ORIGINAL ARTICLE

A modern pollen–climate calibration set from northern Europe: developing and testing a tool for palaeoclimatological reconstructions

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ABSTRACT

Aims and location The potential of pollen records in quantitative climate reconstructions has been widely debated but seldom tested. Our aim is to develop a pollen–climate transfer function for northern Europe and test its performance and inference power by numerical cross-validation with modern climate data. Annual mean temperature (T_{ann}) was assessed as the critical climatic variable because T_{ann} has a distinct south–north gradient (5.5 to −4.7 °C) in the study region with a corresponding zonal vegetation gradient from the hemiboreal zone in the south to the northern boreal zone in the north.

Methods We collected 137 pollen surface samples from small- to medium size lakes from southern Estonia to northern Finland. The transfer function for T_{ann} was developed with weighted averaging partial least squares (WA-PLS) regression. All 102 terrestrial pollen and spore types were included in the calculation sum and all 137 surface samples and all 102 taxa were included in the transfer function. The performance of the WA-PLS transfer function was evaluated by leave-one-out cross-validation.

Results A cross-validated root mean square error of prediction (RMSEP) of our model is 0.89 °C and the coefficient of determination (r^2) between the observed meteorological T_{ann} values and those predicted by the model in leave-one-out cross-validation is 0.88. The RMSEP as a percentage of the gradient length of T_{ann} is 8.8%. These figures indicate high performance statistics for our transfer function compared with other inference models. This is probably because of standardization of our surface-sampling and pollen-analytical procedures, careful selection of the surface sample sites with consideration of the relevant pollen source area, the simple patterns of vegetation zones and climate in the study area, and the mostly natural floristic composition of the forests in northern Europe. However, we also demonstrate the limitations of our model in reliably detecting fine-scale climatic variability.

Main conclusions The study shows the strong influence of T_{ann} on modern pollen composition and demonstrates the potential of pollen data for long-term climate reconstructions in northern Europe. It also provides evidence against simple interpretations of fine-scale variations in a single climate reconstruction. In particular, our results highlight the importance of careful study design and implementation in the construction of pollen–climate transfer functions.

Keywords

Finland, Estonia, pollen, climate, transfer function, validation.

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INTRODUCTION

Pollen has been widely used as a source of quantitative palaeoclimatic information, both in continental-scale reconstructions and in more site-specific reconstructions (e.g. Webb & Bryson, 1972; Huntley & Prentice, 1988; Guiot *et al.*, 1989, 1993; Bartlein & Whitlock, 1993; Allen *et al.*, 1996, 2000, 2002; Cheddadi *et al.*, 1997, 1998a,b; Peñalba *et al.*, 1997; Peyron *et al.*, 1998; Tarasov *et al.*, 1999; Birks *et al.*, 2000; Lotter *et al.*, 2000; Seppä & Birks, 2001, 2002). Most of the reconstructions have utilized modern analogue techniques and the related response surface methodology, or segmented inverse linear regression techniques. All these approaches are based on the collection of modern pollen surface samples and on the comparison of the occurrence and abundance of modern pollen types or modern pollen assemblages with modern climate data in order to produce a pollen–climate calibration or training set. In Europe, many of the continental-scale reconstructions or reconstructions covering previous geological periods have utilized large modern pollen–climate calibration sets derived from data bases. These data sets have often consisted of 1000 to 2000 pollen surface samples from various sedimentary environments (e.g. Cheddadi *et al.*, 1997; Tarasov *et al.*, 1999), and in an extreme case of almost 8000 pollen samples covering the whole of the northern hemisphere (Fauquette *et al.*, 1998). In contrast, some of the site-specific reconstructions have been based on more regionally restricted modern pollen–climate calibration sets with a lower number (100 to 200) of samples (e.g. Birks *et al.*, 2000; Lotter *et al.*, 2000; Seppä & Birks, 2001, 2002; Bigler *et al.*, 2002; Seppä *et al.*, 2002; Heikkilä & Seppä, 2003).

While pollen data have been commonly used in palaeoclimatology, its value as a basis of quantitative climate reconstructions has been intensively discussed (e.g. Davis, 1978; Birks, 1981; Ritchie, 1986, 1995; Webb, 1986; Huntley, 1993) and a number of problems and potential sources of errors have been recognized, as reviewed by MacDonald & Edwards (1991) and Seppä & Bennett (2003). Against this background it is surprising that only rarely has the precision or performance of pollen–climate calibration sets been explicitly investigated and tested or validated. Such validation tests can involve modern meteorological data, meteorological time-series data based on instrumental records, or climatic reconstructions carried out using independent palaeoclimatic proxies (Birks, 1995). Due to the shortness of instrumental time-series records and lack of precision of most of the other proxy records, the first approach is often most useful and rigorous and has been made more reliable by recent developments in quantitative techniques, in particular, cross-validation approaches in regression and model building (Birks, 1998).

One of the basic requirements for reliable quantitative environmental reconstructions is that the calibration set of modern surface samples should be from the same type of sedimentary environment as the fossil samples (Birks, 1995). As most of the pollen-based climate reconstructions are from lake sediments, the most suitable regions for the construction of pollen–climate calibration sets are those where the data set can be based on lake-sediment samples. However, not all lakes are equally suitable for this purpose. Recent modelling experiments have confirmed earlier observations based on empirical investigations that small lakes have smaller pollen source areas than large lakes. The Prentice–Sugita pollen dispersal and deposition model predicts that within the same landscape pollen percentages are highly variable in small ponds but uniform in larger lakes (lakes with diameter >250 m) (Prentice, 1988; Sugita, 1993, 1994; Davis, 2000). Lakes of this size are dominated by the regional pollen rain and have minimal between-site variation, whereas small ponds with a strong local pollen component are not suitable for the construction of pollen–climate calibration sets. Consequently, optimal regions for pollen–climate calibration sets are those where there is an adequate selection of lakes of suitable size.

To test the applicability of pollen data for quantitative climate reconstructions in northern Europe and to develop a tool for future climate reconstructions, we constructed a pollen–climate calibration set from Finland and Estonia (Fig. 1). In this paper we present this data set and the results of the statistical evaluation carried out to check its potential in palaeoclimatic reconstructions in conditions, which, due to the above-mentioned factors, can be regarded as ideal in European context. Our target is purely palaeoclimatological. We do not aim to investigate the modern vegetation–pollen relationships or to produce isopoll maps, as such work has been already carried out in Finland (Aario, 1940; Sauramo, 1940; Birks & Saarnisto, 1975; Prentice, 1978; Hicks, 2000). Finally, on the basis of present data and earlier investigations and discussions, we discuss in a wider context the strengths and potential weaknesses of pollen data in quantitative climate reconstructions in boreal and temperate zones.

PHYSIOGRAPHIC SETTING

Geology, topography and soils

The study area divides into two geological subregions. The bedrock of northern and central Estonia is composed of Ordovican and Silurian calcareous sedimentary rocks and of Devonian sandstone in southern Estonia. Finland is a country of crystalline bedrock with granite and gneiss as the most common rock types. Sedimentary rocks in Finland are rare, calcareous bedrock occurring as small, sporadic exposures. Most of Finland belongs to old metamorphic areas, with a strongly eroded peneplain dominating the landscape. Both countries have an even topography: the highest point in Estonia is 318 m above the sea level (a.s.l.) and the altitudinal variation in southern and central Finland is 0–300 m, but there is more topographical variation in Lapland where the north-western part of Finland reaches to the Scandes Mountains. The highest areas of Lapland are above 1000 m.

Till, a few metres thick and dating from the Weichselian glaciation, is the most common superficial soil deposit but there are also regions with much thicker glacio-fluvial
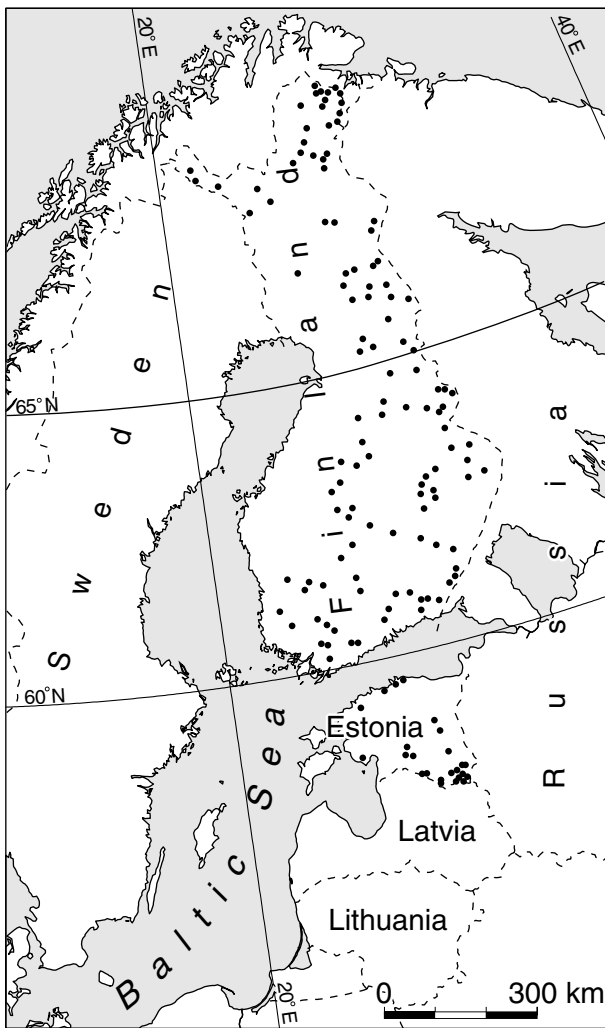
Figure 1 The study region and the location of the 137 surface-sample sites (lakes) in Finland and Estonia.

sediments and glaciomarine clays in both Estonia and Finland. Podsol is the most common soil type in Finland where the soils are in general acid and poor in nutrients. In Estonia, gleysols prevail and the soils are more nutrient-rich due to the carbonaceous bedrock. Peat deposits are the most extensive post-glacial soils. In parts of Estonia, northern central Finland, and southern Lapland they cover over 60% of total land area but in the lake district of eastern Finland only *c.* 10% (Ruuhijärvi, 1983). Ombrotrophic and oligotrophic mire types are dominant.

Climate

The most important atmospheric circulation pattern affecting the climate is the westerly air flow from the North Atlantic. During a typical zonal flow pattern, western and south-western air flow dominates in Finland and Estonia. Cyclones are generated in the Icelandic low and transported to the east. This flow pattern is strongest in the winter and more subdued in

summer when the air flow from the Atlantic is cooler and drier (Johannessen, 1970; Atlas of Finland, 1987). However, this zonal component can be replaced by meridional flow pattern during which there is only minor latitudinal movement of the cyclones and anticyclones. This situation results from the development of a quasi-stationary anti-cyclone over Fenno-scandia. Depending on the location of the anti-cyclone and related cyclones over the western Eurasian continent, meridional flow can enhance warm southern air flow or cold northern air flow. Particularly warm summers are related to the meridional flow pattern in which there is a strong permanent anti-cyclone over northern Russia and a permanent cyclone over the Baltic (Johannessen, 1970; Atlas of Finland, 1987).

Temperature patterns in the study area are relatively simple with decreasing values from the south to the north (Fig. 2). T_{ann} decreases from *c.* 5.5 °C on the south-western Estonian coast to *c.* −4 °C in northern Lapland. July is the warmest month with a mean value of 17.5 °C in southern Estonia and 10.9 °C at the coldest meteorological station in Lapland. There is little variation in July mean temperatures in Estonia and southern Finland, the difference between southern Estonia and central Finland being only *c.* 3 °C. Winter temperatures are more variable, the mean temperature of the coldest months (January and February) on the south-west coast of Finland and Estonia being −4 to −5 °C and in Lapland −14 to −16 °C.

The study area is located on the lee side of the Scandes Mountains, where the influence of the Atlantic air flow on precipitation is subdued by the mountains (Johannessen, 1970), and the annual precipitation values are relatively low. Precipitation is evenly distributed in Finland and Estonia, and the seasonal variation is small. Highest values, 700–750 mm, are recorded in southern and eastern Finland and western Estonia. On the west coast of Finland and in Lapland values are lower, 400–550 mm (Fig. 2). The proportion of snowfall in the precipitation is 45–60% in Lapland and 30–40% in southern Finland and Estonia.

Vegetation

The vegetation zonation of the study area follows the main south–north climatic gradient (Fig. 2). Most of the area is covered by boreal forest dominated by pine (*Pinus sylvestris* L.), spruce [*Picea abies* L. (Karst.)] and birch (*Betula pendula* Roth and *B. pubescens* Ehrh), with alder [*Alnus glutinosa* (L.) Gaertner and *A. incana* (L.) Moench] common on moister sites. Estonia and the south-western and southern coast of Finland belong to the northernmost variant of the nemoral (temperate) vegetation zone, the hemiboreal zone (Ahti *et al.*, 1968; Atlas of Finland, 1988), the northern limit of which follows the distribution limit of oak (*Quercus robur* L.) in Finland (Fig. 2). Of the other temperate deciduous trees, wych-elm (*Ulmus glabra* Hudson), European white elm (*Ulmus laevis* Pallas), lime (*Tilia cordata* Miller), hazel (*Corylus avellana* L.), maple (*Acer platanoides* L.) and ash (*Fraxinus excelsior* L.) occur in the zone. The middle boreal zone, from
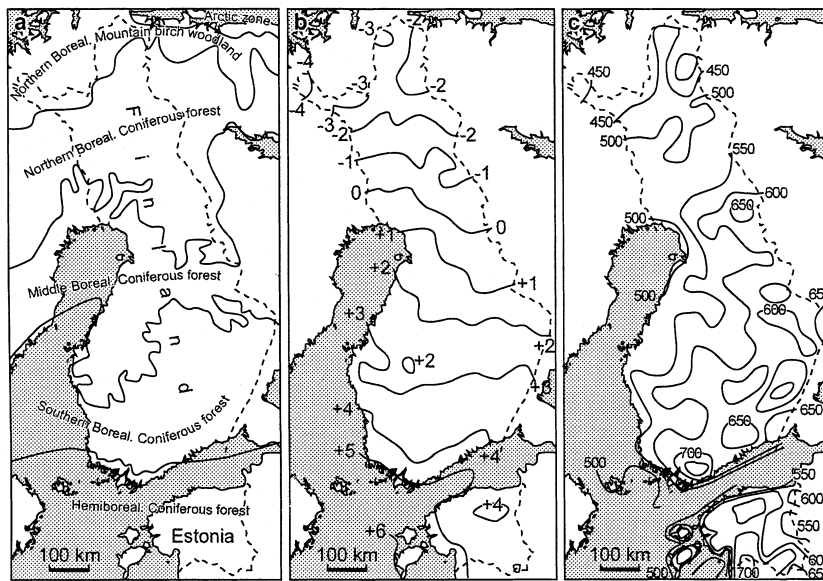
Figure 2 (a) Vegetation zones of the study area (modified from Sjörs, 1963; Ahti *et al.*, 1968), (b) the distribution of annual mean temperature (°C), (c) the distribution of annual precipitation (mm). The climate data are based on Climate Normals Period 1961–90 (Finnish Meteorological Institute, 1991; Jaagus, 1999).

central Finland to southern Lapland, reaches roughly from the northern limit of lime, the northernmost temperate deciduous tree species in Finland, to the northern limit of *Alnus incaca*. Lapland belongs to the northern boreal zone (Ahti *et al.*, 1968). Vegetation is dominated by conifer-birch forests to the northern distribution limits of spruce and pine. Above and beyond the conifer tree-line are mountain-birch [*B. pubescens* Ehrh ssp. *tortuosa* (Lebed.) Nyman] forests and finally treeless oroarctic heaths, where the field layer is characterized by grasses, sedges, herbs and dwarf-shrubs such as *B. nana* (L.), *Calluna vulgaris* (L.), *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher and *Vaccinium* spp.

METHODS

Pollen sampling

For the pollen–climate calibration set, 137 small to medium size lakes were selected, ranging from the oroarctic heaths of northernmost Lapland to the hemiboreal forests of southern Estonia (Fig. 1). Lakes are distributed evenly in Estonia and Finland, apart from two regions in Finland where no lakes have been sampled: the western coastal area on the eastern side of the Botnian Bay and central Lapland. In both areas there are few lakes and the number of the suitable lakes for the present project is limited. Furthermore, the lack of samples from these areas does not cause a major gap in the south–north direction in the data set. Consequently, the lack of samples from these two areas is unlikely to cause problems in the performance or robustness of the calibration set.

Lakes were selected according to the following criteria: size *c.* 20–50 ha, a regular, roundish morphometry, no major throughflows, at least 1.5 m in depth, no extensive peaty shores, no significant telmatic or aquatic vegetation, and no significant human impact (large fields, forest management, housing areas, etc.) in the vicinity of the lake. The lakes from

Finland mostly fulfil these criteria but in Estonia, where the number of lakes is lower, larger lakes of more variable morphometry and with more obvious human impact had to be included in the data set. Data about the lakes are given in Appendix 1.

Field work was carried out in Finland in August and September 1997 and in Estonia in February 2002. In Finland, lakes were sampled from an inflatable rubber boat approximately from the centre of the lakes whereas in Estonia the sampling took place through ice. For the pollen analyses, roughly 10 mm top sediment samples were taken from each lake with a gravity corer. In southern Finland and in Estonia this on average represents *c.* 25–35 years (at 0.3–0.4 mm year^{-1}) and up to 65 years in Lapland (at 0.15 mm year^{-1}) (Prentice, 1978). Samples were stored in plastic bags and stored at 4 °C.

Pollen analysis

Pollen analysis was carried out by H.S. in 1997–98 and 2002. Samples were prepared with the standard KOH, HF, acetolysis and silicone oil method (Fægri & Iversen, 1989). A minimum of 500 terrestrial pollen and spores were counted from each slide. Pollen identification was carried out to the lowest possible taxonomic level, with the help of the identification guide of Moore *et al.* (1991) and a modern pollen reference collection.

The pollen nomenclature of the paper follows Moore *et al.* (1991) with the following exceptions: *Pinus* is termed *Pinus sylvestris*, *Picea* is termed *Picea abies*, *Juniperus*-type is termed *Juniperus communis*, *Aster*-type is termed *Solidago*-type, oblong Cyperaceae grains with large lacunae are termed *Carex*-type, *Plantago major* and *P. media* are termed *Plantago major/media*, Rubiaceae is termed *Galium*, *Diphasiastrum*-type is termed *Diphasiastrum*, and *Typha angustifolia*-type is termed *Sparganium emersum*-type. *Sorbus* is identified as cf. *Sorbus aucuparia*, and a small Umbelliferae with short colpi is termed

Angelica-type. Among small *Rumex/Oxyria* pollen grains the following types were identified: *Rumex acetosa*, *Rumex acetosella*-type, *Rumex acetosa/R. acetosella*-type, and *Oxyria digyna*.

In the pollen diagram (Fig. 3), the percentages of terrestrial pollen and spore taxa were based on their total sum. The pollen diagram was prepared with the TILIA and TILIA.GRAPH programs (Grimm, 1990).

Climate data

Climate data for each pollen surface sample site were derived from the nearest meteorological station. A correction to the values was made according to the altitudinal difference between the meteorological station and the site, using an environmental lapse rate of 0.57 °C per 100 m altitude (Laaksonen, 1976). Meteorological data were collected from the Estonian and Finnish Meteorological Statistic and represent the 1961–90 Climate Normals period.

Numerical analyses

Numerical analyses were performed to answer the following questions: (1) What is the statistical relationship between the modern pollen assemblages and T_{ann} in the data set? (2) What are the statistical relationships between the individual modern pollen and spore taxon values and T_{ann}? (3) Can a statistically robust transfer or calibration function be derived from the modern pollen and spore assemblages and T_{ann} that can then be used to reconstruct past T_{ann} from fossil pollen assemblages?

Prior to all numerical analyses, the modern pollen and spore percentage values were transformed to square roots in an attempt to stabilize the variance and to maximize the 'signal to noise' ratio in the data (Prentice, 1980).

To answer question 1, a detrended correspondence analysis (DCA) (Hill & Gauch, 1980) of the modern pollen data was performed to estimate the gradient length of these data. Detrending by segments, non-linear rescaling and down-weighting of rare taxa were used in the DCA (ter Braak & Şmilauer, 2002). T_{ann} was then regressed on the DCA axes 1 and 2 sample scores to evaluate the strength of the statistical relationship between the modern pollen composition and T_{ann}. A constrained detrended canonical correspondence analysis (DCCA) (ter Braak, 1986) was also performed with annual mean temperature as the sole constraining variable and with the same options as in the DCA. The statistical significance of the relationship between modern pollen assemblages and T_{ann} was assessed by a Monte Carlo permutation test (199 unrestricted permutations). All computations were made using CANOCO version 4.5 (ter Braak & Şmilauer, 2002).
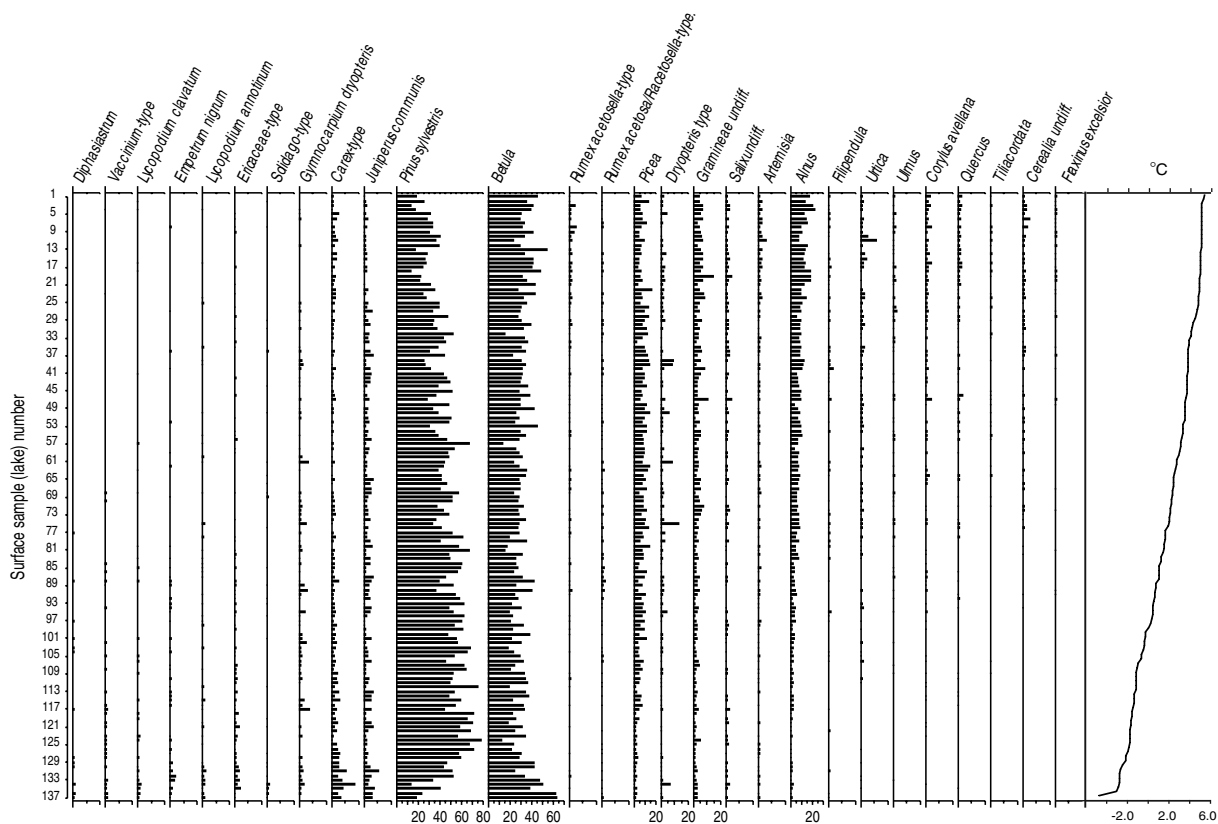

Figure 3 Pollen diagram showing selected pollen and spore types. The samples are arranged from the warmest (top) to the coldest (bottom) and the pollen taxa are arranged from the left to right according to increasing annual mean temperature optima, as estimated by weighted averaging. Annual mean temperatures of the surface-sample sites are indicated on the right hand side of the diagram.

To answer question 2, the statistical relationship of each individual pollen and spore taxon to T_{ann} was assessed using a hierarchical set of taxon response models (Huisman *et al.*, 1993; Oksanen & Minchin, 2002) within the framework of generalized linear modelling (Crawley, 1993). This hierarchical set consists of a skewed unimodal response model (model V), a symmetric Gaussian unimodal response model (IV), a plateau (III), a monotonically increasing (IIi), or decreasing (IId) sigmoidal response model, and a null model (I) of no relationship to T_{ann}. The simplest statistically significant response model for each taxon was found by fitting the most complex first and progressively removing parameters from the regression model in a backward elimination until the model could not be simplified without a significant ($P < 0.05$) change in the deviance of the model. Deviance is a goodness-of-fit statistic based on a likelihood ratio that can be used in *F*-ratio tests (Crawley, 1993). All response models were fitted to square root transformed percentage data by maximum likelihood estimation with a Poisson error structure and a logarithmic link function and were restricted to all taxa with ten or more occurrences in the data set. The weighted average (WA) optima and tolerances (ter Braak & Looman, 1986; Birks *et al.*, 1990) were also estimated to summarize the range of variation in the taxon responses to T_{ann}. The taxon response modelling was implemented using the program HOF version 2.3 (Oksanen & Minchin, 2002) and the WA optima and tolerances were estimated by WACALIB version 3.5 (Line *et al.*, 1994).

To answer question 3, modern transfer function for T_{ann} was developed using the inverse regression approach of weighted averaging partial least squares regression (WA-PLS) (ter Braak & Juggins, 1993; ter Braak, 1995). All 102 pollen and spore taxa included in the calculation sum were used in the WA-PLS model. WA-PLS was selected for deriving the transfer function because it has been shown in many empirical and several theoretical studies to perform as well as or even better than other regression and calibration procedures commonly used to develop organism-environmental transfer functions (see ter Braak *et al.*, 1993; Birks, 1995, 1998; ter Braak, 1995).

The optimal number of components to include in the WA-PLS model was assessed by leave-one-out cross-validation (ter Braak & Juggins, 1993; Birks, 1995). A two-component WA-PLS model was selected on the basis of the low root mean square error of prediction (RMSEP), low maximum bias, high coefficient of determination (r^2) between observed and predicted values of T_{ann}, and the smallest number of 'useful' components (Birks, 1998). ter Braak & Juggins (1993) discuss the importance of using cross-validation to assess and select WA-PLS models. Statistics based on cross-validation provide more reliable measures of the true predictive ability of the transfer functions as they are less biased by sample resubstitution (Birks, 1995). No samples were deleted as outliers or 'rogue' observations and no taxa were deleted. WA-PLS was implemented by the program CALIBRATE version 0.81 (S. Juggins & C.J.F. ter Braak, unpublished program).

In the various regression plots, an LOESS scatter plot smoother (span = 0.25, order = 2) (Cleveland, 1979) was fitted to help highlight the major trends.

RESULTS AND DISCUSSION

Individual pollen types

The pollen data contain 102 pollen and spore types of which the most common taxa are shown in the simplified pollen diagram in Fig. 3. As can be seen in the diagram, the pollen composition is strongly dominated by some wind-pollinated tree taxa, mainly *Pinus sylvestris*, *Picea abies*, *Betula* and *Alnus*. The general features of the pollen data clearly reflect the major vegetation zones of the study area. *Betula* values are highest in the mountain birch zone of northern Finland. The maximum values at the cold end are mostly related to the occurrence of *B. pubescens* ssp. *tortuosa* whereas towards the warm end the pollen is mostly derived from *B. pubescens* and *B. pendula*. The response model of *Betula* is sigmoidal decreasing, as its values increase towards the cooler end of the gradient (Table 1). *Pinus sylvestris* pollen has its highest values in the northern part of the northern boreal zone, where pine forms almost monocultural forests with very sparse understorey vegetation (Fig. 3). *Pinus* values at the warmest, Estonian sites, are as low as they are in the mountain birch zone of Finnish Lapland. *Picea* pollen has a symmetric unimodal response model (Fig. 4) with the highest values in the southern boreal zone in Finland and lower values in the hemiboreal zone and in the north (Fig. 3).

Alnus increases steadily towards the south and it is a strong indicator of higher T_{ann} in our data set. Similar patterns but with considerably lower values are typical for *Corylus avellana*, *Fraxinus excelsior*, *Populus tremula*, *Quercus*, *Tilia cordata* and *Ulmus* (Figs 3 & 4); these pollen types constitute an important indicator group of warmth-adapted, temperate and/or southern boreal pollen types in our calibration set. The temperature sensitivity of the corresponding tree species has been tested and verified (Hintikka, 1963; Skre, 1979; Prentice & Helmisaari, 1991; Dahl, 1998). The northern distribution limits of hazel (*Corylus avellana*) and wych elm (*Ulmus glabra*), for example, are delimited by growing season length and frost sensitivity. Lime (*Tilia cordata*) has a more continental distribution in northern Europe (Hintikka, 1963; Dahl, 1998) and a more northern distribution limit in Finland, where, in contrast to the more oceanic regions in Europe, the mid-summer temperatures are high enough for pollen tube growth and fertilization but the temperature fall during the late summer is so rapid that embryo and endosperm development are incomplete and frequently inhibit the ripening of the seeds (Pigott, 1981). The higher pollen percentages of *Tilia* at the warm end of the calibration set reflect therefore the longer growing season and higher late-summer temperatures.

Due to the low number of samples from arctic or oro-arctic vegetation zones, our data set does not clearly reflect the distribution of arctic or alpine pollen types in northern

Table 1 Optima, tolerances, number of occurrences and response models of all taxa included in the transfer function. The taxa are arranged in alphabetical order. The response models are restricted to taxa with ten or more occurrences in the data set. A, annual mean temperature weighted average optima (°C); B, tolerances (°C); C number of occurrences; D, response models; t., type

Table 1 *continued*

Taxon	A	B	C	D
Acer	4.9	0.2	3	
Achillea-t.	3.5	2.2	13	IIi
Alnus	2.9	2.2	136	IV
Ambrosia-t.	5.2	0.1	6	
Anchusa-t.	5.1		1	
Anemone nemorosa-t.	3.8		1	
Angelica-t.	3.6	2.3	6	
Arctostaphylos	−2.5	2.3	6	
Armeria	−1.8		1	
Artemisia	2.7	2.5	105	IIi
Astragalus danicus-t.	4.9		1	
Athyrium filix-femina	3.1	2.1	4	
Avena/Triticum	3.1	1.9	12	IIi
Betula	2.0	2.7	137	IId
Betula/Corylus/Myrica	1.7	2.7	69	I
Calluna vulgaris	2.3	2.7	60	I
Caltha palustris	4.9		1	
Campanula-t.	4.6		1	
Capsella-t.	2.3	3.0	6	
Carex-t.	1.2	2.9	126	IId
Carpinus betulus	5.2	0.1	9	
Caryophyllaceae undiff.	4.9		1	
Cerastium cerastioides-t.	3.9		1	
Cerealia undiff.	4.2	1.1	59	IV
cf. *Cannabis*	4.8	0.6	14	IIi
cf. *Sorbus aucuparia*	3.5	1.9	23	IIi
Chenopodiaceae	2.7	2.6	73	IIi
Cirsium/Carduus	5.0	0.2	2	
Compositae	3.0	2.1	13	I
Corylus	3.6	2.0	80	IIi
Cyperaceae undiff.	0.9	2.5	78	IV
Diphasiastrum	−1.2	1.6	13	IV
Drosera rotundifolia	−0.3		1	
Dryopteris filix-mas	3.9		1	
Dryopteris-t.	2.4	2.4	117	I
Empetrum nigrum	−0.3	2.6	42	IId
Epilobium	2.4	2.3	42	IId
Equisetum	1.2	3.0	42	IId
Ericaceae-t.	0.2	2.7	70	IId
Fagus sylvatica	3.8		1	
Fallopia convolvulus	5.1		1	
Filipendula	3.1	2.3	63	IIi
Frangula alnus	4.6	0.7	10	IV
Fraxinus excelsior	4.5	1.2	31	IIi
Geum	1.2	3.6	2	
Gramineae undiff.	2.5	2.5	137	IIi
Gymnocarpium dryopteris	0.8	2.3	76	IV
Hippophae rhamnoides	5.5		1	
Hordeum-t.	3.7	0.7	12	IV
Humulus lupulus	5.1	0.1	2	
Huperzia selago	−2.0	1.1	3	
Juniperus communis	1.5	2.7	128	IId
Lychnis viscaria-t.	2.2	2.1	2	
Lycopodium annotinum	0.1	2.5	45	IId
Lycopodium clavatum	−0.5	2.8	30	IId
Lycopodium undiff.	−0.3	2.5	20	IId
Lythrum salicaria-t.	4.9		1	
Melampyrum	2.3	2.6	14	I
Mentha-t.	5.1		1	
Ophioglossum	4.6		1	
Parnassia palustris	−2.7		1	
Picea	2.4	2.3	137	IV
Pinus sylvestris	1.7	2.6	137	IV
Plantago lanceolata	4.5	1.8	20	IIi
Plantago major/media	3.7	1.6	9	
Polygonum aviculare	4.9		1	
Polygonum viviparum	5.0		1	
Populus	3.5	2.4	34	IIi
Potentilla-t.	1.9	2.9	14	I
Prunus padus	3.1	3.5	3	
Pteridium aquilinum	3.9	0.7	8	
Quercus	3.8	2.0	65	IIi
Ranuculus acris	4.9	0.4	2	
Ranunculaceae undiff.	2.9	2.7	24	I
Rhinanthus	5.0	0.3	2	
Rosaceae undiff.	5.2		1	
Rubiaceae	3.3	2.5	17	IIi
Rubus arcticus	1.6		1	
Rubus chamaemorus	−0.3	2.1	8	
Rumex acetosa	2.0	2.4	38	I
Rumex acetosella-t.	3.2	2.3	78	IIi
R. acetosa/acetosella-t.	2.2	2.4	86	I
Sagina	2.4	3.6	2	
Sagittaria	2.3		1	
Salix herbacea-t.	−2.4		1	
Salix undiff.	2.5	2.6	102	IIi
Secale cereale	3.6	1.0	23	IV
Sedum	−2.7		1	
Selaginella selaginoides	−2.1	09	6	
Silene dioica	1.0	4.4	2	
Sinapis-t.	4.2		1	
Solidago-t.	0.5	2.8	30	IId
Thalictrum	1.0	3.4	9	
Thelypteris phegopteris	1.7		1	
Tilia cordata	4.0	1.6	33	IIi
Trifolium pratense	3.6		1	
Trollius europaeus	−1.5		1	
Ulmus	3.5	1.9	56	IIi
Umbelliferae	3.2	2.5	15	IIi
Urtica	3.2	2.1	87	IIi
Vaccinium-t.	−1.1	2.1	30	IId
Valeriana officinalis	5.0		1	

Europe. The few surface samples from the region above the tree-line are characterized by *Betula* due to the proximity of the mountain birch forest. The pollen data, however, show the rise of values of *Empetrum nigrum*, Ericaceae-type, *Vaccinium*-type and *Carex*-type at the sites in and above the mountain birch
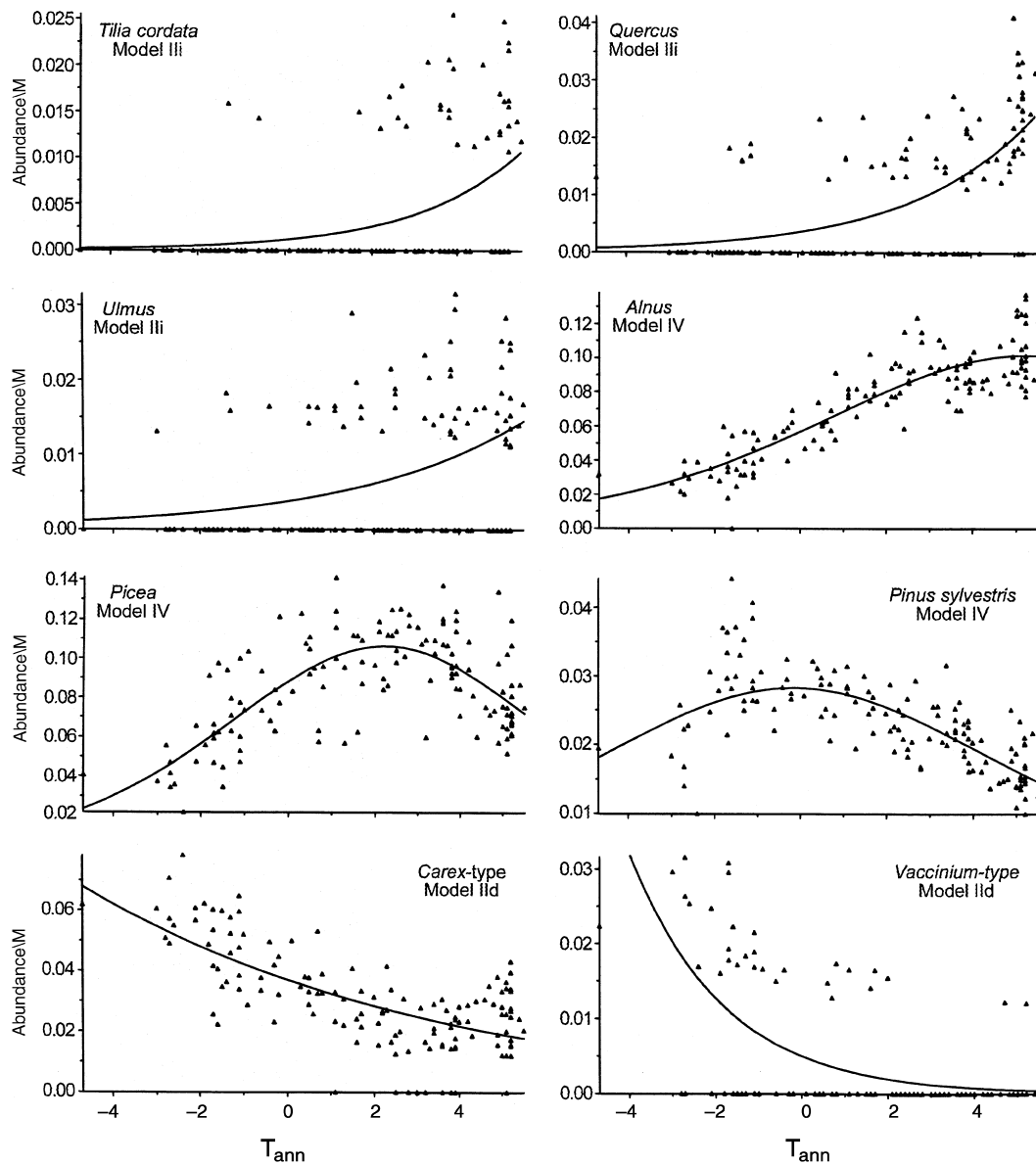
Figure 4 Diagrams showing the simplest statistically significant response models for selected pollen types in relation to annual mean temperature (T_{ann}) as assessed by a hierarchical set of taxon response models within the framework of generalized linear modelling (Huisman *et al.*, 1993; Oksanen & Minchin, 2002). The *x*-axis indicates the modern annual mean temperature (°C) and *y*-axis the abundance of the pollen types (square root transformed percentages) relative to the sample totals (*M*). As the models fitted are non-linear and assume a Poisson error distribution, it is not possible to calculate r^2 or the proportion of variance explained for the models.

forest. Similarly, values of *Huperzia selago*, *Lycopodium annotinum*, *Lycopodium* undiff. and *Lycopodium clavatum* spores increase toward the cold end of the gradient (Figs 3 & 4).

The pollen–climate calibration set

There is a close and statistically significant ($P < 0.001$) relationship between DCA axis 1 and T_{ann} (Table 2; Fig. 5a). There is no significant correlation with DCA axis 2 (Table 2; Fig. 5b). DCA axis 1 is very large (18.4% of the variance) compared with DCA axis 2 (5.6%). The very similar patterns and magnitudes of the DCA and DCCA axes (ter Braak, 1986)

(Table 2) suggest that T_{ann} captures the major gradients of variation in the modern pollen data.

Of the fifty pollen and spore taxa with ten or more occurrences in the data set, 41 have statistically significant relationships to T_{ann} (Tables 1 & 3). The nine taxa that show no statistically significant relationship are *Betula/Corylus/Myrica*, *Calluna vulgaris*, Compositae (Liguliflorae), *Melampyrum*, *Potentilla*-type, *Ranunculus* undiff., *Rumex acetosa/R. acetosella*-type, *Rumex acetosa* and *Dryopteris*-type.

Sigmoidal increasing responses are the commonest response type (twenty taxa), whereas sigmoidal decreasing responses (eleven taxa) and symmetric unimodal responses (ten taxa) are

Table 2 The results of detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA) of the modern pollen–climate data set (SD = standard deviation units)

	DCA		DCCA	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.11	0.03	0.10	0.03
Gradient length (SD)	1.30	0.99	1.21	0.95
Cumulative percentage variance (%)	18.4	24.0	16.6	21.8
Correlation with T_{ann}	0.95	0.15	0.95	–
t-value	3.41	−0.17	3.59	–
P-value	< 0.001	> 0.90	0.005	–

Table 3 The number of pollen and spore taxa (with ten or more occurrences) with different response models

Response model	No. of taxa
Skewed unimodal response (V)	0
Symmetric unimodal response (IV)	10
Plateau (III)	0
Monotonically increasing sigmoidal response (IIi)	20
Monotonically decreasing sigmoidal response (IId)	11
No relationship (I)	9
Total number of taxa	50

less common. Interestingly no taxon shows a skewed unimodal response. Examples of the fitted responses are shown in Fig. 4. Although the total gradient length is only 1.30 standard deviations for DCA axis 1 (Table 2) and sigmoidal increasing and decreasing responses are the commonest statistically significant response model (Table 3), the unimodal-based transfer function on WA-PLS appears to be the most robust statistically, as it is based on the simplest most parsimonous model of only 2 components and has a lower RMSEP than the corresponding linear-based PLS models (three component model RMSEP = 0.90 °C, two component model RMSEP = 0.92 °C). The likely reasons for the superior performance of WA-PLS when applied to compositional data are discussed by ter Braak (1995) and ter Braak et al. (1993) and reflect the 'two faces of compositional data' (ter Braak & Şmilauer, 2002).

The statistical correlation of the modern meteorological data with that predicted by the pollen–climate calibration set in statistical leave-one-out cross-validation reflects the inference power of the data set (Fig. 6). R^2 between predicted T_{ann} and modern T_{ann} is 0.88 (Table 4). By comparison with other corresponding calibration sets this can be considered high. The RMSEP for T_{ann}, 0.89 °C (Table 4), is lower than in most of the other published models for aquatic organisms, based on

similar quantitative methodology (RMSEP$_{jack}$ prediction errors based on WA-PLS). RMSEP as a percentage of the gradient length of T_{ann} is 8.8%, whereas the corresponding figure for eight different diatom-based calibration sets, constructed with similar numerical techniques, ranges from 10.7% to 25.2% (Rosén et al., 2000) and for eight chironomid-based calibration sets from 7.9% to 21.4% (Larocque et al., 2001). The precision and robustness of the data set are further stressed by the fact that we have not deleted any site (lake) or any variable (pollen or spore taxa) as outliers from our data, although the so-called data-screening has been common in many studies based on modern pollen, chironomid, or diatom data sets (e.g. Pienitz et al., 1995; Walker et al., 1997; Weckström et al., 1997; Tarasov et al., 1999).

The relatively high performance of the calibration set is due to a number of factors. First, the lack of outliers and 'rogue' observations is probably due to the large source areas of the pollen records in our calibration-set lakes, making individual samples less sensitive to locally anomalous vegetational and pollen-compositional features. Secondly, Finland and Estonia are characterized by a relatively even relief. Topographical variation and resulting altitudinal temperature variations have been found to be a complicating factor in many pollen-based climate reconstructions. Pollen transport by wind from low altitude sites to the treeless high-altitude sites often leads into too high reconstructed temperatures at high-altitude sites
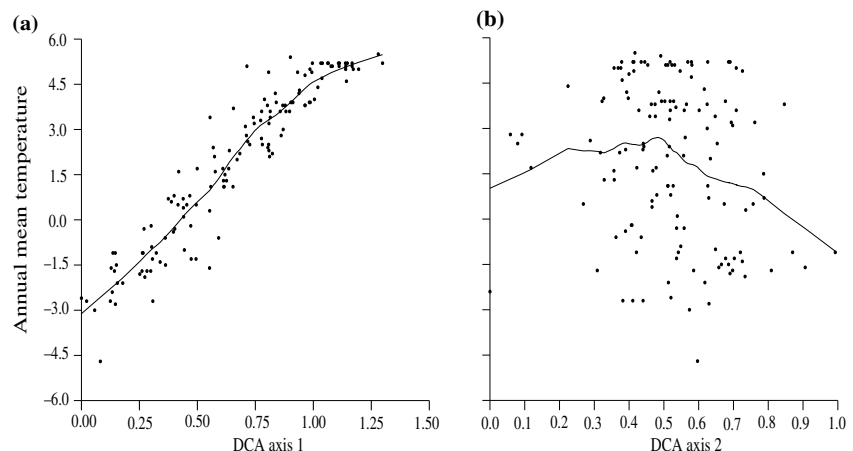
Figure 5 Annual mean temperatures (°C) of the calibration set sites regressed on the detrended correspondence analysis axis 1 (5a) and axis 2 (5b) sample scores. A LOESS smoother with span 0.25 and order 2 has been fitted to highlight the general trends.
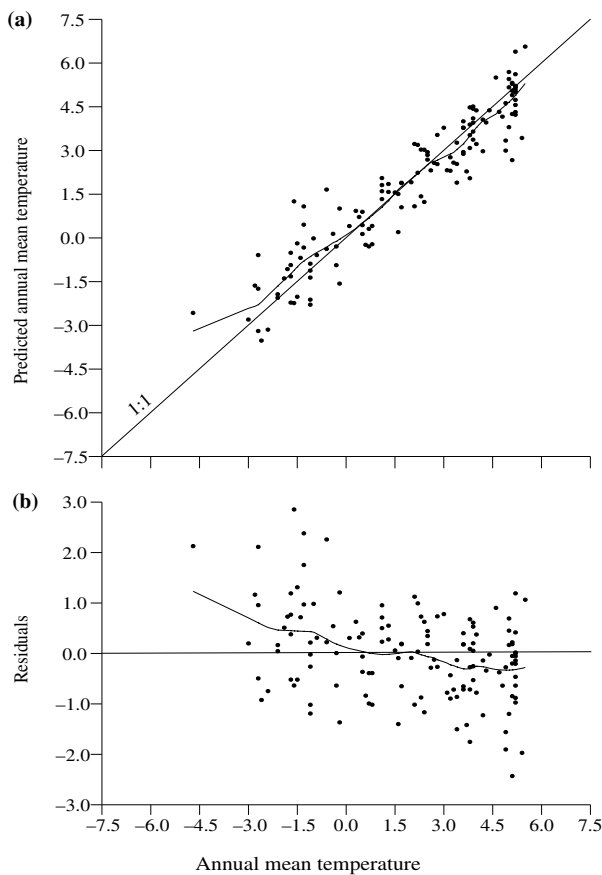
Figure 6 Scatter plots (a) of predicted annual mean temperature (°C) in leave-one-out cross-validation against modern annual mean temperature (°C) and (b) residuals (predicted vs. observed) (°C) against modern annual mean temperature (°C). A LOESS smoother with span 0.25 and order 2 has been fitted to highlight the general trends.

Table 4 Summary performance statistics of the four first components of the WA-PLS pollen–climate transfer function. RMSEP, root mean square error of prediction (°C), r^2, coefficient of determination between predicted and modern annual mean temperatures. The selected 2-component model is shown in bold. These statistics are all based on leave-one-out cross-validation

Components	RMSEP	r^2	Max. bias
1	0.92	0.88	2.36
2	**0.89**	**0.88**	**2.13**
3	0.92	0.87	2.12
4	0.96	0.86	2.28

(Huntley, 1994; Cheddadi *et al.*, 1997). Comparison of the present and the Norwegian (H.J.B. Birks, S.M. Peglar & A. Odland, unpublished data) pollen calibration sets indicate that the Norwegian set has poorer performance statistics,

probably partly due to the more variable topography of Norway and consequently a less simple climatic gradient from the south to the north and the problems of far-distance pollen transport to high altitudes.

Thirdly, our study area has a clear zonal vegetation pattern determined by the latitudinal decrease of T_{ann} and related temperature–climatic variables, such as length of the growing season or length of thermal winter, from the south to the north while other important bioclimatic factors, such as precipitation and effective moisture, do not show any significant regional variation in the area (Fig. 2). Should there be, for example, a major zonal or sectoral variation of precipitation in the study area, the influence of T_{ann} on vegetation and modern pollen assemblages would be less clear, the climate–pollen relationship more complicated, and the statistical performance of the calibration set probably lower. However, the lack of a precipitation gradient makes it impossible to construct a transfer function for precipitation in our study area. In northern Europe, such an effort could be carried out along the major modern west–east precipitation gradient inland from the oceanic Norwegian west coast.

Fourthly, in comparison with densely populated Central Europe, the intensity of human impact on vegetation has been lower in Finland, especially in the north-eastern and northern part of the country. Estonia is characterized by a more long-lasting and locally very intense agricultural influence on vegetation (Veski, 1998; Poska & Saarse, 1999, 2002). This does not confound the correlation between modern climate and modern pollen spectra probably because the regions of most intense human impact in Estonia were avoided during site selection and because the distribution of the main tree species and hence their pollen frequencies still predominantly reflect their original, natural distribution patterns. Forest management in Estonia and Finland has been based on nature-based silviculture, the proportion of exotic, planted trees is low, and 80% of forestland in Finland has been established naturally (Parviainen, 1994). Relatively minor human impact is not the rule, however, and the conclusions from our study cannot be extrapolated to other areas with more extensive forest clearance and planting of exotic trees. The performance of pollen–climate models in Central Europe, for example, should be tested separately. The high number of deleted pollen surface samples in many pollen–climate calibration sets (e.g. Tarasov *et al.*, 1999) may reflect the difficulties of constructing pollen–climate calibration sets in areas where the vegetation has been intensively influenced and altered by human action.

We thus interpret the good performance of our T_{ann} transfer function mostly in terms of suitable regional physiographical and ecological features. It is likely, however, that the high performance partly results from the high degree of standardization and consistency in the design and implementation of the project. It is of critical importance that all the surface samples in the current work are from lakes chosen with similar criteria. Incorporation of a number of different scientists for the fieldwork and for the laboratory analyses of the modern samples may have increased the statistical error of our

calibration set. Many of the existing pollen–climate calibration sets do not meet the requirements of methodological and analytical consistency. It is particularly questionable if pollen surface-sample data sets including samples from open and forested mires, pollen traps, soil samples, moss polsters, and lakes of different size and morphometry, are suitable for pollen-based palaeoclimatic reconstructions.

Potential to detect low- and high-frequency climatic variations

Most quantitative climate reconstructions based on various biological proxies display short-term variability which is usually superimposed on the low-frequency trends. However, it is unclear to what extent this fine-scale variability reflects real climatic variability and how much is intrinsic random variation or 'noise' in data. To assess the role of 'noise' in our calibration set we compared the predicted pollen-based values with the modern meteorological values in Fig. 7, where the modern values are arranged from the coldest to the warmest. This comparison highlights the good correlation of the major trends between observed and predicted values. However, it also shows that several successive predicted values can deviate considerably from the observed values. There are several possible reasons for these observed residuals. There is an inevitable systematic bias in all WA-PLS models (see Fig. 6b) due to the inverse regression used in WA-PLS (ter Braak & Juggins, 1993), resulting in a tendency for an over-estimation of temperatures at the cool end of the temperature gradient and an under-estimation at the warm end. Site-scale non-climatic factors can also influence the pollen assemblages at some site (e.g. the extent of selective forest clearance). The relative magnitude of far-distance transported pollen may also be important, especially in arctic and alpine areas. Whatever the cause of these observed residuals, they have considerable significance for the interpretation of any palaeoclimatological reconstructions based on our calibration set: the model is only really suitable for reconstructing general climatic trends and possibly major short-term fluctuations that significantly exceed the inherent sample-specific reconstruction errors of about 0.9 °C. It is not suitable for detecting fine-scale variation as cold or warm excursions consisting of several successive samples can be due to non-climatic reasons and may thus be 'noise' in the data (Fig. 7). The only way to validate the occurrence of any fine-scale variation is either to replicate the reconstruction from several sites or to use independent palaeoclimatic methods to verify the reconstructed fine-scale patterns. An optimal solution would, of course, be a combination of these two approaches.

CONCLUSIONS

Since the pioneering paper by Webb & Bryson (1972), pollen-based climate reconstructions have been actively carried out in various biogeographical regions of the world. This research activity indicates that pollen data have several advantages as a method of palaeoclimatic reconstructions. From the point of view of the current study we identify the following methodological strengths:

(i) Pollen is abundant, widely dispersed and well-integrated. It provides stratigraphically complete and detailed, widely available material for calibration set construction and for palaeoclimatic reconstructions. Pollen stratigraphies can usually be reliably dated, and, in the case of annually laminated lakes, precise chronologies with annual resolution can be developed.

(ii) The importance of climate from plant ecological, plant physiological, and pollination-ecological points of view is well studied and documented (e.g. Fægri & van der Pijl, 1971; Budyko, 1974; Gates, 1980; Larcher, 1980; Levitt, 1980; Woodward, 1987; Dahl, 1998).

(iii) Due to the importance of climate and individualistic relationships between plant species and climate, pollen records probably not only reflect a single climatic parameter (e.g. annual or July mean temperatures) but also a variety of other climatic inter-related parameters, including the length of
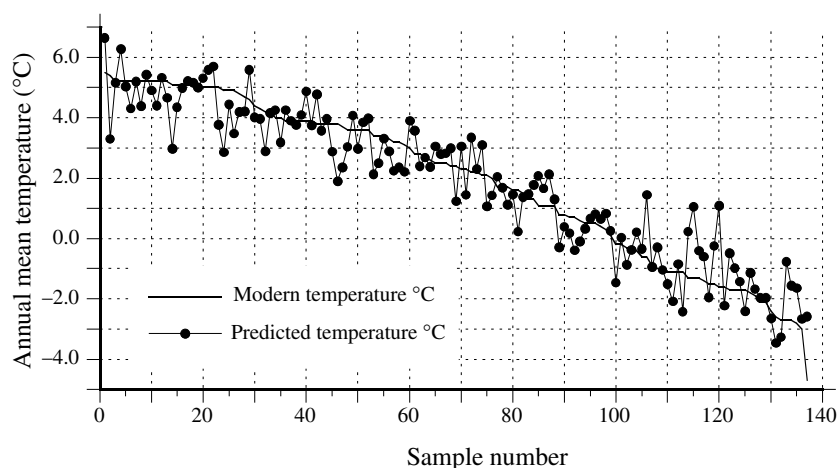

Figure 7 Predicted vs. observed modern annual mean temperatures plotted in order from the site with the highest observed annual mean temperature (left) to the site with the lowest observed annual mean temperature (right).

thermal summer and winter, winter minimum temperatures, precipitation and its seasonal distribution, and effective moisture (e.g. Woodward, 1987; Dahl, 1998). Therefore, pollen-based climate reconstructions can offer a wide, coherent insight into the nature of past climates which is increasingly important for interpreting past dynamics of atmospheric circulation patterns and for comparisons with general circulation model simulations (Masson *et al.*, 1999).

(iv) The relevant pollen source area of lakes with diameter >250 m is large enough to sense the surrounding vegetation on the landscape scale (Sugita, 1993, 1994; Davis, 2000). Due to this, the pollen composition at a given site is usually not biased by local anomalies in geology (bedrock, topography and soil), in local climate (temperature, moisture, protecting snow cover, snow beds and microclimate), or local ecological disturbances (forest fires, storms, pathogen outbreaks, local human impact such as plantations, fertilization, forest clearance and cultivation). For these reasons pollen records from such lakes may be less sensitive to local, non-climatic terrestrial and/or limnological influences than many aquatic organisms, such as diatoms or chironomids, commonly used in quantitative palaeoclimatological reconstructions.

Pollen data also have problems and weaknesses as a palaeoclimatological proxy. From the viewpoint of the present study, the most important are:

(i) The taxonomic resolution of pollen analysis in many cases reaches only the level of family or genus. The original climatic value of many important indicator species is lost. For example, Cyperaceae or *Carex*-type, a pollen type with a sigmoidal decreasing response model in our data set, includes such plant species as *Carex pseudocyperus* (L.), *C. riparia* Curtis, and *Cladium mariscus* (L.) Pohl, all thermophilous species in Finland, and, as macrofossils, important indicators of the Holocene thermal maximum (Backman, 1950; Erkamo, 1956; Hintikka, 1963). Similarly, the pollen type *Ranunculus* undiff. includes plant species that are characteristic of cold, alpine environments [e.g. *Ranunculus glacialis* (L.) and *R. nivalis* (L.)] and warm, southern boreal environments (*Hepatica nobilis* Schreber). This low taxonomic resolution will therefore widen the climatic tolerances, blur the optima of critical taxa, and increase potential biases in the inference model.

(ii) Current palaeoecological theory proposes that most post-glacial migrations have tracked the secular climatic changes in a dynamic equilibrium, with tree species shifting their ranges in response to changing climate (Prentice *et al.*, 1991; Huntley *et al.*, 1997; Davis & Shaw, 2001). However, migrational response to abrupt climatic changes of large amplitude may often be too slow to be in equilibrium with climate (Birks, 1981; MacDonald & Edwards, 1991; Huntley, 1993). In pollen records, this lag may be compensated by non-migratory responses of existing vegetation (Bennett, 1987; Huntley, 1996; Ammann *et al.*, 2000; Shuman *et al.*, 2002a,b) or pollen-production responses which are usually more rapid, as is indicated by climate-induced variations in the annual pollen accumulation rates of the different pollen types in the

northern tree-line regions (Ritchie, 1977; Hicks, 2000). It is difficult to assess, however, whether the amplitude of the non-migratory responses reliably reflects the real amplitude of the climate change (see Lotter *et al.*, 2000; Seppä & Bennett, 2003).

(iii) Pollen–climate reconstruction models can reconstruct one or two climatic variables with the strongest influence on the organism distribution and abundance. However, vegetational and subsequent pollen-compositional patterns are not influenced by a single or few climatic variables, but by a complex combination of many variables which are correlated with each other. Quantitative reconstructions cannot, therefore, capture the total climatic pattern of the past, especially if the past vegetation and pollen samples have been influenced by a climatic variable not present in the modern calibration set (MacDonald & Edwards, 1991).

(iv) The occurrence of long-distance pollen from forested regions in the pollen record from sites beyond and above the tree-line will often lead to a bias towards too high reconstructed temperatures in arctic and alpine environments. Assuming that the bias has remained the same during the study period, this problem can be overcome by presenting the reconstructed climate variable of interest as deviations from the modern inferred value (Huntley, 1994; Cheddadi *et al.*, 1997).

(v) Human impact on vegetation is a potential source of imprecision in climate reconstruction models based on pollen. Selective forest clearance may distort the relative abundances within the species-pool, the modern vegetation–climate relationship, and the relationship between past pollen assemblages and climate. In northern Europe, the role of introduced, exotic plant species is small but the long-term influences of, for example, slash-and-burn cultivation which selectively decimated spruce forests in Finland (Heikinheimo, 1915; Vuorela, 1986), the extensive use of pine for tar production, or the selective logging of oak in Estonia for ship building (Valk & Eilart, 1974) may be more significant.

In conclusion, due to all these confounding factors, pollen-based climate reconstructions are probably not precise enough for reconstructing annual or decadal temperature records beyond the advent of the instrumental meteorological observations in the sense that they could be characterized as 'palaeothermometers'. However, when pollen-stratigraphical studies are carefully designed and implemented they have the potential to provide reliable information about the general, centennial- to millennial-scale climatic trends or about major short-term climatic changes that exceed the inherent sample-specific errors of the reconstructions.

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Appendix 1 Geographical co-ordinates and altitudes of the 137 lakes from which the pollen surface samples were taken. Annual mean temperature (T_{ann}) values for each site are derived from extrapolation of 1961–90 Climate Normals Period data from the closest meteorological station. The lake numbers refer to the pollen diagram in Fig. 3. HB, hemiboreal (boreo-nemoral); SB, southern boreal; MB, middle boreal; NB; northern boreal; MBF, mountain birch forest; OH, oroarctic (alpine-arctic) heath

No.	T_{ann}	Study site name	Lat.	Lon.	Alt.	Veg. zone
1	5.5	Tõhela	58°25′	24°00′	18	HB
2	5.4	Hammersbodaträsk	60.03	22.25	16	HB
3	5.2	Järveotsa	59°06′	24°10′	42	HB
4	5.2	Ubajärv	57°39′	26°35′	72	HB
5	5.2	Väikjärv	57°43′	27°02′	233	HB
6	5.2	Haanja	57°39′	27°05′	225	HB
7	5.2	Preeksa	57°39′	27°09′	183	HB
8	5.2	Palojärv	57°37′	27°09′	179	HB
9	5.2	Murati	57°35′	27°06′	172	HB
10	5.2	Misso Saarjärv	57°37′	27°13′	184	HB
11	5.2	Paidra	57°55′	27°11′	73	HB
12	5.2	Nohipalu Mustjärv	57°56′	27°21′	60	HB
13	5.2	Nohipalu Valgjärv	57°56′	27°21′	54	HB
14	5.2	Alopi	57°57′	26°35′	127	HB
15	5.1	Lillträsket	59.58	23.15	16	HB
16	5.1	Nihu	57°52′	25°53′	71	HB
17	5.1	Kadarbiku	57°53′	25°52′	68	HB
18	5.1	Jaaska	57°45′	26°15′	57	HB
19	5.1	Koobassaare	57°40′	26°24′	72	HB
20	5.1	Rummu	59°27′	25°18′	36	HB
21	5.0	Kvarnträsket	60.02	23.08	36	HB
22	5.0	Päidre	58°16′	25°30′	51	HB
23	5.0	Õisu	58°12′	25°31′	45	HB
24	5.0	Mäeküla	58°07′	25°42′	96	HB
25	4.9	Särkijärvi	60.46	20.21	71	HB
26	4.9	Käsmu	59°35′	25°53′	3	HB
27	4.9	Lohja	59°34′	25°42′	7	SB
28	4.8	Hemträsket	60.04	23.28	2	HB
29	4.7	Männikjärv	58°52′	26°16′	77	HB
30	4.6	Saare	58°39′	26°47′	44	HB
31	4.4	Pernjärvi	60.23	23.25	68	HB
32	4.3	Relusjärvi	61.04	25.28	79	SB
33	4.2	Syväjärvi	60.41	25.55	45	SB
34	4.2	Valkjärvi	60.33	25.48	39	SB
35	4.0	Syväjärvi	60.48	28.08	36	SB
36	4.0	Niemijärvi	60.46	27.04	50	SB
37	3.9	Vihtosenjärvi	61.00	28.20	56	SB
38	3.9	Hinnusjärvi	60.54	28.12	55	SB
39	3.9	Luotoinen	60.42	27.49	49	SB
40	3.9	Hiirlampi	60.31	24.08	73	SB
41	3.9	Neittamojärvi	61.05	22.01	49	SB
42	3.9	Hurmajärvi	60.47	27.17	69	SB
43	3.8	Vahaksenjärvi	60.41	23.45	127	SB

Appendix 1 *continued*

No.	T_{ann}	Study site name	Lat.	Lon.	Alt.	Veg. zone
44	3.8	Iso Ruonajärvi	60.21	23.39	83	SB
45	3.8	Syväjärvi	61.24	23.58	94	SB
46	3.8	Vuorinen	60.58	27.04	78	SB
47	3.8	Veiklampi	60.40	27.08	43	SB
48	3.7	Naarajärvi	61.36	22.40	94	SB
49	3.6	Ruuhilampi	60.20	24.28	70	SB
50	3.6	Heinlammi	60.36	23.53	117	SB
51	3.6	Vaakkoi	60.20	24.36	82	SB
52	3.6	Alinenjärvi	61.29	22.28	135	SB
53	3.6	Hätikkäjärvi	61.22	23.18	115	SB
54	3.4	Palosenlampi	61.34	27.40	81	SB
55	3.4	Lahnajärvi	61.41	24.48	102	SB
56	3.4	Alainen Liesjärvi	61.50	25.14	114	SB
57	3.3	Valtonen	61.45	27.26	108	SB
58	3.2	Valkia Ruokojärvi	61.27	28.26	87	SB
59	3.2	Peltointaustanjärvi	61.21	25.05	129	SB
60	3.1	Etelä-Hiislampi	61.59	26.45	105	SB
61	3.0	Selkäjärvi	61.11	25.11	161	SB
62	2.8	Soitunlahti	62.48	28.24	101	SB
63	2.8	Suurijärvi	62.40	28.00	104	SB
64	2.7	Saarijärvi	62.11	27.54	82	SB
65	2.6	Haapalampi	62.28	28.33	91	SB
66	2.5	Petäjäjärvi	62.22	28.29	106	SB
67	2.5	Iso-Mustiainen	62.21	25.10	158	SB
68	2.5	Muikkulampi	62.26	25.26	163	SB
69	2.4	Humalalampi	62.29	27.29	127	SB
70	2.4	Lehmilampi	62.26	24.40	155	MB
71	2.3	Selkeydenjärvi	63.26	26.35	103	SB
72	2.3	Kutemainen	63.10	25.29	103	SB
73	2.2	Ohenjärvi	63.07	26.47	110	SB
74	2.2	Ruokonen	63.04	26.07	129	SB
75	2.1	Vehkalampi	62.36	30.16	128	SB
76	2.1	Lahnanen	62.42	24.38	205	MB
77	2.0	Pieni Ristijärvi	62.52	25.02	164	MB
78	1.7	Paalikkalampi	63.15	30.40	193	MB
79	1.7	Iso Vihtajärvi	62.57	30.26	187	MB
80	1.7	Rauvanlampi	62.52	28.55	106	MB
81	1.6	Isonlampi	63.18	30.13	124	MB
82	1.6	Korpilampi	62.37	30.46	177	SB
83	1.5	Telkkälampi	63.36	29.55	139	MB
84	1.3	Sainijärvi	64.08	26.32	121	MB
85	1.3	Nuottijärvi	64.09	27.32	156	MB
86	1.1	Kalajärvi	64.28	27.41	187	MB
87	1.1	Toivonlampi	64.01	30.05	207	MB
88	1.1	Kuljejärvi	63.57	29.46	227	MB
89	1.1	Pieni Lantanlampi	64.04	29.29	179	MB
90	0.8	Iso Hakojärvi	65.22	27.36	144	NB
91	0.8	Alajärvi	64.10	28.45	163	MB

Appendix 1 *continued*

No.	T_{ann}	Study site name	Lat.	Lon.	Alt.	Veg. zone
92	0.7	Kilpilampi	64.17	30.10	189	MB
93	0.7	Suukoskenlampi	66.54	25.24	108	NB
94	0.6	Likolampi	64.50	29.31	206	NB
95	0.5	Valkeainen	65.16	29.12	212	NB
96	0.5	Latvajärvi	64.48	28.12	232	NB
97	0.5	Peuro	64.15	30.19	220	MB
98	0.4	Latvalampi	64.11	30.19	242	MB
99	0.3	Aholampi	65.08	29.36	259	NB
100	0.1	Tutulampi	65.29	27.51	186	NB
101	−0.2	Hiltusenjärvi	65.43	28.41	247	NB
102	−0.2	Saarijärvi	65.17	28.24	239	NB
103	−0.3	Keihäsjärvi	66.42	27.40	154	NB
104	−0.3	Karsimusjärvi	66.30	27.12	151	NB
105	−0.4	Kankaanlampi	66.44	27.55	163	NB
106	−0.6	Naumanjärvi	66.12	28.13	247	NB
107	−0.6	Kiviperänlampi	66.04	29.49	258	NB
108	−0.9	Kesäjärvi	66.10	29.08	289	NB
109	−1.0	Saukkolampi	66.10	27.34	270	NB
110	−1.1	M88	69.06	28.35	139	NB
111	−1.1	Iso Kuivajärvi	68.38	27.50	170	NB
112	−1.1	Alanen Aittojärvi	68.29	27.54	160	NB
113	−1.1	Halijärvi	66.43	29.00	281	NB
114	−1.1	Ipojärvi	66.42	28.56	268	NB
115	−1.3	M94	68.39	27.56	202	NB
116	−1.3	Vaara-Uuttulampi	67.28	27.21	225	NB
117	−1.3	Saarijärvi	67.26	27.44	202	NB
118	−1.4	Iso Ivalampi	66.19	29.10	247	NB
119	−1.5	M85	69.19	28.55	198	NB
120	−1.5	M90	68.46	28.41	199	NB
121	−1.6	M66	68.59	27.18	136	NB
122	−1.6	Muotkaseljänlampi	67.18	29.16	246	NB
123	−1.7	M67	69.11	27.17	159	NB
124	−1.7	Nevalahdenjärvet	68.49	26.49	150	NB
125	−1.7	Naruskajärvi	67.25	29.15	263	NB
126	−1.7	J4	67.59	23.41	262	NB
127	−1.8	Kenttälammi	67.18	29.24	277	NB
128	−1.9	Kuonnajärvi	68.26	24.05	309	NB
129	−2.1	Allijärvi	68.17	24.45	338	NB
130	−2.1	J32	68.25	22.54	319	MBF
131	−2.4	J47	68.42	21.34	446	MBF
132	−2.6	M83	69.40	28.58	202	MBF
133	−2.7	J39	68.39	22.01	503	MBF
134	−2.7	J46	69.03	20.40	496	OH
135	−2.7	M70	69.53	28.13	224	MBF
136	−2.8	M71	69.42	28.38	239	MBF
137	−4.7	M81	69.41	28.38	550	OH