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Effect of pollen from regional vegetation on stand-scale forest reconstruction

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Abstract: To investigate the influence of regional pollen inputs on reconstructing local vegetation, we compared modern pollen assemblages deposited in forest hollow sediments from two study areas, Michigan and Wisconsin. Local forest-stand composition (within 50 m) at all sites is dominated by hemlock and northern hardwood trees, but the regional abundance of tree taxa in the two study areas is not the same. Modern pollen assemblages differ between the two study areas, corresponding with differences in regional vegetation. Oak and pine pollen are more abundant in Wisconsin samples, whereas sugar maple, birch and hemlock pollen are more abundant in Michigan samples. Pollen assemblages differed most between study areas for hardwood stands, reflecting lower pollen production of sugar maple and basswood, which exaggerates regional pollen inputs. However, within each study area, surface pollen assemblages are sufficiently different to permit differentiation of hemlock and hardwood stand types, suggesting that regional pollen inputs are similar on the scale of tens of kilometres. Therefore, stand-scale forest histories can be derived from forest-hollow sediments using modern analogues, but our results emphasize the importance of understanding the regional vegetation context and inferring how regional vegetation has changed in the past.

Key words: palaeoecology, vegetation history, pollen analysis, forest hollow, modern analogues, regional versus local pollen, surface samples, hemlock-northern hardwood forest.

Introduction

Pollen preserved in small forest hollows and forest humus can provide histories of vegetation change on a spatial scale relevant to contemporary plant ecologists (Bradshaw, 1988; Björkman and Bradshaw, 1996; Davis *et al.*, 1998; McLachlan *et al.*, 2000). In small basins or under a closed canopy, pollen produced by trees growing nearby (local vegetation) is well represented; whereas, in large basins pollen produced by trees growing far away (regional vegetation) overshadows the local pollen signal (Tauber, 1965; Andersen, 1970; Janssen, 1973; Jacobson and Bradshaw, 1981; Prentice, 1985; Sugita, 1994; Jackson, 1990; 1994, Jackson and Wong, 1994; Jackson and Kearsley, 1998). Identifying and interpreting the local pollen signal requires care, however, because all sedimentary basins contain pollen derived from both local and regional sources. Early estimates of pollen transport distances concluded that most of the pollen in small forest hollows is produced by plants growing only 20–30 m away (Anderson, 1970; Bradshaw, 1981; Heide and Bradshaw, 1982). More recent estimates demonstrate that, in fact, a substantial proportion of total pollen – at least 50–60% – originates from beyond 50–100 m from forest hollow basins (Sugita, 1994; Calcote, 1995; Jackson and Kearsley, 1998).

Even with this large amount of non-local pollen, the relationship between pollen and vegetation for small sedimentary basins is very good. Sugita (1994) explains this apparent discrepancy with the concept of ‘relevant pollen source distance’ (RPSD) which is the spatial scale of vegetation that pollen data records. The RPSD is the distance beyond which the correlation between distance weighted vegetation data and pollen abundance within that basin does not improve significantly. Pollen representation in sediments is necessarily distance-weighted by dispersal characteristics of pollen (Sugita, 1993; 1994; Calcote, 1995; Jackson and Kearsley, 1998) with trees nearby comprising a greater proportion of the pollen sample than trees farther away. Forest patches beyond the RPSD, therefore, blend into a relatively homogeneous background pollen rain, even in areas with heterogeneous vegetation. RPSD varies with the size of the sediment basin, type of vegetation, and patch size and variability (Sugita, 1994).

For forest hollows in the Great Lakes region RPSD has been estimated to be 50–100 m (Sugita, 1994; Calcote, 1995), which is small enough to reflect stand-scale (1–3 ha) differences in vegetation (Calcote, 1998; Davis *et al.*, 1998). This model predicts that pollen assemblages from similar stand types will be similar, as long as regional pollen inputs are homogeneous from site to site (Sugita, 1994). However, regional pollen inputs change in space and time, and the practical implications of variation in regional pollen inputs on the local pollen signal have not been thoroughly explored (Sugita, 1994; Jackson and Wong, 1994;

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Jackson and Kearsley, 1998). In this paper, we pose the following question: how great an effect does a change in regional vegetation have on interpretation of stand-scale vegetation composition from forest hollow sediments?

To address this question, we have assembled a data set of pollen assemblages from the surface of forest hollows and associated vegetation composition surrounding each of the hollows. All surface samples are from stands dominated by similar combinations of northern hardwood and hemlock trees but are distributed in two study areas that differ in regional tree abundance. If regional vegetation has little effect on the local pollen signal at these closed-canopy sites, then pollen assemblages between regions for similar stand types should be indistinguishable. We use a modern analogue approach and multivariate methods to compare pollen assemblages and discuss the implications for reconstructing stand-scale forest composition in the past from forest-hollow sediments.

Methods

Sampling pollen and vegetation

Our strategy for assessing the influence of region pollen inputs on stand-scale reconstructions from forest-hollow sediments was to select sites with similar local stand composition in two areas where regional vegetation composition is different. Calcote (1995; 1998) assembled a set of 66 surfaces samples from the upper Great Lakes region that included stands dominated primarily by hemlock and northern hardwood trees. The sites are located in two areas, one in upper Michigan and one in northwestern Wisconsin (Figure 1), where the regional forest composition differs. In general, the forests in northwestern Wisconsin have a greater abundance of pine and oak and a lesser abundance of hemlock and northern hardwood trees than the forests of upper Michigan. To characterize the difference in forest composition between the two study areas, we summarize data from the US Forest Service's Forest Inventory and Analysis (FIA; Hansen *et al.*, 1992). FIA data can provide only a rough approximation of forest composition on this small spatial scale, and we use them only to confirm broad regional differences in species composition between the two study areas (Table 1). Pine and oak comprise approximately 30% of the basal area in the FIA plots from Wisconsin forests but are uncommon in Michigan. Hemlock trees are three times more abundant regionally in Michigan than they are in Wisconsin. Ideally, forest composition data would be available around each surface-sample site out to several thousand metres, but the effort to collect this amount of data in the field is prohibitive. Remotely sensed forest inventory data might provide a way of describing this extent of forest composition in the future.

Table 1 Regional forest composition (% relative abundance) in the two study areas estimated from FIA plots. Volume estimates of tree abundance were obtained from the FIA World Wide Web site (URL: http://www.srsfia.usfs.msstate.edu/scripts/ew.htm), for FIA plots within 8 km of points located in each of the study areas. For the Michigan study area, FIA plots (n = 39) were selected around the point 89.29°W, 46.22°N. Since surface samples are distributed over a larger area in Wisconsin (*c.* 30 km radius) than in Michigan (*c.* 10 km radius), FIA plots were selected around three points: 91.12°W, 46.17°N; 91.16°W, 46.30°N; 91.58°W, 46.10°N in Wisconsin (n = 56)

	Michigan (% volume)	Wisconsin (% volume)
Pine	2.76	22.05
Red oak	0.00	8.23
Spruce-fir	16.99	5.89
Hemlock	17.13	5.74
Sugar maple	21.55	17.52
Basswood	0.69	3.17
Yellow birch	3.31	1.51
Red maple	11.74	10.57
Ash	2.21	3.70
Aspen	17.40	20.17
Other	6.22	1.44

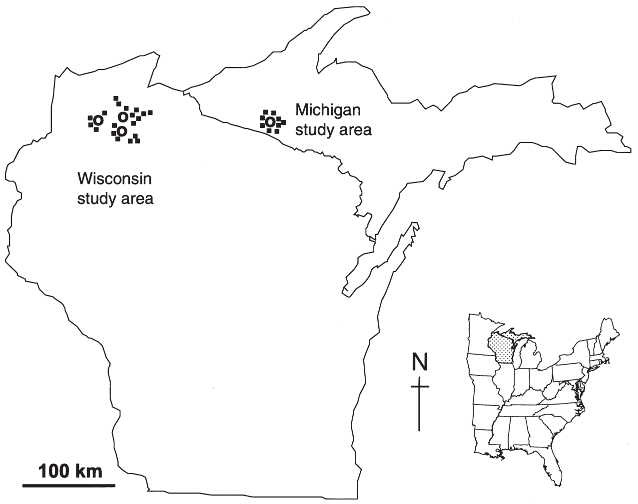

Figure 1 Location of the Michigan and Wisconsin study areas. Circles denote locations of points around which FIA plots were selected to characterize regional vegetation composition (Table 1). Points represent the approximate distribution of the 60 surface samples analysed in this paper. Note that sites are more tightly clustered in the Michigan study area and are not all represented on the map.

We collected additional surface samples from 22 sites that are similar in composition to the hemlock and northern hardwood sites in Calcote's data set. Surface-sediment samples for pollen analysis were taken from the top 1–2 cm of forest-hollow sediments or from soil humus in depressions that morphologically resemble hollows but do not accumulate sediment. Within 20 m of all pollen samples, every canopy tree was mapped and its basal area measured. Basal area for all canopy trees between 20 and 50 metres was estimated with a variable plot prism (Dilworth and Bell, 1982). Pollen was isolated from the sediments by standard methods (Faegri and Iversen, 1989), and at least 600 grains in each sample were counted at 400 × magnification using a light microscope.

Characterizing stand types

To assure that we had collected sites with similar local vegetation, we clustered the forest composition of all stands. Basal area of the 10 most abundant upland tree taxa were used in the classification procedures: hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), birch (*Betula* spp.), basswood (*Tilia americana*), pine (*Pinus* spp.), oak (*Quercus* spp.), fir (*Abies balsamea*), ironwood (*Ostrya virginiana*) and spruce (*Picea* spp.). Though locally abundant in some stands, ash (*Fraxinus* spp., primarily *F. nigra*) and cedar (*Thuja occidentalis*) were not included because their presence often indicates locally wet conditions rather than the composition of the upland forest (Curtis, 1959).

Basal area of all trees was weighted by distance from the sediment sample location based on pollen dispersal characteristics of each tree taxon using Sutton's (1953) equation for dispersal from a ground source. Distance-weighted basal area (DWBA) was calculated for each of five 10-metre concentric rings surrounding each surface sample. Although more work needs to be done to improve the application of pollen dispersal models and their parameters to pollen and vegetation data (Sugita 1993; 1994; Jackson and Kearsley, 1998; Jackson and Lyford, 1999), we used the distance-weighting method of Sugita (1994) based on pollen dispersal estimates of each taxon as the best available approximation of a ‘pollen sample’s view’ of the landscape (Prentice and Webb, 1986). See Sugita (1994) and Calcote (1995) for a more detailed description of this distance-weighting method. Stand classification was based on cluster analysis of percent DWBA (square-root transformed) using Ward’s sum of squares method (Prentice, 1986b; Grimm, 1987).

From the results of this classification, we removed 28 sites, all located in the Wisconsin study area, that were dominated by pine, oak and aspen (*Populus* spp.) from the initial classification of the entire set of 88 surface samples. These stand types are not present in the data set from the Michigan study area, and therefore could not be compared. The remaining 60 sites in both study areas are dominated by hemlock and northern hardwood trees. Classification of these 60 sites, based on the same clustering procedures described above, produced groups of sites with similar local composition that were used for comparing pollen assemblages in this study.

Comparing pollen assemblages

We assessed similarity among pollen assemblages using two common methods (Birks and Gordon, 1985; Overpeck *et al.*, 1985; Prentice, 1986a; Calcote, 1998). First, both pollen percentage data and percent DWBA for the 60 sites were ordinated separately using detrended correspondence analysis (DCA), using the same 10 taxa included in the clustering analysis of vegetation described above. If pollen assemblages are influenced primarily by local pollen inputs, then the ordination of pollen percentages should resemble the ordination of percent DWBA.

Second, we calculated squared chord distance (SCD) of pollen assemblages for all possible site pairs (Prentice, 1980; Overpeck *et al.*, 1985). If there is little effect of regional differences in pollen inputs, then similar vegetation types from the two study areas should have low SCDs (high similarity), similar to values within a region. On the other hand, if regional pollen inputs have a large influence on the pollen spectra, then SCDs should be smaller for vegetation types *within* a study area than *between* study areas.

Results

Forest composition

We identified three stand types from the results of clustering local vegetation composition at the 60 surface-sample sites (Figure 2a). Sites in both Michigan and Wisconsin were distributed evenly among these three stand types (Wisconsin sites are identified in the ‘Region’ column). Local forest composition at sites within the ‘hardwood’ stand type is dominated by sugar maple or a mixture of sugar maple and basswood trees. The ‘hemlock’ stand type includes stands largely dominated by hemlock, although white pine, birch, red maple and balsam fir are often present. The ‘mixed’ stand type is composed of sites with a high abundance of both sugar maple and hemlock, though birch, basswood and red maple are abundant at some sites.

DCA ordination of tree basal area within 50 m of each surface sample demonstrates that vegetation composition in the two study areas is similar (Figure 3a; eigenvalues for the first four axes are 0.487, 0.139, 0.105 and 0.072). The results of this ordination also produced groups of sites that correspond with stand types identified by cluster analysis, further supporting similarity of local forest composition within stand types regardless of study area. The hemlock and hardwood stand types are clearly distinct from each other and overlap only slightly with the mixed stand type.

Correspondence between pollen and vegetation

Pollen abundance in surface samples is related to stand type (Figure 2b). For example, both sugar maple and basswood pollen percentages are higher at hardwood sites and lower at hemlock and mixed sites, whereas hemlock and birch pollen percentages are higher at hemlock sites. Other trends in pollen abundance are related to study area rather than stand type. In mixed and hardwood stands, for instance, birch pollen percentages are higher at Michigan sites, whereas pine and oak pollen percentages are higher at Wisconsin sites. Hemlock pollen percentages are lowest in Wisconsin, especially for hardwood stands.

These two trends appear in the DCA ordination of pollen abundance, though not as strongly (Figure 3b; eigenvalues for the first four axes are 0.121, 0.049, 0.027 and 0.012). First, pollen assemblages from the same stand type tend to be more similar to themselves than to pollen assemblages from other stand types, shown most clearly by the separation of pollen assemblages from hemlock and hardwood stands (Figure 3b). Second, there is a clear effect of study area on pollen assemblage similarity, though the importance of this effect differs with stand type. Separation of hardwood-stand pollen assemblages by study area is most pronounced, in contrast to the basal area ordination where separation between study areas was minimal (Figure 3a). Pollen assemblages from hardwood stands in Wisconsin have more oak and pine pollen and less hemlock and birch pollen than their Michigan counterparts. Mixed stands show a similar pattern, with greater similarity within than between the study areas. Pollen assemblages from hemlock stands are, in general, similar to one another regardless of study area (Figure 3b).

Squared chord distance (SCD) values further demonstrate these patterns (Figure 4). Pollen assemblages collected from the same stand type but from different study areas are not necessarily more similar (do not have lower SCDs) than pollen assemblages from two different stand types (Figure 4a). Median SCD is low (high similarity) when hemlock stands are compared between Wisconsin and Michigan, but pollen assemblages from Wisconsin hemlock stands also have high similarity to hardwood and mixed stands in Michigan. As with the DCA ordination, hardwood stands compared between the two areas show the greatest amount of dissimilarity. Note that hemlock stands in Michigan are very different from hardwood stands in Wisconsin, but the reverse is not true: hemlock stands in Wisconsin are similar to hardwood stands in Michigan. Within each study area, however, pollen assemblages are more similar to each other within the same stand type than between stand types (Figure 4, b and c), especially for hemlock and hardwood stand comparisons.

Discussion

Regional pollen inputs can confound the local pollen signal

One conclusion of our analyses is that forest-hollow pollen assemblages from the same stand type are not necessarily similar if the stands are located within a different regional context. Taxa that show the greatest difference in pollen abundance between study areas are trees that differ most in the regional vegetation. Pine and oak trees are more abundant in Wisconsin than in Michigan, and their pollen is consistently more abundant in Wisconsin pollen assemblages. Hemlock trees are more abundant in Michigan and hemlock pollen percentages there are consistently higher (Figure 2b). Thus, differences in pollen assemblages between study areas are attributed in part to pollen inputs derived from different regional vegetation. There is the possibility that pollen productivity may differ between the two sites and contribute to the patterns that we find here. That differences between pollen assemblages in the two study areas closely match the differences in

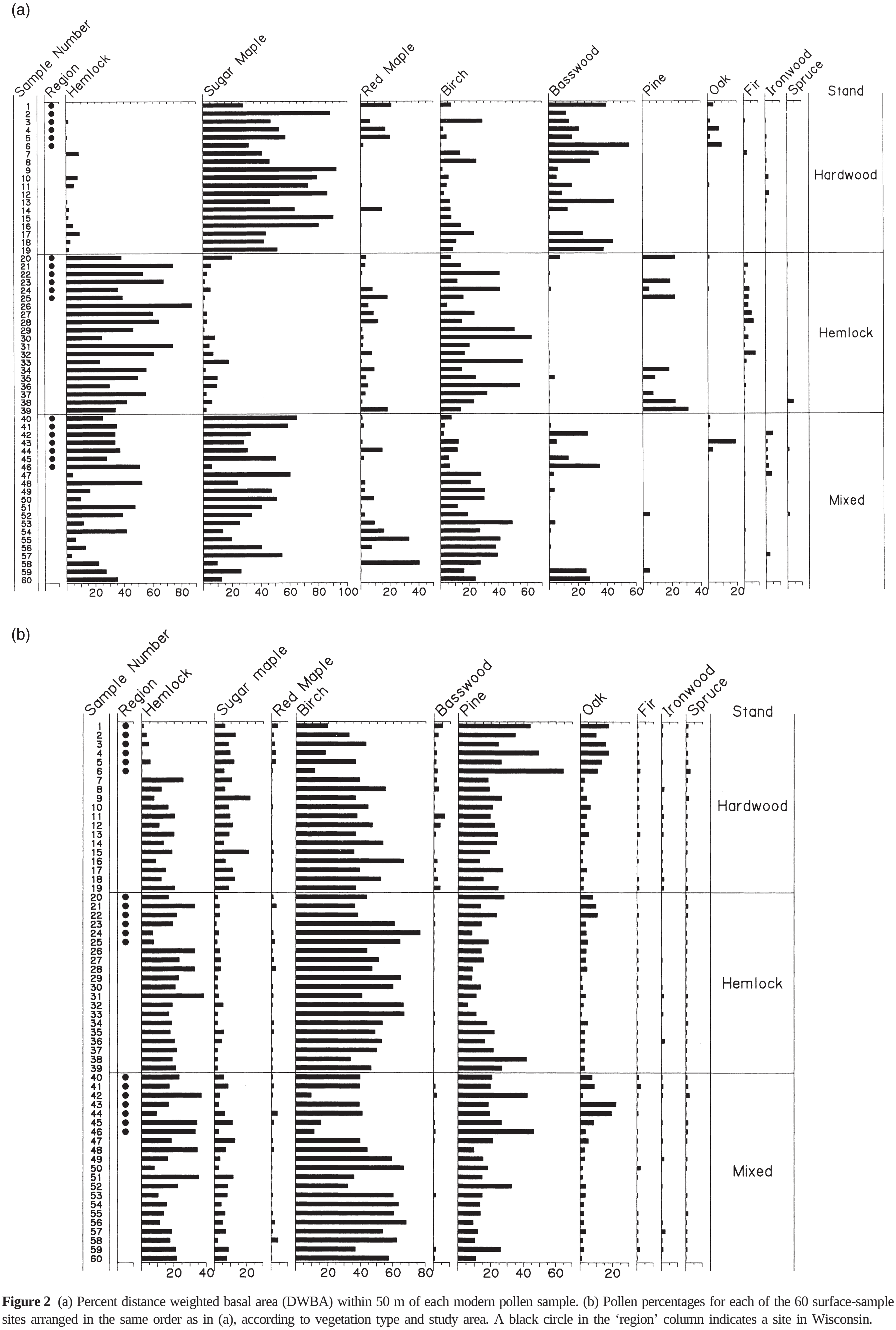

Figure 2 (a) Percent distance weighted basal area (DWBA) within 50 m of each modern pollen sample. (b) Pollen percentages for each of the 60 surface-sample sites arranged in the same order as in (a), according to vegetation type and study area. A black circle in the 'region' column indicates a site in Wisconsin.

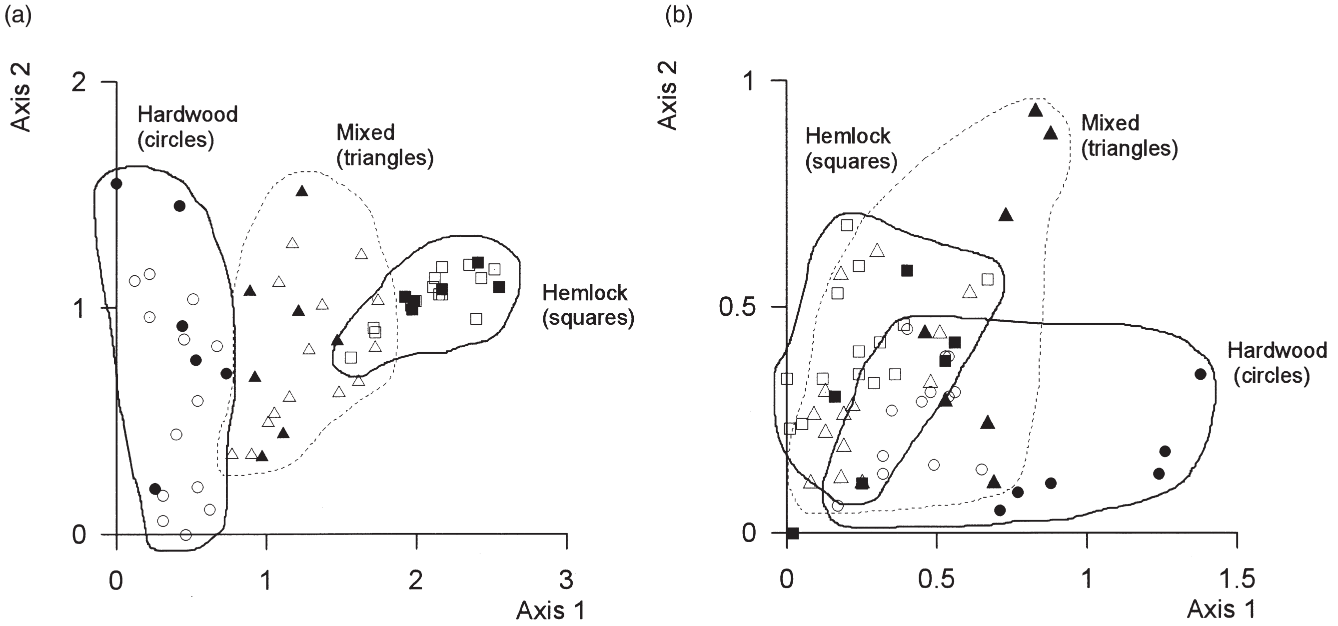

Figure 3 DCA ordination of all 60 surface-sample sites using either (a) percent distance-weighted basal area for trees surrounding each surface sample or (b) percent pollen for each of the 10 tree taxa. Shapes represent sites from each of the stand types identified by vegetation classification (Figure 2). Closed symbols denote sites in the Wisconsin study area; open symbols denote sites from Michigan.

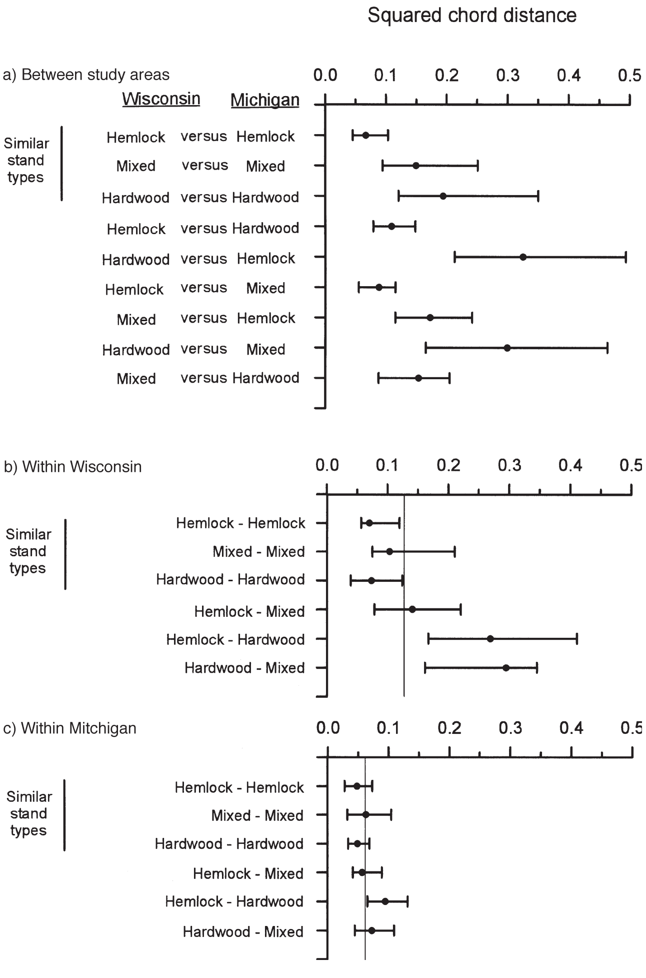

Figure 4 Summary of squared chord distances (SCD, index of dissimilarity) of pollen assemblages between all site pairs. The median (points) and quartile (bars) SCDs are given for all stand comparisons. Summaries are provided for pollen assemblages (a) between stand types in Wisconsin and Michigan; (b) within and between stand types in Wisconsin only; and (c) within and between stand types in Michigan only. Possible SCD cutoff values to identify similar stand types from dissimilar ones are indicated by a line for within-region comparisons.

regional vegetation composition suggests that the effects of variation in pollen productivity is a secondary factor.

Furthermore, not all stand types are influenced by regional vegetation to the same degree. Pollen assemblages from hardwood stands, in particular, differ strikingly between the two study areas, while pollen assemblages from hemlock stands do not (Figures 3b and 4). The dominant trees of hardwood stands, sugar maple and basswood (Figure 2a) are less well represented by pollen than are the dominant trees of hemlock stands, hemlock and yellow birch (Webb *et al.*, 1981; Jackson and Wong, 1994; Calcote, 1995; Jackson and Kearsley, 1998). For this reason, inputs of well-dispersed pollen types from regional vegetation, such as pine and oak, comprise a larger proportion of total pollen in hardwood-stand assemblages than in hemlock-stand assemblages. Higher effective pollen representation of hemlock also explains the high abundance of hemlock pollen at all Michigan sites, including stands where hemlock trees are not present locally. In Wisconsin, hemlock is not a large component of the regional forest, and its pollen is abundant only in samples from sites where hemlock trees occur locally (hemlock and mixed stands; Figure 2b).

Differences in pollen assemblages between the two study areas arise because a minimum of 50–60% of all pollen falling in forest hollows in hemlock-hardwood forest originates from beyond 50–100 m (Sugita, 1994; Calcote, 1995; Jackson and Kearsley, 1998). Given the high proportion of non-local pollen, it is not surprising that differences in regional vegetation cause significant differences among pollen assemblages, even where local vegetation composition is identical. Regional differences in the contribution of non-local pollen can significantly affect estimates of species-specific pollen representation factors (Prentice, 1985; Schwartz, 1989; Sugita, 1994; Jackson and Wong, 1994; Calcote, 1995; Jackson and Kearsley, 1998), and our results demonstrate that the effect of regional pollen inputs can significantly influence forest-stand interpretation using a modern analogue approach.

Local vegetation can be identified successfully within regions

Within each of the study areas, surface pollen assemblages can be used to identify stand types correctly. This point is demonstrated most clearly when pollen assemblages are compared with others from the same study area using squared chord distances

(Figure 4). In Wisconsin, for example, all pairs of pollen assemblages from either hemlock- or hardwood-dominated stands typically have SCD lower than 0.13 when compared to pollen assemblages from stands that are classified as the same type (Figure 4b). Pollen assemblages from dissimilar stand types have higher SCD values. The Michigan data show a similar pattern with a lower SCD threshold (0.06) for stands of the same type (Figure 4c). In contrast, there is no single SCD value that can be specified to separate similar stand types from dissimilar ones when pollen assemblages from both study areas are grouped together (Figure 4a). This supports the view that variation in pollen assemblages within each study area or region represents local differences in forest composition if the composition of non-local (regional) pollen is similar for all of the sites in the group.

This result indicates that once the appropriate scale of a ‘region’ is identified from which to collect surface samples, it is possible to distinguish finer-scale vegetation patterns. Note that the types of forests considered here represent only a portion of the variation in forest composition on the landscape, and that the stands largely contain the same species occurring in different abundances. Our ability to differentiate these slight variations in stand composition using pollen assemblages is remarkable. More disparate upland stand types in this region, such as oak- or pine-dominated stands, can also be differentiated using surface pollen assemblages (Calcote, 1998; Parshall, 1998).

Implications for employing modern analogues with small basins

There are several recommendations that follow from this study on the use of modern analogues to reconstruct local vegetation changes from small sedimentary basins. One is on the compilation of the surface sample data base itself. The data base should include as much of the local variation in vegetation composition as possible, as well as data on the regional context of the sites. An ideal data base would include all possible combinations of local and regional vegetation, but this is impossible given the large number of necessary combinations and the limited variation that exists on the modern landscape. We suggest collecting clusters of surface samples representing a variety of stand types in specific regional contexts. This would provide groups of sites within different regional vegetation, allowing the use of portions of the data base in different parts of a sediment core, once the inferred regional context of that time period is known.

The cluster of surface sample sites in Michigan were collected within a 100 km^2 area, where the regional vegetation is composed primarily of hemlock and northern hardwood trees. In Wisconsin, surface samples were collected over an area of approximately 800 km^2 and encompass a greater variation in regional vegetation among sites. The different sampling scales partly explain why there is less variation within the pollen assemblages from Michigan than from Wisconsin (Figure 4). A more appropriate sampling scheme may lie somewhere in between (i.e., between 100 and 800 km^2), which would decrease the variation in regional pollen inputs among Wisconsin samples and capture a greater variety of pollen assemblages in the Michigan samples.

If regional vegetation composition, and therefore regional pollen inputs, has not changed significantly in the past, then a modern analogue approach can successfully be employed to reconstruct stand-scale forest changes. However, we know that changes in regional forest composition have occurred in the western Great Lakes region, even over the past few thousand years (Webb *et al*., 1983; Davis *et al*., 1986). More recently, vegetation composition has been greatly altered by human land use, especially over the past few hundred years (Behre, 1988; McAndrews, 1988; Houghton, 1994). Characterizing the pollen-vegetation relationship in the absence of widespread human impact would help in this instance. For example, Jacobson and Grimm (1986) used fossil pollen assemblages deposited before European settlement in Minnesota, USA, and presettlement forest composition to reconstruct forest composition for the past 10 000 years with fairly good results. Unfortunately, this approach cannot work for forest hollows because presettlement forest composition is either unavailable or sampled at such a coarse spatial scale that stand reconstructions are not possible.

The challenge is to identify the regional pollen ‘signal’ of the past and separate it from local pollen inputs to reconstruct local vegetation change of the past. Only a few rough methods to do this have been attempted. One approach compares pollen assemblages from many small sites of similar size within the same region (e.g., Davis *et al*., 1998). Assuming that past changes in regional pollen were similar among sites, any differences in fossil pollen assemblages among sites are a result of local vegetation differences. Another approach assumes that regional pollen inputs can be identified from a large sedimentary basin and that this component can be removed from pollen assemblages in a small basin nearby (Heide, 1984; Jacobson, 1979; Foster and Zebryk, 1993). This method, however, does not account for the interdependence of pollen percentage data (Fagerlind, 1952; Prentice and Webb, 1986).

Mechanistic quantitative models may be the best approach for distinguishing local and regional pollen sources. Theoretical models that take into account pollen representation for sediment basins differing in size have been developed (Prentice, 1985; Sugita, 1993; 1994) and can be used to apply correction factors derived from modern pollen-vegetation relationships. Although this is probably the ideal approach toward identifying quantitatively local and regional pollen components of pollen assemblages, the parameters required to develop correction factors (especially taxon-specific productivity and dispersal values) will need to be understood at a higher level of precision than at present (Sugita, 1994; Jackson, 1994; Sugita *et al*., 1997; 1999; Jackson and Lyford, 1999).

Conclusions

The results of this study support previous work demonstrating that pollen assemblages from forest-hollow sediments or closed-canopy sites can be used to identify stand-scale forest composition (Lynch, 1996; Calcote, 1998; Jackson and Kearsley, 1998). Pollen assemblages within either study area could be used to differentiate between hemlock and hardwood stand types. However, the surrounding regional vegetation significantly influenced the correspondence between pollen and local vegetation. Stand types could not be distinguished reliably using pollen assemblages when sites from the two study areas were grouped together because differing regional forest composition contributed different amounts of pollen to the sites. A further complication is the magnitude of this effect among stand types. Hemlock-dominated stands had relatively similar pollen assemblages between the two study areas, but pollen assemblages from sugar-maple stands differed greatly between study areas. These results demonstrate that a better understanding is needed of the relationship between pollen and vegetation, not only in relation to basin size and taxon-specific pollen dispersal characteristics but also in relation to the arrangement of vegetation on the landscape.

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