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Detecting differences in vegetation among paired sites using pollen records

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Abstract: The 'Qualitative Assessment of Difference' method (QAD) is proposed to objectively detect differences in the relative abundance of vegetation between paired sites using pollen percentages. This method corrects for intertaxonomic differences in pollen productivity and neutralizes influences of background pollen on pollen representation of vegetation, using an inverse form of the Extended *R*-value model. We test the method using modern pollen–vegetation data from small hollows in northern Michigan (6 taxa; 45 sites) and from northwestern Wisconsin (7 taxa; 43 sites) in the USA. Compared with pollen percentages, the one-tailed Fisher Exact test shows that the QAD method significantly improves the accuracy of the results for all taxa. The rank order of sites based on QAD is significantly correlated to the rank order of sites based on a survey of vegetation composition surrounding the hollow for each taxon (Spearman's rank-order correlation coefficients; $p < 0.001$). We apply QAD to 9000-yr pollen records from two forest hollows *c.* 6 km apart in northern Michigan. Among seven taxa compared, *Pinus*, a taxon with well-dispersed pollen and a high pollen producer, often displays discrepancies in the direction of difference between QAD and the percentage-based method, demonstrating that pollen percentages alone do not always reflect differences in vegetation composition accurately. When several similarly sized sites are available in the same vegetation zone, QAD can objectively rank-order sites for individual taxa in relation to, for example, differences in soils, topography, patterns of species invasion, natural and anthropogenic disturbances, and other factors.

Key words: Qualitative Assessment of Difference (QAD), pollen percentages, palynology, ERV models, background pollen, vegetation reconstruction, Holocene.

Introduction

Palynologists and palaeoecologists often use pollen percentages as a measure of changes in vegetation, comparing pollen percentages at different time horizons or from different sites. Pollen percentages, however, are not linearly related to vegetation composition; thus differences often fail to accurately reflect changes in vegetation (Fagerlind, 1952; Prentice and Webb, 1986) In addition, pollen transport from distant vegetation can often be substantial and confounding. Several studies have shown that differences in background pollen (ie, pollen coming from beyond the area of interest for vegetation reconstruction) influence relationships between vegetation abundance and pollen percentages (Broström *et al.*, 1998; Sugita *et al.*, 1999; Parshall and Calcote, 2001). Despite recent advances in theoretical and empirical understanding of background pollen (Parsons and Prentice, 1981; Prentice, 1985; Sugita, 1994; Jackson and Lyford, 1999), it is still hard to assess the effects of background pollen on vegetation reconstruction.

Previous studies have attempted to evaluate the direction and amount of vegetation difference between sites by subtracting pollen percentages at one site from those at equivalent stratigraphic levels at another site. Several studies determined the differences in pollen percentages between small sites and large sites, interpreting the results as a measure of differences between local and regional composition of vegetation (Jacobson, 1979; Bradshaw, 1981b; Heide, 1984; Foster and Zebryk, 1993). Pollen percentages and pollen accumulation rates in similarly sized lakes located 150 km apart and on different types of bedrock were compared to assess differences in species abundances related to soils (Ford, 1990). The results from these studies need re-evaluation, however. Comparing pollen percentages from differently sized sites may not provide accurate

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estimates of differences in species composition between local and regional vegetation. Even when similarly sized sites are compared, the sites from different vegetation zones would have different background pollen, affecting the pollen percentages at each site in unknown ways (Broström *et al.*, 1998; Sugita *et al.*, 1999; Parshall and Calcote, 2001).

Although the relationship between pollen percentages and vegetation abundance is fundamentally non-linear, the Extended *R*-value (ERV) model (Parsons and Prentice, 1981; Sugita, 1994) corrects for the non-linear relationship and makes it possible to estimate critical parameters of the relationship from empirical data; pollen productivity and background pollen. Once these parameters are obtained, the inverse forms of the ERV model can be applied for vegetation reconstruction (Prentice and Parsons, 1983). The ERV model is a major methodological advance in palynology, but it has rarely been applied to fossil pollen (Nielsen, 2003). One of the difficulties is that the model assumes pollen productivity and background pollen to be constant for all taxa through time. As a first approximation, constant pollen productivity is a reasonable assumption, at least in the late Holocene (Calcote, 1995; but also see Hicks, 2001). However, it is difficult to justify the assumption that background pollen remains constant through time, because major changes in regional vegetation affect the amount of background pollen (Sugita, 1994, 2007a,b).

We propose a new method, based on an inversion of the ERV model, to evaluate qualitatively differences in the relative abundance of a taxon between similarly sized sites using pollen percentages. This method, the Qualitative Assessment of Difference (QAD) method, effectively neutralizes the effects of changing background pollen and corrects for differences in pollen production among taxa. Although QAD cannot determine the magnitude of difference, it does improve interpretation of the direction of difference in plant abundance, an important step for objective interpretation of pollen percentage data. We describe the theoretical basis of the method, test the method using surface pollen–vegetation data sets from northern Michigan and northwestern Wisconsin, USA, apply it to fossil pollen records from small forest hollows in northern Michigan to demonstrate its relevance, and discuss assumptions and conditions for its application.

Why do we need a new method?

Let us consider hypothetical vegetation landscapes designed to illustrate the potential misinterpretation of plant abundance caused by pollen percentages. Four taxa (*Tsuga*, *Pinus*, *Betula* and *Acer*) that are common throughout northeastern North America are used to simulate pollen assemblages in small forest hollows (circular shape with radius 5 m) as the sedimentary basins for pollen deposition. Small hollows are surrounded by vegetation locally homogeneous within a 100-m radius from a point at the centre of each hollow (Figure 1A). Local and regional components of vegetation landscapes are considered separately. Theoretical and empirical studies for closed forests in northern Michigan (Sugita, 1994, 1998; Calcote, 1995) have shown that differences in pollen assemblages between hollows represent the differences in vegetation composition within a 75–100 m radius and that background pollen coming from beyond that radius is consistent among hollow sites. The local stand surrounding Site A is dominated by *Tsuga* and *Betula* with percentage cover of *Tsuga* (70%), *Betula* (25%), *Pinus* (5%) and *Acer* (0%). Site B is surrounded by a stand dominated by *Tsuga* and *Acer* in which *Pinus* occupies 0%, *Tsuga* 50%, *Acer* 45% and *Betula* 5%.

We next assign two regional landscapes defined by vegetation within a 100-km radius of each site to simulate two different background pollen conditions. Region 1 is dominated by *Pinus* (80%) overall percentage cover, *Tsuga* (5%), *Betula* (5%) and *Acer* (10%). Region 2 is dominated by *Tsuga* (40%) and *Acer* (50%), with lower abundance of *Pinus* (5%) and *Betula* (5%). Regional vegetation is assumed to be homogeneous.

For simulating pollen assemblages, we use Sugita's model of pollen dispersal and deposition (Sugita, 1993, 1994). Wind speed is 3 m/s, and the radius of the hollows is 5 m. Fall speed of pollen in air for these four taxa is listed in Table 1. Relative pollen productivity is 6.0, 3.0, 10.0 and 1.0 for *Pinus*, *Tsuga*, *Betula* and *Acer*, respectively. The assumptions and structure of the model are described in Sugita (1993, 1994, 1998). The sensitivity of the model to parameter selection is discussed in recent papers (Bunting *et al.*, 2004; Nielsen, 2004; Nielsen and Sugita, 2005).

In Region 1, *Pinus* is dominant in the simulated pollen assemblage (Figure 1B). *Pinus* is a high pollen producer and its pollen is well transported by wind (Prentice, 1985; Sugita, 1993). *Pinus* is also the most dominant in Region 1. As a result, *Pinus* pollen percentage becomes higher than the others. In Region 2, pollen percentages of *Betula* and *Tsuga* are high. *Tsuga* and *Acer* are co-dominant in Region 2; however, pollen productivity of these two taxa is low, and their pollen grains are not well dispersed (Sugita, 1993, 1994). On the other hand, *Betula* is a high pollen producer and its pollen is well transported by wind. Thus, *Betula* is overrepresented in pollen assemblages. These results demonstrate that differences in regional vegetation and species composition in both local and regional vegetation simultaneously affect the pollen assemblages. If we did not know the regional vegetation, we would conclude that *Pinus* is more locally abundant at sites in Region 1 than in Region 2, and that *Tsuga* and *Betula* are more abundant locally in Region 2 than in Region 1.

Let us next discuss pollen assemblages from sites located within the same region. Pollen data from small forest hollows are supposed to represent local vegetation (Andersen, 1970). Differences in local plant-abundance between Sites A and B, however, are difficult to evaluate using pollen percentage data (Figure 1B). In Region 1, the pollen percentage of *Pinus* at Site A is lower than at Site B, even though the abundance of *Pinus* within 100 m is 5% at Site A and 0% at Site B. High abundance of *Pinus* in the region and differences in local abundance of *Betula* and *Acer* between Sites A and B, in particular, are affecting the pollen assemblages. In Region 2, the pollen percentage of *Tsuga* is lower at Site A than that at Site B, although its plant abundance is 70% at Site A and 50% at Site B. In addition to the influence of the regional vegetation, differences in pollen dispersal characteristics and pollen productivity among taxa influence the differences in pollen assemblages between sites. Thus, the sign of the difference between local plant abundances do not always agree with that apparent for pollen percentages.

This hypothetical example demonstrates complex effects of regional and local vegetation composition on the relationships between pollen and vegetation (Broström *et al.*, 1998; Sugita *et al.*, 1999). Even when background pollen is constant between sites, differences in plant abundance between sites are hard to evaluate both qualitatively and quantitatively using pollen percentages (Fagerlind, 1952; Davis, 1963; Prentice and Webb, 1986).

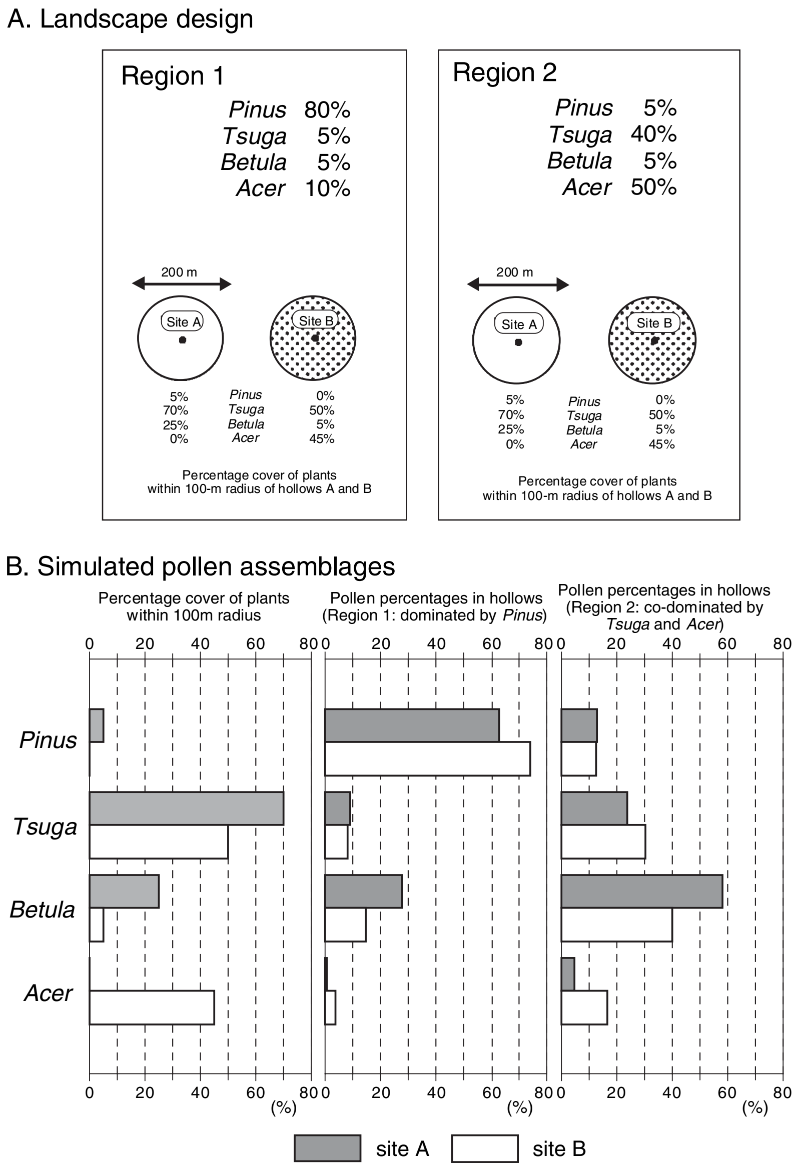

Figure 1 (A) Hypothetical landscapes and vegetation composition used for simulating pollen assemblages at small hollows (5 m in radius; Sites A and B) in two regions (Regions 1 and 2). Species composition in local vegetation (within 100 m from hollows) and in regional vegetation (out to 100 km) is considered separately, although vegetation is homogeneous in both spatial scales. (B) Comparison of vegetation composition within 100 m around Sites A and B to the pollen assemblages at these sites when the hollows are located in either Region 1 or Region 2

Model development

The QAD method uses the inverse form of the Extended *R*-value (ERV) model (Prentice and Parsons, 1983) (see Appendix A). The ERV model correlates pollen percentages to relative vegetation abundance (submodels 1 and 2) or to vegetation abundance in absolute units (submodel 3) (Parsons and Prentice, 1981; Sugita, 1994). The fundamental equation for the Extended *R*-value model assumes a linear relationship between pollen loading (pollen input [grains] per unit area on the surface of a sedimentary basin per unit time) and plant abundance (in absolute units; eg, m^2/ha) for each taxon. In theory, when plant abundance is properly distance-weighted, the slope of the linear relationship represents pollen productivity for each taxon. One of the methodological advantages of the Extended *R*-value model is that it enables us to estimate pollen productivity and background pollen using the non-linear relationships between pollen percentages and vegetation abundance. Detailed description of the Extended *R*-value (ERV) models and assumptions are given in Parsons and Prentice (1981) Prentice and Webb (1986) and Jackson *et al.* (1995).

The method proposed in this paper, QAD (Qualitative Assessment of Difference), effectively neutralizes the background pollen signal and makes it possible to compare plant abundance between a pair of sites in the same region. Even though background pollen may change through time we assume that it remains the same between the two adjacent sites being compared. We express the estimated plant abundance of a given species *i* at site *k*, using the inverse form of the ERV submodel 2 (see Appendix A for all the assumptions required for the submodel and for reasons why this submodel is used in QAD):

$$\hat{v}_{i,k} = \frac{n_{i,k}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,k}/\hat{\alpha}_j}\left(1+\sum_{j=1}^{l}\hat{z}_j/\hat{\alpha}_j\right) - \hat{z}_i/\hat{\alpha}_i \qquad (1)$$

Table 1 Common and taxonomic names of plant taxa used in this paper, and fall speed of pollen of these taxa. These fall-speed values are used to simulate pollen dispersal and deposition in the landscapes in Figure 1, and are also used to calculate distance-weighted plant abundance around forest hollows in northern Michigan and northwestern Wisconsin (see Section 'Data sets and methods for model validation')

Common name	Scientific name	Fall speed of pollen (m/s)
Hemlock	*Tsuga canadensis*	0.071[a]
Sugar maple	*Acer saccharum*	0.056[b]
Birch	*Betula* spp.	0.024[a]
American Basswood	*Tilia americana*	0.032[c]
Red maple	*Acer rubrum*	0.056[b]
Pine	*Pinus* spp.	0.031[a]
Red oak	*Quercus rubra*	0.035[a]

[a]From Eisenhut (1961);
[b]from Sugita (1998);
[c]from Sugita *et al.* (1999).

where $\hat{v}_{i,k}$ is estimate of vegetation proportion of species i at site k. $\hat{\alpha}_i$ is species-specific pollen representation factor for species i estimated for the region. This estimate is equivalent to the pollen productivity estimate of the species, when the vegetation data are properly distance-weighted (Sugita, 1994); $\hat{z}_i$ is species-specific background for species i in the region. The ERV submodel 2 assumes that this is the ratio of background pollen loading of species i (in absolute units) to the total abundance of vegetation within the area of interest surrounding sites. All the ERV submodels (Appendix A) assume that background pollen loading is constant among sites. Therefore the total abundance of vegetation within this area must be the same at all sites to satisfy the assumption that $\hat{z}_i$ is species-specific; $n_{i,k}$ is pollen counts of species i at site k; and l is total number of plant taxa in pollen assemblage.

Then, the difference in abundance of species i between two sites (site k and site m) can be expressed as:

$$\hat{v}_{i,k} - \hat{v}_{i,m} = \left\{ \frac{n_{i,k}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,k}/\hat{\alpha}_j} \left(1 + \sum_{j=1}^{l} \hat{z}_j/\hat{\alpha}_j\right) - \hat{z}_i/\hat{\alpha}_i \right\}$$

$$- \left\{ \frac{n_{i,m}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,m}/\hat{\alpha}_j} \left(1 + \sum_{j=1}^{l} \hat{z}_j/\hat{\alpha}_j\right) - \hat{z}_i/\hat{\alpha}_i \right\}$$

$$= \left(\frac{n_{i,k}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,k}/\hat{\alpha}_j} - \frac{n_{i,m}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,m}/\hat{\alpha}_j} \right) \left(1 + \sum_{j=1}^{l} \hat{z}_j/\hat{\alpha}_j\right) \qquad (2)$$

In equation (2),

$$\left(1 + \sum_{j=1}^{l} \hat{z}_j/\hat{\alpha}_j\right) > 0,$$

because the species-specific background pollen and pollen representation factor are always zero or positive (Appendix A). Therefore, the other term in the right-hand side of equation (2)

$$\frac{n_{i,k}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,k}/\hat{\alpha}_j} - \frac{n_{i,m}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,m}/\hat{\alpha}_j},$$

can provide the *direction of difference* (although not the magnitude of difference) in the abundance of species i between site k and site m. Let us define $\boldsymbol{D_{QAD}}$(species $\boldsymbol{i}$| site $\boldsymbol{k}$ – site $\boldsymbol{m}$) as the sign of the direction of difference, $\hat{v}_{i,k} - \hat{v}_{i,m}$:

$$\boldsymbol{D_{QAD}}(\text{species } \boldsymbol{i} | \text{ site } \boldsymbol{k} - \text{site } \boldsymbol{m})$$

$$= +1, \text{ when } \frac{n_{i,k}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,k}/\hat{\alpha}_j} - \frac{n_{i,m}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,m}/\hat{\alpha}_j} > 0$$

$$= 0, \text{ when } \frac{n_{i,k}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,k}/\hat{\alpha}_j} - \frac{n_{i,m}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,m}/\hat{\alpha}_j} = 0$$

$$= -1, \text{ when } \frac{n_{i,k}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,k}/\hat{\alpha}_j} - \frac{n_{i,m}/\hat{\alpha}_i}{\sum_{j=1}^{l} n_{j,m}/\hat{\alpha}_j} < 0$$

When fossil pollen counts from a pair of similarly sized sites within the same vegetation region, and estimates of pollen productivity are available, we can obtain $\boldsymbol{D_{QAD}}$(species $\boldsymbol{i}$| site $\boldsymbol{k}$ – site $\boldsymbol{m}$). When variances and covariances for the $\hat{\alpha}$-estimates of individual taxa used in data analysis are available, we can incorporate the error estimates of $\hat{\alpha}$'s and pollen counts into the calculation of $\boldsymbol{D_{QAD}}$. See Appendix B.

Examples from the hypothetical landscapes in Figure 1

We can calculate $\boldsymbol{D_{QAD}}$ using the hypothetical examples in Figure 1, and compare with the direction of difference shown by the pollen percentages. Total pollen counts at both Site A and Site B are set to 1000, and the pollen count for each species is calculated using its pollen percentage simulated for each region (Figure 1B). Pollen productivity is fixed at 6.0, 3.0, 10.0 and 1.0 for *Pinus*, *Tsuga*, *Betula* and *Acer*, respectively (Table 2).

Note that the direction of difference in pollen percentage between Sites A and B is not always consistent with the direction of difference in vegetation composition in both Regions 1 and 2 (compare columns 6 and 13 in Table 2).

$\boldsymbol{D_{QAD}}$ reconstructs the correct direction of difference in plant abundance between Sites A and B for all taxa in both Regions 1 and 2 (columns 12 and 13 in Table 2). In both tables, QAD Step 1 (columns 8 and 9) shows pollen counts of individual taxa divided by their pollen productivity (column 7). In QAD Step 2 (columns 10 and 11), each number obtained in QAD Step 1 is divided by the sum of pollen counts divided by their respective pollen productivity at each site (ie, totals at bottom of columns 8 and 9). $\boldsymbol{D_{QAD}}$ (column 12) for each taxon is then assigned as +1 or −1.

QAD provides an objective way to evaluate differences in vegetation abundance between similarly sized sites in the same vegetation region, using pollen percentages. Although these examples are simple and model-based, the results show the potential of the QAD method for real applications.

Table 2 The direction of difference in plant abundance between Sites A and B in Regions 1 and 2, estimated by subtracting pollen percentages and by the QAD method. The results are compared via the direction of difference in plant abundance data used for the simulations for Figures 1 and 2

Col.1	Col.2	Col.3	Col.4	Col.5	Col.6	Col.7	Col.8	Col.9	Col.10	Col.11	Col.12	Col.13
	Pollen counts		Pollen percentages		Pollen percentage-based direction of difference (Site A – Site B)	Pollen productivity	QAD step 1		QAD step 2		QAD-based direction of difference (D_{QAD}) (Site A – Site B)	Direction of difference in plant abundance (Site A – Site B)
	Site A	Site B	Site A	Site B			Site A	Site B	Site A	Site B		
Region 1												
Pinus	627	739	62.7	73.9	−1	6	627/6	739/6	0.625	0.624	+1	+1
Tsuga	90	80	9.0	8.0	+1	3	90/3	80/3	0.179	0.068	+1	+1
Betula	278	144	27.8	14.4	+1	10	278/10	144/10	0.166	0.122	+1	+1
Acer	5	37	0.5	3.7	−1	1	5/1	37/1	0.030	0.186	−1	−1
Sum	1000	1000	100.0	100.0			167.3	197.5	1.000	1.000		
Region 2												
Pinus	129	128	12.9	12.8	+1	6	129/6	128/6	0.103	0.065	+1	+1
Tsuga	239	305	23.9	30.5	−1	3	239/3	305/3	0.382	0.308	+1	+1
Betula	583	400	58.3	40.0	+1	10	583/10	400/10	0.280	0.121	+1	+1
Acer	49	167	4.9	16.7	−1	1	49/1	167/1	0.235	0.506	−1	−1
Sum	1000	1000	100.0	100.0			208.5	330.0	1.000	1.000		

Assumptions necessary for the QAD method

The conditions and assumptions necessary for applying the QAD method for comparing fossil pollen samples between sites are summarized as follows:

(1) Fossil pollen samples are collected from similarly sized and nearby sites, thus we can assume that the background pollen signal, *z,* in equation (1) is a constant for each species, and that the area of local vegetation to be compared is consistent among sites. By definition, this area is the same as the relevant source area of pollen (RSAP; *sensu* Sugita, 1994). The same type of site is preferred (eg, lakes versus bogs).

(2) The inverse form of the ERV submodel 2 used in the QAD method assumes that the sum of vegetation abundance (in an absolute unit) of all taxa within the RSAP is constant among sites. We can relax this assumption a little without losing the accuracy of the method (Appendix A; S. Sugita, unpublished data, 2005). However, if the total abundance of vegetation within the RSAP between sites is different by 30% or more the results should be interpreted with caution.

(3) Chronological control of sediment cores is sufficiently reliable for comparison between sites. The QAD method requires that the samples to be compared are the same age, in order to assure that the same regional vegetation is present.

(4) Pollen productivity is assumed to be constant through time and between regions. This assumption needs to be carefully considered when plants grow at their range limits (Hicks, 2001) or in different soils and other environmental conditions (Brubaker, 1975).

Model validation and application

Data sets and methods for model validation

We use two data sets for surface pollen and vegetation from the upper Great Lakes region in the USA: one from the hemlock-hardwoods forest in northern Michigan (Calcote, 1995, 1998; Davis *et al.*, 1998) and the other from mixed pine-hardwood forest in northwestern Wisconsin (Parshall and Calcote, 2001). All the pollen samples were collected from the surface of small forest hollows or from small depressions topographically similar to forest hollows. Pollen grains were extracted from the samples following a standard method (Faegri and Iversen, 1989) and at least 350 grains counted under compound microscopes. The surrounding vegetation was surveyed out to 50 m at 45 sites in northern Michigan and out to 100 m at 43 sites in northwestern Wisconsin. Basal area of individual species was estimated in concentric rings of 10 m width, using the variable sampling-plot method and the tree-census method together or separately. Calcote (1995, 1998) and Parshall and Calcote (2001) provide detailed descriptions of the field and laboratory methods.

We use the six pollen types most common in northern Michigan (*Tsuga*, *Acer saccharum*, *A. rubrum*, *Betula*, *Tilia* and *Pinus*), and the seven pollen types most common in northwestern Wisconsin (*Tsuga*, *Acer saccharum*, *A. rubrum*, *Betula*, *Tilia*, *Pinus* and *Quercus*). Plant species corresponding to the pollen taxa are *Tsuga canadensis* (eastern hemlock), *Acer saccharum* (sugar maple), *Acer rubrum* (red maple), *Tilia americana* (American basswood) and *Quercus rubra* (red oak). *Betula* represents both *Betula allegheniensis* (yellow birch) and *B. papyrifera* (paper birch); in northern Michigan, *B. allegheniensis* is more abundant, whereas *B. papyrifera* is more common in northwestern Wisconsin. *Pinus* represents *Pinus strobus* (white pine), *P. resinosa* (red pine) and

P. banksiana (Jack pine); *P. strobus* is the most common in both regions (Calcote, 1995, 1998; Parshall and Calcote, 2001).

The ERV submodel 2 (Parsons and Prentice, 1981) was used to estimate pollen productivity ($\hat{\alpha}$'s in the model development section above) and its variance-covariance matrix using erv.v6.1, an Extended *R*-value model program written by Sugita (Sugita, 1994; Sugita *et al.*, 1999; Broström *et al.*, 2004, 2005; Nielsen and Sugita, 2005). Plant abundance was distance-weighted according to the Prentice model (Prentice, 1985, 1988) for each taxon (Calcote, 1995; Parshall and Calcote, 2001). Selection of parameter values for atmospheric conditions in Prentice's model could affect the distance-weighted vegetation abundance (Jackson and Kearsley, 1998; Jackson and Lyford, 1999). We use parameter values appropriate for neutral atmospheric condition with wind speed of 3 m/s as in Prentice (1985) and Sugita (1993, 1994). The taxon-specific fall speeds of pollen necessary for this distance-weighting calculation are listed in Table 1. Other parameter values used in the Prentice model are the same as in Prentice (1985) and Sugita (1993).

Methods of model validation using the modern pollen-vegetation data sets

We use three steps for model validation; (1) estimating pollen productivity of the constituent taxa, (2) calculating $\boldsymbol{D_{QAD}}$ for all pairs of sites in each surface-pollen data set, and (3) evaluating the significance of the results. Computer programs used in Steps (1)–(3) were written by Sugita.

(1) *Estimating pollen productivity.* We estimate pollen productivity, $\hat{\alpha}$, of each taxon using the 'leave-one-out' cross-validation strategy (Efron and Tibshirani, 1998). For example, when sites *i* and *j* are compared, we use all the pollen counts and vegetation data in a data set except those from sites *i* and *j*, estimate pollen productivities, and calculate $\boldsymbol{D_{QAD}}$ for all taxa between the sites. This strategy for validation avoids tautological problems of self-referred parameters using a training data set.

(2) *Evaluating the direction of difference in plant abundance between sites.* $\boldsymbol{D_{QAD}}$ for each taxon is calculated between all pairs of sites, using the pollen count data and the estimates of pollen productivity from Step (1). We then construct matrices of $\boldsymbol{D_{QAD}}$ for individual taxa that include all pairwise comparisons of sites. For example, when $\boldsymbol{D_{QAD}}(\text{species } \boldsymbol{i} | \text{ site } \boldsymbol{k} - \text{site } \boldsymbol{m}) = +1$, a cell at the *k*th row and *m*th column is +1 in the matrix for species *i* (ie, based on the QAD method, the estimated abundance of species *i* at site *k* is higher than that at site *m*.) To evaluate accuracy of the QAD method, matrices of the direction of difference in plant abundance between sites are also constructed in the same way, using the vegetation survey data for individual taxa. Total number of cells used for data analysis is 990 and 903, using the data set from northern Michigan and northwestern Wisconsin, respectively.

(3) *Testing the accuracy of the QAD method.* We evaluate the improvement that the QAD method makes over a method using the differences between pollen percentages alone. In addition to the $\boldsymbol{D_{QAD}}$ matrix, a matrix of the direction of difference in pollen percentage between sites is constructed for each taxon. Then, by comparing with the matrix constructed from the vegetation survey data, the probabilities of the number of cells correctly predicted by QAD (P_1) and by pollen percentage alone (P_2) are calculated for each taxon. The one-tailed Fisher Exact test (Sokal and Rohlf, 1981; Siegel and Castellan, 1988) is used to test the null hypothesis ($\mathbf{H_0}$: $P_1 = P_2$) and the alternative hypothesis ($\mathbf{H_1}$: $P_1 > P_2$). As the second method for evaluation, the correlations are calculated and tested (A) for between rank-orders of sites based on vegetation survey data and based on QAD, and (B) for between rank-orders of sites based on vegetation survey data and based on the differences between pollen percentages. Rank-orders of sites for individual taxa are independently compiled, using the signs of the direction of difference in vegetation suvery data, pollen percentages, and $\boldsymbol{D_{QAD}}$ among paired sites in both northern Michigan and northwestern Wisconsin. For each taxon, Spearman's rank-order correlation coefficient r_s is calculated for both (A) and (B), and the significance of this r_s value is tested (Siegel and Castellan, 1988; Press *et al.*, 1992).

Data sets and methods for the application of the QAD method to fossil pollen

We use fossil pollen data from two forest hollows in Sylvania Wilderness, northern Michigan: one from a hardwood stand (M1 in Davis *et al.*, 1998) and the other from a mixed hemlock-hardwood stand (Plot C in Davis *et al.*, 1994). These two forest hollows, *c.* 6 km apart, are similar in size. The relevant source area of pollen for hollows in this region is *c.* 1–3 ha (ie, within 75–100 m in radius), and consistent background pollen between sites for all the taxa can be assumed for all time periods (Sugita, 1994, 1998; Calcote, 1995). We use $\hat{\alpha}$ values and a variance-covariance matrix estimated from the modern training data set of surface pollen and vegetation used in the Model Validation session above.

Based on the age–depth curves established for the cores from these two sites (Davis *et al.*, 1994, 1998) and pollen data covering the last 9000 years, we calculate pollen percentages at 300-yr intervals by summing pollen counts from all samples in a 300-yr time window. We use seven taxa listed in Table 1. Total number of samples used is 146 for the mixed-stand site and 51 for the hardwood site. We compare the direction of difference in pollen percentages to the QAD-based direction of difference between the two sites.

Results

Testing the QAD method with the modern training sets

Both in northern Michigan and northwestern Wisconsin, the QAD method improves the accuracy of predicting the direction of difference in plant abundance over the method using pollen percentages alone (Table 3). For all the taxa except for *A. saccharum* in northern Michigan, the null hypothesis ($\mathbf{H_0}$) is rejected and the alternative hypothesis ($\mathbf{H_1}$) is accepted: the probability of the number of paired sites correctly estimated by QAD, P_1, is significantly higher than P_2, the probability using pollen percentages alone. Although pollen percentages provide reasonable predictions in general, the QAD method improves the accuracy of interpretation.

The accuracy of the results for *Pinus* is low using both methods in northern Michigan; $P_1 = 0.401$ and $P_2 = 0.337$ (Table 3). Out of 45 sites studied 33 did not include any *Pinus* trees within 50 m from forest hollows (Calcote, 1995), although *Pinus* pollen was counted in pollen samples from all sites. Thus, neither method is always effective for plant taxa at sites where pollen of these taxa comes from beyond the relevant source area of pollen.

Figure 2 shows rank-orders of sites based on (A) $\boldsymbol{D_{QAD}}$ and vegetation survey data, and (B) the differences in pollen percentages and vegetation survey data. Rank-orders of sites

Table 3 Fisher Exact Test to compare the accuracy of the QAD method over a method using pollen percentages alone to evaluate the direction of difference in vegetation abundance between sites

	Based on the QAD method			Based on pollen percentages alone			Probability (p) of the observed outcome or more extreme	Significance level
	Number of cells (A) correctly evaluated	Number of cells (B) incorrectly evaluated	P_1 (= A/(A+B))	Number of cells (C) correctly evaluated	Number of cells (D) incorrectly evaluated	P_2 (= C/(C+D))		
1. Northern Michigan								
Hemlock (*Tsuga canadensis*)	788	202	0.796	684	306	0.691	2.137×10^{-7}	***
Sugar Maple (*Acer saccharum*)	746	244	0.754	732	258	0.739	2.509×10^{-1}	*ns*
Birch (*Betula* spp.)	753	237	0.761	685	305	0.692	3.624×10^{-4}	***
American Basswood (*Tilia americana*)	654	336	0.661	616	374	0.622	4.146×10^{-2}	*
Red Maple (*Acer rubrum*)	699	291	0.706	647	343	0.681	6.997×10^{-3}	**
Pine (*Pinus* spp.)	397	593	0.401	334	656	0.337	1.936×10^{-3}	**
2. Northwestern Wisconcin								
Hemlock (*Tsuga canadensis*)	529	374	0.586	483	420	0.535	1.643×10^{-2}	*
Sugar Maple (*Acer saccharum*)	772	131	0.855	723	180	0.801	1.367×10^{-3}	**
Birch (*Betula* spp.)	685	218	0.759	636	267	0.704	5.389×10^{-3}	**
American Basswood (*Tilia americana*)	703	200	0.779	661	242	0.732	1.238×10^{-2}	*
Red Maple (*Acer rubrum*)	686	217	0.760	649	254	0.719	5.678×10^{-2}	*
Pine (*Pinus* spp.)	636	267	0.704	571	332	0.632	6.853×10^{-4}	**
Red Oak (*Quercus rubra*)	726	177	0.804	692	221	0.766	1.027×10^{-2}	*

Total number of pair-wise comparison of sites (ie, total cells) is 990 using the data from northern Michigan (Calcote, 1995) and 903 using the data from northwestern Wisconsin (Parshall and Calcote, 2003). For each taxon, P_1 is the probability of the number of cells correctly evaluated against the total number of cells using the QAD method, and P_2 is the probability using pollen percentage data alone. The null hypothesis ($\mathbf{H_0}$) is $P_1 = P_2$, and the alternative hypothesis ($\mathbf{H_1}$) is $P_1 > P_2$, thus the one-tailed Fisher Exact Test is used, based on the probability (p) of the observed outcome or more extreme. Significance level is expressed as *ns* when $p \geq 0.05$, * when $0.05 > p \geq 0.01$, ** when $0.01 > p \geq 0.001$, and *** when $p < 0.001$.

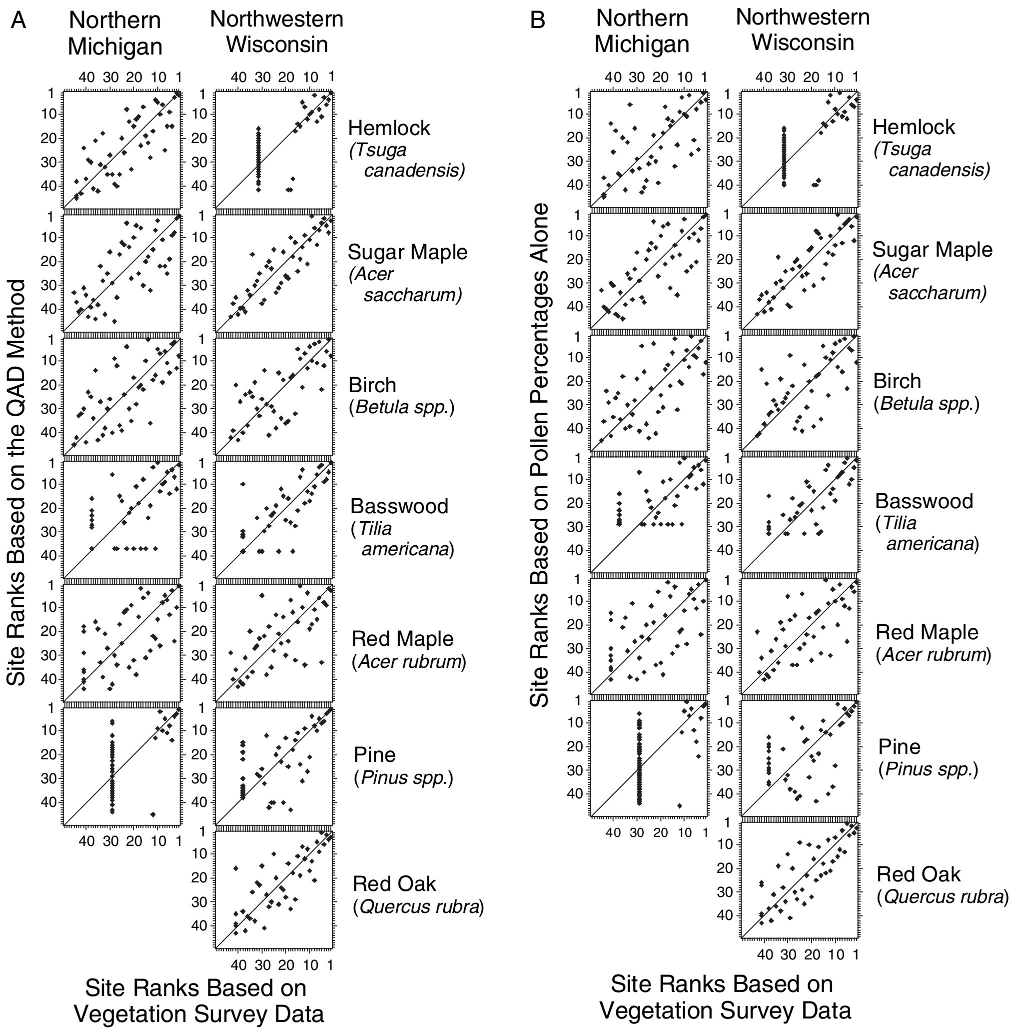

Figure 2 (A) Correlations between rank-orders of sites for major taxa, using QAD-based estimates and vegetation survey data between sites. QAD-based rank-order is estimated using $\boldsymbol{D_{QAD}}$ without considering standard errors. (B) Correlations between rank-orders of sites for major taxa, using differences in pollen percentages and differences in vegetation survey data between sites. Forty-five sites are used in northern Michigan (Calcote 1995) and 43 in northwestern Wisconsin (Parshall and Calcote, 2001). Spearman's rank-order correlation coefficient, r_s, and its two-sided significance level p for individual taxa are presented in Table 4. Many sites have the same rank-order (ie, ties) based on vegetation survey data for *Pinus* in northern Michigan and for *Tsuga canadensis* in northwestern Wisconsin, because these sites did not have any trees of these taxa

based on $\boldsymbol{D_{QAD}}$ and vegetation survey data are all significantly correlated for all taxa. Spearman's rank-order correlation coefficient (r_s) and its probability are listed for each taxon in Table 4. Rank-orders based on pollen percentages alone also have significant correlations with rank-orders based on vegetation survey data for all taxa in both regions (Table 4); however, r_s using the QAD method is equal to or higher than r_s using pollen percentages alone in general.

Site ranks based on vegetation survey data have many ties for *Pinus* in northern Michigan and *Tsuga* in northwestern Wisconsin (Figure 2), because 33 sites did not include *Pinus* trees in the former region and 24 sties did not have *Tsuga* trees in the latter region. Taking into account these ties (Siegel and Castellan, 1988), the correlations are still significant for these two taxa (Table 4).

Data points are more tightly clustered along the diagonal lines, thus having higher Spearman's rank-order correlation coefficients in northwestern Wisconsin than in northern Michigan for all taxa, except *Tsuga* (Figure 2; Table 4). Vegetation data used for the data analysis were collected out to 100 m from hollows in northwestern Wisconsin, and out to 50 m from hollows in northern Michigan. The estimated relevant source area of pollen is within 75–100 m for hollows in both regions (Sugita, 1994, 1998; Calcote, 1995), thus the increased areas sampled in northwestern Wisconsin probably helped improve the correlations.

Comparison of past plant abundance between the hardwood and mixed-stand sites

Figure 3 shows the differences in pollen percentages between a mixed-stand site and a hardwood site in northern Michigan over the last 9000 years. The direction of difference in *Pinus* abundance estimated using the QAD method is often different from the direction of difference in pollen percentages, marked by a solid diamond, even where the difference in pollen percentages is 15% or more. Pollen percentage data suggest that *Pinus* was generally more abundant at the hardwood hollow than at the mixed-stand hollow for most of the last 5500 years. The QAD method, however, provides an opposite conclusion.

Tsuga, *Quercus*, and *Betula* have only a few samples that show discrepancies between the methods in the direction of difference, and these often occur for samples with small difference in pollen percentage between sites. For the other taxa, the direction of difference is consistent. Overall, pollen types that are dispersed short distances, such as pollen of

Table 4 Spearman's rank-order correlation coefficient r_s and its two-sided significance level p between rank-orders of sites based on differences in vegetation and either (1) the QAD method or (2) pollen percentages

	Spearman's rank-order correlation coefficient r_s (two-sided significance level p)			
	Northern Michigan		Northwestern Wisconsin	
	(1) QAD	(2) Pollen percentages	(1) QAD	(2) Pollen percentages
Hemlock (*Tsuga canadensis*)	0.794 ($p = 7.73 \times 10^{-11}$)	0.623 ($p = 4.72 \times 10^{-6}$)	0.741 ($p = 1.33 \times 10^{-8}$)	0.725 ($p = 3.66 \times 10^{-8}$)
Sugar Maple (*Acer saccharum*)	0.719 ($p = 2.62 \times 10^{-8}$)	0.720 ($p = 2.36 \times 10^{-4}$)	0.886 ($p = 3.11 \times 10^{-15}$)	0.869 ($p = 4.53 \times 10^{-14}$)
Birch (*Betula* spp.)	0.703 ($p = 7.33 \times 10^{-8}$)	0.665 ($p = 6.20 \times 10^{-7}$)	0.726 ($p = 3.07 \times 10^{-8}$)	0.665 ($p = 1.13 \times 10^{-6}$)
American Basswood (*Tilia americana*)	0.661 ($p = 7.88 \times 10^{-7}$)	0.669 ($p = 4.96 \times 10^{-7}$)	0.798 ($p = 1.41 \times 10^{-10}$)	0.796 ($p = 1.78 \times 10^{-10}$)
Red Maple (*Acer rubrum*)	0.625 ($p = 4.37 \times 10^{-6}$)	0.571 ($p = 4.14 \times 10^{-5}$)	0.691 ($p = 2.93 \times 10^{-7}$)	0.682 ($p = 4.71 \times 10^{-7}$)
Pine (*Pinus* spp.)	0.621 ($p = 5.14 \times 10^{-6}$)	0.536 ($p = 1.47 \times 10^{-4}$)	0.643 ($p = 3.39 \times 10^{-6}$)	0.534 ($p = 2.29 \times 10^{-4}$)
Red Oak (*Quercus rubra*)	N/A	N/A	0.807 ($p = 6.15 \times 10^{-11}$)	0.812 ($p = 3.94 \times 10^{-11}$)

In northern Michigan, 45 hollows are used and vegetation composition was surveyed out to 50 m from the centre of the hollows (data from Calcote, 1995). In northwestern Wisconsin, 43 hollows are used and vegetation composition was surveyed out to 100 m (data from Parshall and Calcote, 2001).

Tsuga, *A. saccharum* and *A. rubrum*, or pollen types produced in small quantities, such as *Tilia*, tend to produce similar results between the estimates using the QAD method and using pollen percentages.

Pinus, *Betula*, and *Quercus* are all prolific producers of pollen, and pollen grains of these taxa are well-dispersed by wind. Thus, we would expect large quantities of background pollen of these taxa. The reason the QAD method frequently indicates discrepancies in the direction of between-site differences for *Pinus* (Figure 3), is its high background pollen in the region, surrounding local vegetation with low pollen production (*Acer* spp. and *Tilia*).

Discussion

For most taxa, the QAD method improves the accuracy of estimates of differences in plant abundance between sites over the differences in pollen percentages (Table 3). Although pollen percentages approximate results similar to the QAD-based estimates, they have theoretical and empirical limitations. Even when local vegetation composition is the same, pollen assemblages can differ because of different background pollen (Parshall and Calcote, 2001). Where we can assume a constant background pollen between sites as in Figure 1, the direction of difference in plant abundance does not necessarily correspond to the direction of difference in pollen percentages (Figure 1B). The QAD method overcomes these problems.

Modern analogue techniques (Davis, 1969; Prentice, 1980; Overpeck *et al.*, 1985) have been successfully applied to classify past vegetation types in the landscape to regional scales, but also have shown some potential limitations when this technique is applied to identify stand-scale vegetation types (Parshall and Calcote, 2001). When the target spatial-scale of vegetation for reconstruction is stand- to local-levels (ie, 10^4–10^6 m^2), the amount of background pollen cannot be ignored, and in times of regional climate and vegetation changes, the relationships between pollen assemblages and vegetation can vary in unknown ways. There have been advances in statistical procedures for optimal calibration of analogue-matching (Gavin *et al.*, 2003; Oswald *et al.*, 2003; Jackson and Williams, 2004; Wahl, 2004; Lytle and Wahl, 2005). However, the effects

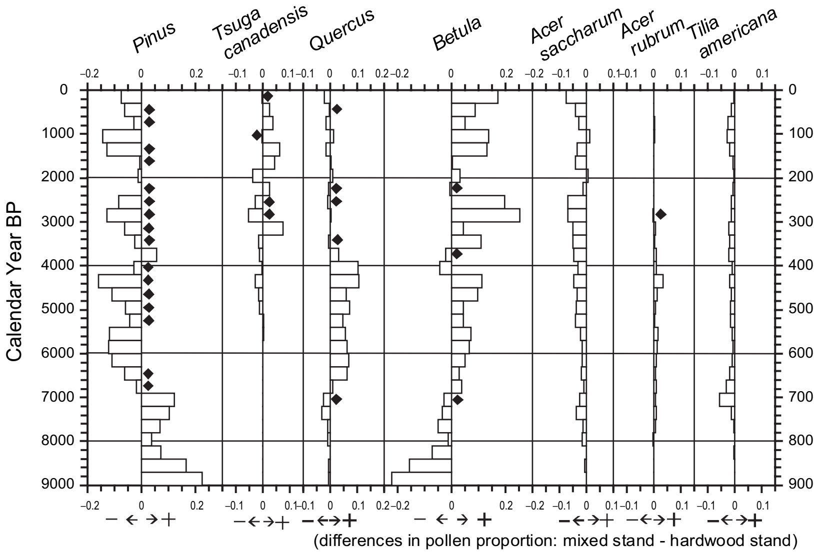

Figure 3 Differences in pollen percentage between a hardwood site and a mixed-stand site in Sylvania, northern Michigan. Negative values indicate that pollen percentages at the hardwood site are higher than those at the mixed-stand site, and positive values indicate the opposite. Solid diamond marks the taxon and age that, according to the QAD method, the direction of difference in plant abundance between the sites is different from that implied from the pollen percentages

of changes in background pollen on analogue techniques remain difficult to assess for the stand- to local-vegetation reconstruction.

Use of the QAD method

The QAD method indicates the direction of differences in plant abundance between sites but provides no quantitative information. As long as pollen percentages are the main measure of pollen records, however, it is important to be realistic about the potential and limits of vegetation reconstruction. Although differences in pollen percentages between sites could approximate the results from QAD for plant taxa that have relatively heavy pollen types or relatively low pollen productivity, interpretation for other taxa requires caution. Fagerlind's critical discussion on the meaning of changes in pollen percentage is still valid (Fagerlind, 1952).

Assuming all the conditions summarized in the Model development section are met, several interesting applications of the QAD method are possible. For example:

(1) Relationships between certain environmental conditions and plant abundance. When multiple sites are available, we can objectively rank sites for individual taxa and correlate rank-order with soil differences, topographic features and other environmental gradients.
(2) Changes in species composition following localized species invasion. Resident vegetation composition can be assessed between sites where a species invaded and where it did not.
(3) Differences in landscape openness between sites. Assuming pollen from grasses and other non-arboreal plants indicate unforested areas, we could rank sites for landscape openness, which could be compared to other indicators of human activity (eg, number of archeological sites).
(4) Effects of disturbance (eg, fire, windthrow, and pathogen/insect outbreak) on species composition. We could rank sites for pre- and post-disturbance vegetation when a regional disturbance event occurred (eg, the *Tsuga* decline in North America (Davis, 1981) and *Ulmus* decline in Europe (Iversen, 1973)) to identify taxa that may have increased in abundance because of competitive release.

Pollen productivity estimates

The QAD method requires reliable estimates of pollen productivity. In practice, good estimates of pollen productivity are very few. Several studies have shown that there is large year-to-year variation in pollen production (Andersen, 1970; Hicks, 2001). Effects of environmental conditions on pollen productivity have also been suspected (Hicks, 1994, 2001). Differences in soil, temperature, precipitation, day-length related to latitude and interactions with other taxa are also thought to affect pollen productivity.

Direct measurement of pollen productivity would be ideal but time-consuming and difficult (Pohl, 1937). Other semi-direct methods, such as flower/litter traps in mono-specific stands (Saito and Takeoka, 1985; Saito *et al.*, 1991) and pollen traps in different vegetation types (Hicks, 2001; and others), can estimate the year-to-year variation in pollen productivity, as well as the impacts of environmental conditions on pollen productivity. It takes several years to evaluate the means and variances that can be derived in this way, however.

In Europe and North America, palynologists and palaeoecologists have indirectly estimated pollen productivities using surface sediments and vegetation data surrounding the sample sites (Andersen, 1970; Bradshaw, 1981a; Webb *et al.*, 1981; Prentice *et al.*, 1987; Calcote, 1995). Assuming that surface sediments of 2–5 cm from forest hollows or moss polsters contain pollen from the previous few years to 10 years (Calcote, 1995; Broström *et al.*, 2004; Hicks *et al.*, 2004; Räsänen *et al.*, 2004), this approach integrates the effects of the year-to-year variation in pollen productivity, providing averaged estimates of pollen productivity over several years. Also, there are ways to reduce the biases caused by dispersal characteristics of different pollen types (Sugita *et al.*, 1997). The number of studies that estimate pollen productivity by reducing dispersal biases has been increasing in Europe and the USA (Calcote, 1995; Broström *et al.*, 2004; Soepboer *et al.*, 2007). Applicability of the QAD method will increase as more reliable estimates of pollen productivity become available.

Conclusions

The QAD method is qualitative but practical for more accurate evaluation of plant abundance between sites than using pollen percentages alone. Reliable estimates of pollen productivity, good chronological control of sediments and pollen counts from adjacent and similarly sized sites are all that is required to take advantage of this method. QAD fosters more objective examination of important ecological properties and processes at the scale of 10^4–10^6 m^2.

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Appendix A: inverse forms of the Extended *R*-value models to reconstruct vegetation composition

Extended *R*-value (ERV) models are used to estimate the pollen representation factor and background pollen for individual taxa from data sets of pollen counts and vegetation composition surrounding study sties. ERV models are constructed in such a way that the slope (ie, the pollen representation factor) and intercept of the linear relationship between pollen loading and vegetation can be estimated, even though a non-linearity exists when pollen percentage values are used (Parsons and Prentice, 1981; Prentice and Webb, 1986). In theory, the pollen representation factor is equivalent to pollen productivity if vegetation abundance is properly distance-weighted (Sugita, 1994). Submodels 1 and 2 require pollen counts and relative measure of vegetation abundance, and submodel 3 requires pollen counts and absolute measure of vegetation abundance (Sugita, 1994).

The inverse form of the ERV models is used to reconstruct vegetation composition with given pollen counts, and independently obtained estimates of pollen representation factor and background pollen (Parsons and Prentice, 1981; Prentice and Parsons, 1983). This method assumes that pollen representation factor and background pollen are species-specific and constant through time. Prentice and Parsons (1983) provide the inverse forms for submodels 1 and 2, and this Appendix provides the inverse form for submodel 3, proposed in Sugita (1994).

Submodel 1 (Prentice and Parsons, 1983)

$$\bar{v}_{i,k} = \frac{\left({}^{n_{i,k}}\big/_{n_{\cdot k}} - \hat{z}_i \right) \big/ \hat{\alpha}_i}{\sum_{j=1}^{l} \left\{ \left({}^{n_{j,k}}\big/_{n_{\cdot k}} - \hat{z}_j \right) \big/ \hat{\alpha}_j \right\}} \qquad \text{(A1)}$$

where $\bar{v}_{i,k}$ is estimated relative abundance of plant species i at site k; $n_{i,k}$ is pollen count of species i at site k; $n_{\cdot k}$ is total pollen counts at site k; l is total number of taxa used; $\hat{\alpha}_i$ is pollen representation factor for species i, estimated from a modern data set of surface pollen samples and vegetation abundance. When the vegetation abundance is properly distance-weighted, this represents estimated pollen productivity of species i. A species-specific parameter, assumed to be constant in the region of interest; and $\hat{z}_i$ is background estimated for species i, defined as a proportion of pollen loading of species i coming from beyond an area, in which vegetation abundance is surveyed, to total pollen loading of this species. A species-specific parameter, assumed to be constant in the region of interest.

Submodel 2 (Prentice and Parsons, 1983)

$$\bar{v}_{i,k} = \frac{{}^{n_{i,k}}\big/_{\hat{\alpha}_i}}{\sum_{j=1}^{l} \left({}^{n_{j,k}}\big/_{\alpha_j} \right)} \left\{ 1 + \sum_{j=1}^{l} \left({}^{\hat{z}_j}\big/_{\hat{\alpha}_j} \right) \right\} - {}^{\hat{z}_i}\big/_{\hat{\alpha}_i} \qquad \text{(A2)}$$

Definitions of the parameters in this equation are the same as in (1) Submodel 1, except $\hat{z}_i$. In the submodel 2, $\hat{z}_i$ is defined as a proportion of pollen loading of species i coming from beyond an area, in which vegetation abundance is surveyed, to the sum of plant abundance for all the species (species 1 to l) within the area of plant survey. $\hat{z}_i$ is a species-specific parameter, assumed to be constant in the region of interest.

Submodel 3, derived from Sugita (1994)

$$\bar{v}_{i,k} = \frac{{}^{n_{i,k}}\big/_{\hat{\alpha}_i}}{\sum_{j=1}^{l} \left({}^{n_{j,k}}\big/_{\alpha_j} \right)} \left\{ 1 + \frac{1}{\Psi_{\cdot k}} \sum_{j=1}^{l} \left({}^{\hat{\omega}_j}\big/_{\hat{\alpha}_j} \right) \right\} - \frac{1}{\Psi_{\cdot k}} \cdot \frac{\hat{\omega}_i}{\hat{\alpha}_i} \qquad \text{(A3)}$$

Definitions of $n_{i,k}$, $\bar{v}_{i,k}$ and $\hat{\alpha}_i$ in this equation are the same as those for submodels 1 and 2. In this form, however, $\hat{\omega}_i$ is background pollen loading (in an absolute unit) estimated for species i, coming from beyond an area of vegetation survey, and $\Psi_{\cdot k}$ is the sum of plant abundance for all the species (in an absolute unit) within the area surveyed around site k. Estimating $\hat{\alpha}_i$ and $\hat{\omega}_i$ requires vegetation abundance data in an absolute unit (Sugita, 1994), not in vegetation proportion as for submodels 1 and 2 (Parsons *et al.*, 1983/1984). $\hat{\alpha}_i$ and $\hat{\omega}_i$ are assumed to be species-specific in a region of interest, and $\Psi_{\cdot k}$ is site-dependent.

Selection of submodel 2 for the QAD method

Among the inverse forms of the ERV submodels, submodel 2 is best suited for evaluation of the direction of difference between sites. The inverse form of submodel 3 is similar to that of submodel 2, except for the inclusion of a term that expresses the site-specific, total abundance of plants (equation (A3)). Submodel 2 assumes that this plant-abundance term is constant among sites, not site-specific (Parsons and Prentice, 1981). Simulation suggest that violation of this assumption would have little effect on the accuracy of the QAD method (S. Sugita, unpublished data). If the total plant abundances are approximately the same among sites, a QAD method based on submodel 3 is identical to the QAD method using submodel 2 proposed in this paper.

The inverse form of submodel 1 is structurally different from that of submodel 2 (Appendix A, equation (A1)), and does not make it possible to evaluate the direction of difference in plant abundance in a consistent way. Parsons and Prentice (1981) and Parsons *et al.* (1983/1984) stated that there is no specific reason to select one submodel over the other for data analysis. However, empirical and simulation studies (Sugita, 1998; Sugita *et al.*, 1999; Broström *et al.*, 2004; S. Sugita, unpublished data, 2005) have suggested that estimates of pollen productivity and background could be unstable with submodel 1 when the sum of background pollen loadings is high. Therefore the inverse form of submodel 1 is not useful for detecting differences in plant abundance among sites.

Appendix B: error estimates for the QAD method.

$\boldsymbol{D_{QAD}}$(species ***i***| site ***k*** – site ***m***), the sign of the direction of difference in vegetation composition of species i between sites k and m, is determined by

$$\frac{{}^{n_{i,k}}\big/_{\hat{\alpha}_i}}{\sum_{j=1}^{l} {}^{n_{j,k}}\big/_{\hat{\alpha}_j}} - \frac{{}^{n_{i,m}}\big/_{\hat{\alpha}_i}}{\sum_{j=1}^{l} {}^{n_{j,m}}\big/_{\hat{\alpha}_j}} \qquad \text{(B1)}$$

See Appendix A for notation.
Let's define $f_{i,k}$ and $f_{i,m}$ as

$$f_{i,k} \equiv \frac{{}^{n_{i,k}}\big/_{\hat{\alpha}_i}}{\sum_{j=1}^{l} {}^{n_{j,k}}\big/_{\hat{\alpha}_j}} \quad \text{and} \quad f_{i,m} \equiv \frac{{}^{n_{i,m}}\big/_{\hat{\alpha}_i}}{\sum_{j=1}^{l} {}^{n_{j,m}}\big/_{\hat{\alpha}_j}}.$$

Then, equation (B1) is expressed as $f_{i,k} - f_{i,m}$. Taking into account $s.e.(f_{i,k})$ and $s.e.\ (f_{i,m})$, the standard errors of $f_{i,k}$ and $f_{i,m}$, respectively, $\boldsymbol{D_{QAD}}$(species ***i***| site ***k*** – site ***m***) is evaluated as:

$\boldsymbol{D_{QAD}}$(species ***i***| site ***k*** – site ***m***)

$$\begin{aligned} &= +1,\ \text{when } f_{i,k} - s.e.(f_{i,k}) > f_{i,m} + s.e.(f_{i,m}), \\ &= 0,\ \text{when } f_{i,k} - s.e.(f_{i,k}) \le f_{i,m} + s.e.(f_{i,m}) \text{ and } f_{i,k} \\ &\qquad + s.e.(f_{i,k}) \ge f_{i,m} - s.e.(f_{i,m}), \\ &= -1,\ \text{when } f_{i,k} + s.e.(f_{i,k}) < f_{i,m} - s.e.(f_{i,m}) \end{aligned}$$

Variance of $f_{i,k}$ for species i at site k can be approximated using a hybrid of the delta method (Stuart and Ord, 1994) and Monte Carlo simulations (Sandy Weisberg, Statistics Department, University of Minnesota, personal communication, 2005). Its variance is expressed by the delta method as:

$$\operatorname{var}(f_{i,k}) \cong \left(\frac{\dfrac{\hat{q}_{i,k}}{\hat{\alpha}_i}}{\displaystyle\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}} \right)^2 \times \left[\frac{\operatorname{var}\left(\dfrac{\hat{q}_{i,k}}{\hat{\alpha}_i}\right)}{\left(\dfrac{\hat{q}_{i,k}}{\hat{\alpha}_i}\right)^2} + \frac{\operatorname{var}\left(\displaystyle\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}\right)}{\left(\displaystyle\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}\right)^2} - \frac{2 \cdot \operatorname{cov}\left(\dfrac{\hat{q}_{i,k}}{\hat{\alpha}_i}, \displaystyle\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}\right)}{\dfrac{\hat{q}_{i,k}}{\hat{\alpha}_i} \cdot \displaystyle\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}} \right] \tag{B2}$$

where $\hat{q}_{i,k} = \dfrac{n_{i,k}}{n_{\bullet k}}$ and $n_{\bullet k} \equiv \displaystyle\sum_{j=1}^{l} n_{j,k}$. $Var\left(\dfrac{\hat{q}_{i,k}}{\hat{\alpha}_i}\right)$ and $\operatorname{var}\left(\displaystyle\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}\right)$ in equation (B2) are approximated in a similar way as Parsons *et al.* (1984/1984) did, using the delta method:

$$\operatorname{var}\left(\frac{\hat{q}_{i,k}}{\hat{\alpha}_i}\right) \cong \left(\frac{\hat{q}_{i,k}}{\hat{\alpha}_i}\right)^2 \times \left\{ \frac{\hat{q}_{i,k} \cdot (1 - \hat{q}_{i,k})}{n_{\bullet k} \cdot \hat{q}_{i,k}^2} + \frac{\operatorname{var}(\hat{\alpha}_i)}{\hat{\alpha}_i^2} + \frac{2 \cdot \operatorname{cov}(\hat{q}_{i,k}, \hat{\alpha}_i)}{\hat{q}_{i,k} \cdot \hat{\alpha}_i} \right\} \tag{B3}$$

and

$$\operatorname{var}\left(\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}\right) \cong \sum_{j=1}^{l} \operatorname{var}\left(\frac{\hat{q}_{j,k}}{\hat{\alpha}_j}\right) + \sum_{j \neq m}^{l} \left\{ -\frac{\hat{q}_{m,k}}{\hat{\alpha}_m} \cdot \frac{\hat{q}_{j,k}}{\hat{\alpha}_j} \cdot \left(\frac{1}{n_{\bullet k}} - \frac{\operatorname{cov}(\hat{\alpha}_m, \hat{\alpha}_j)}{\hat{\alpha}_m, \hat{\alpha}_j} \right) \right\} \tag{B4}$$

$\operatorname{cov}\left(\dfrac{\hat{q}_{i,k}}{\hat{\alpha}_i}, \displaystyle\sum_{j=1}^{l} \frac{\hat{q}_{j,k}}{\hat{\alpha}_j}\right)$ in equation (B2) and $\operatorname{cov}(\hat{q}_{i,k}, \hat{\alpha}_i)$ in equation (B3) are estimated by Monte Carlo simulations. Variance and covariance of $\hat{\alpha}$'s in equations (B3) and (B4) can be obtained from training data sets of modern pollen deposition and vegetation in a region of interest (Parsons *et al.*, 1980; Prentice and Webb, 1986; Calcote, 1995; Broström *et al.*, 2004), using computer programs for the Extended *R*-value models (Parsons and Prentice, 1981; Parsons *et al.*, 1983/1984; Sugita, 1994; Jackson *et al.*, 1995; Sugita *et al.*, 1999; Broström *et al.*, 2004).

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