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We have pleasure in dedicating this paper to Magdalena Ralska-Jasiewiczowa on the occasion of her 70 th birthday, and in recognition of her many outstanding contributions to Quaternary vegetational and environmental history.

Pollen-based reconstructions of late-Quaternary climate in Europe – progress, problems, and pitfalls

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ABSTRACT: This paper reviews the basic concepts of pollen – climate transfer functions used to reconstruct quantitative past climates from fossil pollen assemblages. The various assumptions and requirements are outlined and progress in developing detailed regional pollen – climate calibration sets and resulting transfer functions in Europe is discussed. Current problems in the existing approaches are presented, and the inherent pitfalls of pollen-stratigraphical data as a climatic proxy are discussed. Despite these problems and pitfalls, pollen-based climate reconstructions in northern Europe are generally consistent and agree well with other independent climatic reconstructions, at least at broad millennial scales.

KEY WORDS: pollen, climate, transfer functions, weighted averaging partial least squares, reconstruction, evaluation, validation, assumptions

INTRODUCTION

Pollen-stratigraphical data are increasingly used as a basis for quantitative palaeoclimatic reconstructions (e.g. Davis et al. 2003, Kühl & Litt 2003). Such reconstructions can be at a broad continental scale (e.g. Davis et al. 2003) or at finer regional scales (e.g. Seppä & Birks 2002). Climate reconstructions at a range of scales are increasingly needed in response to demands for quantitative reconstructions of past climate as inputs to, or validations of, simulations by intermediate complexity Earth System models of past, present, and future climate patterns (e.g. Claussen et al. 2002). There are three main approaches to the quantitative reconstruction of past climates from pollen-stratigraphical data (Birks 1981, 2003, Guiot 1991) – (1) the indicator-species approach, (2) the assemblage approach, and (3) the multivariate numerical transfer function approach. All these approaches require information about the modern climate preferences and tolerances of the taxa found as fossil pollen and spores. The basic assumption throughout is methodological uniformitarianism (Birks & Birks 1980, Birks 2003), namely that modern-day observations and relationships can be used as a model or analogue for past conditions and, more specifically, that pollen – climate relationships have not changed with time, at least in the late Quaternary.

Since the pioneering work on the quantitative reconstruction of past climates by Iversen

(1944) using the indicator-species approach, by Guiot (1990) using the assemblage-approach and associated modern analogue techniques (MAT), and by Webb and Bryson (1972) using transfer functions, there have been considerable methodological advances in all these approaches (e.g. Kühl et al. 2002, Huntley 1993, ter Braak 1995). This paper concentrates on the multivariate transfer-function approach in late-Quaternary palynology. It presents the basic concepts of transfer functions and outlines the assumptions and requirements of pollen – climate transfer functions. It briefly reviews progress in this approach. It discusses in detail some of the major critical ecological and numerical problems and pitfalls in the approach and suggests possible future developments and research needs in relation to these problems and pitfalls. Our review concentrates on pollen – climate transfer functions in Europe. Grimm and Jacobson (2004) discuss current approaches to Holocene climatic reconstructions in North America. The paper avoids, as far as possible, details of the mathematical methods involved in transfer functions. Readers interested in such details should consult ter Braak (1995), ter Braak and Juggins (1993), ter Braak et al. (1993), and Birks (1995, 1998). In this paper we draw, in part, on previous reviews by Birks (1981, 1995, 1998, 2003), MacDonald and Edwards (1991), and Seppä and Bennett (2003) and on our experiences of reconstructing past climates from European pollen-stratigraphical data.

BASIC CONCEPTS OF POLLEN – CLIMATE TRANSFER FUNCTIONS

The basic idea of using transfer or calibration functions to reconstruct past climate quantitatively from pollen-stratigraphical data is summarised in Figure 1 (Birks 2003). We assume that there is one or more climate variable $\mathbf{C_o}$ that we wish to reconstruct from fossil pollen assemblage $\mathbf{P_o}$ that consists of *m* taxa in *t* samples. To reconstruct $\mathbf{C_o}$ we model the responses of the same *m* taxa today in relation to the modern climate variable(s) of interest ($\mathbf{C_m}$). This involves compiling a modern "training set" or "calibration set" of *m* taxa at *n* sites ($\mathbf{P_m}$) represented as pollen assemblages preserved in surface (0–1 cm) sediments such as surficial lake muds with an associated set of modern climate variable(s) ($\mathbf{C_m}$) for the same *n* sites. The modern relationships between $\mathbf{P_m}$ and $\mathbf{C_m}$ are modelled numerically and the resulting function is used as a transfer function to transform the fossil pollen assemblage $\mathbf{P_o}$ into quantitative estimates of the past

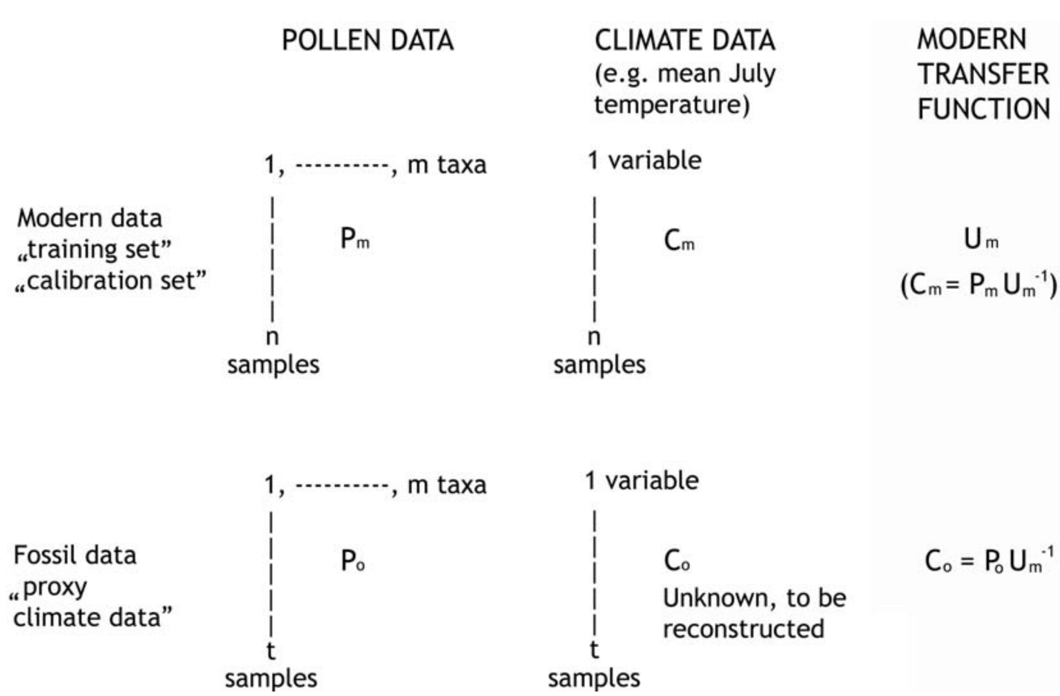

Fig. 1. The principles of quantitative palaeoclimatic reconstruction showing $\mathbf{C_o}$, the unknown climatic variable, to be reconstructed from fossil pollen assemblages $\mathbf{P_o}$, the essential role of a modern "training set" or "calibration set" consisting of modern pollen ($\mathbf{P_m}$) and climate ($\mathbf{C_m}$) data, and the resulting transfer function ($\mathbf{U_m}$)

climate (C_o). The various practical stages are schematically represented in Fig. 2. In standard statistical terminology, the taxa within P_m are assumed to respond to the climatic variables in C_m, and thus notationally P_m is equivalent to **Y** (response variables) and C_m is equivalent to **X** (predictor or explanatory variables) in regression modelling.

The palynological and ecological bases for using pollen as a means of reconstructing past climate are as follows (modified from Webb & Bryson 1972).

1. Modern pollen assemblages (P_m) are a function, admittedly a complex and non-linear function, of modern vegetation (V_m), namely

$$P_m = V_m R_m \quad (1)$$

where R_m represents modern pollen representation or “correction” factors.

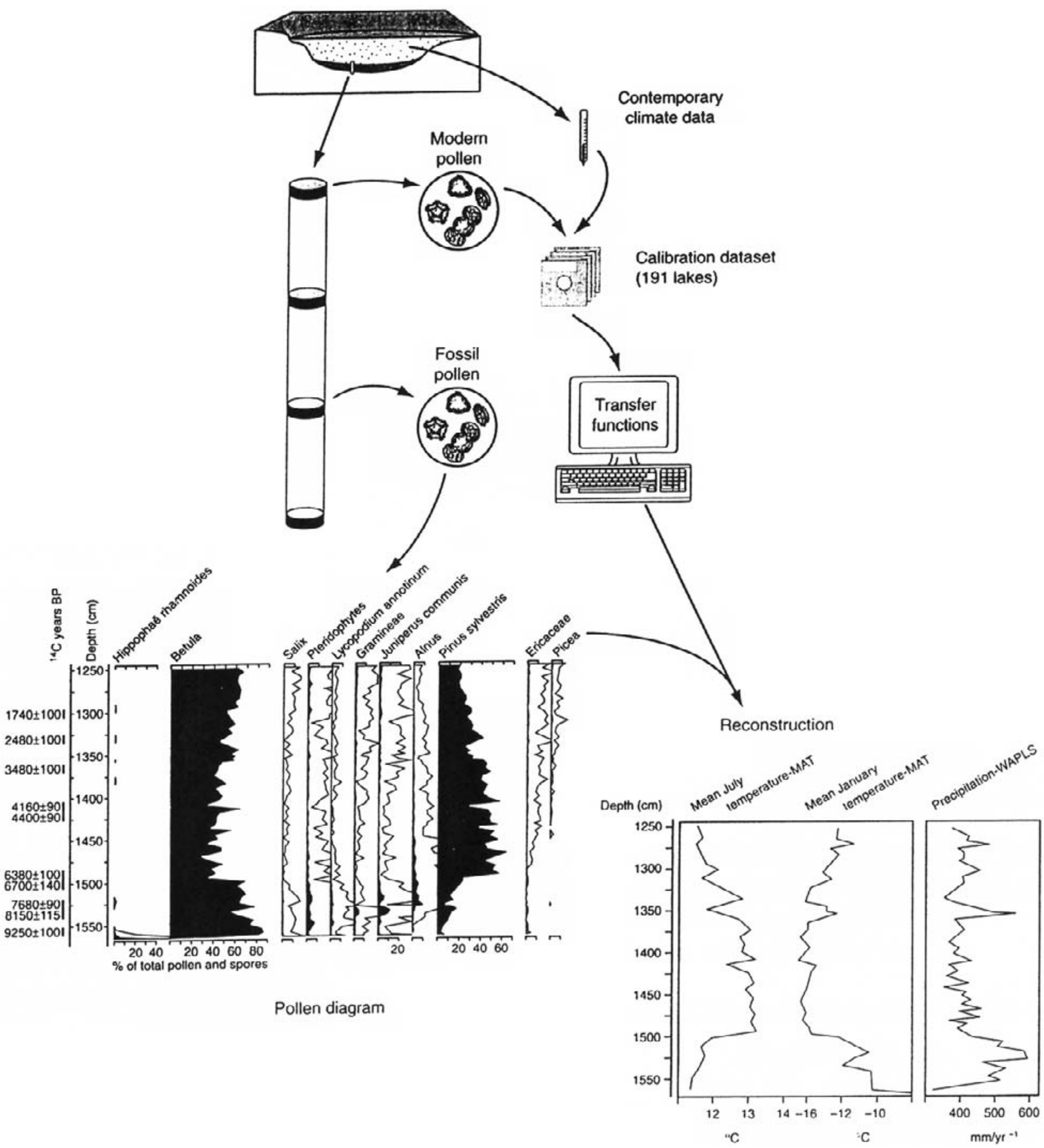

Fig. 2. A schematic representation of the various stages involved in deriving a quantitative reconstruction from pollen-stratigraphical data using a modern calibration set. Modified from an unpublished diagram by Steve Juggins

This is, of course, the basic assumption of pollen analysis, namely that there is a modern pollen – vegetation relationship (Birks & Birks 1980).

2. Past vegetation (V_o) can be reconstructed from fossil pollen assemblages ($\mathbf{P_o}$) by means of $\mathbf{R_m}$, namely

$$V_o = \mathbf{P_o R_m}^{-1} \quad (2)$$

This is the basic quantitative interpretation of fossil pollen assemblages in terms of past populations (Birks & Birks 1980).

3. Modern vegetation ($\mathbf{V_m}$) is a function of modern climate ($\mathbf{C_m}$), at least at a broad scale such as Fennoscandia, namely

$$\mathbf{V_m} = \mathbf{C_m D_m} \quad (3)$$

where $\mathbf{D_m}$ represents the modern ecological response functions and climatic preferences and tolerances of the taxa that comprise the contemporary vegetation. This is the assumption of broad-scale ecology and plant geography, namely that there are broad-scale modern vegetation – climate relationships (Woodward 1987, Dahl 1998, Moen 1999).

4. Past climate (C_o) can be inferred qualitatively from the reconstructed vegetation (V_o) by means of $\mathbf{D_m}$, namely

$$C_o = V_o \mathbf{D_m}^{-1} \quad (4)$$

This is the basis of all environmental reconstructions using modern ecological knowledge applied to fossil pollen assemblages interpreted initially as past vegetation (Birks & Birks 1980).

5. Expressions (1) and (3) can be combined to derive a quantitative reconstruction of C_o directly from fossil pollen-stratigraphical data, namely

$$\mathbf{P_m} = \mathbf{V_m R_m} \quad (1) \quad \text{and} \quad \mathbf{V_m} = \mathbf{C_m D_m} \quad (3)$$

$$\mathbf{P_m} (\mathbf{R_m D_m})^{-1} = \mathbf{C_m} = \mathbf{P_m U_m}^{-1} \quad (5)$$

where $\mathbf{U_m}$ represents modern pollen – climate transfer functions (Fig. 2).

6. Given a fossil pollen assemblage ($\mathbf{P_o}$) and modern estimates of $\mathbf{\hat{U}_m}$, we can derive quantitative estimates of past climate (C_o) from

$$C_o = \mathbf{P_o U_m}^{-1} \quad (6)$$

There are many numerical procedures now available for deriving modern transfer functions, as reviewed by Birks (1995, 1998) and ter Braak (1995). Within these procedures, there are major distinctions between methods that assume (1) linear or monotonic responses or (2) non-linear or unimodal responses between pollen taxa and climate, and between classical and inverse approaches for estimating transfer functions (ter Braak 1995). It is a general feature of ecology that organism – environment relationships are usually non-linear and pollen abundance is often a unimodal function of climate (e.g. Seppä et al. 2004). Each taxon has its highest values at a particular "optimum" value of a climate variable and is rare or absent where the value of that variable is too low or too high. Thus all taxa tend to occur over a characteristic but limited environmental range and within this range to be most abundant near their climatic optimum (Hengeveld 1990, ter Braak 1996).

The distinction between classical and inverse approaches is also important (ter Braak 1995). In the classical approach, pollen responses $\mathbf{P_m}$ are modelled as a function of climate ($\mathbf{C_m}$) with some error

$$\mathbf{P_m} = f\,(\mathbf{C_m}) + \text{error}$$

The function f ( ) is estimated by linear, non-linear, and/or multivariate regression from the modern calibration-set. Estimates of f ( ) are then "inverted" in some way so that the unknown past climate ($\mathbf{C_o}$) can be inferred from a fossil pollen assemblage ($\mathbf{P_o}$). "Inversion" involves finding an estimate of the past climate variable that maximises the likelihood of observing the fossil pollen assemblage in that climate. If f ( ) is non-linear, which it almost always is, non-linear optimisation procedures are required and these can be computationally difficult and demanding (Birks 2003).

In the inverse approach, this difficult inversion is avoided by estimating directly the inverse function from the calibration-set by "inverse" regression of $\mathbf{C_m}$ on $\mathbf{P_m}$, namely

$$\mathbf{C_m} = \mathbf{q}\,(\mathbf{P_m}) + \text{error}$$

The inferred past climate ($\mathbf{C_o}$), given fossil pollen assemblage ($\mathbf{P_o}$), is simply

$$C_o = \mathbf{q}\,(\mathbf{P_o})$$

(Note that $\mathbf{q}$ would correspond to $\mathbf{U_m}^{-1}$ in expressions (5) and (6) above.)

Of the various numerical techniques used to derive pollen – climate transfer functions and to reconstruct past climate, only the smooth response-surface approach with locally weighted averaging (e.g. Prentice et al. 1991, Bartlein & Whitlock 1993, Huntley 1993, Allen et al. 2002, Grimm & Jacobson 2004) is a classical approach assuming an unknown underlying non-linear response model. All the widely used remaining techniques fall within the inverse approach and assume linear, non-linear, or unimodal pollen – climate response models (ter Braak 1995). These techniques include segmented inverse linear regression (e.g. Bartlein & Webb 1985, Huntley & Prentice 1988, Bartlein & Whitlock 1993), modern analogues or *k*-nearest neighbours (e.g. Guiot 1990, Bartlein & Whitlock 1993, Peyron et al. 2000,), artificial neural networks (e.g. Peyron et al. 1998, 2000), and weighted-averaging partial least squares regression (WA-PLS) (e.g Lotter et al. 2000, Seppä & Birks 2001, 2002, Seppä et al. 2002).

There is no consensus amongst statisticians about the relative merits of the classical and inverse approaches. Inverse methods perform well if the fossil assemblages are similar in composition to samples in the central part of the calibration-set, whereas classical methods may be better at the extremes and under some extrapolation (ter Braak 1995). There have been surprisingly few comparisons of these two major approaches but the few comparative studies suggest that inverse methods (e.g. WA-PLS) nearly always perform as well as classical methods but often with a fraction of the computational demands of classical approaches (ter Braak et al. 1993, ter Braak 1995, Birks 1998).

The bulk of this paper only considers WA-PLS as it represents a simple, robust approach to climate reconstructions. ter Braak et al. (1993) concluded their comparative study with "until such time that such sophisticated methods mature and demonstrate their power for species – environment calibration, WA-PLS is recommended as a simple and robust procedure."

WA-PLS fulfils the basic numerical requirements (see below) for quantitative palaeoclimatic reconstruction: it performs well with a range of data-sets, it does not involve an excessive number of parameters to be estimated, it is relatively robust statistically, it is computationally economical, and suitable software is widely available (Birks 1995, 2003, Juggins 2003). The basic idea of WA-PLS is to estimate parameter values for each pollen type that summarise the climatic preferences for each type in the modern calibration-set. These values are estimated in such a way so as to maximise the numerical power of the modern calibration-set as a whole to model and to predict the climatic variable of interest today. By means of the statistical tool of cross-validation where the modern data are divided into a training- or calibration-set for model development and a test-set for model assessment, the simplest (fewest number of components) WA-PLS transfer-function model is selected that gives the lowest root mean square error of prediction (RMSEP) and bias in cross-validation using the modern data. This model with its taxon parameters is then used as the transfer function to transform fossil pollen assemblages into quantitative estimates of past climate. Ter Braak and Juggins (1993), ter Braak et al. (1993), ter Braak (1995), and Birks (1995, 1998, 2003) discuss the theory and application of WA-PLS, methods of cross-validation, and stages in model selection and assessment.

POLLEN – CLIMATE TRANSFER FUNCTION ASSUMPTIONS AND REQUIREMENTS

As in all scientific procedures, there are several hidden assumptions in pollen – climate transfer functions (Imbrie & Webb 1981, Birks 2003). These biological and methodological assumptions are:

1. The m taxa in the modern pollen data ($\mathbf{P_m}$) are systematically related to the modern climate ($\mathbf{C_m}$).

2. The climatic variable(s) to be reconstructed ($\mathbf{C_o}$) is, or is linearly related to, an ecologically important climatic determinant in the system studied.

3. The m taxa in the modern calibration data ($\mathbf{P_m}$) are the same biological entities as in the fossil data ($\mathbf{P_o}$) and their ecological responses ($\mathbf{U_m}$) to the climate variable(s) of interest have not changed over the time represented by the fossil assemblage. Thus contemporary spatial patterns of pollen taxon abundance ($\mathbf{P_m}$) in relation to $\mathbf{C_m}$ can be used to infer changes in climate through time.

4. The mathematical methods used adequately model the biological responses to the climate variable(s) of interest and provide transfer functions with sufficient predictive power to yield accurate and unbiased estimates of $\mathbf{C_o}$.

5. Other environmental variables than

the climatic ones of interest have negligible influence, or their joint distribution with the climatic variable(s) in the past is the same as today.

Properties of modern and fossil pollen data critical to transfer-function development are that the data usually contain many taxa (e.g. 50–200 types) and there may be 50–300 samples or more. The data are usually expressed as percentages of the total terrestrial pollen and the data are thus multivariate "closed" compositional data. They often contain many zero values (up to 50% of all values) because some pollen taxa may be absent from many samples.

After Birks (1995, 2003) there are eight major requirements for all quantitative palaeoenvironmental reconstructions (including past climate) from biological "proxy" data (including pollen). These are:

1. A biological system (e.g. vegetation) is required that produces abundant identifiable and preservable fossils (e.g. pollen assemblages) and is responsive to the climatic variable(s) of interest today at the spatial and temporal scales of the study.

2. A large high-quality calibration-set is available that is representative of the likely range of past climate and past fossil assemblages, has consistent taxonomy and nomenclature, is of comparable quality (sampling methods, preparation procedures, counting techniques, count size, etc.), and is from the same sedimentary environment and site type (e.g. small or medium-sized lakes; Seppä & Bennett 2003).

3. Fossil data-sets used for reconstruction should be of comparable taxonomy and quality, and from the same sedimentary environment and site type as the modern calibration-set.

4. Robust statistical methods are required that model the non-linear relationships between modern taxa and their environment and take account of the numerical properties of the biological data.

5. Reliable estimates of prediction errors are required. As the reliability of the reconstructed climatic values can vary from sample to sample, depending on composition, preservation, etc., sample-specific RMSEP are needed for individual fossil samples.

6. Critical evaluation and validation of all reconstructions are essential as any numerical procedure will give results. It is important to assess if the result obtained is ecologically sensible and numerically reliable.

7. The numerical methods used are theoretically sound statistically and ecologically, easy to understand, robust, perform well with large and small data-sets and taxon-rich and taxon-poor assemblages, and are not too demanding in terms of computing resources.

8. The relevant computer software is available within the research community.

Recent work at developing consistent, high-quality modern pollen – climate calibration-sets in Fennoscandia (Seppä & Birks 2001, 2002, Seppä et al. 2004) and Switzerland (Lotter et al. 2000) using consistent field and laboratory methodology, WA-PLS, sample-specific error estimation by bootstrapping (Birks 1995), quantitative evaluation and validation procedures (Birks 1995, 2003), and widely available software (Birks 1995, 2003, Juggins 2003) is an attempt to fulfil these eight basic requirements. We will return to the five underlying assumptions below.

PROGRESS

Two approaches have been adopted to develop modern pollen – climate calibration data-sets in Europe (Seppä et al. 2004). Palaeoclimatic reconstructions at a continental scale or over long glacial – interglacial time scales have been based on large calibration data-sets consisting of 1000–3000 surface pollen samples from various sedimentary environments derived from databases (e.g. Cheddadi et al. 1997, 1998b, Peyron et al. 1998, Tarasov et al. 1999, Davis et al. 2003) or even data-sets of over 8000 modern samples covering much of the northern hemisphere (e.g. Fauquette et al. 1998, Allen et al. 2002). Inevitably, such large data-sets based on surface samples from a range of sedimentary environments and sites of different sizes, and collected and analysed by different workers using different techniques and with no analytical quality control are heterogeneous and can only consist of the major pollen taxa that are identified and counted consistently by all analysts (Seppä & Bennett 2003). An alternative approach has been to develop regional modern pollen – climate calibration data-sets with a smaller number of samples (100–300) but with a high internal methodological, analytical, taxonomic, site-type, and sedimentary consistency and using over 150 pollen and spore taxa (e.g. Seppä & Birks 2001, Lotter et al. 2000, Seppä & Bennett 2003, Seppä et al. 2004).

The available regional data-sets in Europe are summarised in Table 1 in terms of numbers of samples and terrestrial pollen and spore taxa included, range of the climatic variables sampled, and three performance statistics (RMSEP, maximum bias, and the coefficient of determination (r^2) between observed and inferred values). These performance statistics are all based on leave-one-out cross-validation and the simplest WA-PLS model selected using the criteria presented by Birks (1998) (usually 2 or 3 component models). The RMSEPs for these regional models are about 0.64–1.25°C for mean July or mean summer temperature, which is about 8–13% of the climate gradient sampled. The RMSEPs for mean January temperature are 1.5–2.6°C, about 11–14% of the sampled range. The annual precipitation models have the highest RMSEPs (58–418 mm; 11–32% of the sampled range). The combined Finland and Estonia data-set for annual mean temperature has particularly good performance statistics with a RMSEP of 0.89°C (9% of the sampled range). The RMSEP values of these regional pollen – climate models (Tab. 1) are similar or lower than the comparable performance statistics for other biological proxies (e.g. chironomids, cladocera, diatoms) used in palaeoclimatic reconstructions (Seppä et al. 2004).

An important but neglected model performance statistic is the so-called maximum bias. This is estimated by dividing the sampled climatic gradient into 10 equal intervals, calculating the mean bias per interval, and reporting the absolute maximum of the 10 values calculated as the maximum bias (ter Braak & Juggins 1993). Maximum bias is considerably larger than the RMSEP and is 11–43% of the sampled climatic gradient. Maximum bias is particularly high for mean July temperature and annual precipitation in the Norway + N Sweden and Norway + N Sweden + Finland models and for mean January temperature in Finland (Tab. 1).

Overall the performance statistics for the regional pollen – climate models (Tab. 1) suggest that the mean July, summer, or annual temperature can be inferred from modern pollen data (in leave-one-out cross-validation) with a RMSEP of about 0.6–1.3°C, whereas models for mean January temperature and annual precipitation have a higher RMSEP. There is, however, a high maximum bias in almost all the regional models. This bias most commonly occurs at the low end of the sampled temperature gradient, presumably because far-distance pollen from low altitudes or from areas further south result in elevated temperature inferences with a bias of 2–3.5°C. Although the RMSEPs for annual precipitation are seemingly very high, when expressed as a percentage of the precipitation gradient sampled, the RMSEP is about 11–32% of the sampled gradient.

It is difficult to compare the relative performance of the regional and continental pol-

Table 1. Details of the regional pollen – climate calibration data-sets in Europe and their WA-PLS performance statistics based on leave-one-out cross-validation

Region	No. of samples	No. of taxa	Climate range	RMSEP	Maximum bias	r^2	References
Norway + N Sweden	191	152					
Mean July temp °C			7.7 – 16.4°C	1.03°C	3.53°C	0.54	Birks et al. 2000
Mean Jan temp °C			–17.8 – +1.1°C	2.57°C	3.31°C	0.74	Birks et al. 2000
Annual precipitation (mm)			300 – 3234 mm	417.5 mm	951.5 mm	0.68	Birks et al. 2000
Finland	113	84					
Mean July temp °C			10.9 – 17.1°C	0.64°C	1.06°C	0.81	Seppä & Birks unpubl.
Mean Jan temp °C			–16.8 – –3.6°C	1.46°C	5.66°C	0.54	Seppä & Birks unpubl.
Annual precipitation (mm)			395 – 717 mm	57.8 mm	79.5 mm	0.77	Seppä & Birks unpubl.
Annual mean temp °C			–4.7 – +5.4°C	0.91°C	2.12°C	0.85	Heikkilä & Seppä 2003
Norway + N Sweden + Finland	304	156					
Mean July temp °C			7.7 – 17.1°C	0.99°C	3.89°C	0.73	Seppä & Birks 2001
Mean Jan temp °C			–17.8 – +1.1°C	2.34°C	2.13°C	0.76	Seppä & Birks unpubl.
Annual precipitation (mm)			300 – 3234 mm	333.6 mm	951.0 mm	0.73	Seppä & Birks 2001
Finland + Estonia	137	102					
Annual mean temp °C			–4.7 – +5.5°C	0.89°C	2.13°C	0.88	Seppä et al. 2004
Switzerland	126	284					
Mean summer temp °C			4.5 – 20.6°C	1.25°C	2.13°C	0.90	Lotter et al. 2000

len – climate models as performance statistics based on cross-validation are very rarely reported for the continental-scale models (Seppä & Bennett 2003). The RMSEPs for mean July temperature for the regional models (0.64–1.03°C) are about 50% lower than the RMSEP presented by Davis et al. (2003) for their 2363 sample European-scale calibration model (2.25°C). In contrast, the RMSEPs for mean January temperature for the regional models (1.46–2.57°C) are similar to the European model's RMSEP of 2.58°C.

The Norway + N Sweden model (Tab. 1) has been used to derive quantitative estimates of Holocene and late-glacial climate in northern Sweden (Bigler et al. 2002, Hammarlund et al. 2002, Birks & Birks 2003) and in western Norway (Birks et al. 2000, H.J.B. Birks, S.M. Peglar, and A.E. Bjune unpubl.). The combined Norway + N Sweden + Finland model (Tab. 1) has been used to infer Holocene and Younger Dryas climates in northernmost Finland (Seppä & Birks 2001, 2002, Fig. 3) and northern Norway (Seppä et al. 2002, Bjune et al. 2004). The Finnish annual mean temperature model (Tab. 1) has been used to reconstruct Holocene climate changes in southern Finland (Heikkilä & Seppä 2003), the Finland + Estonia model has been used for Holocene annual mean temperature reconstructions in Estonia (Seppä & Poska 2004), and the Swiss model (Tab. 1) has been used to reconstruct late-glacial and Holocene climate in Switzerland (Lotter et al. 2000, Wick et al. 2003). The resulting reconstructions are consistent and accord well with several independent palaeoclimatic records (e.g. Lotter et al. 2000, Seppä & Birks 2001, 2002, Hammarlund et al. 2002, Fig. 3). These reconstructions based on modern regional pollen – climate data-sets indicate that quantitative reconstructions of Holocene and even late-glacial climate in parts of Europe are possible from pollen stratigraphical data, at least at a broad temporal scale. The next section will outline some of the problems associated with these reconstructions.

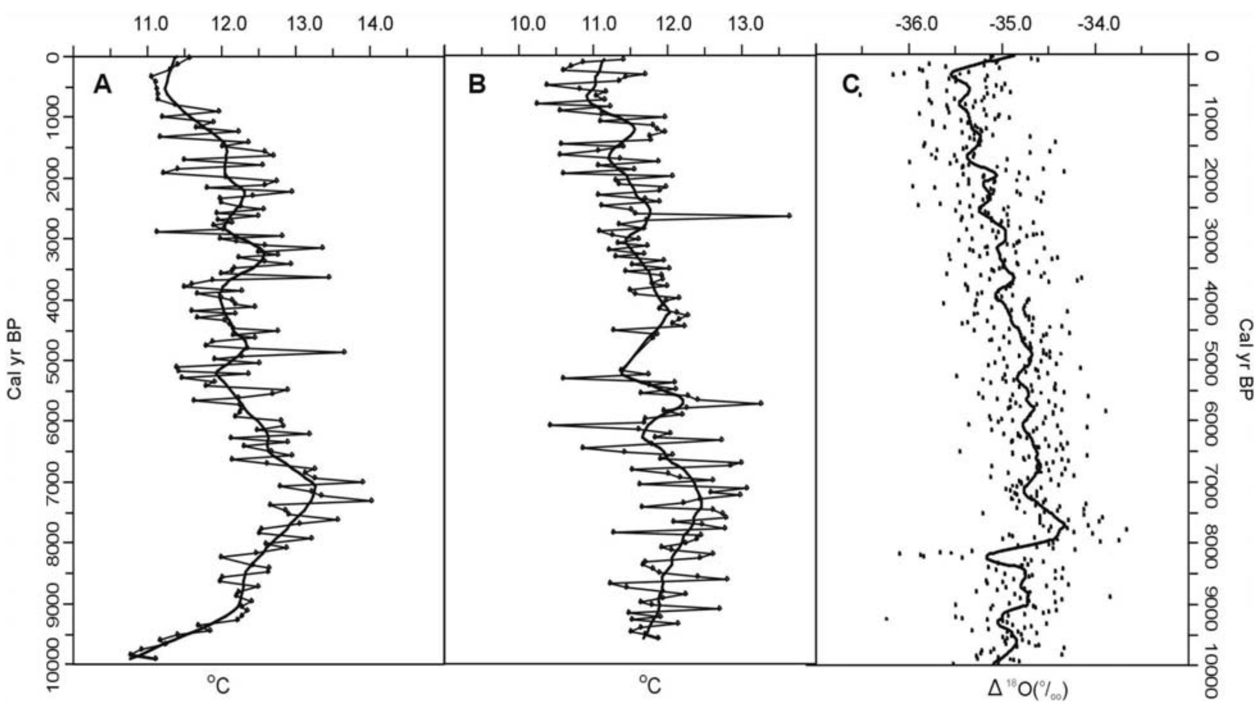

Fig. 3. Two pollen-based quantitative July mean temperature reconstructions for the last 10 000 years from two small lakes in the tree-line region of Finnish Lapland, reconstructed using a combined Norwegian-Finnish calibration set (Tab. 1). **A** = Tsuolbmajavri, 68°41′N, 22°05′E (Seppä & Birks 2001), **B** = Toskaljavri, 69°12′N, 21°28′E (Seppä & Birks 2002). The original reconstructed data points are shown as circles and the thicker black lines represent LOESS smoothers with span 0.10. The estimated modern July temperature of Lake Tsuolbmajavri is 11.0°C and Lake Toskaljavri 9.7°C. The section between 5150 and 4700 cal yr BP of the Toskaljavri record has been deleted due to an inferred redeposited sediment layer. The main trends of the two records are roughly similar, indicating the highest July mean temperatures at about 8000–65 000 cal yr BP and gradual cooling during the late Holocene. Tsuolbmajavri has about 1.0°C higher temperature all through the study period. **C** = the $\delta^{18}O$ record of the NorthGRIP ice core from central Greenland and is shown for comparison (Johnsen et al. 2001). The record has been smoothed by fitting a LOWESS smoother with span 0.05 to the data points which represent 20-years moving averages

PROBLEMS

There are currently several unresolved problems in quantitative pollen – climate reconstructions, several of which we believe can be resolved with further statistical, palynological, and climatic research.

1. Statistical model selection. Modern pollen data, when sampled over long climate gradients, commonly show a mixture of symmetric unimodal (ca. 40%) and sigmoidal monotonic responses (ca. 40%), a few skewed unimodal responses (<5%), and some null responses (ca. 15%) implying no statistically significant responses to the climate variable of interest. The data also show considerable variation in the tolerances or ecological breadths of different taxa and have a compositional turnover or "gradient length" of 2–3 standard deviation units (e.g. Seppä et al. 2004, Birks unpubl.). Such data show too many monotonic responses for the investigator to feel comfortable with using a unimodal-based calibration method such as WA-PLS and too many unimodal responses for linear-based methods such as linear-PLS (Birks 1995). Flexible "classical" methods that can cope with a mixture of unimodal and monotonic responses like Gaussian or multinomial logit regression and calibration should be re-investigated. They were tried in the late 1980s and early 1990s (ter Braak & van Dam 1989, Birks et al. 1990) but discarded because of computational limitations and programming problems at that time.

2. Statistical model bias. Different numerical methods, all with an implicit underlying model, can give very different reconstruction results (e.g. C.J.A. Birks 2001, Birks 2003) even though they can have very similar modern model performance statistics. There is accumulating evidence of model bias when applied to fossil data. For example, reconstructions based on modern analogue techniques (MAT) generally show low variability within the Holocene, whereas WA-PLS and its linear counterpart PLS show considerably more variability. In terms of modern model performance alone, all seem good in terms of RMSEP and maximum bias. These results raise questions as to whether one should try to select one model for reconstruction or whether one should use several reconstruction results and develop a consensus reconstruction (e.g. Bartlein & Whitlock 1993, Birks 1995, Birks & Birks 2003).

The general insensitivity of MAT-based reconstructions of Holocene climates may result from the occurrence of so-called "multiple analogues" (ter Braak et al. 1996), namely compositionally similar modern pollen assemblages from different contemporary climates. Attempts to circumvent these problems and to sharpen the sensitivity of MAT-based reconstructions include constraining the possible modern analogues to be within the pollen-inferred biome (e.g. taiga, cold conifer forest) from which the fossil pollen assemblages are inferred to have originated from (e.g. Magny et al. 2001, 2003). An additional constraint used is to constrain the possible modern analogues to those that would infer a past climate compatible with the reconstructed lake-level status at particular times in the past (Guiot et al. 1993, Cheddadi et al. 1997, Magny et al. 2001, 2003, Muller et al. 2003). Interestingly, MAT-based reconstructions without any such constraints but based on a modern regional data-set of 636 samples from the western Mediterranean (Cheddadi et al. 1998a) rather than a continental-scale data-set suggest considerable variation in annual precipitation during the Holocene at a site in the Middle Atlas Mountains of Morocco. The inferred precipitation trends match reconstructed lake-level changes in the same core based on independent palaeolimnological data (Lamb et al. 1995).

Davis et al. (2003) used a MAT-approach to reconstruct Holocene climate at 510 sites across Europe. They converted the modern pollen data (2363 samples) to 21 plant functional types (PFT) (Peyron et al. 1998) and then compared modern and fossil pollen assemblages expressed as plant functional types, rather than as individual taxa. Plant functional types are broad classes of plants defined by stature, life-form, phenology, physiology, leaf form, and climatic tolerances (Prentice et al. 1996).

3. Sample-specific errors of reconstruction for individual samples. These are generally 1–1.7°C for mean July or mean summer temperature for Holocene pollen assemblages (e.g. Birks 2003). These errors are close to the likely magnitude of summer temperature in the Holocene. When the sample-specific errors are plotted stratigraphically (e.g. Birks 2003), there is commonly a consistent temporal trend in the reconstructed values but continuous overlap in the associated errors (e.g. Bigler et al. 2002, Birks 2003, Heikkilä & Seppä 2003,

Seppä & Poska 2004). A critical problem is thus how to identify the underlying long-term temporal "signal" from the inherent "noise" and chance variation in the stratigraphical data on which the reconstruction is based, and how to incorporate the sample-specific errors in interpretations, comparisons, and syntheses. An approach that Seppä & Birks (2001, 2002) and Bigler et al. (2002) have used to identify long-term temporal "signals" is to fit locally weighted least square regression smoothers (LOWESS) to the reconstructions (e.g. Cleveland 1993). As Birks (1998, 2003) discusses, there is a considerable variety of potential smoothers to use and problems in deciding which smoother to use and what degree of smoothing to apply. More sophisticated smoothers such as SiZer (Chaudhuri & Marron 1999) have considerable potential because they provide a statistical basis for assessing which features seen in a series of smoothers are statistically significant (see Korhola et al. 2000).

4. Presentation of palaeoclimate reconstructions. Palaeoclimatologists are often most interested in climatic "anomalies" or "deviations" from present-day values (e.g. Δ = –1.2°C, Δ = +2.4°C). There are several options available in the presentation of pollen-based climate reconstructions – (i) as the inferred value in °C, mm precipitation, etc, (ii) as deviations (Δ) from the observed present-day value at the study site, (iii) as deviations (Δ) from the pollen-inferred present-day value at the study site, (iv) as deviations (Δ) from the mean of all reconstructed values for the last 100, 200 (Heikkilä & Seppä 2003, Seppä & Poska 2004) or 250 years, or (v) as deviations (Δ) (possibly standardised) of the mean of all reconstructed values for the sequence under study. Despite the considerable advances that have been made in techniques for reconstructing past environments from fossil assemblages, much work is needed on how to present optimally the reconstructed climatic temporal-series and how to detect consistent trends and patterns within such temporal-series (Birks 2003).

5. Validation of palaeoclimatic reconstructions. An important aspect of quantitative reconstructions is to attempt an independent validation of the climatic reconstructions. It is clearly possible to develop modern transfer functions with good modern model performance statistics in terms of low RMSEP and maximum bias (Tab. 1). How reliable are the resulting reconstructions for 6000 BP, 8000 BP, etc? Although there is a series of reconstruction-evaluation statistics (Birks et al. 1990, Birks 1998, Bigler et al. 2002), what is needed is rigorous comparisons with independent climate "proxies" such as ice-cores, stable isotopes, or other biological proxies. Unpubl. work in Norway in which chironomid-based transfer functions are applied to reconstruct mean July temperatures in the Holocene (Brooks et al. unpubl.) shows that pollen-based and chironomid-based reconstructions can give very different results for the same stratigraphical sequence (see also Rosén et al. 2003). The critical question is thus, which reconstruction is the more reliable? Additional means of independent validation are needed to help decide which reconstruction should be accepted. One approach (Birks & Birks 2003) is to use plant macrofossil evidence as proof of local presence of, for example, tree *Betula* or *Pinus sylvestris*. On the basis of modern ecological studies, their local presence can set lower limits (e.g. mean July temperature of 11°C or more) for the climate at the times when macrofossils occur. Another approach is to use the newly developed probability density function (PDF) technique (Kühl et al. 2002, Kühl 2003, Kühl & Litt 2003). This estimates modern "climate envelopes" for a range of taxa that commonly occur as macrofossils or as scattered pollen grains (e.g. *Dryas octopetala*). The PDFs for a range of indicator taxa present in a fossil assemblage can then be used as an independent validation of pollen- or chironomid-based climate reconstructions based on the quantitative aspects of the assemblage. Other biological and physical variables can also be used in reconstruction validation (see Birks 1986, MacDonald & Edwards 1991, Huntley 1996, 2001).

An obvious approach to validating pollen – climate models is to compare inferred climate values with historical instrumental data series, as has been done with chironomid (Larocque & Hall 2003) and diatom data (Bigler & Hall 2003) in northern Sweden. A major problem in this approach is to derive a reliable chronological basis for comparing inferred climatic values with historical values. Every pollen sample and resulting climatic reconstruction integrates several years. Even with very high-resolution pollen stratigraphy and ^{210}Pb-dating, it is not possible to say that a particular pollen sample represents, for example, AD 1930–1936 and can thus be compared with the mean of the historical data for that period. Results from the European MOLAR palaeolimnology project in which a range of palaeolimnological data were compared with instrumental climatic records at mountain lakes across Europe (Battarbee et al. 2002) highlight the chronological problems in such comparisons.

In this respect the most promising approach is to use annually laminated sediments in such regions where it is possible to use long instrumental or documentary meteorological records for comparison and validation. In work currently in progress in Estonia, pollen analyses are carried out with samples that comprise on average 3 years (3 laminae) and with an average sample interval of 10 years (Veski & Seppä unpubl.). The annual mean temperatures since AD 1500 are reconstructed from this data set using the Finnish-Estonia pollen – climate calibration set (Tab. 1). The reconstructed temperature patterns can be compared with the unique historical record of the break-up dates of the sea ice in the harbour of Tallinn, Estonia. This data set has been transformed by linear regression into a mean winter temperature (December to March) record back to AD 1500 (Tarand & Nordli 2001). One problem with this approach is that the pollen record may be more responsive to spring-summer temperature than winter temperature. Hence, the pollen-based reconstruction is also compared with a spring-summer (April to June) temperature record, derived from historical meteorological records back to AD 1731 (Tarand & Nordli 2001). The preliminary results suggest that the pollen-based temperature reconstructions show similar long-term trends both with the winter temperature and the spring-summer temperature records, with a marked cold period at about 1570 to early 1800s, followed by warming towards the present. However, this work has also highlighted a new problem associated with validation efforts using the historical meteorological data series, namely the role of varying human influence of vegetation. Thus, it is currently impossible to know if the reconstructed low values at about 1570–1800 in Estonia are due to a cold climate and resulting decreased regeneration and pollen production and increased mortality of the thermophilous plant species or due to human impact, especially clearance of mixed oak forests for agriculture and timber production.

6. Obtaining reliable climate values for sites today. A major practical problem in developing modern pollen – climate calibration data-sets even at a regional scale is deriving reliable estimates of present-day climate for individual sites, especially in mountainous areas. In all the regional data-sets discussed here (Tab. 1), modern climate values for individual lakes have been derived by standard procedures of interpolation from existing meteorological stations with allowances for lake altitude and geographical location (see Korhola et al. 2001). The basic climatic data used in these interpolations are the 1961–90 normals data. It is unknown if this climate period is appropriate for comparison with modern pollen assemblages preserved in the uppermost 1 cm of surficial lake sediment, which may represent 5–50 years. It is possible that geographical information systems and spatially-explicit statistical modelling and robust interpolation procedures (e.g. Fotheringham et al. 2000) may improve the estimation of climate data for individual sites. Such data are an essential and critical part of modern pollen – climate calibration data (Fig. 1).

7. Improving the numerical techniques for deriving transfer functions. In theory, the numerical procedures could include information about the tolerances or ecological breadths of different taxa today, so that taxa with broad tolerances would carry less weight in the model and the resulting reconstructions than taxa with narrow tolerances (ter Braak & van Dam 1989, Birks et al. 1990). In the case of pollen and spores, the taxa may represent entire families (e.g. Rubiaceae), ecologically diverse categories (e.g. *Ranunculus acris* type), individual genera (e.g. *Quercus, Ulmus*), or individual species (e.g. *Plantago lanceolata*) because of pollen-morphological limitations. In such instances it is unclear what information would be gained by incorporating some form of tolerance weighting in the transfer functions, as the actual tolerances of a pollen taxon may change with time, depending on the composition of the actual plant species in the "species pool" that, at a given time, produces the pollen taxon *Ranunculus acris* type or Rubiaceae.

Improvements in numerical methodology may come from using artificial neural networks or adopting a Bayesian framework (Birks 2003). Artificial neural networks (ANN) have been used by Peyron et al. (1998, 2000) to reconstruct past climates from fossil pollen. In their study on European data at 18 000 BP, Peyron et al. (1998) assigned 93 pollen taxa into 17 "plant functional types" (PFT) and used the PFT scores as $\mathbf{P_m}$ (Fig. 1) in an ANN estimation of modern transfer functions. It is currently unclear what advantage assigning taxa to PFTs has on the final reconstruction, compared with using all taxa individually as in WA-PLS. Although there are clear advantages in developing transfer functions based, for example, on diatoms or chironomids (e.g. Korhola et al. 2002) within a Bayesian framework, it is unclear what major advantages such a framework would provide for pollen data because of the pollen-morphological limitations discussed above. However, recent and as yet unpubl. work by John Haslett and colleagues (Whiley et al. 2004 a, b) adopts the Bayesian perspective in climate reconstructions from pollen-stratigraphical data from a site in Ireland, in an attempt to take advantage of expressing the reconstruction problem in explicit hierarchical terms and to model the myriad of uncertainties involved in pollen – climate reconstructions (Haslett, pers. comm.). This work uses flat prior probabilities but the methodology clearly allows the use of other priors if appropriate.

8. Existing pollen – climate reconstruction models reconstruct one or two climatic variables (Tab. 1) that have a high statistical relationship with pollen distribution and abundance today (Seppä et al. 2004). Vegetation and pollen assemblages may not be directly influenced by these variables but by a complex combination and interaction of many variables which may be correlated with each other (Woodward 1987, Dahl 1998). Quantitative reconstructions of, for example, mean July temperature and annual precipitation, cannot represent the total past climate, especially if there were interactions between climatic variables in the past that are different from present-day interactions (see MacDonald & Edwards (1991) and Assumption 5 above).

These are all problems that, in theory at least, can be overcome by improving data collection and quality, developing new numerical methods, applying novel statistical approaches and new graphical tools, and improving validation procedures. There are, however, several pitfalls in the use of pollen-stratigraphical data as a means of reconstructing past climate in Europe. These pitfalls are an inherent function of pollen-analytical data and of European ecology. At present there are no obvious ways of resolving these pitfalls.

PITFALLS

1. Far-distance pollen. Long-distance dispersed "extra-regional" pollen is blown into sites from areas at lower altitudes or further south. This is a major and well-known problem of pollen analysis of sites above or beyond the tree-line (e.g. Rosén et al. 2003). Plant macrofossils are a valuable guide to local species presence (Birks & Birks 2000, 2003). However, the absence of macrofossils does not mean that the species was absent locally. The net result of far-distance pollen on pollen-based climate reconstructions is that resulting climatic estimates are higher than the actual values. This effect is well illustrated today by the high maximum bias in the modern pollen – climate models at sites with low summer temperatures today that are above or beyond the present-day tree-line (Seppä & Birks 2001). Far-distance pollen results in $\mathbf{P_m}$ being an even more complex function of $\mathbf{V_m}$ than is represented in Expression (1) above.

2. Human activity. In the underlying theory of modern pollen – climate reconstructions, we assume that

$$\mathbf{P_m} = f_1\ (\mathbf{V_m})$$

where f_1 is some function related to pollen representation (production and dispersal biases) and relevant pollen source area.

We also assume that

$$\mathbf{V_m} = f_2\ (\mathbf{C_m})$$

where f_2 is a function linking modern vegetation to modern climate.

In reality, in much, if not all, of the present European landscape, vegetation is a reflection of

$$\mathbf{V_m} = f_2\ (\mathbf{C_m}) + f_3\ (\mathbf{H_m})$$

where $\mathbf{H_m}$ is human impact at a range of spatial scales.

In all pollen – climate models $\mathbf{H_m}$ is largely ignored (MacDonald & Edwards 1991, Seppä & Bennett 2003). In northern Europe, the effects of human impact increase the pollen percentages of Poaceae, Ericaceae, and *Juniperus communis*, all of which (in the absence of human activity) are associated with low temperatures (Seppä et al. 2004). Holocene climate reconstructions may therefore be difficult to evaluate, especially when there is independent evidence for human activity in the study region.

3. Pollen production and climate. Pollen representation is a function of vegetation which, in turn, is a function of climate PLUS a function which is the interaction between vegetation and climate. The same vegetation type in different climates may have different pollen productivities and hence different pollen representations. This can be expressed as

$$\mathbf{P_m} = f_1\ (\mathbf{V_m}) + f_4\ (\mathbf{V_m} \cdot \mathbf{C_m})$$

In eastern Norway, for example, the relative pollen representation of *Pinus* and *Picea* appears to be considerably greater than in western Norway (Birks & S.M. Peglar unpubl.).

4. Biological interactions. The pollen – climate model does not explicitly consider or include biological interactions. Modern vegetation is, in all reality, a function not only of climate, human activity, and soils, but also a function of biological interactions between different taxa, namely

$$\mathbf{V_m} = f_2\ (\mathbf{C_m}) + f_3\ (\mathbf{H_m}) + f_5\ (\mathbf{S_m}) + f_6\ (\mathbf{B_m})$$

where $\mathbf{S_m}$ = modern soils and $\mathbf{B_m}$ = biological interactions.

As climate, human activity, soils, and biological processes may themselves interact, the model for modern vegetation is thus something like

$$\mathbf{V_m} = f\ (\mathbf{C_m} + \mathbf{H_m} + \mathbf{S_m} + \mathbf{B_m} + \mathbf{C_mH_m} + \\ + \mathbf{C_m}\ \mathbf{S_m} + \mathbf{C_mB_m} + \mathbf{H_mB_m} + \ldots\ \mathbf{S_mB_m})$$

In the case of Fennoscandia it is unknown if there were significant lags in tree spreading in the early-Holocene. There is evidence to suggest that the expansion of *Betula* in the early-Holocene in western Norway was delayed by about 500 years when pollen and plant macrofossil records are compared with chironomid-based temperature inferences (Birks et al. 2000). Because of the discordance between middle- and late-Holocene chironomid-based temperatures and other biological proxies, it is not currently possible to say if the asynchronous spread and expansion of *Alnus, Quercus,* and *Picea* in Fennoscandia are a result of migrational lags, dating uncertainties, or interactions between climate change and biotic factors. MacDonald and Edwards (1991) and Seppä and Bennett (2003) discuss in detail the question of lags and the resulting problems in pollen-based climate reconstructions.

5. Pollen morphological and identification limitations. These are a major pitfall. An obvious problem is the near impossibility of consistently separating pollen of *Betula nana* from tree birch (*B. pubescens, B. pendula*). There is considerable macrofossil evidence to indicate that the earliest Holocene rise of *Betula* pollen in southern and western Norway reflects the local abundance of dwarf birch rather than the spread of tree birch (van Dinter & Birks 1996). Because *Betula* pollen cannot be consistently separated into *B. nana* and tree *Betula*, the resulting pollen-based mean July reconstructions of 12–13°C in the earliest Holocene in southern Norway are probably 2–3°C higher than the likely past climate based on plant macrofossils. In general, pollen-based climate reconstructions tend to give higher July estimates than would be inferred from plant macrofossils alone (H.H. Birks & H.J.B. Birks unpubl.). Such over-estimates may result from several factors including far-distance pollen transport and pollen-morphological "bluntness".

6. Gradient ends. An inherent pitfall of all unimodal-based reconstruction procedures using weighted-averaging estimation (e.g. WA-PLS) is the "edge effect" that results in distortions at the ends of the environmental gradient sampled (ter Braak & Juggins 1993). Although an inverse deshrinking regression within WA-PLS helps to reduce these edge effects, an inevitable bias remains with over-estimates at low modern values and under-estimates at high modern values. At present there seems to be no way to reduce the truncation of taxon responses and hence under- or over-estimation of taxon parameters except by using shorter climatic gradients, linear-based models, and thus environmentally restricted local calibration sets (Birks 1998, 2003).

7. Problems of "no-analogue" assemblages. WA-PLS performs surprisingly well and considerably better than direct analogue matching procedures when none of the fossil pollen assemblages are similar to the modern data (ter Braak et al. 1993, ter Braak 1995, Birks 1998). WA-PLS is, in reality, a multivariate

"indicator species" approach where all fossil taxa are used in the climate reconstruction and estimates of the taxon parameters are derived from the modern calibration data rather than modern autecological observations. The resulting climate reconstruction is a weighted summation of these taxon parameters. Problems do, however, arise in the late-glacial where the ability to extrapolate beyond the modern calibration data-set is limited and the resulting pollen-based climate reconstructions are consistently warmer than are suggested by plant macrofossils (Birks et al. 2000). Seppä & Bennett (2003) discuss possible approaches to reconstructing late-glacial and full-glacial climates from no-analogue assemblages using plant functional types (Peyron et al. 1998) and inverse vegetation modelling approaches (Guiot et al. 2000).

BASIC ASSUMPTIONS REVISITED AND FINAL CONCLUSIONS

In conclusion, we revisit the five basic assumptions presented earlier in light of the various problems and pitfalls that we have discussed.

Given the importance of human activity on European vegetation and landscapes, it is unlikely that all the taxa in all parts of Europe in modern pollen data ($\mathbf{P_m}$) are systematically related to modern climate ($\mathbf{C_m}$) (assumption 1). To what extent this assumption is violated is difficult to evaluate as it depends on the spatial scales of study. At the scale of Fennoscandia, it is likely that this assumption is violated, to some degree, for taxa such as Poaceae, Ericaceae, and *Juniperus communis*.

Climatic reconstructions are usually made for mean temperature of the warmest month, coldest month, or annual means, whereas plant growth and distribution are probably influenced more by parameters such as growing-season degree days, moisture availability, and temperature extremes (Dahl 1998). Many climate variables are highly inter-correlated, so assumption 2 (the climatic variable reconstructed is ecologically important or is linearly related to an ecologically important climatic variable) is probably valid. There is currently no means of testing assumption 3, namely that the taxa in the modern calibration data are the same biological entities as in the fossil data and that their ecological responses to climate have not changed over time. Davis & Shaw (2001) and Seppä & Bennett (2003) discuss the question of genetic adaptations in the context of the late-Quaternary.

Performance statistics of the modern pollen – climate models (Tab. 1) suggest that the mathematical models adequately model the biological responses to climate (assumption 4).

The fifth assumption, namely that environmental variables other than the climatic variables of interest have negligible influence or their joint distribution with the climate variable(s) in the past is the same as today remains largely untested. There is increasing evidence (e.g. Davis et al. 2003) to suggest that winter and summer temperatures show a high degree of independence during the Holocene. The ecological implications of independent changes in winter and summer temperatures on plant distribution and abundance and hence on pollen assemblages are unknown. Other important ecological factors today such as human activity cannot have had the same joint distribution with climate in Fennoscandia during the Holocene. There is thus the need to test the robustness of pollen-climate reconstruction models to violations of this assumption, along the lines that Le & Shackleton (1994) developed in their work using simulated data in the marine realm.

Quantitative reconstructions of past climate from pollen-stratigraphical data are possible in Europe. The resulting reconstructions are generally consistent, sensible, and agree well with other independent reconstructions (Fig. 3), at least at broad spatial and temporal scales (Seppä & Bennett 2003). There are several unresolved methodological problems such as developing models that can combine both linear and unimodal responses, detecting "signal" from "noise" in the resulting reconstructions, understanding potential methodological bias, interpreting sample-specific errors of reconstruction, presenting reconstructions in a clear and unbiased way, and attempting more rigorous independent validations of the reconstructions. Hopefully some of these methodological problems will be addressed in future research. However, there are also several pitfalls in pollen-based climate reconstructions in Europe, such as far-distance pollen, possible migrational lags and biotic interactions, human activity, pollen morphological limitations, no-analogue pollen assemblages, and geographical variation in pollen production and representation. The relative importance of these pitfalls that may result in the violation of some of the basic assumptions could be investigated by carefully designed numerical experiments using simulated data (both calibration and test data) of known properties (ter Braak et al. 1993, ter Braak 1995). The magnitude of far-distance extra-regional pollen, the extent of taxonomic discrimination, the effect of geographical variation in pollen production, and the impact of taxa with no direct relation to climate to simulate the anthropogenic factor on pollen – climate models could be studied and quantified.

Compared with other biological climatic proxies, pollen are probably one of the most useful and ubiquitous terrestrial sources for climatic reconstructions, at least at broad millennial scales. There is, however, a clear need for improvements in methodology and increased caution in the interpretation of the resulting reconstructions. Seppä & Birks (2001, 2002) reconstructed Holocene climate for two sites in north-west Finland. The reconstructions are generally consistent and resemble the Holocene palaeotemperature records from the Greenland ice-cores (Fig. 3). There are, however, considerable differences in the fine-scale variability of the two reconstructions. It is uncertain how much of this variability reflects local-scale climatic variation, noise resulting from inherent non-climatic variability in pollen-stratigraphical data, and prediction errors and biases in the modern pollen – climate transfer functions (Seppä & Bennett 2003). It remains unclear if stratigraphical pollen percentage data are sensitive enough to detect fine-scale centennial or decadal climatic shifts, because of the complex of biological factors that may influence pollen – climate relationships at fine-scales.

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