Spatial scale and sampling strategy in paleoecological studies of vegetation patterns in mountainous terrain

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INTRODUCTION

Consideration of spatial scale is fundamental to the successful design of paleoecological studies of previous vegetation patterns. For pollen data to record a particular pattern, the paleoecological sampling sites should be spaced appropriately to allow for: (1) the size of the pollen source areas of the individual sites, i.e. the area from which most of the pollen reaching a basin originates; and (2) the spatial scale of the vegetation patterns of interest, e.g. regional vegetation zones and landscape-level mosaics within the zones. These considerations are particularly important in mountainous landscapes where vegetation gradients are often steep. Sampling sites must be closely spaced and consequently pollen source areas of individual sites may include several vegetation zones. Analytical procedures are then required to highlight vegetation patterns recorded by the pollen data. In this paper, we review the advantages and difficulties of paleoecological studies in mountainous regions, discuss the spatial-scale considerations required when interpreting the data from such studies, and illustrate these issues using our recent studies in the mountains of eastern North America.

Paleoecological studies in mountainous regions
The vegetation history of mountainous regions has interested paleoecologists since the pioneering efforts of Gams (1923), Ludi (1932) and Welten (1944; 1952) in the Alps, and

the extensive research of van der Hammen and his colleagues and students in the Andes (van der Hammen & Gonzales 1960; van der Hammen *et al.* 1973; van Geel & van der Hammen 1973; Salomons 1986; van der Hammen 1988). Tectonic activity and the high relief of mountainous regions has led to certain mountain basins being the source of some of the longest continuous sections of Quaternary lake sediments in the world (Wijmstra 1969; Woillard 1979; Hooghiemstra 1984; Adam 1988; Dodia 1988). The pollen sequences from these sediments are invaluable guides to Quaternary history and provide unique opportunities for linking terrestrial and marine records (Woillard & Mook 1982; Heusser & Shackleton 1979). Such linkage is critical to understanding biospheric and climatic dynamics during the past 2×10^6 years (Shackleton *et al.* 1988).

Palynological records of vegetation history in mountainous regions offer the potential advantage of recording large changes within a relatively small spatial area. Elevational gradients compress broad latitudinal climatic gradients into relatively short distances along mountain slopes. Therefore shifts in vegetation zones, treeline, or individual species ranges of 100–1000 m elevation can record climate changes that might be represented on a latitudinal gradient by vegetational shifts on the order of 100 to >1000 km. Records of vegetation history from montane regions are therefore potentially sensitive to short-term and low-magnitude climate changes not represented at lowland sites.

The potential sensitivity of montane pollen records is compromised, however, by pollen dispersal across compressed vegetation gradients (Maher 1963; Birks 1973; Markgraf 1980; Solomon & Silkworth 1986). Lakes and peatlands receive their pollen from relatively large source areas and hence may collect pollen from several vegetation zones. The problem increases with elevation because the geometry of most mountain regions dictates that areas at high elevations usually comprise a relatively small proportion of the total pollen source area for lakes within these zones (Jackson & Whitehead 1990). The problem is amplified further in treeless alpine zones where pollen is blown in from large distances and from forests at lower elevations (Spear 1989). The problem of pollen transport has frustrated paleoecologists trying to interpret data from mountain sites. Aspects of spatial scale (e.g. the size of the pollen source area) must therefore be incorporated into the design and interpretation of paleoecological studies of montane vegetation patterns.

Spatial scale considerations

Paleoecologists face the problem of inferring the composition and pattern of the source vegetation from individual pollen and plant–macrofossil assemblages recovered from spatially separated sites. A useful approach for interpreting these assemblages is to view pollen (or macrofossil) data as remotely sensed information about the vegetation, analogous to the information provided by aerial photographs or satellite images. This perspective leads to the recognition that interpretation of pollen data, like any remotely sensed data, requires some form of analysis to transform the original data (e.g. frequencies of different pollen types, which are analogous to the different wavelengths and intensities of radiation recorded by satellites) into information about the composition and pattern of the vegetation that either produced and released the pollen, or analogously, emitted and reflected the radiation. Such analysis requires, in turn, both a theoretical understanding of the fundamental properties of the sensing system (e.g. spatial scale, sensor-induced distortions, etc.) and empirical studies comparing remotely sensed data (pollen) with the emitting entity (vegetation). This perspective has led to research efforts involving collection of modern pollen and vegetation data (Davis 1963; Webb 1974; Prentice 1978; Grabandt 1980; 1985; Melief 1985; Jackson 1990), calculation of empirical pollen/vegetation

calibrations (Prentice & Webb 1986; Grabandt 1985; Melief 1985), numerical searches for analogues (Overpeck *et al.* 1985) and discussion of the effects of scale (Webb *et al.* 1978; Delcourt *et al.* 1983; McDowell *et al.* 1989).

Recent studies have revealed the complexity of the problem of calibrating pollen percentages in terms of plant abundances and have demonstrated the need to know more about the size of the pollen source area (Bradshaw & Webb 1985; Prentice & Webb 1986; Prentice *et al.* 1987; Jackson 1990). Other recent studies have shown how well graphical methods, applied to the data in their original uncalibrated form, can be used to illustrate spatial patterns in the data (Jacobson 1979; Webb *et al.* 1983; Gaudreau & Webb 1985; Gaudreau 1986; 1988a; 1988b; Woods & Davis 1989; Jackson & Whitehead 1990). Underlying this graphical approach is the recognition that vegetation reconstructions are both theoretically and empirically easier to obtain from spatial arrays of samples than from time series (i.e. pollen diagrams) at single sites (Gaudreau 1988a; Prentice 1988).

The importance of spatial scale considerations in the interpretation of paleoecological data has led us first to describe a recent study that compares modern pollen and vegetation and provides information about the relative size of the pollen source areas for different taxa. We then review various graphical methods that can be used to illustrate spatial patterns in pollen data. We show how the different graphical methods combined with appropriate sampling strategies can be used to assess the pollen source area and thus determine the resolution of vegetation patterns that can be obtained from the fossil data. The types of vegetation patterns we discuss are macroscale geographical gradients, mesoscale physiographical gradients, and landscape-level gradients, including montane gradients in plant distribution. The sampling strategies we discuss include varying (1) the spatial arrays of sites (paired sites, site transects, site networks), (2) site spacing (e.g. closely spaced along mountain slopes vs. broadly spaced across the regional landscape), (3) site size (e.g. small vs. moderate-sized lake basins), and (4) the types of paleoecological data (pollen vs. macrofossils). The graphical methods used include (1) maps of pollen data to show spatial patterns in pollen records for regional site networks, (2) difference diagrams to emphasize contrasts between pollen records of adjacent paired sites, and (3) elevation-time diagrams to show how differently pollen and macrofossil data record the same elevation gradient in vegetation.

STUDIES IN EASTERN NORTH AMERICA

Study area

The weathered Paleozoic Appalachian and Precambrian Adirondack mountains comprise a southwest- to northeast-trending highland system that bisects eastern North America (Fig. 1a & c). Relief in the region is relatively moderate with maximum elevations approximately 1900 m in the Appalachians and 1600 m in the Adirondacks. Major lowlands occur along the Hudson and St Lawrence rivers, the Great Lakes, and the Atlantic Coast.

Vegetation of the region (Fig. 1b) includes deciduous forests (with temperate hardwoods such as *Quercus, Carya, Castanea*), mixed forests of conifers and central/northern hardwoods (*Tsuga, Pinus, Acer, Betula, Fagus*), spruce-fir and boreal forests (*Picea, Abies, Betula*), and alpine sedge/herb/shrub tundra. Pine-dominated (*Pinus*) forests occur in coastal areas. The deciduous, mixed and spruce-fir forest associations dominate along a south–north latitudinal gradient in the study region. These three associations comprise the montane vegetational gradient in mountains of the southern to central parts of the region. Farther north montane vegetation grades from mixed forests into sub-alpine spruce-fir forests, with alpine tundra above approximately 1500 m.
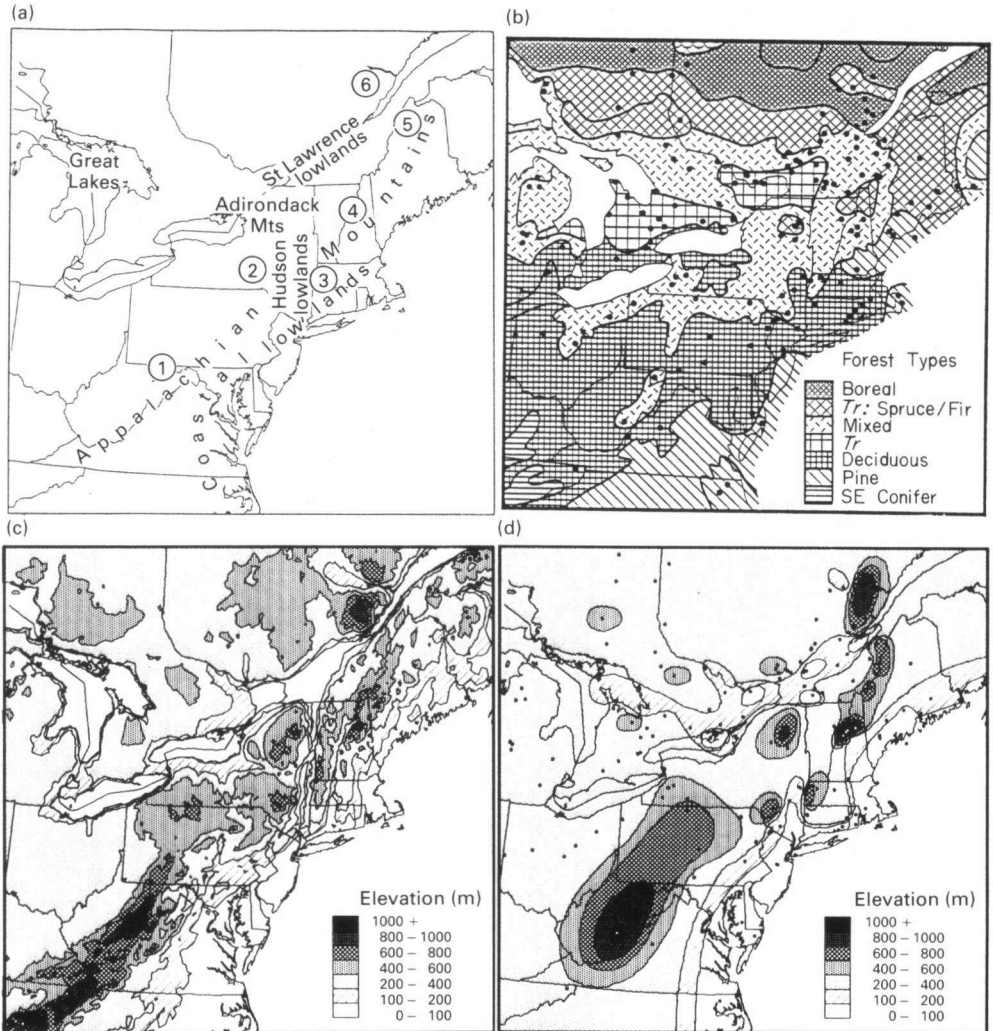
Fig. 1. Maps of eastern North American (35–50°N, 65–85°W) showing (a) physiography, (b) vegetation, (c) topography, and (d) site-specific topography. In maps (b) and (d) the dots show the locations of the 166 sites in a data base of postglacial records at Brown University. Map (a) shows the physiographical features that are represented in the pollen data base. Major highlands include the Adirondack mountains, the Appalachian mountain system including the 1—Allegheny, 2—Catskill, 3—Taconic, 4—White, 5—Longfellow/ Notre Dame, 6—Laurentian mountain ranges. Major lowland areas occur along the Coast, the Great Lakes, and the Hudson and St Lawrence rivers. Map (b) shows major vegetation regions including the South-eastern Conifer, coastal Pine, Deciduous, Mixed, and Boreal Forests (Tr indicates transitional forest) (modified from Gaudreau 1988a; 1988b). Map (c) shows elevation contours derived from a 5-min grid of elevations. Map (d) shows elevation contours derived from the elevations of the 166 pollen sites.

The macroscale distribution of the vegetation reflects broad geographical (latitudinal and longitudinal) climatic gradients. In addition, topography emplaces localized climatic gradients that superimpose mesoscale patterns on the vegetation. For example, Figure 1 shows that mixed forests extend southward in the highlands of the Appalachian mountains, and the deciduous forests reach their northernmost extent in the St Lawrence lowlands.

Similarly, spruce-fir forests extend southward at high elevations in the Adirondacks (Fig. 1b). The finer-scale montane vegetational gradient is incompletely represented in the maps because of the decreasing spatial area of higher-altitude vegetation, a function of the geometry of mountains. For example, the spruce/fir forests that occur in the high elevations of the southern Appalachians are not shown in Fig. 1b, nor is the alpine tundra vegetation of the Adirondacks and northern Appalachians (the White, Notre Dame/Longfellow, and Laurentian mountains).

Relative pollen source area among different taxa

Graphical method. Theoretical and empirical studies indicate that the pollen source areas for different taxa vary by orders of magnitude (Bradshaw & Webb 1985; Prentice 1985). An effective way of studying pollen source areas is to compare scatter plots of pollen percentages versus tree percentages that show how the pollen/vegetation relationship varies at different vegetation-sampling radii (Fig. 2). These graphical relationships can be used along with statistical parameters from regression analysis to identify the radius that yields the best linear fit between pollen and tree percentages, which should be closely related to the radius of the pollen source area for a taxon (Bradshaw & Webb, 1985; Prentice *et al.* 1987).

Sampling strategy. Studies using coarse site grids (sites spaced 5–100 km apart) over large areas (10^5–10^7 km^2) show that while most *Fagus* and *Picea* pollen derives from within a 4·5 km radius, significant amounts of *Betula* pollen originate from within 30 km of the sites (Bradshaw & Webb 1985; Webb *et al.* 1981; Delcourt *et al.* 1984; Prentice *et al.* 1987). The coarse-scale sampling strategy employed by these studies leaves unanswered the question of how sensitive pollen assemblages are to vegetation patterns at spatial scales of less than 10 km. One strategy is to determine the pollen source areas of lakes spaced in tighter grids (i.e. sites spaced < 10 km apart) using finer-scale vegetation surveys. Jackson (1990) did this for 19 small lakes (< 0·5 ha) situated in two clusters, one in the deciduous forest of southern New England and another in the mixed forest of northern New York. Pollen assemblages were compared with landscape-scale forest composition, estimated within concentric radial distances of 20 m, 100 m, 500 m, 1 km and 2 km of each lake.

Results. The results of this study show that spruce pollen derives from relatively short distances (*c.* 100 km) (Fig. 2a), most beech pollen from intermediate distances (*c.* 1 km) (Fig. 2b) and most birch pollen from much greater distances (> 1 km) (Fig. 2c). The study also showed that most of the tree pollen in sediments of the small lakes is derived from trees growing more than 500 m from the lakeshores.

These and other results of Jackson (1990) demonstrate that pollen assemblages of small lakes are potentially sensitive to fine-scale tree abundance patterns of some taxa (e.g. *Picea, Fagus*). However, fine-scale patterns of tree abundance were poorly recorded for some well-dispersed taxa (*Betula, Pinus, Quercus*). These results confirm the relative rankings of pollen source areas estimated by Bradshaw & Webb (1985) for a coarser site grid while also illustrating how sampling design can increase the spatial resolution of pollen assemblages (e.g. by using poorly dispersed pollen types in closely spaced small lakes). Both studies show that the pollen source area varies by at least an order of magnitude depending on the pollen type. The differences in pollen source area among pollen types result from differences in their dispersibility as predicted by Tauber (1965) and Prentice (1985). Within a given pollen type, pollen source area increases with lake size
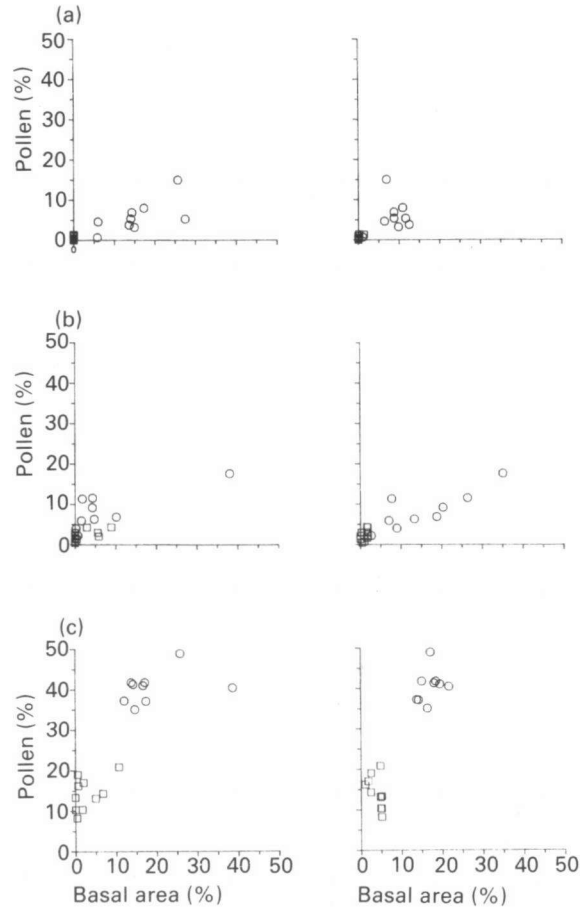
Fig. 2. Scatter diagrams showing relationship between modern pollen percentages (based on a sum of arboreal taxa) and percentage basal area of tree populations within 100 m (left) and 1 km (right) of 19 small lakes (<0·5 ha) for (a) *Picea*, (b) *Fagus* and (c) *Betula*. (O) Data from northern New York, and (□) from southern New England. Eight of the New York sites are within 6 km of each other in the central Adirondack mountains; a ninth site is about 50 km away in the eastern Adirondacks. Three New England sites are within 6 km of each other in south-central Massachusetts, and seven sites are within 2 km of each other in southern Rhode Island, 60 km to the south. Modified from Jackson (1990).

(Jacobson & Bradshaw 1981; Prentice 1985). Because of the small size (<0·5 ha) of the lakes studied, Jackson's (1990) results indicate the lower limit of spatial resolution possible using pollen assemblages from lakes in forested landscapes.

Site networks: isopoll maps

Graphical method. Isopoll maps (Figs 3 & 4) show how well spatial patterns in pollen data from site networks resolve vegetational gradients and thus these maps are a graphical approach to the issue of pollen source area. The isopolls (contours of pollen isofrequency) are a graphical method of low-frequency filtering that removes the site-specific (here the high-frequency) signal (e.g. the over-representation of local trees in pollen assemblages), while emphasizing between-site differences. The amount of filtering or smoothing (and thus the scale emphasized) is controlled by site spacing (site number and distribution), site
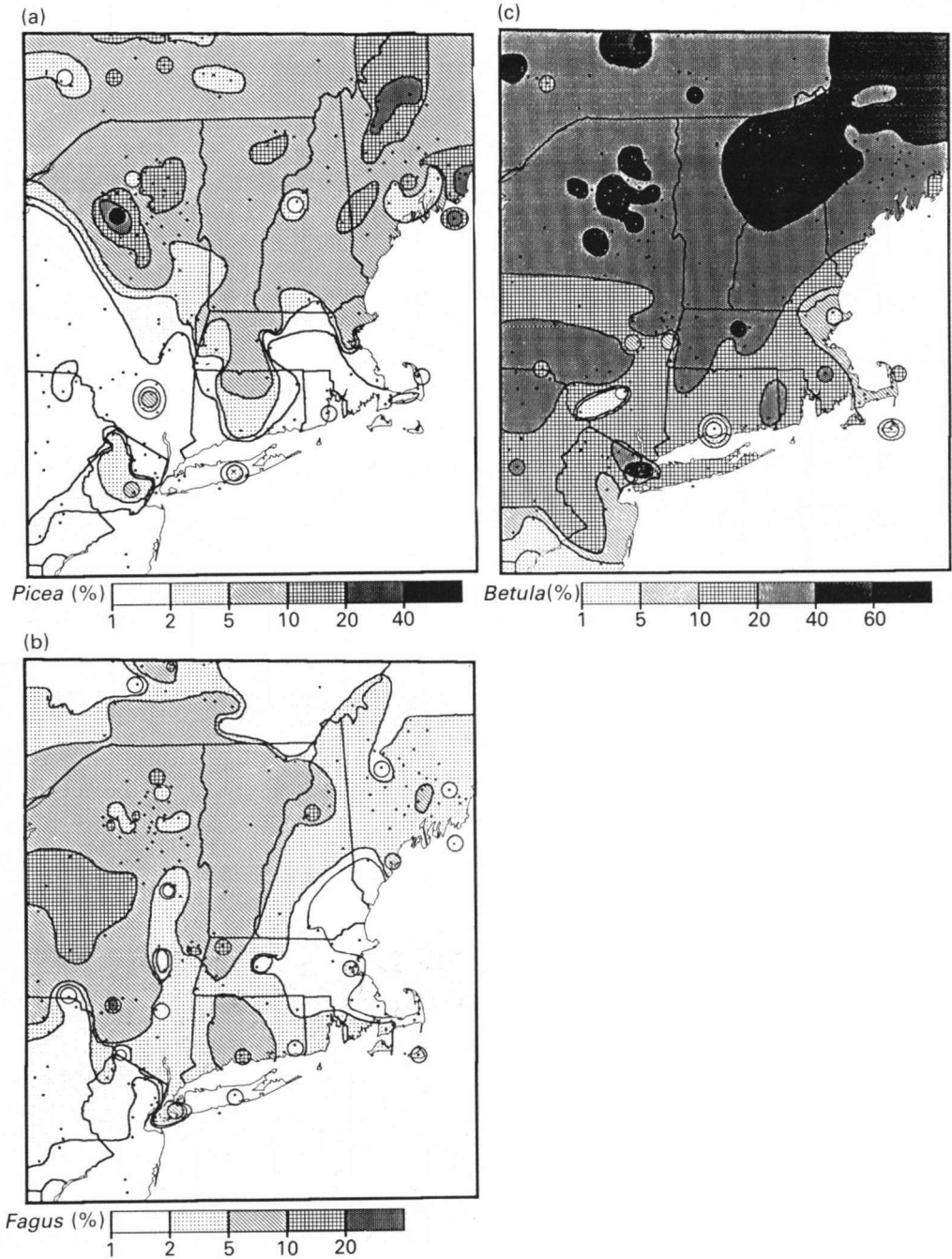
Fig. 3. Isopoll maps of greater New England showing the modern distribution of (a) *Picea*, (b) *Fagus* and (c) *Betula* pollen at 232 sites. Percentages are based on a sum of tree plus shrub pollen (Gaudreau, unpublished observations). The region (39–46°N; 69–76°W) is a subset of that shown in Fig. 1. The dots represent 232 surface-sediment samples from the modern pollen data base at Brown University. Physiographical features represented in the 232-site data base include (refer to Fig. 1): highlands associated with the Adirondack mountains, and the Catskill, Taconic, White and Longfellow/Notre Dame mountains of the Appalachian system; and lowland areas associated with the Atlantic coast and the Hudson and St Lawrence rivers.

(a)

Picea (%)

1 5 20
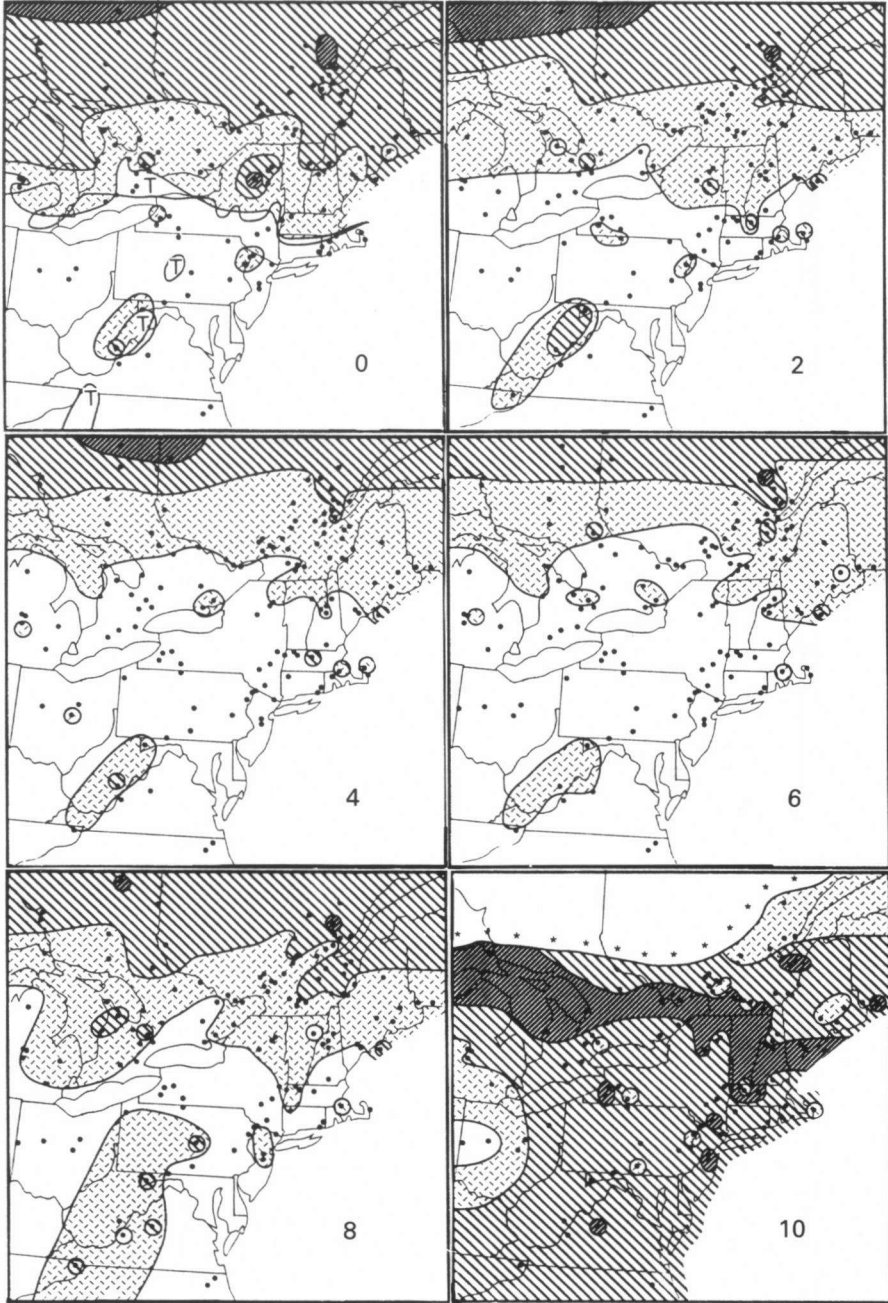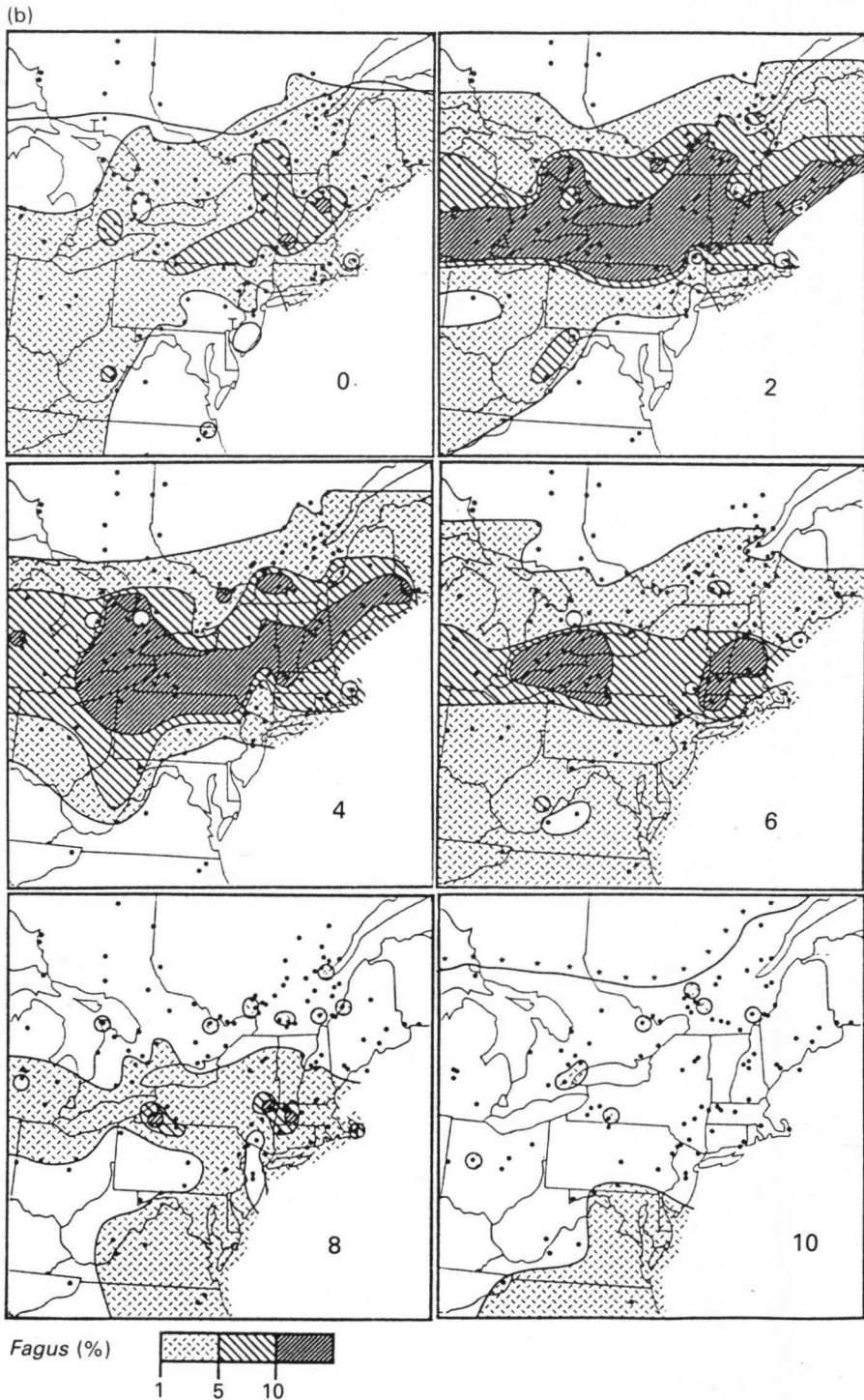
Fig. 4. Isopoll maps of eastern North America showing the changing distribution of (a) *Picea* pollen percentages and (b) *Fagus* pollen percentages at 2000-year intervals from 10 ka (10) to present day (0) at 161 sites. Pollen percentages are based on a sum of tree, shrub and herb pollen. The only paleogeographical feature shown is the ice sheet (delimited by a contour labelled with *). The modern tree-range limits for *Picea* species and for *Fagus grandifolia* are shown (delimited by a contour labelled with T; T is positioned within the tree range) on the 0 ka maps. (Map (a) modified from Gaudreau 1988a; 1988b; (b) modified from Gaudreau 1986)).

attributes (e.g. basin size and type such as lake, bog), pollen attributes (e.g. dispersal, representation) and mapping techniques (e.g. map scale, choice of contouring intervals).

Sampling strategy. For existing site networks, one strategy to change the filtering of the pollen data is to vary the size of the geographical area mapped and thus emphasize patterns at the macro-, meso- or other scales. Another strategy is to map several pollen types that vary in the size of their source regions owing to differences in their dispersal and representation and in the number of species lumped in the pollen type.

Gaudreau (1986; 1988a; 1988b; manuscript in preparation) used existing networks of pollen sites in North-eastern USA and Canada to test the sensitivity of pollen distributions to topographic gradients in plant distributions between major physiographical features. The spatial sensitivity was evaluated (1) at two map scales of different pollen-site densities: a scale showing both latitudinal and topographical gradients based on 166 sites in eastern North America encompassing 3×10^6 km^2 and many forest types (Figs 1 & 4), and a scale focusing on topographical gradients based on 232 sites in greater New England encompassing 0.5×10^6 km^2 that includes deciduous, mixed and spruce/fir forests (Fig. 3); (2) in time, based on maps of modern (0 ka) pollen distribution (Figs 3 & 4) and map-series of Holocene (0–10 ka) pollen distribution (Fig. 4); and (3) for pollen types with source areas that vary by orders of magnitude.

Comparison of an elevation map contoured according to the elevations of the individual pollen sites in the 161-site network (Fig. 1d) with a map of evenly spaced elevational data (Fig. 1c) shows that the pollen-site grid includes many of the major physiographical features of the mapped region (see Fig. 1a). Similar comparison for the 232-site network shows this same level of resolution (Gaudreau, unpublished observation). Both the 161- and 232-site grids are irregular with respect to geographical and topographical gradients, and the between-site distances range from about 1 km up to 100 km. Thus, the contours can constrain physiographical features that are minimally of the order of 10 km in breadth.

Results: modern maps (Figs 3 and 4 (0 ka)). *Picea* trees have a southern range limit in the north-east (Fig. 4a) and dominate in northern vegetation regions, the spruce-fir and boreal forests (Fig. 1b). *Picea* isopolls (Fig. 4a) show this geographical gradient. For example, the 1% isopoll correlates with the southern range limit of *Picea* trees; the isopolls also show a monotonic northward increase in pollen abundance. Superimposed on this geographical gradient in the isopolls are patterns that match topographical gradients. The topographical gradients in turn correlate with the northern-centered distribution of *Picea* species. For example, the tree range limit (Fig. 4a) extends locally southward in the highlands; the 1% isopoll reflects this topographical gradient deflecting southward along the southern Appalachians, and in the Taconic highlands of New England (in contrast to the Hudson lowlands). Topographical gradients in which *Picea* pollen abundance increases with elevation are evident northward as well, where the 5% and 20% isopolls deflect about the Adirondacks and northern Appalachians.

Changing the map scale to focus on New England (Fig. 3) increases the resolution of these geographical and topographical gradients. For example, Fig. 3a shows that *Picea* pollen values in the southern Appalachians, Catskills and Taconics are large (2–5%) relative to values in adjacent lowlands of the coast and Hudson River (0.1%). Also, in the north, values in the Adirondacks and northern Appalachians (e.g. the Longfellow/Notre Dame mountains) are larger (10 to >40%) than in surrounding lower elevations

(5–10%); with a further decline in elevation toward the St Lawrence lowlands, values decrease further (1–5%).

Fagus grandifolia has a northern range limit in southern Canada, a localized southern limit (coastal New Jersey) (Fig. 4b), and dominates in mixed forests of central latitudes (Fig. 1b). *Fagus* isopolls (Fig. 4b) show this geographical gradient. For example, the 1% isopoll correlates with the northern range limit of *Fagus* trees and is conservative with respect to the southern range limit. The isopolls show a geographical gradient in latitude in which values (0–1%) are low in the south, increase in central latitudes (5–>10%) where the mixed forest dominates, and then decrease northward (to <1%). The geographical gradient in the *Fagus* isopolls also has a longitudinal component, an east–west abundance gradient that, like the latitudinal gradient, is non-monotonic. Superimposed on these geographical gradients in the isopolls are patterns that match topographical gradients. The topographical gradients in turn correlate with the central-latitudinal distribution of *Fagus*. For example, in the southern part of the distribution, values in the Hudson lowlands are smaller than in adjacent highlands, and accordingly the 5% isopoll deflects northward in the lowlands. In northern areas this abundance gradient is reversed and the 5% isopoll deflects northernmost in the St Lawrence lowlands relative to adjacent highlands.

Changing the map scale to focus on New England (Fig. 3) increases the resolution of these geographical and topographical gradients. Figure 3b shows a non-monotonic latitudinal gradient in pollen abundance, a longitudinal gradient in which pollen abundance increases inland, and topographical gradients which are most evident in the southern part of the distribution where pollen abundances are smaller in lowlands of the coast and Hudson River relative to adjacent highlands.

Betula species range throughout the region and dominate in the mixed forests and more northern forest regions (Fig. 1b). *Betula* pollen (Fig. 3c) is widespread and abundant in the north-east and is an over-represented, highly dispersed type. Nevertheless, *Betula* isopolls resolve geographical and topographical gradients in tree abundance even within greater New England (Fig. 3c). The isopolls show a monotonic northward increase in pollen abundance and the 20% isopoll correlates with the southern limit of the mixed forest in which *Betula* is a dominant taxon. Superimposed are patterns in the isopolls that match topographical gradients and correlate with the northern-centered distribution of *Betula* species. Larger values of *Betula* pollen occur southernmost in highlands relative to adjacent lowlands. For example, in the south the 20% isopoll deflects southward (as does the distribution of mixed forest) in the highlands of the Catskills and the Taconics. Also, in the north the 40% isopoll deflects southward along the northern Appalachians (e.g. Longfellow/Notre Dame and White mountains) and the Adirondacks.

Results: map time-series (Fig. 4). Isopoll map series show biogeographical changes in *Picea* and *Fagus* for the last 10 000 years.

Picea isopolls (Fig. 4a) show a macroscale distributional change from southern to northern latitudes following deglaciation after the last glacial maximum about 18 ka. By 8 ka the *Picea* isopolls show their modern geographical and topographical gradients consisting of a northern-centered distribution with abundances decreasing southward monotonically. Correlated with this geographical gradient, the topographical gradient in pollen abundance shows greater values in the highlands relative to adjacent lowlands. Though these gradients persisted for most of the Holocene, they shifted in geographical location and in steepness in response to environmental change.

Fagus isopolls (Fig. 4b) show a macroscale change from southern to central latitudes by 8 ka. This latitudinal shift in the distributional centre is accompanied by changing longitudinal abundance gradients both at the range limits and the central part of the *Fagus* distribution. For example, in the early Holocene (10–8 ka) an east/west or southeast/ northwest trend is most evident in the *Fagus* range and by the mid-Holocene (6 ka to present) a north/south trend becomes more evident. These longitudinal trends could complicate the otherwise simple correlation between latitudinal and topographical gradients in pollen abundance. However, at the scale of the maps in Fig. 4b, the *Fagus* isopolls generally show simple, correlated latitudinal/topographical gradients in which, in the southern and central parts of the *Fagus* distribution, abundances are greater in highlands relative to lowlands, while near the northern range limit (e.g. around the Great Lakes and in the St Lawrence lowlands) this topographical gradient is reversed.

Results: summary. The isopolls of *Picea, Fagus*, and *Betula* showed mesoscale (i.e. topographical) patterns superimposed on the macroscale (i.e. geographical latitudinal/ longitudinal) patterns. That these macro- and mesoscale gradients record vegetational gradients is corroborated by the fact that the latitudinal and topographical gradients in the isopolls are correlated in simple and biogeographically reasonable patterns. For example, at the northern part of the distribution of a pollen type, relatively larger pollen values extended locally northward in lowlands than in highlands, while at the southern part they extended southernmost in highlands.

For the isopoll maps based here on two irregular size-grids of variously sized basins with between-site distances from about 1 km to 100 km, the fine-scale vegetational resolution noted by Jackson (1990) for closely spaced small lakes is filtered out, but the vegetational pattern associated with major physiographical features becomes the signal in the pollen distributions. These patterns are robust signals in the pollen data in that they could be resolved when the pollen data were differently filtered in space and time. The isopoll maps in Figs 3 and 4 differentially filter the pollen data because of differences in the source regions of pollen types, in the pollen sum, in the site grids, and in the map scale and contouring intervals. As expected at the broader scale of eastern North America, the isopoll patterns are smoothed; but the increased detail in the fine-scale maps of New England is not noise but rather increased signal of mesoscale vegetational patterns.

Paired-site studies can test the limits of resolution of vegetation pattern from pollen distributions at an even finer scale. However, as the next example illustrates, the between-site contrasts can be understood better in the broader context of regional changes that isopoll maps display.

Paired sites: difference diagrams

Graphical method. Contrasts in the pollen records at two sites can be emphasized in difference diagrams, in which the values for pollen types at one site are subtracted from those at another site. When applied to sites along vegetation gradients between adjacent physiographical features, difference diagrams become a high-frequency filtering method that removes the regional, macroscale (low-frequency) signal that is common to both sites and emphasizes the sub-regional, mesoscale signal (high-frequency) unique to each site.

Sampling strategy. One strategy to test the sensitivity of pollen distributions to environmental gradients is to space sites so that the major difference between them involves a

single key factor such as soil composition or elevation. Consistent differences in pollen abundance between the sites can be used as an index of the sensitivity of pollen data to the environmental gradient. Jacobson (1979) introduced this method for paired sites on contrasting soils, and Gaudreau (1986; 1988a) extended it to a pair of moderate-sized lakes in similar edaphic settings but at different elevations, one in the Hudson lowlands of New York (Gaudreau, 1986), and the other 20 km to the east in the Taconic mountains of Massachusetts (Whitehead, 1979) (Fig. 5). These two physiographical features are each approximately 20 km in geographical (longitudinal) breadth in the vicinity of the two pollen sites, and they are associated with a vegetational gradient in which deciduous forest is distributed across the lowland while mixed forest dominates in the highland.

Results. The pollen stratigraphies from the two sites (Fig. 5) show similar temporal trends in three pollen types with different source areas (small for *Picea*, moderate for *Fagus*, large for *Betula*). *Picea* pollen was initially abundant, then declined in the early Holocene around 8 ka and increased by 2 ka. *Fagus* pollen was common from 8 ka to the present, and *Betula* pollen was abundant throughout the Holocene. These similarities show that the pollen sequences at both sites record macroscale regional vegetation changes. However, the difference diagrams for each taxon reveal significant topographical patterns in pollen abundance and thus in forest composition during the Holocene.

Difference diagrams for the last 9000 years (the time-interval over which the two sites share pollen records) show that when pollen percentages differed between the highland and lowland sites, *Betula* (Fig. 5c) and *Picea* (Fig. 5a) were more abundant at the highland site. This topographical gradient is predictable given the locations of the two pollen sites with respect to the regional Holocene distributions of *Picea* (Figs 3a & 4a) and *Betula* (Fig. 3c). Pollen percentages are expected to be higher in the highlands than in lowlands in the southern part of a taxon's range. For *Picea* the topographical contrast evident in the difference diagram in the early and late Holocene disappears from about 8–2 ka (Fig. 5a). These changing topographical trends are consistent with the regional changes in the *Picea* isopoll maps (Fig. 4a), which show the southern range of *Picea* populations in New England at 8 ka and earlier, the range retreating northward during the mid-Holocene, and then re-expanding southward in New England by 2 ka.

As in the cases of *Picea* and *Betula*, the difference diagram for *Fagus* shows a topographical signal, but in contrast the topographical gradient is not unidirectional (Fig. 5b). In the early to mid-Holocene until about 5 ka, *Fagus* pollen was generally more abundant in the lowlands but after that time it became more abundant in the highlands. The changing elevational contrasts agree with regional changes in the *Fagus* isopoll maps (Fig. 4b), if the 5% isopoll is assumed to approximate the boundary of *Fagus* population centres (e.g. Fig. 3b). The isopoll maps show that during the early Holocene (e.g. by 8 ka), central New England was near the northern edge of the 5% isopoll and therefore *Fagus* pollen would be expected to be more abundant at the lowland site. However after 6 ka, central New England was near the southern edge of this isopoll, and accordingly the pollen percentages became greater at the highland site.

In summary, the results show that pollen types with source areas across the range of empirically determined sizes can sense the vegetational gradient between physiographical features such as a highland and lowland. Their pollen source areas are small enough relative to the site spacing of 20 km so that pollen dispersal does not blur the vegetational pattern when the vegetational gradient is also at approximately this scale.
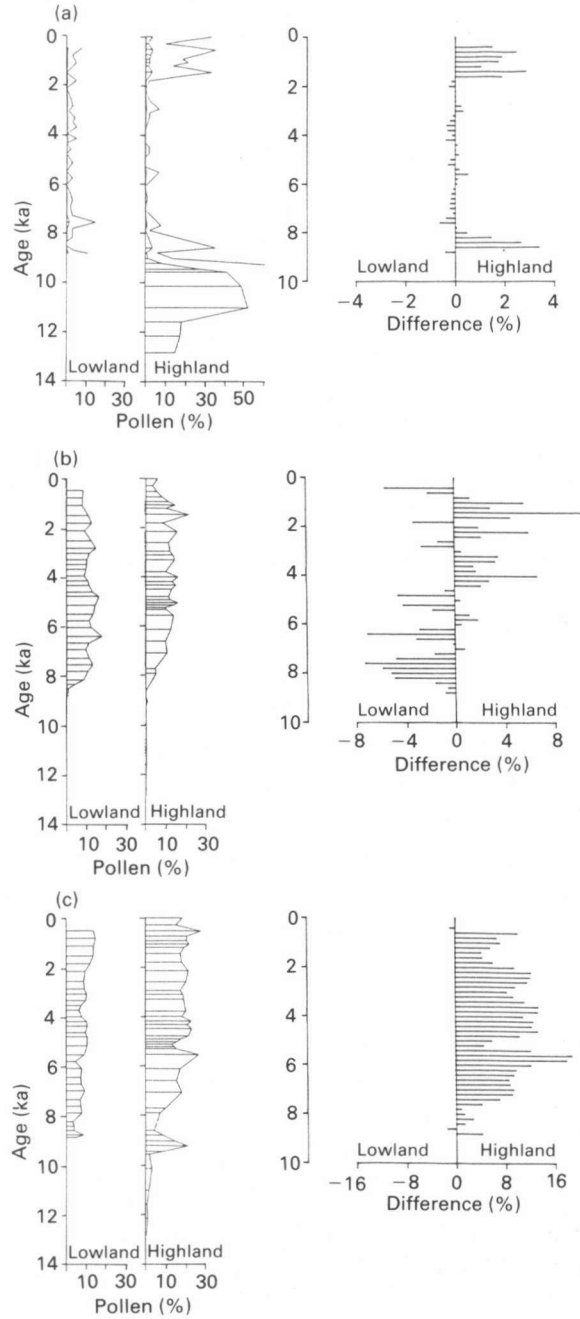
Fig. 5. Pollen stratigraphies (left) and difference diagrams (right) for (a) *Picea*, (b) *Fagus* and (c) *Betula* pollen for Burden Lake in the Hudson River lowlands and Berry Pond in the Taconic mountains. (Figs. (a) and (c) from Gaudreau 1988a; (b) modified from Gaudreau 1986.) See Fig. 1 to locate the physiographical regions. The pollen stratigraphy from Burden Lake dates back to about 9 ka (Gaudreau 1986; 1988a); the Berry Pond pollen record dates back to about 13 ka (Whitehead 1979).

Site transects: elevation-time diagrams and macrofossil vs. pollen data

Graphical method. Temporal changes in taxon abundance patterns along spatial gradients can be displayed and analysed using space-time contour plots of paleoecological data (Dexter *et al.* 1987). Space-time diagrams can be used as a high-frequency filter to emphasize elevational patterns when applied to data from closely spaced sites along an elevational gradient (Jackson & Whitehead 1990).

Sampling strategy. The effectiveness of any high-frequency filter is limited if sites must be spaced so closely that pollen source areas of individual sites overlap substantially. This is frequently the case in montane areas with steep vegetation gradients. An alternative strategy is to use plant macrofossils from lake or peatland sediments as a source of paleoecological data to be used in elevation–time plots. In lakes and bogs without influent streams, macrofossils derive from trees growing less than 30 m from lakeshores. Dunwiddie (1987) demonstrated that relative abundances of conifer needles in lake sediments were closely related to tree abundances within 30 m of lake shores in north-western North America. Jackson (unpublished observations) confirms this scale of resolution in lakes of north-eastern North America.

Jackson & Whitehead (1990) studied pollen and macrofossils in sediment cores from six lakes of various sizes (0·2–11·2 ha) along an elevational gradient from 660 to 1320 m in the Adirondack mountains. The lakes were spaced at approximately 200-m elevational intervals across a vegetational gradient from mixed forest to sub-alpine spruce/fir forest to sub-alpine fir forests. Distances between individual sites ranged from 2 to 15 km.

Results. Elevation–time plots of pollen data reveal the relative insensitivity of pollen data to elevational vegetation patterns in the Adirondacks (Fig. 6). However, these same plots for macrofossil data show elevational trends that correspond to expected gradients in tree abundance (Fig. 6). For example, macrofossils of *Abies, Picea* and *Betula* show clear elevational patterns (Fig. 6a, b. c). In contrast, only *Abies* pollen shows a distinct spatial pattern of abundance along the elevational gradient (Fig. 6a).

The disparity between the spatial patterns of *Betula* pollen and macrofossil data (Fig. 6c) results from the high dispersal capacity and hence large source area of *Betula* pollen (Bradshaw & Webb 1985; Prentice *et al.* 1987; Jackson 1990). Even though *Picea* pollen is relatively poorly dispersed, it also fails to show elevational patterns corresponding to the vegetation gradient evident in the macrofossils (Fig. 6b). *Abies* pollen is more-poorly dispersed than either *Picea* or *Betula* pollen (Prentice 1985; Jackson & Whitehead 1990) and does show spatial patterns along the gradient similar to those in the macrofossils (Fig. 6a). However, *Abies* pollen is also severely under-represented relative to tree abundances, limiting its ability to resolve *Abies* tree distributions. Therefore, even for *Abies*, the macrofossil data show the sharp elevational contrasts in tree abundance better than do the pollen data.

The contrasting patterns in the pollen and plant-macrofossil data in the elevation–time diagrams indicate that pollen dispersal is widespread relative to the spatial scale of this montane elevational gradient. Whereas macrofossils in lake sediments can potentially record elevational variations in vegetation down to a scale of 100 m elevation or less, widespread pollen dispersal has the effect of smoothing vegetation patterns along the entire elevational gradient. Modern pollen assemblages from lakes in the sub-alpine spruce/fir forests of the Adirondacks are composed mainly of pollen from low and
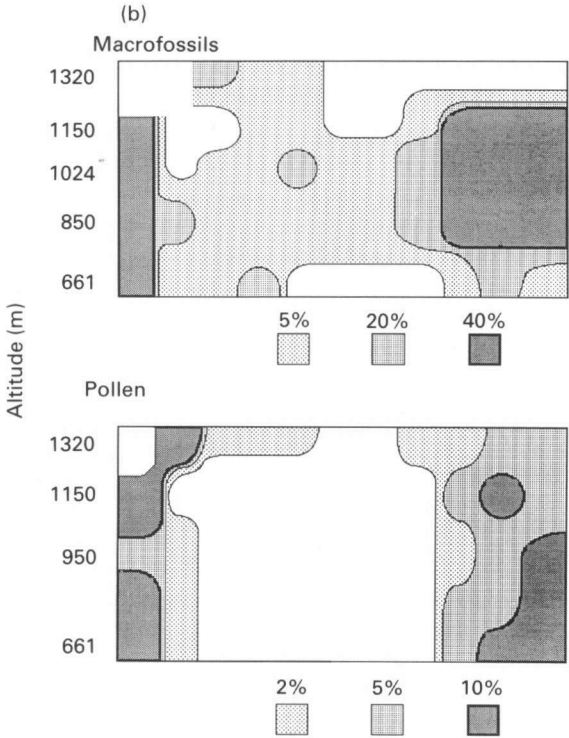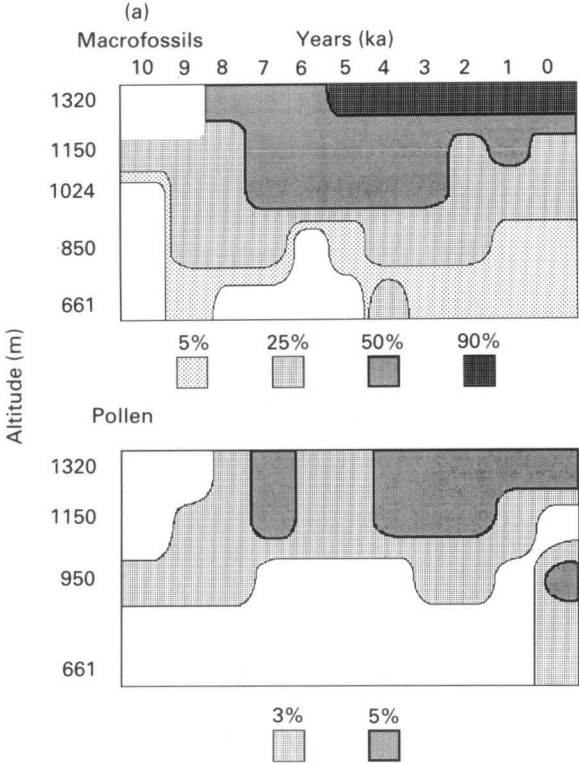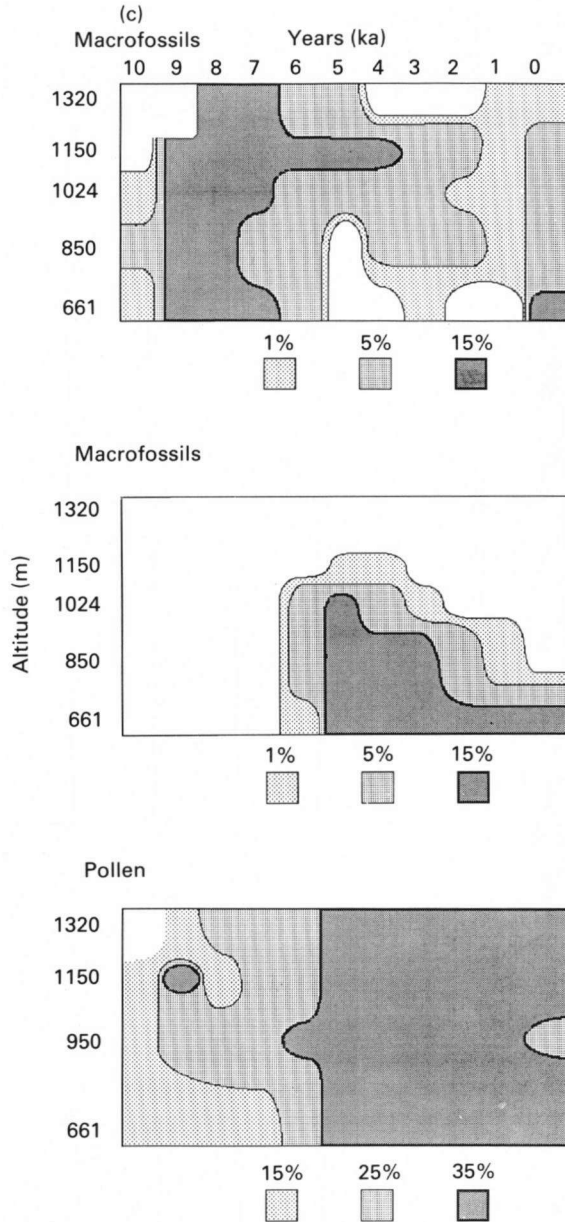
Fig. 6. Elevation–time diagrams for pollen and macrofossil percentages in an elevational transect of sites in the central Adirondack mountains from 10 ka to the present (a) *Abies*, (b) *Picea* and (c) *Betula papyrifera* (top), *Betula lutea* (middle) and *Betula* sp. (bottom). Modified from Jackson & Whitehead (1990)

mid-elevation mixed forests 2–10 km away (Jackson & Whitehead unpublished observations). Pollen data from lake basins are therefore relatively ineffective in revealing fine-scale abundance and distribution patterns for many tree taxa along steep elevational gradients.

DISCUSSION

Consideration of spatial scale aids the design of paleoecological studies of vegetation history (Jacobson & Bradshaw 1981). Our studies illustrate how choices of site spacing, basin size, type of fossil data collected (e.g. pollen types, macrofossils) and method of display affect the interpretation of data in paleoecological studies of mountainous regions.

First we described a study of tightly spaced (< 10 km apart) grids or transects of small lake basins to illustrate the differential size of the pollen source area among taxa and to test whether pollen distributions can resolve the landscape-level mosaics in taxon abundance within the vegetation region. The results showed that pollen source distances for upland trees have a lower limit of the order of 100 m and can be large (much greater than 1 km radius) depending on the pollen type (Jackson 1990). Secondly, we considered various sizes of lakes and bogs in two networks of sites (sites 1–100 km apart), both distributed across major physiographical features. Here the aim was to test whether networks of pollen samples can resolve the regional topographical gradients in taxon abundance patterns across vegetation zones. The results showed that maps of contoured pollen abundance for types ranging widely in the size of their source area can resolve vegetational contrasts (of the order of 10 km) created by physiographical features such as major rivers and highlands (Gaudreau 1986; 1988a; 1988b; unpublished observations). Thirdly, difference diagrams for paired sites (20 km apart) from adjacent lowland and highland areas (400 m relief) illustrated a way to emphasize the vegetational contrasts between these areas (Gaudreau 1986; 1988a). Our last example was at the scale of a forested mountain range with steep elevational gradients and vegetational gradients. We showed that except for poorly dispersed types, pollen from small to moderate-sized lakes cannot resolve the vegetational pattern along a fine-scale elevation gradient even when the lakes were 2–5 km from other vegetational zones. However, the small size of the source regions allowed macrofossils to resolve this landscape-scale gradient (Jackson & Whitehead 1990).

Our examples illustrate how the spatial patterns of pollen abundance smooth the vegetational patterns to varying degrees depending on choices of spacing among sample sites relative to the size of the pollen source area and to the scale of the vegetational pattern itself. For example, on mountain slopes, topographical gradients and their associated vegetational gradients are often so steep that sites cannot be spaced far enough apart to resolve an elevation-specific 'image' of vegetational composition. In contrast, because they can be resolved with less spatial precision, the vegetational gradients between major physiographical features can be resolved in pollen assemblages. (Fig. 1b, which shows physiographical patterns in vegetation types but not the fine-scale montane gradients, illustrates this point about spatial precision.) Our examples showed how spatial resolution varied among pollen types that differ by orders of magnitude in the size of their source areas. For the scales we studied, types with smaller source areas showed systematic variation among sites spaced more closely than did better-dispersed types. Of *Picea, Fagus,* and *Betula* (with small to large source areas, respectively), none showed the montane vegetational gradient in the Adirondacks, and only *Picea* pollen matched landscape-level patterns of tree abundance at the 100 m scale. However, all three showed pollen abundance gradients that correspond to topographical gradients between major physiographical features at the 10 km scale in eastern North America.

We showed how a variety of graphical methods can be applied to pollen and macrofossil data in order to highlight vegetation patterns at various scales. Scatter plots emphasize patterns for direct pollen/vegetation comparisons, difference diagrams for comparison of time-series data from paired sites, isopoll maps for site networks, and elevation–time

diagrams for time-series data from site transects. Isopoll maps at different spatial scales reveal topographical contrasts in the vegetation at different levels of resolution. For example, isopoll maps at the continental scale for Europe (Huntley & Birks 1983) and eastern North America (Webb 1988) show broad macroscale vegetational changes, but smooth some of the patterns evident in our regional maps. At the same time, our regional maps smooth the high-resolution patterns visible in isopoll maps based on a high-density pollen-site network in the St Lawrence lowlands and adjacent Appalachian mountains of southern Quebec, Canada (Webb *et al.* 1983). Tsukada's (1988) elevation–latitude diagrams for Japan and those of Barnosky *et al.* (1987) for north-western North America are examples of additional graphical methods to summarize vegetational patterns along major elevational gradients.

The high spatial resolution of macrofossils has led to their wide application in vegetational reconstructions of mountain regions (Baker 1976; Davis *et al.* 1980; Jackson, 1983, 1989; Lang & Tobolski 1985; Dunwiddie 1986; Anderson 1987; Spear 1989). Packrat middens are a type of 'collecting basin' for pollen and macrofossils in arid climates and have yielded detailed information on past vegetational patterns in the mountains of western North America (Cole 1982; Spaulding *et al.* 1983; van Devender *et al.* 1987; Thompson 1988). Pollen samples from small hollows, moss polsters, and forest soils can match the high spatial resolution of macrofossils from small lakes. Graphical summaries of pollen data from such collecting sites show fine-scale elevational contrasts in vegetation (Heusser 1973; Davis 1984; Grabandt 1985; Anderson & Davis 1988), but the direct application of such results to fossil data from lake sediment is not straightforward (see cautionary comments in Grabandt (1985) and Dunwiddie (1987); and compare results of Heide & Bradshaw (1982) with those of Webb *et al.* (1981)). The latter two studies showed how pollen/vegetation relationships can differ substantially between data from lake sediments and data from moss polsters within the same region.

In addition to the factors reviewed above, the size of the pollen source area is also related to the physiognomy of the vegetation. Our work has focused on forested landscapes, but the limitations of spatial resolution for pollen from lakes and bogs are compounded in mountainous areas of treeless vegetation (e.g. montane grassland, shrub steppe, deserts). The zone of treeless vegetation covers a relatively small area due to the geometry of mountains. Also, pollen production per unit land area is low compared to forested landscapes. These factors, coupled with pollen dispersal, usually result in collecting sites above the treeline having a larger pollen source area than those in forests. Modern pollen assemblages from lake sediments and moss polsters in such vegetation include large amounts of tree pollen blown in from distant forests (Maher 1963; McAndrews & Wright 1969; Heusser 1973; Mack & Bryant 1974; Baker 1976; Grabandt 1980; Markgraf 1980; Davis 1984; Graf 1986; Solomon & Silkworth 1986; Anderson & Davis 1988; Mathewes 1988). For example, Spear's (1989) sites in the sub-alpine and alpine zones of the White mountains of north-eastern North America derive > 80% of their pollen from forest trees growing below the treeline. Differences between pollen assemblages from lakes above and below treeline are subtle and recognizable primarily by the presence or absence of trace amounts of a few 'indicator' types (Spear 1989).

CONCLUSIONS

Increased understanding of how pollen data sense vegetation patterns is leading to the establishment of guidelines for designing and interpreting paleoecological studies that

provide maximum information about vegetation patterns at different scales. We have focused on some of the issues important to paleovegetation studies in mountainous terrain, including the scale of the vegetation pattern, the size and density of the study-site grid, and the size of the pollen source area. Pollen data from spatial networks of lake and peatland sites can resolve vegetation patterns at macro- and mesoscales. However, finer-grained vegetation patterns such as those within montane regions are often smoothed owing to the large pollen source areas of lakes. Such patterns can frequently be resolved using plant macrofossils. Further understanding of pollen source areas, combined with sampling strategies and development of new display methods should increase the resolution of paleoecological and paleoclimatological inferences made for montane regions. Such details will add to the solid foundation of research developed by Professor dr. T. van der Hammen and his associates for the Andes and elsewhere.

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