Some Implications of Paleoecology for Contemporary Ecology

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I. Abstract

The paleoecological record allows contemporary ecologists to put current pheno-mena into the context of a longer time-frame, thereby providing the opportunity to evaluate the importance of slowly operating processes, past cyclic or unusual events, disturbance regimes, and historically constrained phenomena. We briefly outline the environmental history of the Quaternary, discuss the spatial and temporal resolution of the paleoecological evidence for biotic change, and summarize data relevant to such current issues as the nature of the biotic community, the role of disturbance, stability versus rapid change, evolutionary theory, explanations of species diversity, and refugia theory. Finally, we offer examples of the utility of paleoecological tech-niques for ecologists and environmental scientists.

Sommaire

Le dossier paleoécologique peut aider les écologistes contemporaines à mettre les phénomènes actuels dans le contexte d'une periode plus longue, ainsi fournissant l'occasion d'évaluer l'importance des processus qui s'effectuent lentement, d'événements cycliques ou inhabituels du passé de régimes perturbatrices, et du phénomènes historiquement contraints. Nous tracons brièvement l'histoire du milieu environnement du Quaternaire, discutons la résolution spaciale le temporelle de l'evidence paleoécologique du changement biotique et résumons les donneés applicable à des issues actuels tel que la nature de la communauté biotique, le role du dérangement, la stabilité contre le changement rapide, la théorie d'évolution, les explications de la diversité des espèces, et la théorie d'évolution, les explications de la diversité des espèces, et la théorie de refugia. Finalement, nous présentons des exemples de l'utilité des techniques paleoécologique pour les écologistes et les savants qui etudient l'environnement.

II. Introduction

The earth's biota responds to environmental changes that range in time from milliseconds to millions of years and affect areas from 10^{-6} to 10^{14} m^2 (Fig. 1). Most ecologists study organisms on a time scale of less than 100 years (and are usually limited to the time span of a field season, grant or dissertation) but many patterns and processes in nature can be better understood over a longer period. By providing information on vegetation and environmental change, especially during the past 15,000 years, paleoecology can broaden the interpretation of issues that are specifically relevant to modern ecologists, e.g., the prevalence of stability versus rapid change in ecosystems, the concept of an integrated community, the importance of disturbance in regulating community organization, alternative explanations of species diversity, and refugia theory. Paleoecological approaches also have many uses for applied ecologists and environmental scientists concerned with landscape management, restoration ecology, and the design of nature preserves.

The ecological implications of paleoecological data have been noted both by community ecologists and paleoecologists (cf. various authors in Barbour & Billings, 1988; Braun, 1950; Clements, 1924; Davis, 1983; Delcourt et al. 1983; Foster et al., 1990; Ogden, 1985; Walker, 1982; Watts, 1970; West, 1964). Because paleoecology is essentially community ecology stretched backward through the fourth dimension of time, it offers the ecologist a vast temporal vista from which to view present patterns, processes and phenomena. While the number of paleoecological studies and the variety of temporal and spatial scales therein has increased, contemporary community ecologists have become more aware of the importance of processes occurring over extended periods of time. In the past two decades enough paleoecological data have accumulated to allow analysis and mapping of multiple data sets, which has resulted in temporal/spatial maps relevant to many ecologists.

As ecologists are beginning to extend the scales at which contemporary phenomena are addressed (Hubbell & Foster, 1986; Ricklefs, 1987; Urban et al., 1987), and as paleoecologists are contributing to ongoing discussions of ecological theory (Bennett, 1988; Davis, 1986; Delcourt & Delcourt, 1987; Prentice, 1988; Huntley & Webb, 1989), the interrelationships of the two fields are becoming more apparent.

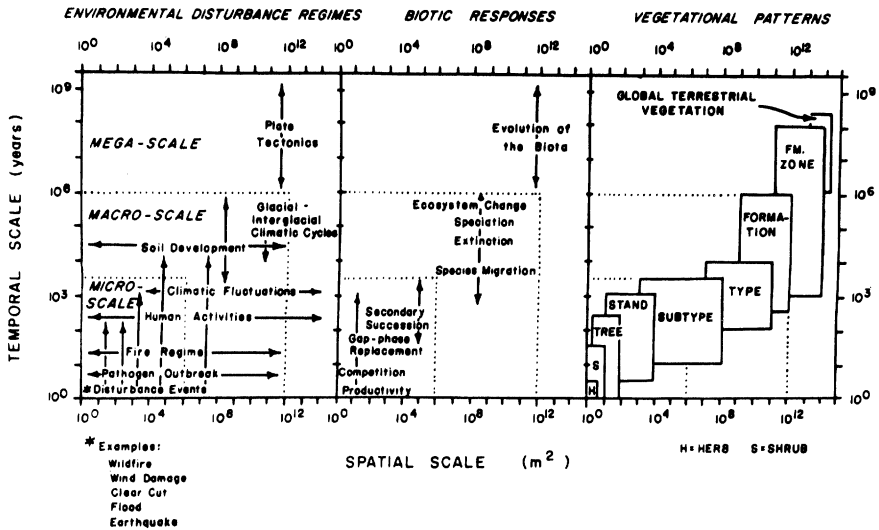This paper emphasizes this interdependence with examples drawn mainly from

Fig. 1. Spatial and temporal scales at which disturbance, biotic responses and vegetation patterns can be detected. Paleoecological data can detect micro- and macro-scale disturbance regimes, and are useful at all but the finest scales of biotic responses (productivity and competition) and vegetation patterns (individual organisms). (From Delcourt et al., 1983.)

eastern North America and western Europe. A brief outline of the environmental history of the last 1.6 million years (the Quaternary Era) sets the stage for describing the response of vegetation to environmental change during the last 18,000 years of the recent post-glacial period. Within this context we will examine the relevance of recent developments in the field of paleoecology to the fields of community ecology, evolutionary biology, and environmental science.

III. Quaternary Environments and Vegetation

A. CLIMATIC CHANGE DURING THE QUATERNARY

The Quaternary Era encompasses the last 1.6 million years and some 24 glacial events (van Donk, 1976), and is recognized as a predominantly cold period following the relatively warm and equable Tertiary (Nilsson, 1982). Within the Quaternary, glacial stages have usually lasted 50–100,000 years, with a 41,000 year cycle dominant in the early Quaternary and a 100,000 year cycle dominant after 700,000 years BP (Shackleton et al., 1988). During glacial stages large ice sheets slowly accumulate in high latitudes in an oscillatory fashion. These glacial stages generally end with a rapid decay of the ice sheets, followed by relatively warm interglacials of 10–20,000 years similar to the current Holocene Epoch, which began about 10,000 years ago and may end within the next few thousand years (Emiliani, 1972; Imbrie & Imbrie, 1986). Thus glacial stages are periods of relative climatic stability followed by rapid environmental change and relatively brief interglacials. Shorter-term environmental changes occur within this glacial-interglacial time frame.

The alternating warm and cold periods of the Quaternary are generally believed to result from changes in insolation caused by cyclical alteration in the earth's orbit around the sun as set forth by the Milankovich theory (Berger et al., 1986; Milan-
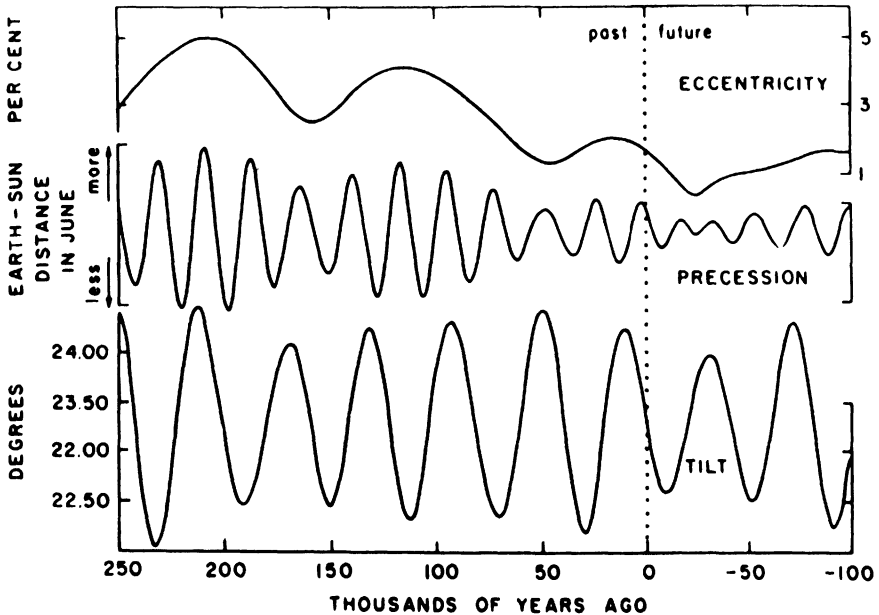
Fig. 2. Changes in the geometry of the earth's orbit during the last 250 ka and projected for 100 ka into the future. Glacial-interglacial cycles roughly correspond to periods when the extremes of these cycles reinforce one another. (From Imbrie & Imbrie, 1986.)

kovich, 1941). This theory describes three components of the geometry of the earth's orbit, each with its own long-term cycle, that combine to give an overall cyclicity. Eccentricity (the degree to which the earth's orbit deviates from being circular) varies from 0% to 5% or 6% on a 100,000 year cycle. Obliquity (the tilt of the earth's axis) changes from 22 to 24.5 degrees on a 41,000 year cycle, and primarily affects the latitudinal distribution of solar radiation. Precession (the time of year when the earth-sun distance is a maximum or minimum) alters approximately 10% on a 22,000 year cycle, and affects seasonality. Long-term climatic variation is caused by the interplay of these three cycles (Figs. 2 and 3). Climatic changes are variable because the three cycles have different effects at various latitudes; they also amplify and/or interfere with each other at various times and cause time-transgressive events like glaciation and oceanic heating/cooling. In general, warm and cold stages in the Quaternary roughly correspond to periods when these cycles amplify one another, although the effects of orbital forcing are modified by surface boundary conditions, positive feed-back, and lag effects.

The occurrence and duration of glacial cycles during the Quaternary is well documented by the study of glacial geomorphological features, fluctuations in ocean and lake levels, stable isotope ratios in ocean sediments and ice cores, planktonic assemblages in ocean and lake sediments, plant (especially pollen) and animal fossils in lake and bog sediments, and changes in sedimentation and chemistry in peat and lake sediments (Bradley, 1985). In particular, radiometric and paleomagnetic methods of dating and stable isotope analysis revolutionized the field of paleoecology in the 1950's and 1960's (Cox et al., 1963; Godwin, 1980; Shackleton and Opdyke, 1973; Thompson & Oldfield, 1986). These methods helped to extend previous estimates of the number of glacial episodes during the Quaternary from 4 to about 24
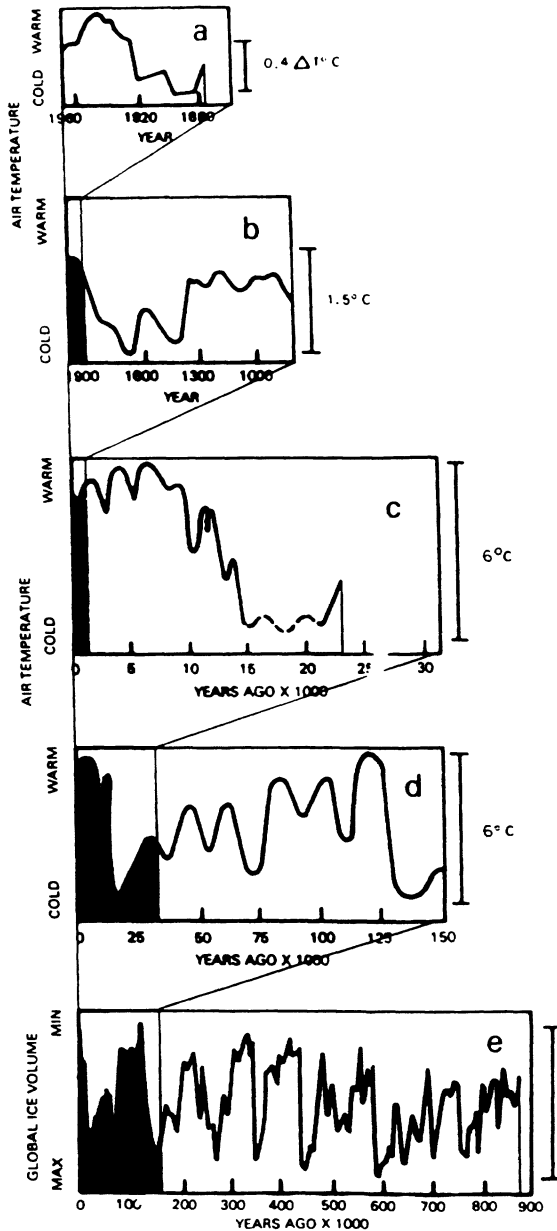
Fig. 3. Global temperature (a–d) and ice volume (e) on different time scales shows that we are currently living at the end of a brief warm period in a predominantly glacial climate. Note that interpretation of apparent patterns depends on the scale at which they are viewed. For example, the dramatic rise in temperature from 1880 to 1960 (a) appears to be a continuation of a steady warming trend since the end of the little ice age (b), which in turn appears to be a brief reversal of a slow cooling trend beginning about 6000 years ago when global temperatures during the current interglacial reached their maximum. (From Webb, 1986.)

(Fig. 3). They also provided a more detailed chronology for these glacial cycles and for shorter-term events such as the environmental and biotic changes since the end of the most recent glaciation.

A few marine and terrestrial records show climatic changes at the frequency of Milankovitch cycles for at least the past 3 million years (Hooghiemstra, 1984; Shackleton et al., 1988). This suggests that orbital cycles, albeit unaccompanied by glaciations for the most part, have occurred throughout earth history and have gone undetected by temporally coarse geologic evidence (Bennett, 1990).

The nature of late-glacial and Holocene climate change is being refined through the use of general circulation models coupled with a global network of paleoclimatic data (Bartlein et al., 1989; COHMAP, 1988; Kutzbach & Guetter, 1986; Webb et al., 1987). Simulations run on these models are in reasonably close agreement with the paleoclimatic data, and the integration of these data and models are the basis for the following brief summary of the climatic history of North America for the last 18,000 years.

At the time of the last glacial maximum 18,000 years ago, solar insolation was similar to that of the present (Fig. 4), but global climate was considerably different, with air and sea-surface temperatures generally lower, and global air and ocean circulation altered. The large 3 km thick Laurentide ice sheet covering most of Canada and the northeastern United States split the westerly jet stream, which was stronger than it is presently, into northern and southern sectors. The more southerly track of the jet stream brought more moisture to the American southwest, while a strong anticyclone centered on the ice sheet brought drier air to the Pacific Northwest. Although the central and eastern United States were colder than at present, cold arctic air masses were trapped behind the ice sheet in the Arctic Basin. When this air mass was able to flow down to the mid-continent plains during winter, it would have been warmed adiabatically by 20° to 30°C. Yet summer temperatures would have been cooler near the ice sheet. Thus the climate of the eastern and central United States, although cooler than at present, may have been less seasonable and more equable.

From 18,000 to 11,000 years BP the earth–sun distance decreased in northern summer and the axial tilt increased, thereby increasing average solar radiation and seasonality for northern latitudes. Ice sheets stabilized and began to retreat as early as 16,000 years BP, although widespread melting did not begin until 14,000 years BP. By 12,000 years BP increasing solar insolation (and perhaps feedback mechanisms such as bedrock rebound, increased iceberg calving, moisture starvation and elevated CO_2 concentrations) reduced the Laurentide ice sheet so that it no longer deflected a somewhat weakened westerly jet stream northward. Maximum rates of glacial decay lagged the solar insolation maximum at 11–10,000 years BP by about 1000 years, as did maximum mid-continental temperatures. The transition from late-glacial to Holocene climates from 14,000 to 10,000 years BP was not continuous spatially or temporally. Climate change accelerated to a maximum toward the end of this period, and at least one significant cool interval (possibly resulting from oceanic cooling caused by rapidly decaying ice-shelves) is recorded for many sites adjacent to the North Atlantic Ocean before a rapid warming that marked the beginning of the Holocene about 10,000 years BP (Fig. 3).

From 9000 to 6000 years BP summer temperatures reached their maximum of 2° to 4°C above present (except at the boundaries of the rapidly melting ice sheet), and thereafter declined to present values. During this time climatic regimes in the west
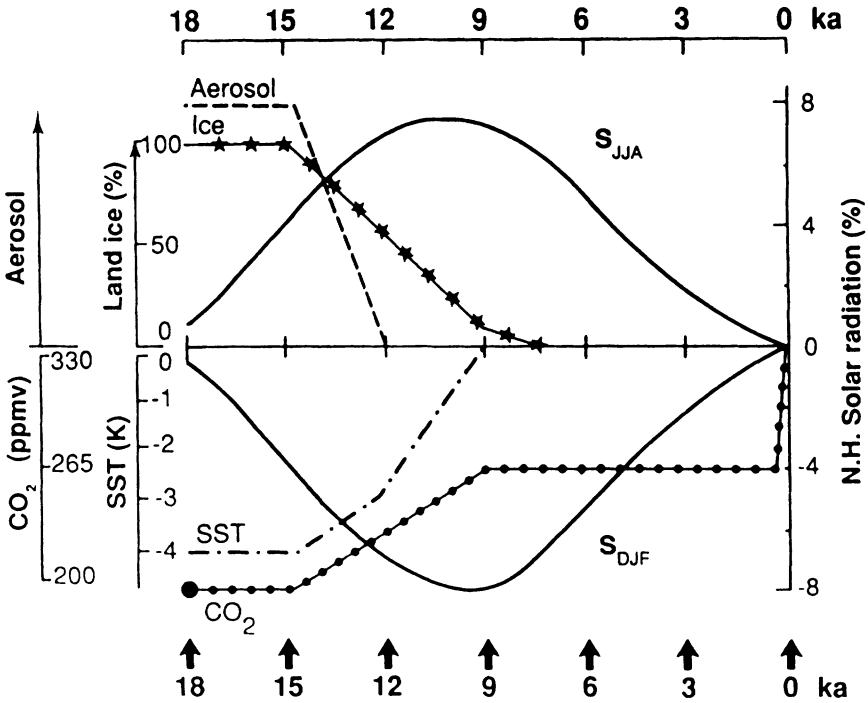
Fig. 4. Boundary conditions for various parameters in the COHMAP global climate simulation model for the past 18 ka, expressed as the percentage departure from present values for: S_{JJA}, S_{DJF}, Northern Hemisphere solar radiation for June–August and December–February, respectively; SST, global mean annual sea-surface temperature. Land ice is expressed as the percent difference from that of 18 ka. CO_2 is parts per million by volume, and excess glacial-age aerosol is drawn on an arbitrary scale. (From COHMAP, 1988.)

approached modern values as temperatures increased, and precipitation patterns shifted from predominantly winter to summer monsoonal in the southwest; in the Pacific Northwest temperatures were warmer and moisture levels lower than at present until 6000 years BP (COHMAP, 1988; Ruddiman & Wright, 1987).

Although paleoclimatic data are adequate only for North America and western Europe, the reasonably close agreement of the data with general circulation models suggests the following: First, complex climatic changes have occurred over the entire earth, driven by orbital forcing, yet modified by the interplay and feedback of such factors as changes in ice sheet albedo, extent of sea ice, iceberg calving, jet-stream deflection by ice sheets, sea surface–land temperature differences, consequent oceanic and atmospheric circulation, and elemental cycling. Second, climate has varied along a continuum of space and time, and climatic changes may have been time-transgressive with lag effects in certain regions such as at the boundaries of ice sheets. Third, there were past climatic regimes for which there are no modern analogs. For example, there are probably no modern climate analogs for North American climates from 18,000 to 12,000 BP, or for the increased seasonality in the Northern Hemisphere approximately 9000 years BP (Fig. 4).

B. EVIDENCE FOR BIOTIC CHANGE

The evidence for long-term vegetational change comes from fossil plant parts such as pollen, seeds, leaves and twigs contained in lake muds and peats, and in drier environments, pack-rat middens (Berglund, 1986; Betancourt et al., 1990; Birks & Birks, 1980). Most late-glacial and Holocene vegetational data come from studies of fossil pollen in which samples are taken from lake and peat sediments. The pollen within these sediment samples is concentrated, sub-sampled, counted, and displayed on a pollen diagram (Fig. 5). Macrofossils such as seeds, leaves, and twigs offer more taxonomic and spatial resolution than pollen, but are less abundant in most sediments so that problems of sampling and temporal resolution can arise. Information derived from fossil pollen lacks the spatial, temporal and taxonomic resolution of living material, but offers a long-term perspective unavailable to ecologists who study living organisms.

The principles of pollen analysis, briefly enumerated below, have been rigorously tested and refined for over 70 years.

1. Most pollen and spores are produced in abundance.
2. Most of these fall to the ground from a well-mixed pollen rain that represents the surrounding vegetation.
3. Pollen is preserved under anaerobic conditions, for example in lake and bog sediments.
4. Small amounts of sediment (≤ 1 cm^3) contain enough taxonomically identifiable pollen (up to 10^6 grains) to represent the surrounding vegetation at the time the sediment was deposited.
5. Pollen spectra obtained from several levels of a sedimentary column represent the history of the vegetation at that place.
6. Two or more series of pollen spectra obtained from different sites represent changes in vegetation at different places.

Pollen analysts have taken great strides in understanding differential pollen production, dispersal, deposition and preservation (Andersen, 1974a, 1974b; Calcote & Davis, 1989; Clark, 1988a; Cushing, 1967; Davis, 1973; Davis & Brubaker, 1973; Havinga, 1967; Jackson, 1990; Raynor et al., 1975). Recent advances have also been made in sampling, numerical analysis and multivariate techniques (Berglund, 1986; Birks & Birks, 1980; Clark, 1988b; Gordon & Birks, 1985; Green, 1981, 1988; Jacobson & Grimm, 1986; Maher, 1972, 1981; Prentice & Webb, 1986; Schwartz, 1989; Webb et al., 1981). These studies have helped to define the taxonomic, numerical, spatial, and temporal confidence limits of pollen data, and have provided methods for reducing the complexity of the data so that pollen assemblages can be interpreted more clearly with regard to stratigraphic relationships, environmental gradients, and rates of change.

Paleoecologists can address various ecological problems along a broad continuum of spatial and temporal scales through the careful selection of study sites, organisms, and field, laboratory and analytical techniques. In general paleoecologists want to know about the presence, abundance, location, and temporal occurrence of taxa, communities and environments. Many studies combine pollen analysis with analyses of plant/animal macrofossils, charcoal, sediment lithology and chemistry, human artifacts, tree-rings, historical records, and modern vegetation. These studies reveal

LAKE OF THE CLOUDS, MINNESOTA

A. M. Swain   1973
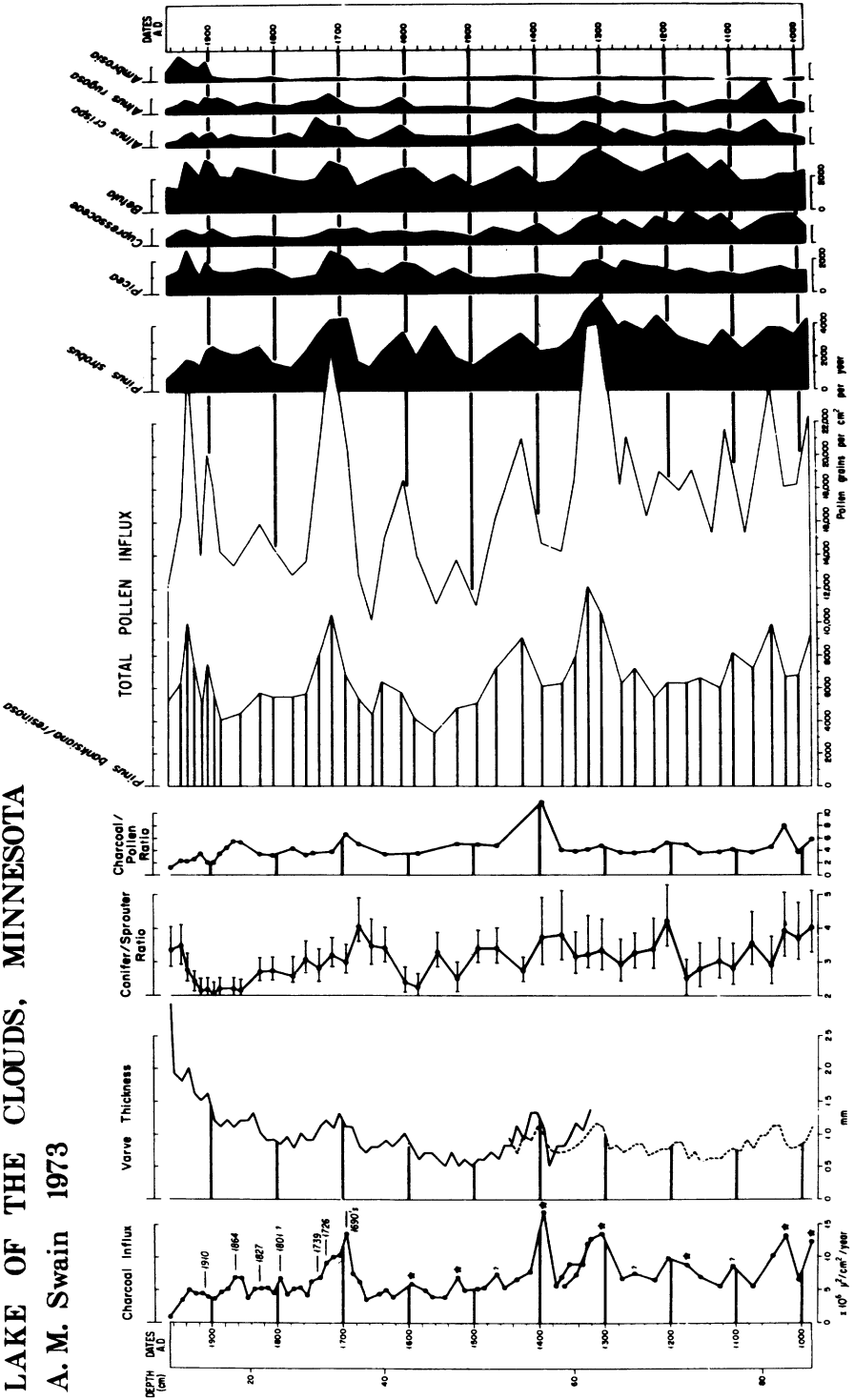
patterns of climate change, natural and anthropogenic disturbance, soil development, erosion, community composition and diversity, migration, invasion and succession (for examples and techniques see Berglund, 1986; Birks & Birks, 1980; and Huntley & Webb, 1988).

A few examples illustrate the spatial, temporal and ecological resolution available at various scales (Fig. 1). Tree-ring analysis, vegetation reconstruction and historical records provide very fine resolution, often comparable to data from permanent plots. Henry and Swan (1974) and Oliver and Stephens (1978) analyzed the growth rates of live and dead stems on small plots (0.04 and 0.36 ha respectively) in conjunction with historical records. They detected disturbances such as fire, windthrow and tree-cutting, and subsequent changes in vegetation composition. Many studies (e.g., Foster, 1988; Heinselman, 1973; Hemstrom & Franklin, 1982; Romme, 1982) have used less intensive techniques to document disturbance and vegetation change at the landscape level. Tree-rings also provide paleoclimatic information at the local, re-gional and global level, detecting phenomena such as the "little ice age" 1450–1850 A.D. (Fritts, 1976).

Annual laminations in lake sediments may provide yearly records of vegetation and environmental change (Saarnisto, 1986; Clark, 1990). Swain (1978) analyzed varved sediments from Hell's Kitchen Lake in north-central Wisconsin for pollen, charcoal and seeds. He found a successional sequence of aspen, birch, white pine, and hemlock following fires whose frequency of 100 to 140 years was affected by available moisture of the prevailing climate. He concluded that major vegetational change occurred on two different time scales. Short-term changes related to individual fires were superimposed on longer term changes resulting from increases or decreases in the frequency of these fires.

Basin size (in addition to morphometry, in/outflow, and surrounding vegetation) determines to a large degree the source area of pollen falling onto the surface of a lake or pond (Fig. 6). Moderate sized lakes (10 to 100 ha) receive pollen mainly from within a 20 to 30 km radius. Finer spatial resolution is available through the analysis of mor humus and sediments from small forest hollows (Bradshaw, 1988). These sites, overhung by a tree canopy that contributes abundant pollen and also filters the regional pollen rain, collect pollen from a smaller source area than ponds and lakes, allowing stand-level interpretations of vegetational change over thousands of years in some cases (Andersen, 1970; Jacobson & Bradshaw, 1981; Mitchell, 1988). Aaby (1983) analyzed pollen and fungal hyphae from two soil profiles only 7 m apart and found clear differences, substantiated by historical records, between the two sites. Andersen (1984) analyzed pollen from a suite of small hollows and soil profiles in the Eldrup forest in Denmark, producing a detailed history of forest change at the stand level. Analysis of pollen from small hollows and mor humus is a well known technique in northern Europe, but has been adopted by North American paleoecol-ogists only recently (Davidson, 1985; Frelich et al., 1989; Heide, 1984; Schoonmaker & Foster, 1989; Schwartz, unpubl.). Although mor humus and small forest hollows have been thought to collect most of their pollen from a radius of 20 to 30 m (Jacobson

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Fig. 5. Charcoal influx, varve thickness, and pollen influx for the last 1000 years of Lake of the Clouds, Wisconsin. Sediment in this lake is deposited in discrete annual laminations or varves, which allows for precise dating of events. A fire frequency of 60 to 70 years (peaks in the charcoal influx marked by stars or dates) has maintained a relatively stable vegetation composition. (From Swain, 1973.)
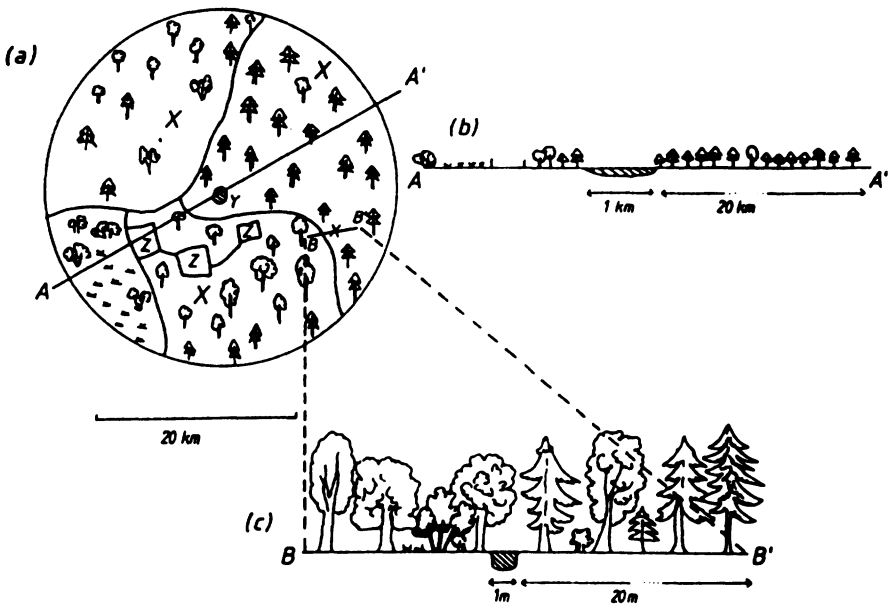
Fig. 6. a) Aerial view of hypothetical study area with pond (y) and forest hollows (x). b) View of pond with pollen source area (diameter A–A') and c) hollow with pollen source area (diameter B–B'). (From Bradshaw, 1988.)

& Bradshaw, 1981; Prentice, 1985), recent evidence suggests that the pollen collection properties of these sites vary considerably, and that extra-local and regional pollen may contribute a substantial amount of pollen input (Calcote & Davis, 1989; Jackson, 1990; Schoonmaker & Foster, 1990). Pollen analysts must be careful to test and acknowledge the spatial and temporal limits of data from small hollows and mor humus.

A combination of fine spatial scale pollen analysis and vegetation reconstruction should produce a long record of both high spatial and temporal resolution (Schoonmaker & Foster, 1990). Reconstruction of the establishment, growth and death of live, dead, and downed stems provides a spatially and temporally detailed 100 to 1000 year history of vegetation dynamics. These data can be used to interpret the longer but less spatially precise record available through pollen analysis. Because seeds, leaves and woody plant parts are less mobile than pollen, macrofossil analysis should be included in studies whose aim is high taxonomic and spatial resolution (e.g., Jackson, 1989, 1991).

Landscape-level phenomena can be investigated by selecting small to medium size basins (that collect pollen from the surrounding 10 to 100 km²) at distances such that pollen source areas do not overlap extensively (Gaudreau et al., 1989). Brubaker (1975) analyzed pollen from lake sediments on three different soil types in Michigan and found that the same regional climate change resulted in different communities on different soils. Gaudreau (1986) compared two sites less than 15 km apart but with an elevational difference of 440 m in the northeastern United States and found that physiographic position affected the arrival dates of migrating plant species. Clark (1990) combined a stratigraphic analysis of charcoal on petrographic thin sections

from varved sediments from three small (5 ha) lakes having adjacent catchments with a study of fire scars on red pine trees. This combination of techniques produced a detailed picture of fire history and environmental conditions for a 1 km² area.

Radiocarbon-dated pollen spectra from thousands of basins throughout the world have been analyzed in the last few decades (Fig. 7). This large number of late-glacial and Holocene paleoecological studies has enabled the detailed mapping of the distribution of taxa through time on a regional or subcontinental scale in Europe and North America (Figs. 8–11). Huntley and Birks (1983) presented isopoll maps (contour lines connecting similar pollen percentages) of pollen sampled from 423 sites in Europe covering a period from 13,000 to 0 years BP with a resolution of 500 years. Bernabo and Webb (1977), Gaudreau (1986, 1988), and Webb et al. (1983) have drawn similar maps for the eastern United States (Fig. 8). Davis (1981), Gaudreau and Webb (1985), and Webb et al. (1983) constructed isochrone maps (contour lines representing migrational fronts of taxa at different times in the past) for eastern North America (Fig. 9). Delcourt and Delcourt (1981, 1985) and Davis and Jacobson (1985) mapped inferred vegetation for eastern North America during the late-glacial and Holocene. Most recently, Delcourt and Delcourt (1987) have produced a large set of maps based on 162 sites in eastern North America that present tree percentages at different times during the Holocene as interpreted by modern pollen/vegetation analogs (Fig. 10). Gaudreau (1984) and Jacobson et al. (1987) mapped different taxa simultaneously using colored isopolls to reveal population centers and overlap of different taxa at ≥500 year intervals over the past 18,000 years (Fig. 11). This latter method may offer the most insight into species interactions. A further step might be computer enhanced interpolation providing continuous output. These and other studies carefully select the data for proper and consistent analytical technique, time control and resolution. As more sites become available, the spatial and temporal resolution of the maps will continue to improve.

C. VEGETATION CHANGE DURING THE LATE-GLACIAL AND HOLOCENE

The maps of changing vegetation as implied by changing pollen percentages present the following picture: At the time of maximum glaciation 18,000 years ago, when ice covered much of northwestern Europe, Canada and the northeastern United States, the vegetation in the area immediately south of the ice sheet (the periglacial area) consisted of species drawn from a range of present day environments and life history strategies (pioneer, ruderal herbs, arctic-alpine, steppe). Some of these communities, which included sedges, grasses and taxa such as *Alnus, Betula, Dryas,* and *Artemisia,* might be recognized as tundra or steppe (Birks, 1986).

Other communities such as the open polar desert (dominated by chenopods, grasses, and *Artemisia*) that occupied northwestern Europe between the ice sheet and the Alps have no modern analogs (Iversen, 1973). The absence of modern analogs for fossil assemblages is not so surprising when we consider that climatic and edaphic conditions during the past were not merely different from those of the present, but may have combined to create unique habitats resulting in unique vegetation, for example, spruce–poplar and spruce woodland–tundra assemblages (Huntley, 1990; King, 1981; McAndrews, 1965; Prentice, 1986; Wright, 1987).

South of the 50- to 100-km-wide periglacial areas, steppe and gallery forests occurred in Europe with true forests found south of the Alps, especially in southeastern
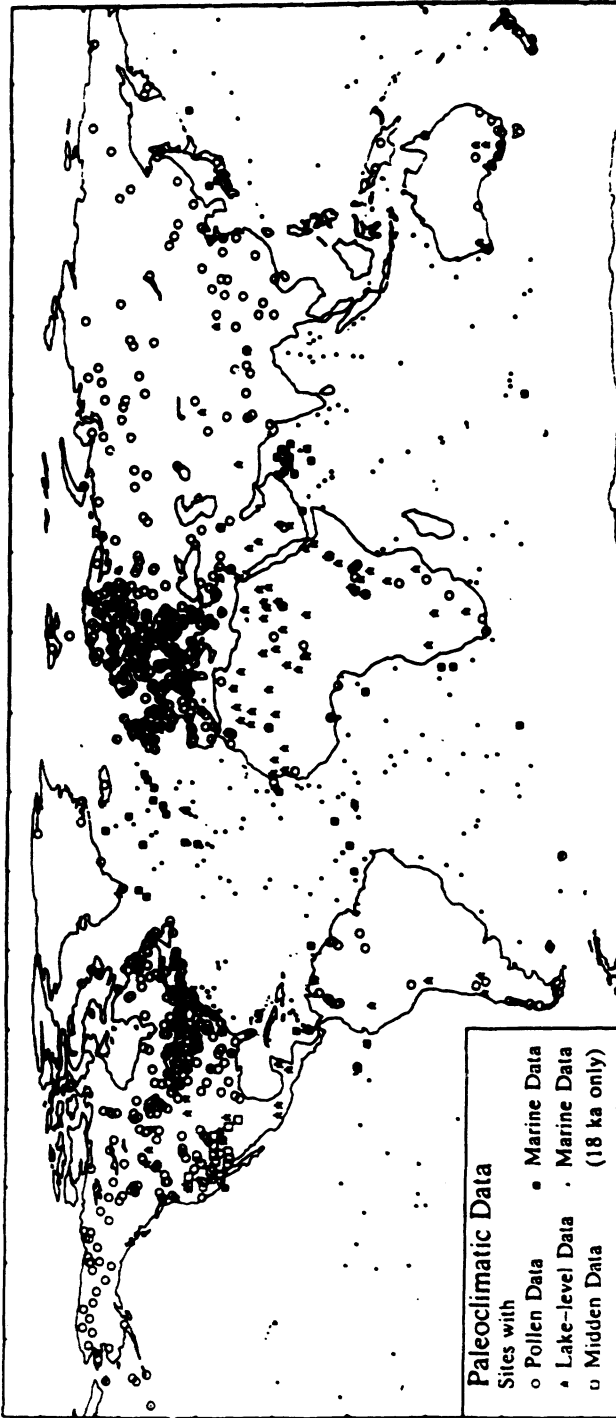
**Fig. 7.** Location of sites in COHMAP global paleoclimate database, which does not include all radiocarbon dated pollen records. Note the high number of sites in the Northern Hemisphere, especially in eastern North America and western Europe, and the scarcity of sites in the humid tropics. (From COHMAP, 1988.)

Europe in locally mesic refugia surrounded by an otherwise arid environment sup-
porting steppe and possibly sclerophyll woodland (Bennett et al., 1991; Huntley &
Webb, 1988; Van der Hammen et al., 1971). In North America south of the periglacial
area, an open spruce and larch forest dominated in the central United States well
into the Great Plains, with jack pine becoming more important toward the Appa-
lachians and reaching dominance along the Atlantic Coastal Plain and southeastern
United States. Deciduous trees may have occurred as minor elements throughout
much of the conifer forest (Jacobson et al., 1987). These deciduous species became
more important in the lower Mississippi River Valley and had isolated refugia in the
southern Appalachians (Delcourt & Delcourt, 1977; Delcourt et al., 1983; Wright,
1983).

   As temperatures increased, ice sheets began to retreat in a spatially and temporally
patchy manner about 14,000 years BP. Species on the periphery of the glacial boun-
dary invaded exposed substrate followed by species from further south. In Europe,
boreal species such as pine and birch invaded followed by elm, beech, hornbeam
and spruce, among others. Although most taxa migrated from southeast to northwest,
each took a somewhat different route, and moved at a different and variable rate
(Huntley & Birks, 1983). Spruce, a late-comer, migrated along a double front both
westward into central Europe and northwest into Scandinavia. Birch and pine have
continued to migrate southward along the Scandinavian peninsula in the last few
thousand years.

   As the ice retreated in eastern North America, tundra species preceded spruce,
jack pine and balsam fir, which moved northward at different rates and in different
directions, creating open and then closed conifer forests. Further to the south, white
pine and hemlock (Fig. 9) migrated up the Atlantic seaboard, while oak appears to
have migrated north-northwestward along a broad front. Following these species,
elm, maple, beech and chestnut appear to have moved in that order from the southern
Mississippi River Valley or further west, while hickory diverged into two fronts
apparently split by the higher Appalachians. Not all species migrated in a general
south to north direction. During the late-glacial, ash appears to have been restricted
to small microhabitats south of the ice sheet in the midwest. In the late-glacial to
early Holocene, ash expanded its range, becoming a component of a spruce–ash–
poplar assemblage, and then part of an ash–ironwood–elm asemblage, before its range
began to shrink again about 10,000 years BP. During this time the geographic center
of ash's range remained relatively fixed, just to the south of the Great Lakes (Jacobson
et al., 1987) (Fig. 11). Birch appears to have expanded to the southwest from the
northeastern United States and then later northward (Gaudreau, 1988) (Fig. 8). As
in Europe, each species took a somewhat different route (generally northward) and
migrated at variable rates (Davis, 1981a) (Table I). When we inspect the isochrone
maps (Fig. 9), we can clearly see that different taxa migrated at different rates, from
different origins and in different directions. Hickory invaded deciduous forests in
Ohio 4000 years before beech, but beech arrived in southern New England 3000
years before hickory. Beech and hemlock arrived in the Appalachian Mountains at
about the same time, but hemlock migrated more quickly thereafter and reached
central New England and upper Michigan 2000 and 2500 years respectively before
beech. Some species such as chestnut were still migrating northwards as recently as
2000 years BP, thousands of years after a well-developed forest had become estab-
lished and climatic cooling had begun. Most species have retracted their ranges
somewhat to the south in response to this recent cooling (Davis, 1983). The inde-
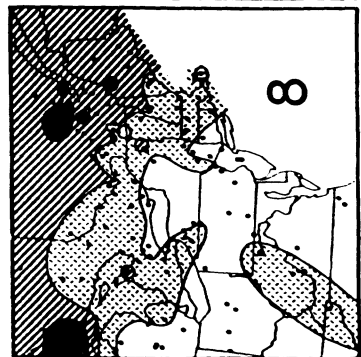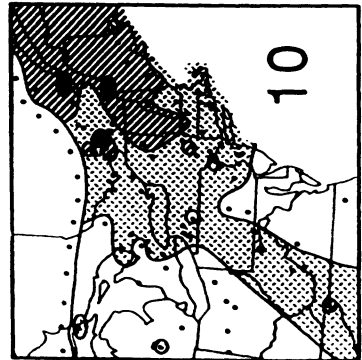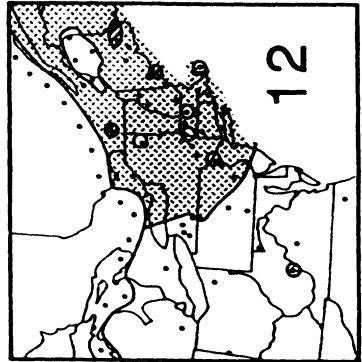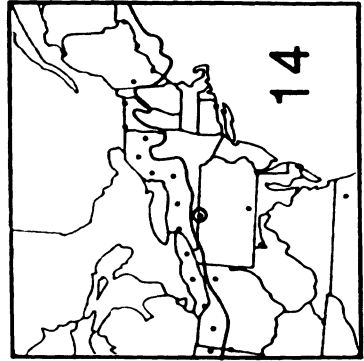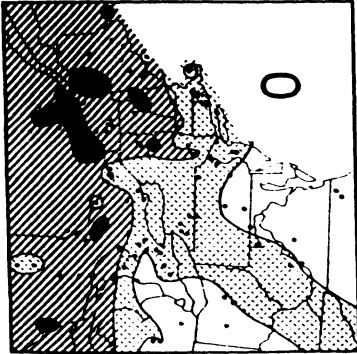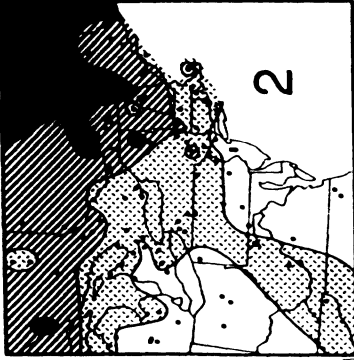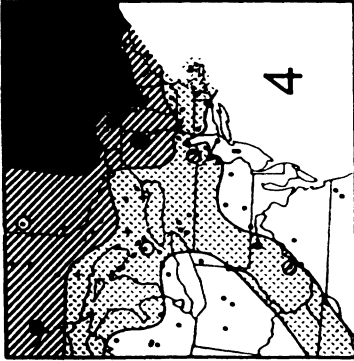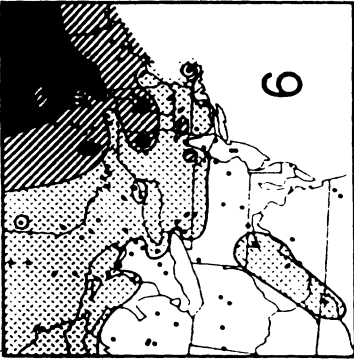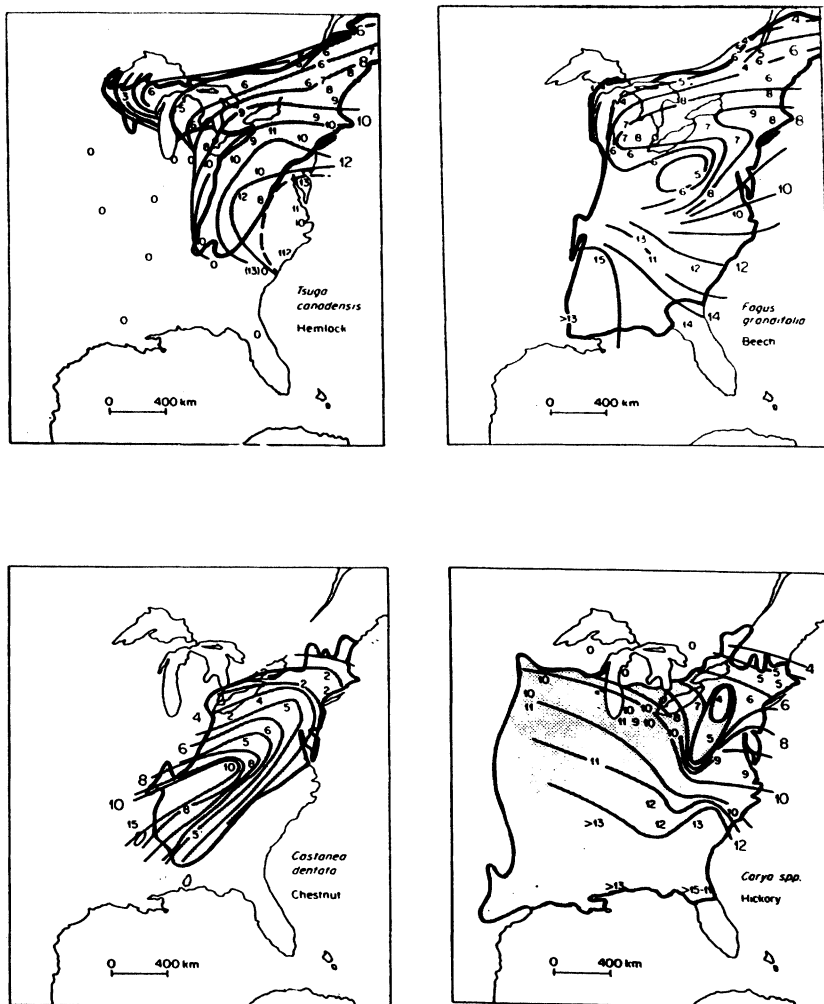
Fig. 9. The migration front of hemlock, beech, hickory, and chestnut depicted by isochrone maps (12 ka to present) with lines connecting arrival dates of taxa as inferred from increases in pollen or presence of macrofossils at 1000 year intervals. Heavy lines show present or recent range of taxa. (From Davis, 1982.)

pendent response of organisms to changing environments has far reaching implications for ecological theory. What we see today is merely a snap-shot of a dynamic and changing environment and biota that have come about through evolutionary and historical forces operating on several temporal and spatial scales.

←

Fig. 8. Isopoll map for birch pollen 14 ka to present with contour lines connecting values of 5% (stippled), 20% (diagonal lines), and 40% (black) birch pollen. Birch appears to have had a more northerly range during the last glacial period than many other arboreal taxa. Ice sheet appears in the northern part of 14, 12 and 10 ka maps. Dots are fossil-pollen sites. (From Gaudreau, 1988.)
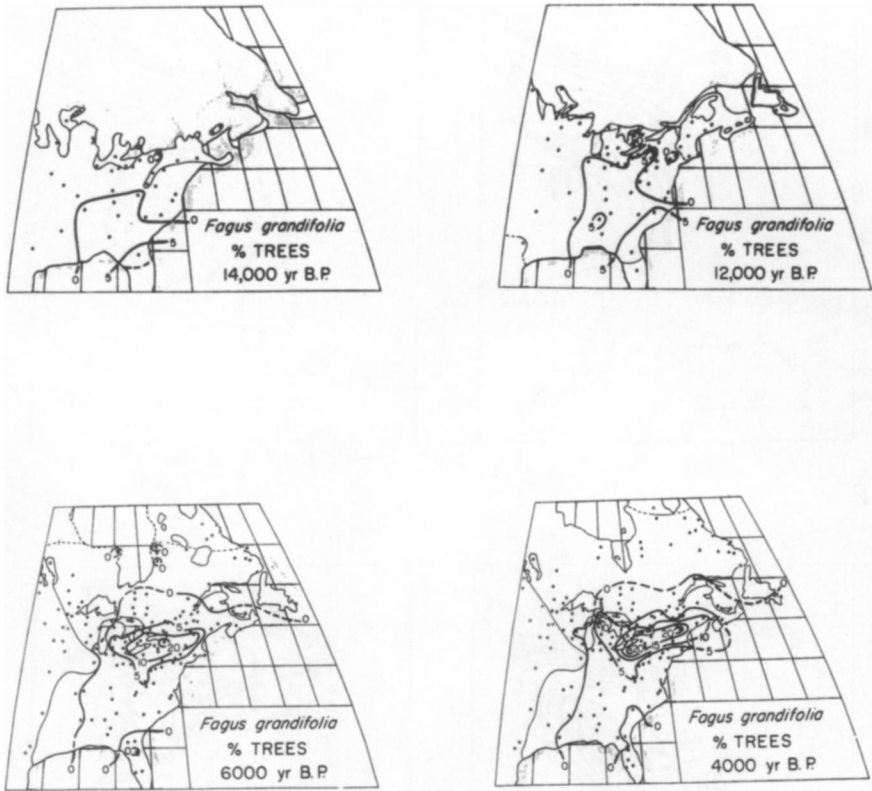
Fig. 10. Isophyte map of beech tree abundance, 14 ka to present, transformed from the pollen data to an estimate of tree abundance with a transfer function based on modern pollen samples and forest inventory data. Dots are fossil-pollen sites. (Delcourt & Delcourt, 1987.)

IV. Paleoecological Insights for Community Ecology

A. THE NATURE OF THE BIOTIC COMMUNITY

The nature of the biotic community has long been a source of disagreement and controversy among ecologists (Pickett & Davis, 1990). The "organismal" concept of Clements (1916) was criticized by ecologists who recognized the individualistic nature of species within assemblages (Cain, 1947; Gleason, 1917, 1926; Livingston & Shreve, 1921; Ramensky, 1924) and the continuous (vs. discrete) distribution of species along environmental gradients (Curtis, 1955, 1959; Curtis & McIntosh, 1951; Whittaker, 1951, 1956, 1975). It is interesting to note that Clements recognized the importance of disturbance in structuring some communities (Clements, 1910), and was well aware of the paleoecological perspective (Clements, 1924).

Recent definitions of "communitiy" have been purposely vague, ranging from "a set of species populations that occur in some place" (Schoener, 1986) to "all organisms in an area" usually restricted for the convenience of the researcher "spatially, trophically, taxonomically or by life form" (Roughgarden & Diamond, 1986). A temporal restriction is not mentioned, but is often implicit (i.e., the time period during which the community is studied).
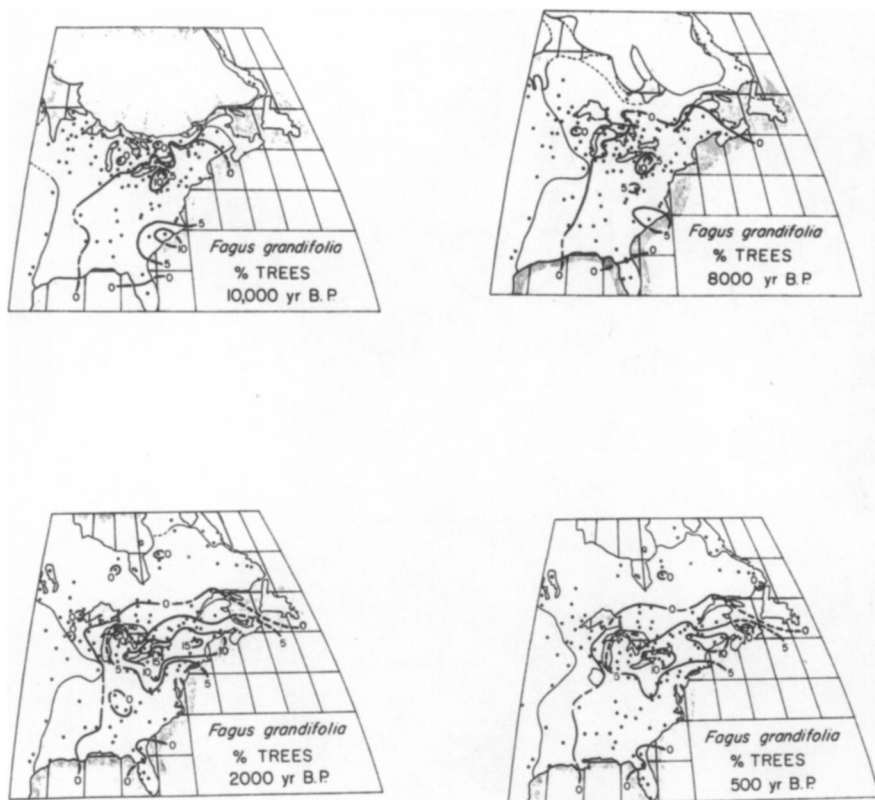
Fig. 10. Continued.

Several lines of paleoecological evidence suggest that plant communities are loose and relatively ephemeral assemblages of species populations. The individualistic response of tree species to climatic change described above, and the apparent ease with which species migrate into and subsequently leave assemblages demonstrate the absence of cohesive communities. For example, chestnut invaded the mature hardwood forest of the northeastern United States 2000 years ago with only modest readjustments in the densities of resident species (Davis, 1983). When chestnut was eliminated as a canopy dominant in these forests in the first half of this century, other species, especially oaks and hickories, merely increased their abundance (Keever, 1953; Mackey & Sivic, 1973). The sudden and temporary decline of hemlock in North America, and of elm in Europe around 5000 years BP also resulted in the increased dominance of remaining species (Allison et al., 1986; Davis, 1981b, 1983; Iversen, 1973). Both hemlock and elm recovered within a few hundred to a thousand years and rapidly regained their former abundance. Thus forests are relatively open communities that may suffer apparently little reorganization or ecosystem disruption upon the invasion or decline of a dominant species.

The ephemeral and transitory nature of plant communities is demonstrated by the independent migration of species and by historical changes in abundance and distribution of modern species assemblages. The forests with which we are familiar
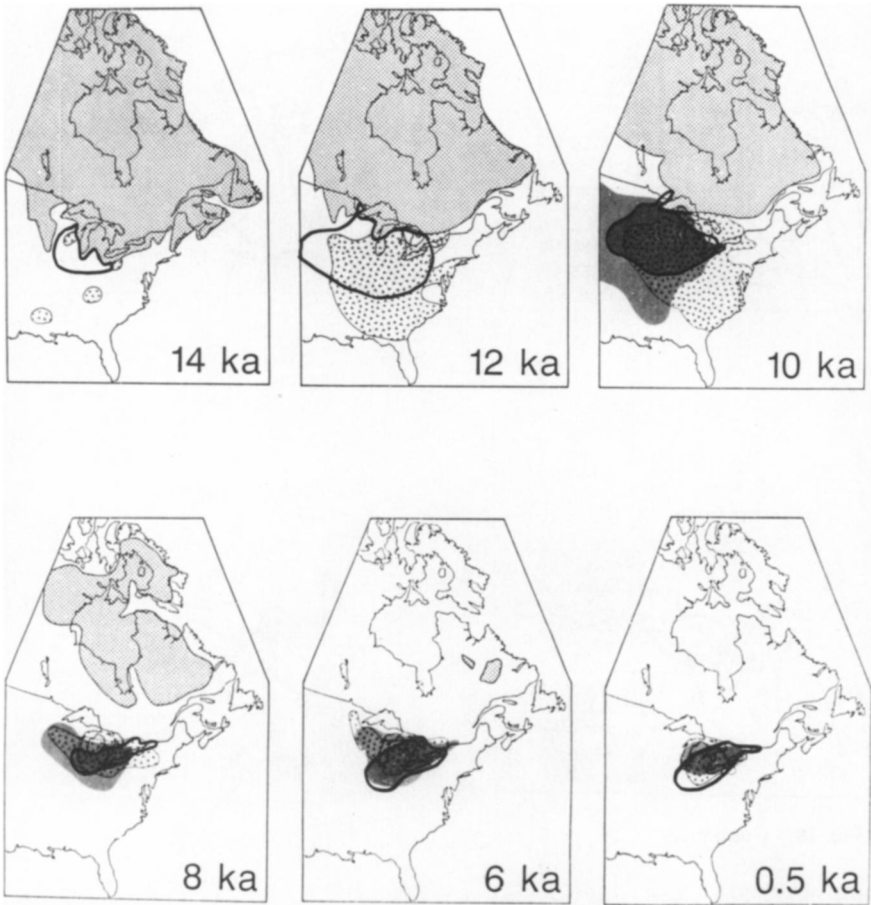
Fig. 11. Isopoll maps, 14 ka to 0.5 ka, with ice sheet to north stippled. Elm (light grey), ash (heavy outline), and ironwood (symbol < >) showing overlapping ranges (e.g., dark grey for elm–ash). The ranges of all three taxa have decreased throughout the Holocene, to the point that their present ranges might be considered refugia. (From Jacobson et al., 1987.)

today are composed of species that arrived at different times from various glacial refugia, responding independently to changing climatic and disturbance regimes and biotic interactions. As a particular species migrated in response to climatic change, it would have encountered other species to form dynamic and constantly changing assemblages. At the height of the last glaciation, a spruce woodland–tundra assemblage with no modern analog existed in the central and eastern United States (Wright, 1984, 1987); several thousand years later, the hardwood (black ash–ironwood–elm) component of this community was left behind as conifers moved northward (Jacobson et al., 1987). By the time most tree species were migrating northward (12,000–10,000 yrs BP), ephemeral communities, such as the black ash–oak–spruce–graminoid assemblage in north central Illinois (King, 1981) were not uncommon. The animal fossil record also has many examples of no-analog assemblages or what Graham (1986) calls "interminglings" of species that have separate ranges today.

Table I

Average rates of late-glacial to Holocene range extensions in eastern North America
(modified from Delcourt & Delcourt, 1987)

Genus	Rate (m/yr)
Salix	287
Populus	263
Betula	212
Tilia	209
Tsuga	202
Larix	189
Fagus	169
Abies	159
Picea	141
Juglans	140
Pinus (Northern group)	135
Ulmus	134
Acer	126
Quercus	126
Fraxinus	123
Carya	119
Castanea	100*
Pinus (Southern group)	81
Nyssa	70

* From Davis, 1982, roughly comparable to data from Delcourt and Delcourt, 1987.

This is not to say that all species assemblages have been ephemeral at all times. There are examples of constancy over long periods of time (Delcourt & Delcourt, 1987; Green, 1982; Jacobson & Grimm, 1986), but in general, change appears to be more characteristic of the late-Quaternary.

B. EVIDENCE OF DISTURBANCE IN THE PALEOECOLOGICAL RECORD

We define disturbance here sensu White and Pickett (1985) as "any relatively discrete event in time that disrupts ecosystem, community or population structure, and changes resources, substrate availability or the physical environment" and include both destructive events and environmental fluctuations. Most ecologists consider disturbance in a diurnal, seasonal, decadal, or centennial time frame, yet the disturbance regime (sensu Heinselman, 1981) of destructive events and environmental fluctuations with profound effects for the vegetation of an area is best characterized over longer time periods. The use of the long paleoecological record enables ecologists to avoid the space-for-time substitution that, although employed by most successional studies, may be highly misleading because of the difficulty of assuring between-site uniformity (Clark, 1990; Pickett, 1988).

Natural disturbances of varying size, frequency and severity have been documented throughout the paleoecological record. Fires may be detectable in sediment as charcoal layers and as peaks in charred particles counted on slides prepared from sediment (Clark, 1988a, 1988b; Patterson et al., 1987) (Fig. 5). Geomorphological features and sediment lithology record erosional events (Campbell & Fraily, 1984), and tephra layers indicate volcanic eruptions (Sarna-Wojcicki et al., 1983). Sudden changes in pollen assemblages often correlate with catastrophic events or anthropogenic activity
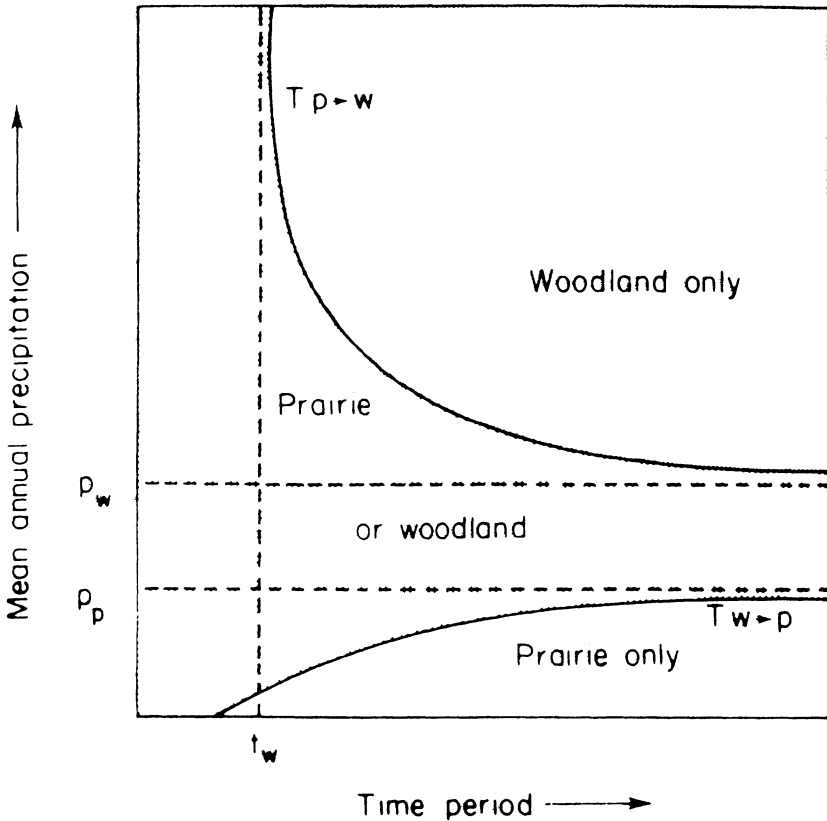
Fig. 12. Schematic diagram showing a two-dimensional cross section of the subspaces in which prairie and oak woodland will persist in an n-dimensional hyperspace in which the axes are time period and the independent climatic variables influencing fire frequency. The curves are the thresholds for the changes from oak woodland to prairie and the reverse from prairie to oak woodland. (From Grimm, 1983.)

(Brugam, 1978; Green, 1981). The paleoecological record also reveals changing patterns of disturbance as environmental conditions change. Grimm (1983) documents the invasion of oak woodland in southern Minnesota by more mesic tree species as the result of decreasing fire frequency caused by the cooler, moister climate of the "little ice age." He presents a model suggesting that climate, physiography, vegetation pattern and fire interact to cause thresholds for vegetation change to vary in space and time (Fig. 12). Thus different vegetation types can persist adjacent to one another in essentially identical environments, their locations being historically contingent on past disturbances.

The paleoecological record allows us to better understand the spatial as well as temporal dynamics of disturbance. The extent and nature of discrete and periodic events may not be observable over an entire landscape or region in a lifetime. For example, in southern New England the overall frequency of fire is relatively low. However, studies of charcoal and pollen along a transect of sites suggests that a very strong gradient of decreasing fire frequency from the coastal oak–pine forests to the

northern hardwood forest parallels a climate/vegetation gradient (Patterson & Backman, 1988; Winkler, 1986). The history of coastal oak–pine vegetation repeatedly returning after fire illustrates another point: certain types of vegetation are remarkably resilient.

Recent and paleoecological evidence confirm that the regional vegetation mosaic in communities with fire-dependent species appears to have been maintained by naturally recurring fires (Cwynar, 1987; Habeck & Mutch, 1973; Heinselman, 1973; Minnich, 1988; Romme, 1982; Swain, 1978). In these communities, fire is responsible for long-term stability; the lack of fire, owing to climatic change might be considered more of a disturbance to the overall system, causing widespread species replacement (Grimm, 1983). Conversely, during a time of climatic change, a community showing some inertia may be opened up to invasion by fire. Green (1982) documented rapid, long-term species replacement following fire in the early Holocene in Nova Scotia.

Disturbance in tropical areas has been characterized as less severe than that in temperate regions (Connell, 1978; Whitmore, 1975), but there is evidence to the contrary, such as hurricanes that have their genesis in the Tropics of Cancer and Capricorn (Lugo et al., 1983; Wadsworth & Englerth, 1954), and the 1983 El Niño event that unleased torrential rains along the eastern Pacific rim but resulted in drought and fire in the western Pacific (Leighton & Wirawan, 1986). Nevertheless, stand-level disturbance in the tropics has received more attention in the last decade (Brokaw, 1985; Denslow, 1980; Lieberman et al., 1985; Uhl et al., 1988).

The paleoecological record further extends the evidence for disturbance in the tropics at several scales. Catastrophic deluges of rain along the west coast of South America even stronger than that in 1983 have occurred periodically throughout the Holocene and are especially evident in areas of human settlement (Nials et al., 1979). Sedimentological and geomorphological evidence suggests equally catastrophic flooding in the Amazon basin during the Holocene (Campbell et al., 1985; Liu & Colinvaux, 1988). River channel meanders revealed by satellite photography have inundated forests with the result that 12 percent of the forest along rivers in the western Amazon is successional (Salo et al., 1986). Another 14.6 percent lies on the floodplain and has been disturbed in the recent past. Thus a quarter of this region of the Amazon basin has been disturbed by flooding probably within the last few hundred years. Evidence of fire has been found in tropical rainforests dated back to 6000 years BP (Saldarriaga & West, 1986; Sanford et al., 1985).

Past human activities have had major impacts on the landscape and often serve as convenient time horizons. Neolithic man most likely caused the sudden decline of elm in Europe around 5000 years BP by girdling trees and using the foliage for animal fodder (Birks, 1986; Iversen, 1973). North American Indians are generally believed to have had a sophisticated understanding of the use of fire as a tool for hunting and clearing land (Day, 1953; Patterson & Sassaman, 1988; Pyne, 1982). Human presence drastically altered vegetation in parts of central America during Mayan times (Binford & Leyden, 1987). A distinct settlement horizon of *Ambrosia* in most palynological records throughout North America is a consequence of the clearance of forests for agriculture by colonists from Europe.

C. COMMUNITY STABILITY AND EQUILIBRIUM

With the recognition that disturbance is an integral part of many ecosystems and that climate has been changing continuously in the past, ecologists have begun to

debate the relative importance of equilibrium vs. nonequilibrium explanations of community structure (Connell, 1978; Hubbell & Foster, 1986; Pickett & Davis, 1990). Organisms encounter and respond to environmental changes throughout the entire spectrum of spatial and temporal scales. Indeed, we must first define the taxonomic, spatial and temporal scales at which we wish to investigate questions of stability and equilibrium. We might ask if two populations are in equilibrium with each other. Or whether an entire community is at an equilibrium state. Or whether a species is in equilibrium with its environment. The answer may be positive at one intersection of the various scales under consideration and negative at another.

A further complication with pollen data is determining how to quantify stability and change. Paleoecologists traditionally have recognized different pollen assemblages or zones, and numerous multivariate statistical approaches have been adapted to allow for more objective zonation (Gordon & Birks, 1985). Jacobson and Grimm (1986) and others have applied detrended correspondence analysis (DCA) to modern and fossil pollen data matrices. With appropriate application, the results show the rate and direction of change (Figs. 13 and 14). Using this method, Jacobson et al. (1987) have shown that the highest rates of widespread vegetational change in eastern North America occurred at two discrete times: 11–9000 years ago, reflecting rapid migration of taxa in response to climate change, and since European settlement, reflecting a response to pervasive anthropogenic disturbance.

An ongoing debate among biogeographers and paleoecologists concerns how closely vegetation tracks environmental change. The consensus seems to be that the answer depends on the time scale under consideration, the rapidity and amplitude of the climate change and the particular vegetation under investigation (Prentice, 1986). At a frequency of 1000 years, vegetation usually appears to be in dynamic equilibrium with climate (Birks, 1989; Webb, 1986). On shorter time scales, between 1 and 500 years, vegetation may often lag behind climatic change (Davis, 1986).

In an environment that varies between long periods of glacial stasis and relatively abrupt interglacials, organisms must cope with conditions that may favor stable equilibrium communities during glacial times and more dynamic communities during interglacials. The paleoecological record provides evidence that communities in the past and present have been both stable and unstable, and in disequilibrium and equilibrium states (e.g., Delcourt & Delcourt, 1987; Green, 1981; Jacobson & Grimm, 1986; McAndrews, 1965; Payette & Filion, 1985; Ritchie, 1986). However, ecologically dynamic and nonequilibrium communities probably have been more characteristic throughout the Holocene as species migrated independently in response to climatic change.

The independent migration of tree species and their penetration of established deciduous forests in the northeastern U.S., the hemlock and elm declines, and the transient nature of species assemblages in general demonstrate the disequilibrium nature of communities during the Holocene. Time lags shown by organisms in response to environmental change are evidence for both stability (in the sense that organisms remain where they are—inertia, sensu Gorham, 1957) and disequilibrium (in the sense that other organisms join or depart from the assemblage). Cole (1985) has shown that some plant species growing near the Grand Canyon at the beginning of the Holocene were slow to move northward with warmer climates and were joined by faster moving arrivals from the south resulting in a transient species-rich assemblage. Davis and Botkin (1985) have modeled tree species' responses to climate change in computer simulations and predicted 200 year response lags. Davis (1986)
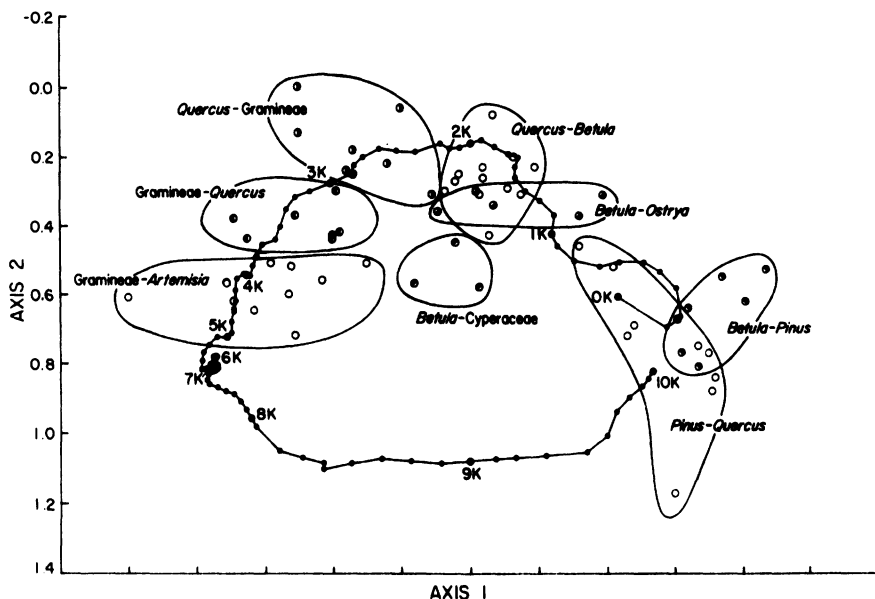
Fig. 13. Direction and rate of vegetation change in central Minnesota during the past 10,000 years. Ordination of 100 years BP analog pollen assemblages (open and half-filled circles), and a five-sample running average of fossil pollen for the last 10,000 years from Billy's Lake, central Minnesota (dots connected by line). Points on the running average curve represent the position every 100 years (rather than the position of each sample). (From Jacobson & Grimm, 1986.)

has also summarized data showing that various animals including barnacles, birds, insects and small mammals have lagged anywhere from a few years to decades behind environmental changes. Migration maps do show, however, that present temperate communities probably have been roughly in equilibrium with the environment on a regional scale since about 2000 years BP.

If instability and disequilibrium are characteristic of the Holocene, models of population and community dynamics based on equilibrium conditions, while heuristically useful, may be even less realistic than empirical ecologists often claim (Franklin et al., 1987). Most models of population growth, competition and predation ignore migration for simplicity's sake, but the paleoecological record suggests that migration and dispersal are fundamental to understanding the above phenomena. Thus modelers should be exlicit about the time and space scales under consideration, and recognize that models of short time-scale phenomena may not extrapolate to long-term ecological or evolutionary time scales.

D. EVOLUTIONARY CONSIDERATIONS

Paleoecological data from the Quaternary should be of considerable interest to those concerned with rates of evolution and speciation, and related processes including the evolution of diversity, coevolution, selection, competition, and extinction. Bennett (1990) has even suggested that Gould's (1985) three-tier temporal hierarchy of evolutionary processes should be expanded to include glacial-interglacial cycles, thus yielding a four-tier hierarchy consisting of: ecological time (thousands of years),
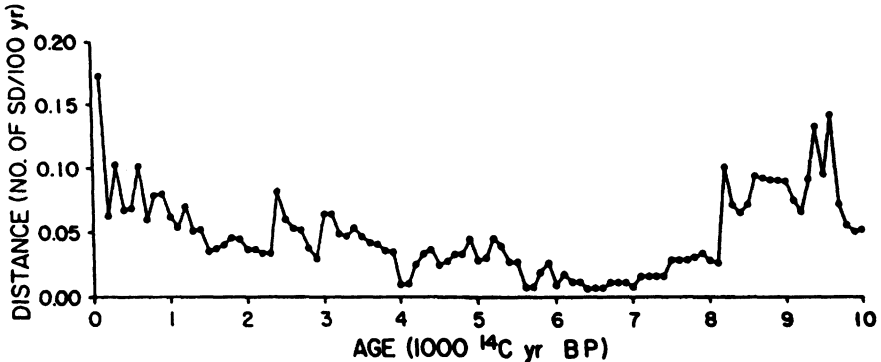
Fig. 14. Rate of vegetation change in central Minnesota during the past 10,000 years. Graph of distance (number of standard deviations) moved every 100 years in the first three dimensions of the ordination depicted in Figure 13 vs. age. Greater distance indicates greater change in pollen spectra in 100 years. The graph shows high rates of vegetation change from 10 to 8 ka, as forest taxa were replaced by prairie taxa (see Fig. 13), relative stasis from 8 to 4 ka, and then higher rates of change again as different forest taxa invaded from 4 ka to the present. Highest rates of change are associated with settlement. (From Jacobson & Grimm, 1986.)

orbitally forced climate changes (20,000–100,000 years), geological time (millions of years), and mass extinctions (approximately 26 million years).

Viewed over the entire Quaternary, taxa have constantly migrated in response to glacial-interglacial cycles, often resulting in alternation between widespread populations in favorable times, and small, fragmented populations during unfavorable periods. These oscillations in population size, location and genetic composition should favor rapid evolution through geographic isolation and founder effects (Huntley & Webb, 1989).

The rapid migration of tree species during the Holocene provides examples of how allopatric speciation by geographical isolation might occur. Migration maps show taxa moving in two different directions at different rates (e.g., Figs. 8 and 9). Rapid speciation during the last glacial-interglacial cycle is suggested in the paleoecological record, e.g., the recent divergence of jack pine and lodgepole pine (Critchfield, 1985; Cwynar & McDonald, 1987). On a longer time scale, spruce has become rarer since the early interglacials, failing to reach England during the Holocene, while hazel has become more common. West (1980) speculates that these trends are likely a result of evolutionary changes in these two species based on the observation that abundances of other species have remained roughly similar during Quaternary interglacials. Mengel (1964) shows how modern species of wood warblers could have arisen from repeated migration of an ancestral species northwestward from the southeastern United States during interglacials and subsequent isolation of western populations upon glacial advance. These examples suggest that environmental changes that induce varying rates and directions of migration and other individualistic responses play an important role in determining rates and directions of speciation. Webb (1988), however, points out that the time scale of glacial-interglacial cycles may be too short for many populations to develop major morphological differences and become genetically isolated.

Species interactions should be profoundly affected by glacial-interglacial cycles. In contrast to a more stable environment where species may have time to adapt to one

another, species reacting individualistically to oscillating environments may form looser associations. A particular species migrating northward in the Holocene would have competed with several species along its route, and even may have occupied various ephemeral communities in different places at different times or simultaneously. Thus while speciation may be facilitated by repeated isolation and contact of populations and species, the individualistic nature of species responses implies diffuse interactions with less time for coevolutionary relationships to develop. Furthermore, some microevolutionary changes that arise in a stable environment may be lost upon widespread environmental change during more dynamic phases of glacial-interglacial cycles (Bennett, 1990). Diffuse interactions and loss of microevolutionary changes may be common to both temperate and tropical regions, since widespread environmental change has been documented for both areas.

This last point is particularly relevant to current thinking on the evolution of diversity in the tropics. If species responses are as individualistic in the tropics as they are in temperate regions, and species interactions are at times diffuse, then the hypothesized evolution of diversity through competition and niche differentiation in a stable environment becomes questionable as does the importance of long-term coevolutionary relationships. Instead, speciation by repeated geographical isolation would be the driving evolutionary force. Van Devander (1986) speculates that because climatic fluctuations are less severe toward the equator, species with refugia at lower latitudes are less likely to go extinct. Hence they should survive to speciate allopatrically, with intense competition after sympatry leading to niche separation and high diversity in the tropics. Alternatively, the majority of evolutionary differentiation could have taken place in stable environments before the onset of the Quaternary glacial-interglacial oscillations. More paleoecological data are needed from the tropics to test these hypotheses, but we must recognize the limits of the paleoecological record in this regard. Any search for the ghost of competition past is likely to produce only circumstantial evidence. Fine resolution pollen analysis may suggest competitive interactions (Bennett, 1986), and paleoecologists have applied competition equations to fossil pollen data (Delcourt & Delcourt, 1987). But with the difficulty of defining competition and proving it has happened in extant populations, it is unlikely that most sites provide the taxonomic and spatial resolution to infer mechanisms of competitive interactions using pollen data as a proxy for biomass or reproductive success. We can, however, document that taxa occurred in the same locality at the same time, that their abundances changed, and that their ranges diverged, separated, and coalesced. This provides us with circumstantial evidence that competition or speciation by geographical isolation has had the chance to occur, and with a timeframe within which to place these processes.

Given the fluctuating environments of the Quaternary, we can probably assume that selection pressure and direction on species have been in a state of flux. During a long stable glacial period competition for resources may be of primary importance in areas where the environment is not extreme. But during a rapid environmental change, ability to adapt quickly or disperse to more suitable habitats may be favored. This should be true in the tropics as well as in temperate regions. The variable nature of selection pressure suggests that those species (especially plants) that are most flexible in their response to environmental change may have been favored during the Quaternary. Some organisms that exist today may have been able to rapidly alter their life history strategies to adapt to changing environments and selection pressures. This would be possible in populations where alleles for alternate life history strategies

exist in a small percentage of the population. However, some strategies such as rapid dispersal might be at least adequate at all times, and other more stress tolerant and competitive strategies (sensu Grime, 1977) might be viable for organisms inhabiting regions where the environment has fluctuated less rapidly or severely than others. But the record of environmental oscillation during the Quaternary indicates that, in general, those species or populations unable to respond rapidly to a changing environment should be the ones most likely destined for extinction.

The paleoecological record also demonstrates the stochastic and historically constrained nature of evolution and community structure. The structure of some communities can be traced in part back to climatic fluctuations that began and ended hundreds of years ago (Clark, 1990; Grimm, 1983) (Fig. 12). Periodic global events with regionally catastrophic effects, such as the 1983 El Niño event (as yet poorly understood on a paleoecological scale) may have important effects on the evolution of species (Gibbs & Grant, 1987). Species also may migrate into areas that constrain their evolutionary future. An example of this is the cloud forest of Amazonian affinities that is isolated in pockets along the western foothills of the Andes (Koepcke & Koepcke, 1958).

Tree species diversity in Europe is much lower than in eastern North America, quite possibly because the east–west trending Alps trapped species retreating southward from advancing glaciers and caused their extinction, while small relict southern populations also became extinct (Bennett, 1991; Davis, 1983; Reid, 1935). Slow-migrating and late-arriving species were probably unable to spread throughout the British Isles at the beginning of the most recent interglacial because the English Channel and Irish Sea were flooded about 8000 years BP by the rising Atlantic Ocean (Birks, 1989; Godwin, 1975).

Because of the complex nature of past climate change and biotic response, historical constraints have probably compounded in many cases so that it is highly unlikely that species responses to past glacial-interglacial cycles have been identical to responses during the most recent Wisconsin glacial–Holocene interglacial. Species probably encountered various competitors, predators, mutualists and pathogens during different glacial stages that have influenced their course of evolution. West (1970) presents some evidence for different community composition during each of the last 7 interglacials (Table II). Thus, on an evolutionary time scale, we might think of past climatically dynamic interglacials as times when the biotic cards are reshuffled, setting the stage for glacial periods when species in more stable assemblages have a better chance of playing an extended game. If Milankovitch cycles do indeed extend beyond the Quaternary, this scenario might be characteristic of biotic interactions throughout earth history.

E. REFUGIA IN THE PALEOECOLOGICAL RECORD

The individual nature of species as revealed by the paleoecological record has important implications for refuge theory, which has gained more attention with the acceptance of wide-spread climatic change in the tropics during the Pleistocene (Binford & Leyden, 1987; Colinvaux, 1987; Van der Hammen, 1988; Walker & Chen, 1987). The refuge hypothesis states that climatic oscillations have caused species ranges to contract and expand, and has focused on tropical rainforest species whose ranges are thought to have contracted and fragmented during the cool, dry glacial periods and expanded and agglomerated during warm, moist interglacials (Whitmore

Table II

Occurrences of genera in fossil deposits from seven interglacial stages, including the Holocene, in England (modified from West, 1970)

Genus	Interglacial stage						
	Lud-hamian	Antian	Pas-tonian	Cro-merian	Hoxnian	Ip-swichian	Holocene
Quercus	+	+	+	+	+	+	+
Ulmus	+	+	+	+	+	+	+
Tilia	−	−	−	+	+	−	+
Carpinus	+	+	+	+	+	+	+
Picea	+	+	+	+	+	−	−
Abies	−	−	−	+	+	−	−
Tsuga	+	+	+	−	−	−	−

& Prance, 1987). Thus forest communities would have been constantly changing, and the opportunity for speciation by geographic isolation would have arisen many times during the Pleistocene. Various areas have been identified as probable refugia in the Amazon, based on present diversity, endemism, contact zones and climatic conditions (Prance, 1982). This approach is probably too simplistic in light of what we know of long-term forest dynamics in temperate zones and the complexity of climatic change. Global climate simulations of full glacial climate suggest, for example, that much of the tropics was cooler, but that rainfall was similar or slightly less than at present, with decreased seasonality and less intense summer rains in the southern tropics (COHMAP, 1988). These climate simulations do not disprove the refuge hypothesis, but neither do they present compelling evidence for locating specific refugial areas in the tropics.

The paleoecological evidence for rainforest contraction and expansion in the tropics is scanty. Walker and Chen (1987) compiled a list of 118 sites that have been investigated by pollen analysis in the tropics (Table III). Only 24 of these sites are from lowland everwet rainforests, and of these sites, 13 contain less desirable records from swamps and riverine lakes. None of these contain evidence of full-glacial refugia.

In the Amazon, for example, there is no complete palynological record back to full-glacial times for lowland rainforest. However, Liu and Colinvaux (1985) produced radiocarbon-dated evidence for a 700-meter lowering of the lowland rainforest–lower montane rainforest boundary between 33,000 and 26,000 years BP. Absy and Van der Hammen's (1976) pollen diagram for Rondônia shows that land currently supporting seasonal rainforest was occupied by savanna sometime in the early Holocene. Hence, the palynological evidence for lowland rainforest refugia in Amazonia is circumstantial, suggesting only that refugia probably occurred. Paleoecological evidence does suggest, however, intermediate disturbance processes such as flooding, erosion, and fire as possible mechanisms for generating diversity (Campbell & Frailey, 1984; Colinvaux et al., 1985; Salo et al., 1986; Sanford et al., 1985; Saldarriaga & West, 1986).

Elsewhere, some lowland rainforest in Africa occupies what was savanna or dry woodland only 10,000 years BP (Livingstone, 1975), and an apparent Pleistocene refuge has been documented for montane rainforest in east Africa (Hamilton, 1982). In northeastern Australia, savanna woodland changed to seasonal rainforest from 10,000 to 5000 years BP (Chen, 1986; Kershaw, 1983). Clear evidence exists for the

Table III

Number of radiocarbon dated pollen records for non-arid environments in the tropics
(modified from Walker & Chen, 1987)

Lowland everwet rainforest	11
Lowland everwet swamps and riverine lakes	13
Lowland seasonal forest	7
Other low to mid altitude forests and woodlands	7
Savanna, shrub and grassland, some secondary forest	6
Lower montane rainforest	28
Upper montane and subalpine forest	17
Subalpine and alpine nonforest	29
Total	118

lowering of forest zones in the upper Amazon, central America, tropical Africa and
southeast Asia during glacial times (Bush and Colinvaux, 1990; Flenley, 1979, 1984;
Hamilton, 1982; Liu and Colinvaux, 1985).

The tropics, especially, require extensive palynological and geological investigation,
such as the ongoing work of Colinvaux (1991) and co-workers in the Amazon basin,
before any hypothesis of refugia composition, size, location, and history can be
confidently accepted (Campbell et al., 1985; Colinvaux, 1987; Connor, 1986). Ex-
amples of testing the locations of proposed refugia are provided by Campbell et al.
(1985) who found one proposed refugium overlain by Holocene alluvial deposits,
and by Bush and Colinvaux (1990) who produced palynological evidence suggesting
climatic cooling inconsistent with proposed refugial areas in Panama.

In summary, no tropical rainforest refugia have been documented, and some pos-
tulated refugial areas have been disproven. Many pollen studies have found, however,
that non-rainforest vegetation was more widespread during the late-glacial, implying
that rainforest ranges were restricted, perhaps to the point of functioning as refugia.

Although most interest in the refuge hypothesis has been in connection with tropical
rainforest species, refugia (or at least sites where sparse populations occurred) are
best documented by paleoecological evidence in temperate regions. The proposed
Mixed Mesophytic Forest refugium, believed by Braun (1950) and others to have
included most tree species presently growing in eastern North America, has never
been documented in the paleoecological record. Instead it appears that taxa had
various refugia independent of each other (Davis, 1983; Delcourt & Delcourt, 1987).
Refugia may have occurred in some surprising places. For example, white pine and
hemlock appear to have had a refugium located partially on the continental shelf of
the Carolinas which was above sea level during glacial times (Davis, 1983). Many
hardwoods may have occurred along the bluffs of the southern Mississippi Valley,
and in isolated pockets of suitable habitat in the southern Appalachians (Delcourt
& Delcourt, 1977; Delcourt et al., 1983).

The higher diversity of tree species in eastern North America compared to Europe
generally has been attributed to tree species being able to migrate independently
down the Appalachian mountain chain and find appropriate refugia throughout the
south. European trees on the other hand, would have had to migrate southward over
or around the Alps during climatic deterioration (Campbell, 1982; Davis, 1983). The
difficulty of reaching proposed refugia near the Mediterranean and Asia Minor may
have resulted in a significant loss of species. Bennett et al. (1991), however, maintain
that species repeatedly became extinct in their northern ranges upon initiation of

glacial stages, while relict populations survived in the south. Thus the crucial factor in the elimination of a species would be the extinction of its relict populations in the Balkans and southern Europe. There is evidence that the biogeographic barrier presented by high mountain ranges can be breached (Davis et al., 1988), but rapid climate change may preclude this for some species.

Refuge theory should take into account the dynamic nature of species behavior and the complexity and interdependence of past climates, edaphic factors and disturbance regimes. It also should recognize that refugia for various species are probably constantly forming and expanding and contracting: species that are limited to refugia today (e.g., plant and animal species isolated in mountain ranges and surrounded by desert in the Great Basin, Fraser fir in the central Appalachian mountains) may be widespread during glacial stages and vice versa. Finally, given the independent nature of species' migration and life history traits (fecundity, wind vs. animal pollination, seed dispersal mechanisms, environmental tolerances, etc.) the concept of a 'refuge' may not be appropriate for many species. The response of species to unfavorable conditions probably spans a continuum from migration towards refugia having no overlap with the former range, to range contractions, to survival of sparse populations in suitable microhabitats throughout the former range. Many other scenarios are possible and indeed can be observed in contemporary biota.

V. Prescriptions and Applications

The greatest advantage of a paleoecological perspective is that it extends knowledge of spatial patterns into the very useful fourth dimension of time. Patterns can be observed over long periods of time and processes can be inferred from these patterns. These patterns and inferred processes can be compared with currently occurring phenomena to interpret and perhaps predict environmental and biotic change.

Most ecologists are aware of the geology and recent history of their study sites, but few take full advantage of the available paleoecological data to better understand disturbance regimes and other historical constraints that may operate at several spatial and temporal scales (Hamburg & Sanford, 1986). For example, Hamburg and Cogbill (1988) present long-term data that suggest climatic warming (in addition to recent pollution) as the causal factor for red spruce decline in New Hampshire.

Paleoecological data also can provide tests for hypotheses that infer temporal processes from spatial patterns. Jackson et al. (1988) cored a dune pond on the shore of Lake Michigan and showed that Cowles' (1899, 1901) classical hydrosere was a product of human disturbance commencing 150 years ago. Campbell et al. (1985) demonstrated that the diverse biota of a proposed refugium in the western Amazon must have invaded the site after several meters of Holocene-age alluvium were laid down.

The comparison of paleoecological and current data not only allows the community ecologist and evolutionary biologist to place current phenomena into the context of a longer time-frame, it also can be helpful in the area of applied ecology. For example, global climate circulation models that relate orbital geometry of the earth and climate can be tested with paleoecological data to refine the models and help predict future climate and biota (Davis, 1990; Davis & Zabinski, 1991). We also know from geomorphological data, and from increases in paludification and retrogression of certain forested areas that soils have become increasingly leached and nutrient poor in northern temperate areas during the latter half of the Holocene (Engstrom & Hansen,

1985; Godwin, 1975; Iversen, 1964). Long-term ecosystem acidification driven by climate and vegetation change during interglacial periods has been shown to occur especially under certain conditions (Ford, 1990). Vegetationally mediated soil change is an ongoing process and should have important implications for foresters and agronomists (Birks, 1986). On a shorter time scale, tree-ring chronologies and historical records may be helpful in characterizing current climate in relation to recent climatic changes, and in determining what changes constitute a long-term trend (such as global warming) vs. a recent cycle (such as the 20-year precipitation pattern across much of Saharan Africa) vs. random short-term variation (a two-year drought in parts of North America).

Information on species responses to past environmental change can help us predict future behavior of species. One area of much concern is the possible warming of the earth's atmosphere owing to increased emissions from the burning of fossil fuels. In theory, it should be possible to suggest future scenarios of community change and species migration by integrating past vegetation changes with a global circulation model that includes anthropogenically generated global warming (Davis & Zabinski, 1991). In practice this may not be so easy. First, the predicted climatic changes will take place over a time span of decades to a few hundred years instead of hundreds to thousands of years. Second, the predicted global warming will be caused by changes in atmospheric chemistry affecting radiation transmittance, reflectance and absorption rather than by orbitally induced changes as in the past. Third, the effects of an altered global climate will be confounded by the physiological effects of greenhouse gases, such as CO_2, on plants. Fourth, the earth's predicted future orbital geometry indicates global cooling, a trend reflected in global climate and vegetation over the last 2000 years up to the 19th century. Furthermore, general circulation models and paleoecological evidence suggest that disturbance regimes will likely change with changing climate and vegetation (Grimm, 1983; Rind et al., 1989). Predictions of future greenhouse effects on the earth's biota must take into account all these factors, and recognize that future climate may not simply be warmer or drier but entirely different across a continuum of spatial scales.

In light of the difficulties of predicting climate change, what generalizations can we make about biotic responses? First, the type and rate of response will vary taxonomically, even phenotypically. Second, response will vary locally with the severity of climatic change. Third, where climatic change is severe response rates will be at or near their maximum. Fourth, even at a maximum response rate, the earth's biota will likely lag behind climate change. Fifth, in general most species will move poleward or upward in altitude. Sixth, populations at poleward extremities of landmasses and near mountaintops will be the most likely to become extinct. Seventh, species that are more phenotypically and genotypically flexible in their responses will be favored over less flexible ones. Eighth, as species migrate at different rates, assemblages of species will change.

The prediction of species responses to impending environmental changes is particularly important with regard to wilderness preserves and refuges that protect endangered species (Graham, 1988; Hunter et al., 1988). Rapid migration of species in response to environmental change and the variable nature of past Quaternary refugia suggest that planning refuges is a more complicated task than most conservationists realize. Communities as we know and classify them will add and lose species, perhaps producing assemblages that have never occurred in the earth's history. Simply marking off an area may not be enough. Instead, nature preservation

will have to take on a fourth, temporal dimension. Hunter et al. (1988) emphasize continental scale migration corridors and large reserves encompassing a variety of physical environments. This contrasts with the present strategy of preserving specific communities or ecosystems.

One practical application of paleoecological techniques that should be employed more widely is the documentation of an area's history before a decision is made to preserve it in its assumed natural state. Backman and Patterson (1984) found that a scrub oak–pitch pine forest in southeastern Massachusetts, which was managed to maintain that unique habitat, had been a white pine–hardwoods forest in pre-colonial times, and was likely altered by land-clearing associated with settlement and extensive fire. Such information may not deter the effort to preserve an area, but might greatly alter the management procedures.

Fire histories can be reconstructed to help the forest manager understand natural fire cycles and plan accordingly (Wright, 1974). A large body of such literature exists for many regions in North America (e.g., Harmon, 1983; Heinselman, 1973; Morrison & Swanson, 1990; Romme, 1982), and has been employed in the implementation of National Park management strategies (e.g., Hemstrom & Franklin, 1982; Kilgore, 1973; Kilgore & Taylor, 1979; Romme, 1982).

Another applied use of paleoecological data is as baseline information with which to compare environmental changes caused by humans. One may want to know, for example, the various characteristics of the previous natural community before attempting to restore a natural ecosystem (Engstrom & Wright, 1984). Past abundances of organisms sensitive to acidity, toxic compounds and eutrophication can give us an idea of natural conditions in presently polluted lakes (Battarbee, 1984; Battarbee et al., 1989; Davis, 1987). Brugam (1978) documented past limnological conditions in Linsley Pond using pollen, diatoms, other algae, chironomids, cladocerans, rotifers, and chemical analysis of the sediments. By studying diatom assemblages buried in lake muds, Stockner and Benson (1967) detected changes in eutrophication in Lake Washington associated with the development of and sewage input from the city of Seattle. After sewage was diverted from the lake, Shapiro et al. (1971) recorded improvements in water quality by comparing the chemistry of pre- and post-sewage sediment cores. Davis (1987) describes an extensive effort to document changes in lake acidification by analyzing past diatom populations from a network of lakes in the northeastern United States.

Paleolimnological studies in Central America and the Caribbean suggest that widespread environmental destruction in some over-exploited areas occurred in Mayan times (Binford & Leyden, 1987). Contemporary patterns similar to those in early Mayan times should help to alert us to areas prone to incipient environmental destruction. In summary paleoecological data can help answer the question, "what is a 'natural' ecosystem?" in addition to such questions as, "how did the ecosystem arise, what is its history, and which processes are implied by past patterns?"

VI. Summary

Most ecologists study organisms on a scale of less than 100 years, but many patterns in nature can be better understood on a scale of hundreds to thousands of years or more. The paleoecological record can help contemporary ecologists put current phenomena into the context of a longer time-frame, allowing us to see processes taking longer than a lifetime, and to gauge the importance of past cyclic or unusual events, disturbance regimes, and historically constrained phenomena. The Holocene has been

a time of rapid environmental change following a more stable glacial. The biotic response to this change has been complex and probably different in detail in each of the preceding glacial-interglacial cycles. Species react in an individualistic manner to long-term environmental change; when considered on a paleoecological scale, communities are transient assemblages of species. Species populations and ranges have responded to and sometimes lagged behind environmental changes in the Quaternary; these populations and ranges can vary between states of stasis and equilibrium vs. instability and disequilibrium. Paleoecological studies indicate that disturbances of various sizes and intensities play an important role in structuring communities. The environment has been highly cyclical during the Quaternary, and perhaps throughout earth history. Such cyclicity should: 1) select for flexibility in species responses to environmental changes and biotic interactions; 2) allow for allopatric speciation by geographic isolation; 3) cause some loss of microevolutionary change as biotic assemblages are reorganized. Paleoecology can be helpful in explaining present processes in light of past patterns, making comparisons, and predicting future patterns.

VII. Acknowledgments

VIII. Literature Cited

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