetation records. Documentation of this shift is complicated by sampling uncertainty and much of this difference can be attributed to differential utilization of tree species by settlers or the particular successional stage of the forest at the time of sampling. However, the dominant trend in the pre/postsettlement forest differences – a decrease of *Fagus* from the pressettlement to the present time – had been occurring for at least 500 years prior to settlement of the region by Europeans (Fig. 2). It is likely that some of the difference between the presettlement and present day forests is the continuation of a trend begun well before settlement (see also Bennett, 1985). Further work is needed to separate the impact of human activities on forest communities from natural variability.

Climatic effects on vegetation

This study was originally motivated by recent attempts to derive quantitative estimates of climate from pollen records on two time scales; the Holocene (Webb & Bryson, 1972; Bartlein *et al.,* 1984, and others), and the past 1000–3000 years (Berna-

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*Editorial note: See also various papers in the special issue on Vegetation-climate equilibrium, Vegetatio 67(2).

bo, 1981; Gajewski, 1983). Although there are many factors that affect vegetation composition (for example, climate, soil type, fire frequency), any ecological or geophysical process operates on a characteristic time scale (Imbrie, 1982; Delcourt *et al.*, 1983; Prentice, 1983). If the climate forcing is of prime interest, other factors can be ignored, if they do not bias (in some way) the climate estimates (see Imbrie, 1982).

The pollen diagram (either the whole diagram, some particular pollen types, or some linear combination of pollen types such as principal components) can be thought of as one realization of some underlying stochastic process. The pollen catchment area is a system with an input of climate, and the output of a pollen diagram. Fluctuations in the output (pollen diagram) can come from 1) fluctuations in the climate input to the system, transformed by the system to the observed output, or 2) interactions of subsystems, including the component species, disturbances, the soil subsystems or other environmental factors, or 3) chance variations.

These multiple sources of variation cannot be separated by the analysis of one diagram in isolation (Webb, 1981). The local vegetation response to a large scale circulation change depends on such factors such as the pre-existing state of the vegetation, topographic diversity and local hydrology (Bernabo, 1981; Green, 1983; Grimm, 1983). A single pollen diagram may also be influenced by local disturbances (Swain, 1978; Cwynar, 1978; Green, 1981) and chance variations. Finally, the specific changes in the local climate, such as temperature, precipitation or net radiation, due to a uniform regional change in large-scale circulation patterns varies from place to place (e.g., Jones & Kelly, 1983; Bryson, 1985).

Many of these local uncertainties can be avoided by considering a regional analysis of a network of pollen cores. Atmospheric circulation changes are large scale in nature, and for the scales that we are interested in, should affect all of the diagrams analyzed in this study (Bryson & Padoch, 1980). If the above-mentioned complications can be avoided or taken into account, then these large-scale patterns can be determined. For example, by mapping the spatial patterns of abundance of pollen for various times in the past, Bernabo & Webb (1977) were able to show that pollen changes were consistent for large areas and long time periods. These patterns could be explained, at least qualitatively, by changes in the atmospheric circulation patterns. Bernabo & Webb (1977) interpreted changes in the major biomes, the boundaries of which can be represented by the change in abundance of characteristic species, e.g., *Picea, Pinus, Quercus,* and herbs. Their analysis retained only the very large scale pollen changes by greatly smoothing the pollen percentages.

The pollen changes seen in the data from this study are of a different scale. All of the sites are located within one biome. While representative species could presumably be used, it is not clear which species to use. The appropriate species may change across the biome that we are analyzing or may not be present at some sites. These pollen records are therefore hard to interpret, both because of the relatively small changes in abundance during the past two millennia, which are obscured by local variability and disturbances (Green, 1981; Swain, 1973, 1978; Walker, 1982), and because the nature of the climatic changes will usually be different from north to south or from east to west. Therefore, to identify the large scale changes, the strategy used here was to ignore individual species responses to climate by calculating the principal components of correlation between species and then comparing the community change of several diagrams through time. It was found that all of the pollen diagrams show a long term trend that can probably be associated with the changes in atmospheric circulation associated with final phases of the gradual 'Milankovitch cooling' of the past several thousand years – as summer temperatures have steadily declined with decreased summer insolation (Kutzbach, 1981). Medium frequency fluctuations (with timescales of several centuries) were also found to be coherent at many sites and therefore could be associated with climatic changes, even though the immediate forcing on the vegetation might be changes in the climate-related fire frequency (Loucks, 1970). High frequency fluctuations were also identified at all cores, but either these reflect local events, or, if climatically-controlled, a more detailed network of time and space sampling would be required to resolve the climatic signal.

This study further documents that one need not search for climatic effects on vegetation only at ecotones or 'sensitive' sites (c.f. Watts, 1980; Woods & Davis, 1982; Prentice, 1983; Grimm, 1983). Davis (1982) and Davis & Botkin (1985) have argued that century-scale fluctuations, such as the Little Ice Age, would rarely be seen in pollen diagrams, and that these fluctuations may only be apparent at ecotones or other special situations where the vegetation is in equilibrium with the climate (Davis, 1978). However, climate fluctuations are identified by the analysis of the spatial distribution of pollen assemblages. For example, *Fagus* may expand or contract in one portion of its range (at the ecotone), and this can be discerned by careful sampling of several nearby lakes (Davis 1978; Bennett, 1985). In other parts of the range, the change may be less, or even of the opposite direction. While *Tsuga* and *Fagus* expanded in the midwest during the past 500 years, there was a major decrease in these types in northern New England. The response of *Fagus* to a climate change will be less in the center of the range presumably because the threshold of response of *Fagus* to the particular climatic change has not been crossed, or the changes were too small to be detected above the noise of the diagram. But by analyzing the multivariate community response to a climatic change, some other taxa may change and the vegetational response to the climatic fluctuation would be recorded.

This method of presentation has also emphasized the continuous nature of climate changes and vegetation response to these changes. While it is generally acknowledged that the climate changes at all scales, emphasis has been on certain episodes – e.g. the Little Ice Age (Lamb, 1977; Davis & Botkin, 1985). While it may certainly be true that climate changes are episodic, this should not obscure the fact that these changes are occurring continuously and at all scales (Bryson, 1975). The Little Ice Age was one of a series of events of this frequency, duration, and magnitude. These century-scale climate changes are superimposed on a long-term cooling in eastern North America (see also Fisher, 1982). However, the most drastic changes observed in these pollen diagrams are those starting about 500–600 years ago (Swain, 1980).

There may be a scale interaction between the long term cooling and the apparent severity (as sensed by the vegetation) of the most recent medium frequency 'Little Ice Age' event. As the mean climate cools, there may be a greater probability that a century-scale climate fluctuation would affect the plant populations in the region. Fig. 5, modified from Schumm (1977) illustrates the importance of a threshold of response of a species to climate changes. Subsequent century-scale climate fluctuations would be more evident, even if their magnitude about the trend is the same (although it need not be). The long-term cooling can be considered as increasing the susceptibility (cf. Campbell, 1983) of the site to change by the medium frequency climate fluctuations, in the same way that the location of a site (e.g. on an ecotone) increases the susceptibility to climatic fluctuations. Local increases of e.g., *Picea* occur when higher frequency climatic fluctuations change the competitive advantage in favor of *Picea*, or a disturbance permits an increase of *Picea*, *Abies*, *Betula* or *Pinus*. The resulting vegetation history is a time analogue of a spatial ecotone, where some variables (e.g. radiation) change smoothly while others change abruptly (Bryson, 1966). The interaction of these different frequency changes, in either space or time, causes physical boundaries that can be abrupt in some places and gradual in others.

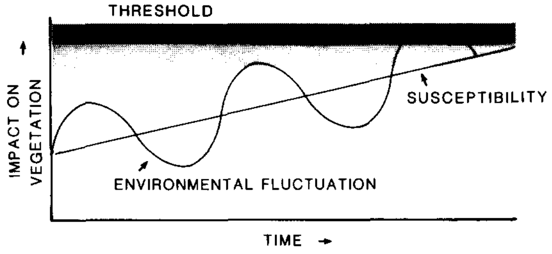

Fig. 5. Scale interaction in the response of vegetation to climatic changes of several frequencies.

Succession of communities following a disturbance is an important paradigm of ecology, and is usually described as unidirectional and non-stationary. Loucks (1970) noted that repeated fires and subsequent successions could be considered a stationary process, when viewed in a longer term context. However, environmental changes of many frequencies are affecting ecosystems. This landscape level process of repeated fires and successions may be non-stationary, when it is viewed in an even longer-term context of the neoglacial climate changes.

This study has confirmed the vegetation response to a long-term Late-Holocene climatic trend. In addition, this study has suggested that vegetation responds rapidly to century-scale climate changes. This was shown by using a spatial array of pollen diagrams and analyzing the community fluctuations at each site. Although specific mechanisms by which climate changes affect plant populations is not known, climate changes can, in this way, be identified.

Natural environmental variability and environmental impact assessment

The examples discussed above indicate that there is temporal variability in the forests on a scale that is important for the interpretation of the modern landscape. The increase in *Picea* across the whole area and the east-west shift in *Tsuga* and *Fagus* are examples of major changes in this forest region that occurred quite rapidly.

A rough indication of the impact of the environmental changes discussed above can be obtained by comparing the values of some pollen percentages in the cores to samples of modern pollen. Surface samples as far away as southern New England and New York are needed to provide reasonable 'analogues' to conditions in Conroy Lake and Basin Pond prior to 600 years ago. Thus climatic shifts equivalent to latitudinal shifts of 500 km appear to have occurred. This seems to indicate a major and significant decrease in *Tsuga* and *Fagus* in Maine in response to a recent climatic change.

While these changes are too slow to be discerned by an individual in their lifetime, they are certainly of the frequency and magnitude to be considered in environmental impact planning. These pollen diagrams provide good examples of the natural climatic variability, as sensed by the vegetation. Furthermore, these changes can occur anywhere, not just at particular sensitive sites such as biome margins. Models to predict the impact of human effects on ecosystems may have to account for the interaction of human-induced influences and natural changes of many scales.

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