Veget Hist Archaeobot (2006) 15: 235–251
DOI 10.1007/s00334-006-0066-6

REVIEW ARTICLE

Hilary H. Birks · H. John B. Birks

Multi-proxy studies in palaeolimnology

Received: 28 April 2005 / Accepted: 8 March 2006 / Published online: 27 July 2006

Abstract Multi-proxy studies are becoming increasingly common in palaeolimnology. Eight basic requirements and challenges for a multi-proxy study are outlined in this essay – definition of research questions, leadership, site selection and coring, data storage, chronology, presentation of results, numerical tools and data interpretation. The nature of proxy data is discussed in terms of physical proxies and biotic proxies. Loss-on-ignition changes and the use of transfer functions are reviewed as examples of problems in the interpretation of data from multi-proxy studies. The importance of pollen analysis and plant macrofossil analysis in multi-proxy studies is emphasised as lake history cannot be interpreted without knowledge of catchment history. Future directions are outlined about how multi-proxy studies can contribute to understanding biotic responses to environmental change.

Keywords Data interpretation · Loss-on-ignition · Multi-proxy studies · Palaeoecology · Palaeolimnology · Project design · Transfer functions

Introduction

Ecosystems can be thought of as an almost infinite network of interactions among biotic and abiotic components balanced between internal and external driving factors. In a stable ecosystem the interactions are in balance, but when they become unbalanced the character of the ecosystem will change. The change may be small or substantial and may occur suddenly in a short time or slowly over an extended period. A rapid change occurring in the present may be monitored by regular observations. However, many changes have been proceeding over a long period before observation was possible, and some rapid and extensive changes have occurred far back in the past. In order to study the dynamics of these ecosystems we have to look back into the past by using the record of changes in fossil organisms and sediment characteristics ('proxy' data) to reconstruct past ecosystems and biotic responses. Because of the complex network of interactions throughout the ecosystem, it is desirable to study as many proxies as possible in order to gain a wider overview of the situation than could be acquired from a single proxy (Smol 2002; NRC 2005). Such an investigation is called a multi-proxy study. In this essay about multi-proxy studies we shall concentrate on lake-sediment studies (palaeolimnology) in temperate areas, although one should be aware that successful multi-proxy studies have been carried out on peats (e.g. Booth and Jackson 2003; Pancost et al. 2003; Booth et al. 2004; Chambers and Charman 2004; Charman and Chambers 2004; Mighall et al. 2004), dendrochronological series (e.g. McCarroll et al. 2003), archaeological sites (e.g. Clark 1954; Wasylikowa et al. 1985; Davies et al. 2004; Selby et al. 2005), salt-marsh sediments (e.g. Gehrels et al. 2001), freshwater-marsh sediments (e.g. Finkelstein et al. 2005) and marine sediments (e.g. Andersson et al. 2003; Oldfield et al. 2003a; Risebrobakken et al. 2003; Haug et al. 2005), and in tropical (e.g. Verschuren et al. 2000; Vélez et al. 2005) and extreme polar (e.g. Birks et al. 2004; Hodgson et al. 2005) environments.

The earliest multi-proxy studies, reviewed by Wright (1966) and Birks and Birks (1980), used the palaeolimnological record to test ideas of lake ontogeny and biotic responses over time to external perturbations and internal processes. Although these studies used selected taxa and proxies and there was little or no statistical or numerical

Communicated by Pim van der Knaap

H. H. Birks (✉) · H. J. B. Birks
Department of Biology, University of Bergen,
Allégaten 41,
5007 Bergen, Norway
e-mail: Hilary.Birks@bio.uib.no

H. H. Birks · H. J. B. Birks
Bjerknes Centre for Climate Research,
Allégaten 55,
5007 Bergen, Norway

H. H. Birks · H. J. B. Birks
Environmental Change Research Centre, University College London,
London WC1H 0AP, UK

analysis, they provided elegant and carefully argued narratives, emphasising limnological processes and the role of catchment changes on lake dynamics. They are major contributions and in many ways they present a challenge to palaeolimnologists today to make further advances in our understanding of lake development and dynamics (Deevey 1984; Likens 1985). In palaeolimnological studies these days, a multi-proxy approach is the norm, but the aims of investigating ecosystem dynamics have turned more towards the reconstruction of past environments and climate changes (Lotter 2003). The synthesis of multi-proxy results in successful studies exceeds the sum of the component parts. However, as knowledge and experience expand, problems have become apparent in the use of some of these component parts for ecosystem reconstruction.

Extensive and detailed reviews of multi-proxy studies in palaeolimnology and palaeoecology include Wright (1966), Birks and Birks (1980), Delcourt and Delcourt (1991), Smol (2002), Cohen (2003), Lotter (2003), Pienitz et al. (2004) and NRC (2005). The four volumes on palaeolimnological methods edited by Last and Smol (2001a, b) and Smol et al. (2001a, b) provide detailed accounts of the full range of field and analytical techniques currently available in palaeolimnology.

The essential aspect of any multi-proxy study is that several proxies are used simultaneously to address the aims of the project. The methods used will, of course, be related to the research question under investigation. The study of lake sediments can be directed towards reconstructions of the aquatic environment and/or of the terrestrial catchment of the lake, even including the regional landscape beyond the catchment. The factors or processes behind the reconstructed changes (patterns) in the lake ecosystem can be sought in terms of causal processes such as changes in climate, both temperature and precipitation, or human activity that affect most aspects of lake ecosystem functioning. Often, more specific questions are asked concerning both natural and human-induced changes in lake-water quality and catchment characteristics, especially changes in vegetation and the catchment that affect the lake either directly or indirectly (Birks et al. 2000; Lotter and Birks 2003).

The results of a multi-proxy study are usually presented and discussed in a descriptive or narrative way (Birks 1993a), using all the lines of evidence to reconstruct various aspects of the past ecosystem and to deduce the range of changes it has undergone. The value of any multi-proxy study clearly rests on the reliability of the proxies used to reconstruct the past environmental conditions. Different proxies reflect different environmental factors at a range of spatial scales and consequently show different strengths and weaknesses. By combining proxies, strengths can be exploited and weaknesses can be identified (Mann 2002). However, weaknesses exposed by multi-proxy studies should not be ignored. They demonstrate shortcomings in methodology and resolution, limitations in taxonomic identifications, lack of understanding of the taphonomy of fossils, and gaps in our knowledge of the relationships of proxies, both biological and physical, to environmental factors. Thus important new lines of research may be stimulated.

There have been many major advances in palaeolimnology in the last 25 years, as reviewed by Smol (2002). In the context of multi-proxy studies discussed here there have been at least six major areas of development. (1) the study of new proxies such as stable isotopes, near-infrared spectroscopy, organic chemistry and bio-markers, chironomids and organic contaminants; (2) improved chronological tools including the discovery of lakes with annually laminated sediments, improvements in ^{14}C dating, ^{14}C calibration and ^{210}Pb dating, and the development of other dating techniques; (3) increasing use of quantitative methods for summarising patterns in complex stratigraphical data and for deriving transfer functions to reconstruct quantitatively past environmental variables from biological proxy data; (4) an increase in fine-resolution studies, often utilising laminated sediments; (5) increasing concern for careful and rigorous project design, site selection, and hypothesis testing; and (6) an emphasis, perhaps an over-emphasis, on palaeoenvironmental reconstructions, with a corresponding neglect of lake biotic responses to changing internal or external factors, of lake dynamics and processes, and of the underlying biology and ecology of the organisms preserved as proxy records in lake sediments. The aim of this essay is to outline some of the methodological and conceptual aspects and challenges of multi-proxy studies in palaeolimnology. It makes no attempt to be exhaustive and inevitably reflects our personal interests and biases, particularly towards quantitative approaches and to recent (last 100–300 years), Holocene, and late-glacial palaeolimnology. It also reflects our research experiences in temperate areas, and our collaborations with colleagues in the UK, Fennoscandia, USA, Canada, The Netherlands, and Switzerland.

Basic requirements and challenges for a multi-proxy study

1. As in any scientific investigation, clear research questions are needed at the outset that the study aims to address. This is especially important in multi-proxy studies as they inevitably involve several scientists collecting a large amount of data. This process is often very time-consuming and therefore expensive in time, effort, and resources.
2. A good leader is required, with effective communication and co-ordination skills, a broad knowledge, a flexible approach, and an enthusiasm and determination to synthesise and publish the results. Multi-proxy studies accumulate large amounts of data (e.g. an estimated 25,000 data points were collected in the Kråkenes Project; Birks et al. 1996, 2000; Birks and Wright 2000). Thus the project has to be carefully planned and co-ordinated from the outset so that all the data are available to all the participants at the synthesis and writing-up stages. A major benefit from a well co-ordinated study is that all the participating scientists are involved and

cross-disciplinary links and collaboration can be established.

3. Because so much work goes into a multi-proxy study it is vital that the site or sites for investigation are chosen in locations that will potentially provide answers to the original aims of the project. Once a site is chosen, the collection of the sediments must be done in the most careful and precise way possible from an appropriate place in the lake. It is vastly preferable to undertake all the analyses on one core, as precise correlations can then be made between proxy records. It is therefore worth spending time on site selection, establishing the basic morphometry and sediment stratigraphy of the basin, and on obtaining continuous large-diameter (10–11 cm) cores (e.g. Nesje 1992) or a series of overlapping large-diameter cores (e.g. Cushing and Wright 1965). Such cores usually provide enough material for the majority of analyses to be performed, but perhaps not enough for studies of fossil beetles or some organic bio-markers. If more than one core is required, for example a central core in deep water and a littoral core in shallow water, or a transect of cores, then the cores should be correlated as precisely as possible. This can be done using sediment lithology and comparison of percent loss-on-ignition or magnetic susceptibility measurements. If several lakes are to be investigated, the cores can be correlated using dating techniques (^{14}C, ^{210}Pb) or by correlating events in a regional record such as anemophilous pollen, tephra, or atmospheric contaminants such as sphaeroidal carbonaceous particles.

   In practice there are three sampling and analytical situations in a multi-proxy study–(1) the 'ideal' situation where all the analyses of the various proxies are made at the same levels in the same core, (2) the 'worst' situation where the analyses are made at different levels in two or more cores from the same part of the basin, and (3) the 'compromise' situation where different proxies are studied at different levels but in the same core. To help alleviate the 'worst' situation, reliable core correlation can often be achieved using sequence-slotting procedures (Birks and Gordon 1985; Thompson and Clark 1989) or other numerical procedures (Kovach 1993) with percent loss-on-ignition [percentage weight loss after burning at 550 or 900°C], magnetic susceptibility, and other sedimentary variables as the basis for core comparison and correlation. In the 'compromise' situation of sampling different levels in the same core, it may be necessary to interpolate the different data sets to constant sampling interval or temporal resolution to permit various types of time-series analysis (Birks 1998) and to allow comparisons between different proxies. A wide range of interpolation procedures is available (Davis 2002; Weedon 2003). They all inevitably result in some loss of information and temporal resolution. The interpolation approach adopted depends very much on the research questions under study.

4. Because so many data are collected, it is important to store and co-ordinate them efficiently. A multi-proxy relational data-base (e.g. Juggins 1996) ensures compatibility and consistency between data types and provides a rapid and effective means of bringing together, comparing, and cross-correlating different proxy records within and between cores. It provides archival and research tables of, for example, basic core data, physical and chemical variables, biological data, chronological information, age-depth model results, and correlations. A data-base allows rapid retrieval of data and provides the basis for subsequent data manipulation and output for further analysis.

5. For almost all multi-proxy studies a reliable chronology is essential. This is usually provided by high-resolution radiocarbon dating, preferably AMS ^{14}C dating of carefully determined terrestrial plant material (e.g. Gulliksen et al. 1998). Recent sediments can be dated by the ^{210}Pb method and associated radiometric techniques involving ^{137}Cs and ^{241}Am (e.g. Appleby 2004) and age-depth models of recent peat profiles have been made by ^{14}C dating (Goslar et al. 2005). In rare instances, lake sediments may be annually laminated and an absolute, or at least a 'floating' absolute, chronology can be established (Bradbury and Dean 1993; Anderson et al. 1995, 1996; Ralska-Jasiewiczowa et al. 1998, 2003; Lotter 1999, 2001; Smith et al. 2004) and used to establish rates of compositional change in different proxies (e.g. Lotter et al. 1992), to detect decadal or even annual environmental changes (e.g. Smith et al. 2004), and to infer catchment–lake interactions at a decadal scale (Anderson et al. 1995, 1996).

6. Clear presentation of the wealth of results from a multi-proxy study is necessary. An important first step, essential if the data-sets are from different cores, is to establish age-depth models for each core, so that all the data can be plotted on a comparable age basis. Calibration of radiocarbon dates into calendar years is needed to provide a linear age scale into which other chronologies (e.g. ^{210}Pb) can be combined. Techniques for radiocarbon calibration (e.g. Buck and Millard 2004) and the underlying radiocarbon calibration data-sets (Reimer et al. 2005) are continually evolving. There are many approaches to age-depth modelling (e.g. Bennett 1994; Telford et al. 2004b; Heegaard et al. 2005), all with strengths and weaknesses. The limiting factor of all age-depth models is the number and reliability of the available radiocarbon or other types of dates (Telford et al. 2004b).

   Once a robust and realistic age-depth model is established, the variables from the core(s) can be plotted stratigraphically using computer software such as TILIA, TILIA.GRAPH, and TGView (Grimm 1991–2004) or PDP (Palaeo Data Plotter, Juggins 2002), now superseded by C2 (Juggins 2003). These programs allow stratigraphical variables with different sampling intervals to be plotted on a common depth or age basis (e.g. Oldfield 1996; Oldfield et al. 2003a) or stratigraphical variables with different sampling intervals and from different sites or cores to be plotted on a common age basis (Oldfield 1996).

7. Numerical techniques for detecting the major patterns of variation in a range of stratigraphical data, often

consisting of a large number of variables, and for summarising the main stratigraphical patterns are an invaluable tool in synthesising data in multi-proxy studies. The major numerical techniques are reviewed by Birks (1998). A valuable philosophical concept is the principle of parsimony and hence the statistical concept of the 'minimal adequate model' in numerical analysis and model selection (Crawley 1993).

There are three classes of numerical techniques that are useful for analysing multivariate multi-proxy stratigraphical data. Independent zonations of different stratigraphical proxies (e.g. pollen, diatoms, chironomids, sediment geochemistry) using Gordon's (1982) optimal, non-hierarchical partitioning (see also Birks and Gordon 1985) and subsequent comparisons of the various partitionings with the broken-stick model (Bennett 1996) will detect the minimal number of potentially 'significant' zones. Zonation schemes based on different proxies can then be compared visually (e.g. Lotter and Birks 2003) or statistically (e.g. Gardiner and Haedrich 1978). Sequence-splitting (Walker and Wilson 1978; Walker and Pittelkow 1981) is a potentially valuable tool for summarising multi-proxy data. It was developed for pollen-stratigraphical data and it has not, as far as we know, been applied in palaeolimnology. It 'zones' each stratigraphical variable (like individual pollen taxa) into sections with distinct but homogenous means and standard deviations. The statistical significance of each split is tested (Walker and Wilson 1978) and the occurrence of all splits in time can be tested statistically (Gardiner and Haedrich 1978). Birks and Gordon (1985) discuss the approach in detail and Birks and Line (1994) present a palaeoecological application involving statistical testing within and between sequences. The procedure requires statistically independent stratigraphical variables (like accumulation rates). A simple way of transforming relative percentage stratigraphical data into independent variables is to represent them as principal component or correspondence analysis axes that are, by definition, orthogonal and uncorrelated. Each axis can be used as a variable in sequence splitting. The temporal occurrence of significant splits in the data can then be compared with the occurrence of splits in other data-sets from the same core, thereby identifying consistent periods of change in different individual proxy variables.

Ordination techniques (e.g. principal components analysis, correspondence analysis) provide valuable summaries of the major stratigraphical patterns in a particular palaeolimnological variable (e.g. diatoms), particularly when the sample scores on ordination axes 1, 2, etc. are plotted stratigraphically. Such plots (e.g. Ammann et al. 2000; Birks et al. 2000; Birks and Birks 2001; Lotter and Birks 2003) highlight the major patterns of variation, and illustrate and summarise the nature of the temporal changes. It is most parsimonious to consider only those ordination axes that are statistically significant, namely that have eigenvalues larger than expected under the broken stick model (Jolliffe 2002; Jackson 1993). For biological data, detrended correspondence analysis (DCA) (Hill and Gauch 1980) is preferable because the sample scores are scaled in 'standard deviation' units of compositional change or turnover (β-diversity). It is thus possible to obtain a graphical summary of the magnitude of compositional change within a stratigraphical proxy (like chironomids) and between stratigraphical proxies (e.g. chironomids, pollen, diatoms) from the same stratigraphical sequence (e.g. Birks et al. 2000; Birks and Birks 2001). When interest is focussed on the magnitude of compositional change in a group of organisms over a specific time interval between sites, a series of constrained DCCAs (= detrended canonical correspondence analysis with detrending by segments and non-linear rescaling: ter Braak 1986) using sample age as the constraining variable can be made and the estimates of compositional change for the time interval at each site can be mapped and compared (e.g. Smol et al. 2005).

8. Interpretation and publication of the large amounts of data resulting from a multi-proxy study are major challenges.

Firstly, there are often too much data to assimilate readily and it is here that numerical techniques for data summarisation are their most useful and powerful (see above, Birks 1998; Bradshaw et al. 2005a).

Secondly, there is the challenge to avoid the natural tendency to believe that one type of proxy is, in some way, more reliable or more informative than another proxy record, and hence to give subconsciously greater weight to some proxies than to others.

Thirdly, it is a major challenge to avoid the 'reinforcement syndrome' (Watkins 1971; Thompson and Berglund 1976; Bennett 2002) or the tendency to adopt a 'confirmatory' approach where data interpretation is forced to fit into a particular favoured paradigm or stratigraphical sequence of environmental changes. This syndrome was articulated in the field of palaeomagnetism when Watkins (1971) wrote "It is infinitely more difficult, if not impossible, to prove that a given magnetic field behaviour has not taken place, than to 'show' it has occurred. Superimposed on this is an important human element: it is far more reasonable to generate the energy and the belief (? faith) required for publication of data confirming a discovery than to publish more negative data of a pedestrian nature. Thus the initial discovery is reinforced." In palaeolimnology there is a tendency to try to match small changes in proxy data-sets ('signal') to fit or to confirm the current paradigm or model and to ignore other, perhaps equally large, changes as 'noise'. To avoid the reinforcement syndrome it is important to let the data speak for themselves. Lotter et al. (1995) and Ammann et al. (2000) provide striking examples where numerical techniques helped the data to speak for themselves. The relative sensitivities of different proxies were revealed and the presence or absence of lags in biotic response to rapid climate change could be assessed. An invidious effect of the reinforcement syndrome is so-called publication bias (Möller and Jennions 2001; Meiri et al. 2004) where only confirmatory results are published, especially in so-called 'high-impact journals' and non-confirmatory results are published in other journals or, worst of all, are never published. As Watkins (1971) noted, "it would be instructive to compile examples of other applications of this 'reinforcement syndrome' to see if there are any natural laws governing the blossoming or survival of possibly spurious, or at least only partially correct, observations or ideas." Examples of this syndrome may exist in the palaeoclimatological literature concerning, for example, cycles or periodicities in Holocene climatic change, the global extent of rapid and short-lived climatic changes in the Late-glacial and early Holocene, and the early Holocene thermal maximum.

Fourthly, a potentially rewarding approach to the interpretation of large amounts of multi-proxy data is so-called 'data-splitting'. One proxy (e.g. pollen) may be used to reconstruct mean July air temperature and this reconstruction is then used to interpret stratigraphical changes in another independent proxy (e.g. chironomids, diatoms) in terms of biotic responses to climate change (e.g. Ammann 1989a, b, 2000). Lotter and Birks (2003) adopted this approach in their interpretation of Holocene multi-proxy data at Sägistalsee. Plant macrofossil data were used to reconstruct catchment vegetation, and these reconstructions were then used, along with insolation and other independent climate proxies, as 'predictors' in statistical modelling to see which 'predictors' best explained, in a statistical sense, the observed changes in five different types of limnological variables (chironomids, cladocera, sediment geochemistry, sediment magnetics, and sediment grain-size). This hypothesis-testing approach is relatively new and has great potential for future research development. It is a powerful way of testing ideas and it should be undertaken more widely in the future (Birks 1993a, b, 1996, 1998), in an attempt to test hypotheses about the possible processes driving biotic and lake-ecosystem changes. Ammann et al. (2000) used the oxygen-isotope stratigraphy from late-glacial sediments as a record of climate change against which observed biotic changes (pollen, chironomids, cladocera, beetles, plant macrofossils) could be compared and evaluated in terms of lags in response to rapid climate change. Other examples of this 'data-splitting' approach as an effective means of using one or more proxy types to help interpret the observed changes in another proxy type include Seppä and Weckström (1999), Seppä et al. (2002), Heiri et al. (2003), and Shuman et al. (2004).

Fifthly, it is a major challenge not only to interpret and synthesise the results from a multi-proxy study in as fair and as objective a way as possible, but also to write up the results and to publish synthesis papers, which are, by their very nature, often rather complex and long. There is a tendency today towards the publication of more and more short papers. This has the disadvantage that papers can easily be overlooked because of the ever-increasing number of publications and 'information-overload' for readers. A reader can become frustrated when, for example, environmental reconstructions from the same core but based on different numerical methods or calibration data-sets or on different types of proxies are published in different journals, and presented and plotted in different ways and on different scales. If the potential of multi-proxy studies is to be maximised, it is essential that the results be synthesised in a common format presenting points of similarity and points of difference, the potential strengths and weaknesses, and the different potential sensitivities of different proxies, so that their contribution to the conclusions can then be evaluated. It will be vastly more interesting to discuss apparent contradictions in interpretation as these will raise important questions about the proxies, what aspects of the environment they may be reflecting and responding to, and how to interpret them. Contradictions or anomalies also raise important and productive research questions concerning the appropriate use of calibration data-sets and the limitations of our existing ecological, environmental and limnological understandings (see Bigler et al. 2002; Rosén et al. 2003). Palaeoceanographers now recognise that different proxies (diatoms, planktonic foraminifera, benthic foraminifera, sediment grain-size, chemical ratios and stable isotopes) reflect different aspects of the ocean system in terms of stratification, currents, and rates of overturn (Andersson et al. 2003; Risebrobakken et al. 2003). Palaeolimnologists could, with profit, adopt a similar approach in their interpretation of multi-proxy data.

The complex nature of proxy data

The essential feature of multi-proxy studies is that several stratigraphical proxies are used to investigate a common aim. Each proxy takes its own unique place in the ecosystem network and may be used to reconstruct different facets of the ecosystem. Besides the standard much-used proxies, new techniques and proxies are continually being developed, often for specific purposes. Rather than trying to discuss all the various types of proxies available in palaeolimnology, we illustrate the complexities of deriving reliable and robust palaeoenvironmental inferences in multi-proxy studies by focusing on the interpretation of a commonly used physical proxy, namely sediment loss-on-ignition, and on the interpretation of biological proxies using transfer functions.

Physical proxies

Percent loss-on-ignition (% LOI) is the most widely used and perhaps the most useful, simple, physical proxy in palaeolimnology. It reflects the proportion of organic carbon, carbonate, and mineral matter in the sediment (Dean 1974; Boyle 2004). Loss-on-ignition at 550°C (Heiri et al. 2001) has been found to be a remarkably good summarising proxy for many changes in a lake ecosystem (e.g. Levesque et al. 1994; Birks et al. 2000; Battarbee et al. 2001, 2002). However, it is a percentage, and thus an increase can reflect an absolute increase in organic matter or an absolute decrease in mineral matter, or some combination of both. In addition, organic and mineral matter can both originate in the lake (bioproduction, biogenic silica and carbonate) and/or in the catchment (bioproduction, humus or mineral inwash due to catchment instability). Thus % LOI is a simple measurement that can have a complex interpretation (Shuman 2003). Livingstone et al. (1958) were the first to realise this, but few absolute estimates of organic accumulation have been made. Recently, Velle et al. (2005a) estimated the rates of accumulation of organic and mineral matter at Råtåsjoen, central Norway, and were able to interpret changes in % LOI as processes related to early Holocene increased lake productivity and decreased mineral inwash resulting from stabilisation and vegetation of the catchment. Maximum organic matter deposition occurred around 5000 cal B.P. and was related to the climate-induced loss of trees from the catchment. The organic matter stored in the soils was released and washed into the lake. Velle et al. (2005a) were also able to show that % LOI was not related to diatom productivity of biogenic silica. It was slightly correlated with Holocene temperature changes as deduced from the chironomid record, but the organic matter accumulation rate was not. The absolute amount of carbon in the sediments was related much more strongly to changes in catchment vegetation, as deduced from the plant macrofossil and pollen records. The predominant catchment origin of organic matter in sediments in upland lakes was long-ago proposed by Mackereth (1965, 1966), and has been elegantly confirmed by whole-lake additions of ^{13}C (Pace et al. 2004).

% LOI has also been interpreted more directly as a climate signal (e.g. Willemse and Törnqvist 1999). At Lochan Uaine, Scotland, changes in the chironomid assemblage could be related to small temperature changes coinciding with changes in the % LOI curve (Battarbee et al. 2001), suggesting that the % LOI was reflecting greater bioproduction and preservation during times of either warm or cool temperatures. In the Jotunheim mountains of central Norway, Nesje and Dahl (2001) found sharp decreases in % LOI in several lakes at around 8200 cal B.P. that were related to times of glacier re-advance, the so-called Finse event. This cool and/or wet event is correlated in time to a major cool period in the Greenland ice cores (Alley et al. 1997). It is unlikely that the dips in % LOI in the Jotunheim lakes were caused by changes in bioproduction, as the sediments are visibly more silty, suggesting that the % LOI is reflecting minerogenic inwash from the catchment. At Lake Tsuolbmajavri in northern Finland, the % LOI (Seppä and Weckström 1999) follows the annual precipitation reconstruction more closely than the summer temperature curve reconstructed from the pollen data (Seppä and Birks 2001), suggesting that precipitation effects on the catchment may have influenced the minerogenic input and thus the % LOI in this sub-arctic lake. Shuman (2003) emphasises that changes in % LOI in a single core may be difficult to interpret because of within-lake processes and thus multiple cores increase the interpretability of the % LOI record.

Various other chemical and physical proxies have been measured in lake sediments, most notably stable isotopes of H, O, C and N, and carbonate content, chemical composition and magnetic properties. Developing proxies include near-infrared spectroscopy (Rosén et al. 2000, 2001) and bio-markers in sediment organic geochemistry. The last is particularly useful as it is a record of organic compounds produced by organisms that leave no visible remains, such as algal groups, bacteria and cyanobacteria (e.g. Fritz 1989; Lotter 2001). Long-chain lipids from leaf cuticles have been used to characterise terrestrial vegetation changes in response to changes in precipitation and run-off into near-shore marine sediments in Venezuela (Hughen et al. 2004). A new approach by Huang et al. (2004) has shown the potential of studying isotopes in specific lipid biomarkers preserved in lake sediments as a record of environmental change.

Biotic proxies

Environmental reconstructions

Biotic proxies are as numerous as the organisms that leave a record in lake sediments (Smol et al. 2001a, b). As specialist knowledge is needed to identify the fossil material, the organisms are usually studied as groups, such as diatoms, pollen, plant macrofossils, chironomids etc. If enough is known about the biology and ecological tolerances of a taxon, that taxon may be used as an indicator species for the reconstruction of past habitat, community, and environment, including climate (Birks and Birks 1980). Similarly if an assemblage of taxa resembles a modern community that lives in a defined ecological range today, that assemblage may be used to infer past conditions. The indicator species and assemblage approaches rely on modern analogy and assume that the limiting conditions in the past were the same as they are today (Birks and Birks 1980; Birks 2003). The assemblage approach has been quantified as the Mutual Climatic Range Method (MCRM) used with Coleoptera (Atkinson et al. 1987), with molluscs (Moine et al. 2002) and with plant macrofossils (Sinka and Atkinson 1999; Pross et al. 2000). It is also the basis of probability density functions used with plants (Kühl et al. 2002; Kühl 2003; Kühl and Litt 2003) and modern analogue techniques, often used on marine assemblages (e.g. Telford et al. 2004a; Telford and Birks 2005), but also on terrestrial pollen assemblages (e.g. Bartlein and Whitlock 1993; Davis et al. 2003). These methods are designed to reconstruct past environments from fossil assemblages of taxa whose environmental limits have been either determined or assumed by correlation of taxon distributions and abundance with climate or other environmental data.

Another approach to environmental and climate reconstruction is the transfer function approach (Birks 1995, 1998, 2003). Within a group of organisms, taxa from surface-sediment samples are related numerically to environmental parameters by means of a quantitative transfer function. Using the transfer function, past environmental parameters are reconstructed from fossil assemblages. The most widely used transfer functions are between diatoms and lake-water pH, salinity, and total P, pollen and mean July and January temperature and annual precipitation, chironomids and mean July air temperature and water temperature, and Cladocera and mean July air temperature. The use of transfer functions to reconstruct past climate has often been an aim of multi-proxy studies, but surprisingly few multi-proxy studies have compared the resulting reconstructions. When the mean July temperature reconstructions using various methods (transfer functions for pollen, chironomids, and cladocera; MCRM for Coleoptera; indicator species and assemblages for plant macrofossils) were compared for the Late-glacial and early Holocene at Kråkenes (Birks and Ammann 2000) the results were somewhat surprising. Although the patterns of the temperature curves were all the same, as one might expect given the temperature-driven changes through the Late-glacial, the estimated temperature values of the reconstructions were different. The reasons for the discrepancies need to be sought in a more detailed examination of the performance of the numerical reconstruction methods and the representativity of the training sets, especially near the limits of biological existence that prevailed during the Younger Dryas in western Norway.

Transfer functions perform well when the environmental changes are large and are within the central range of the modern training set (Birks 1998). In the Late-glacial, the large temperature changes are well reconstructed. However, reconstructions become less reliable when the values of the environmental variables are near the limits of the training set (Birks 1998). In cold climates, diversity is reduced and the same cold-adapted assemblage of e.g. chironomids, may exist over a wide temperature range. The same restriction applies to pollen, but there is the additional complication of the presence of long-distance-transported pollen from trees in warmer regions into the pollen assemblages deposited beyond the arctic or alpine tree-lines (Birks and Birks 2003). Thus, the reconstruction of cold temperatures and associated precipitation levels from pollen assemblages is difficult (Birks et al. 2000; Larsen and Stalsberg 2004). A similar imbalance is present in diatom/total phosphorus reconstructions; diatoms are sensitive to low and medium total-P concentrations but relatively insensitive to high total-P situations. Related problems of insensitivity can arise when inferring Holocene temperature changes from fossil chironomid assemblages. Temperature changes in the Holocene are smaller and more subtle than late-glacial changes. Reconstructed changes are nearly always within the inherent prediction error range of reconstruction, although trends may be apparent (Birks 2003), and the reconstructions may also be rendered insensitive by the overall predominance of common species with wide ecological tolerances. Small reconstructed environmental changes may result from the chance occurrence of species with narrow tolerance ranges (Velle et al. 2005b).

Apparent discrepancies in quantitative environmental reconstructions based on transfer functions and a range of organisms raise important and critical questions about transfer functions and their robustness. There are several assumptions behind the transfer-function approach (Birks 1995). The most relevant here are the assumptions that (1) the environmental variable(s) to be reconstructed is, or is linearly related to, an ecologically important determinant in the ecosystem of interest; and (2) environmental variables other than the one of interest have negligible influence, or their joint distribution with the environmental variable of interest in the past is the same as in the modern calibration data-set (Birks 1995). Transfer functions are, by necessity, correlative in character; they model numerically the relationship between the observed occurrence and abundance of organisms in surface-sediment samples and modern environmental variables, for example the relationships between chironomid assemblages and mean July air temperature. It is probable that chironomids respond to water temperature rather than directly to air temperature (Brooks and Birks 2001; Brooks 2003). Although there is a strong correlation today between lake-water and air temperatures (Livingstone and Lotter 1998; Livingstone et al. 1999), and transfer functions for modern chironomid assemblages and air temperature perform well as assessed by statistical criteria in cross-validation using *modern* samples, the critical question is whether the relationship between lake-water and air temperature would be the same if winter precipitation as snow increased by 100–200% or more, as it probably did in parts of the Holocene in the Norwegian mountains (Nesje et al. 2001; Bjune et al. 2005; Bakke et al. 2005a). Large amounts of snow melt-water would result in cool lake-water even though the mean summer air temperature may be the same as in the periods with less winter precipitation. Brooks and Birks (2001) discuss two lakes today in Norway with cold-water modern chironomid assemblages but with high summer air temperatures. Both lakes are 'outliers' when chironomids are used to infer modern summer air temperatures, giving estimates of air temperature 4°C cooler than the observed values. Observed differences between reconstructed values of mean July air temperature based on pollen and plant macrofossils and on chironomids in the Holocene (Brooks and Birks unpublished) may be, in part, a result of the relationship between mean July air temperature and July water temperature not having the same joint distribution in the past. A further complication in the use of chironomid transfer functions for inferring past climate is the strong covariance between modern temperature and lake trophic conditions (Broderson and Anderson 2002). Velle et al. (2005b) discuss possible additional confounding variables in chironomid-inferred air temperatures for the Holocene in western Norway. A similar problem may arise in the use of diatom–climate transfer functions as several limnological variables (e.g. alkalinity, pH, conductivity) may covary with temperature (Anderson 2000).

Although there are several numerical procedures for evaluating transfer function models (e.g. Birks 1995; Telford and Birks 2005), the most powerful means for assessing the reliability and sensitivity of a particular transfer function is to compare palaeolimnological reconstructions using transfer functions with known historical records (e.g. Renberg and Hultberg 1992; Fritz et al. 1994; Bennion et al. 1995; Lotter 1998; Teranes et al. 1999; Bradshaw and Anderson 2001). In general the environmental reconstructions based on transfer functions parallel the trends in the historical records but do not always match the absolute values.

Discrepancies emerging from multi-proxy studies (e.g. Birks and Ammann 2000; Rosén et al. 2003) encourage researchers to ask what particular transfer functions really reflect – air temperature, water temperature, length of growing season, trophic status, pH, lake habitat, or a complex interaction of these and other variables? Recent work by Heegaard et al. (2006) indicates that there are significant differences between modern chironomid, cladoceran, and diatom assemblages along an altitudinal gradient in the Swiss Alps in terms of where major compositional changes occur. There appears to be no consistent 'aquatic ecotones' between the three groups of organisms. This suggests that each is responding to different environmental variables or complexes of variables that may influence the rates of compositional change between the taxonomic groups with altitude. Thus different proxies and their responses to different aspects of the environment can be utilised to demonstrate varying degrees of inertia and different thresholds (Smith 1965; Maslin 2004). This adds to the challenges of interpreting multi-proxy data and illustrates its potential to differentiate a range of biotic responses to environmental change.

Environmental reconstructions using transfer functions may depend on a surprisingly small number of taxa (e.g. Racca et al. 2003). If there is a preponderance towards abundant taxa with wide ecological tolerances in Holocene fossil assemblages and taxa with narrow tolerances are rare or absent, transfer functions may be rather insensitive, as they appear to be in several reconstructions of Holocene past climate (e.g. Brooks and Birks 2001; Rosén et al. 2001, 2003; Bigler et al. 2002; Korhola et al. 2002; Velle et al. 2005b).

Given current uncertainties about what environmental variables are the major determinants of the occurrence and abundance of different groups of organisms, it is advisable to avoid any attempts to derive 'consensus' reconstructions based on different groups of organisms. Given the hidden biases and assumptions in different numerical reconstruction procedures (Telford et al. 2004a; Telford and Birks 2005), 'consensus' reconstructions based on the same group of organisms but involving different numerical techniques may conceal important differences in the behaviour of the numerical procedures and are similarly not recommended (cf. Birks 1995, 1998).

A further problem associated with environmental reconstructions in multi-proxy studies is distinguishing between 'signal' and 'noise' (Birks 1998). The SiZer smoothing procedure of Chaudhuri and Marron (1999) helps to assess which features in a smoothed time-series are statistically significant and hence which features may represent 'signal'. Korhola et al. (2000) provide a palaeoecological application of SiZer. The approach could be extended to consider several stratigraphical records from a multi-proxy study to help distinguish 'signal' from 'noise'.

There have been considerable advances in the theory, methodology, and development of quantitative transfer functions in the last 20 years (Birks 1995, 1998, 2003). However, as a result of recent multi-proxy studies, problems in some transfer functions are emerging. There is thus the need to 'return to basics', in particular to study the environmental requirements and niche parameters of species commonly found as fossils (e.g. Broderson et al. 2004). There is considerable scope for incorporating ecological knowledge into environmental reconstructions and interpretations of multi-proxy studies within a Bayesian framework for inference and prediction – see Ellison (2004) and Clark (2005) for recent lively discussions about why ecologists (and thus palaeoecologists) are becoming or should become Bayesians.

A wider-based multi-proxy approach is now developing where transfer functions, involving whole groups of organisms, are being used in combination with indicator species information. The interest is shifting away from climate or pH reconstruction as ends in themselves and more towards whole lake ecosystem reconstructions and the causes behind the changes. To do this, one has to look inside the proxy group and seek reliable indicator species. This was the original approach to palaeolimnology. It is particularly appropriate for aquatic macrophytes, where individual species ecology has always been important (e.g. Iversen 1954; Watts 1978; Birks et al. 1976, 2001; Birks 2000, 2001). Less is known about the ecology of freshwater algae, including diatoms, but ecological studies of arctic and Antarctic lakes and ponds (e.g. Douglas et al. 2004) are contributing much to our knowledge of diatom and chrysophyte ecology. The modern ecology of chironomid taxa has recently been used to help to rationalise anomalous temperature reconstructions made from chironomids (Brodersen et al. 2004; Velle et al. 2005b). Cladoceran ecology has always been of more interest than climate reconstruction from the whole group (e.g. Hofmann 1996, 2000; Duigan and Birks 2000; Milecka and Szeroczyńska 2005). Coleopteran ecology has also always played a large role in palaeoecological investigations although climate reconstructions using MCRM have now become dominant (e.g. Elias 1994, 1997, 2001; Elias et al. 1999). The ordination method detrended correspondence analysis (DCA) can be used to summarise compositional turnover for groups of organisms that can then be directly compared among groups (e.g. Birks et al. 2000). Individual species changes can then be investigated to seek the reasons for rapid changes in turnover and ecological factors can be inferred to explain the changes (e.g. Birks and Birks 2001).

Pollen analysis and plant macrofossils

As palaeolimnology has made considerable methodological and conceptual advances in the last 20 years (e.g. Battarbee 2000; Smol 2002; Brooks 2003; Fritz 2003; Mackay et al. 2003), it has increasingly developed its own identity, with its own journal, meetings and research agenda. Pollen analysis has not, however, played a major part in the recent development of palaeolimnology (Birks 2005) even though pollen analysis and the associated study of plant macrofossils can provide the main evidence for catchment vegetation over long time periods. Pollen and plant macrofossil analysis (e.g. Wick et al. 2003) are becoming increasingly important in multi-proxy palaeolimnological studies as the role of the lake's catchment and its vegetation and soils is so important in understanding lake biotic and sedimentary changes (e.g. Anderson et al. 1995; Korsman and Segerström 1998; Seppä and Weckström 1999; Lotter 1999, 2001; Birks et al. 2000; Bradshaw et al. 2000, 2005a; Bradshaw 2001; Lotter and Birks 2003; Oldfield et al. 2003b). Limnologists are exploring links between water chemistry and nutrient status and catchment vegetation (Maberly et al. 2003; van Breemen and Wright 2004). There is also a resurgence of interest in biogeochemistry (Jackson and Hedin 2004). Palaeolimnological techniques such as sediment geochemistry can also be used to address critical questions in understanding changes in vegetation history by providing information about catchment soil development and change (e.g. Engstrom and Hansen 1985; Ford 1990; Willis et al. 1997; Ewing 2002; Ewing and Nater 2002). There is thus an increasing need for close collaboration and interaction between pollen analysts, vegetation historians, and palaeolimnologists in multi-proxy studies.

Another area where close collaboration is needed is the analysis of plant macrofossils. Besides providing unique evidence for the local presence of taxa in or near the study lake, macrofossils of aquatic macrophytes are a record of a major component of the lake ecosystem, namely the macrophyte flora (Birks 2000, 2001). Aquatic macrophytes are a major habitat for other aquatic biota, are sensitive to changes in lake level and nutrient status, and represent one alternative equilibrium state in shallow lakes. Interest in plant macrofossils is greatly increasing, not only to provide terrestrial material for ^{14}C AMS dating, but also to help understand changes in aquatic biota in multi-proxy studies (e.g. Sayer et al. 1999, 2006; Birks et al. 2001; Brodersen et al. 2001; Odgaard and Rasmussen 2001; Bradshaw et al. 2005b; Davidson et al. 2005).

Pollen and plant macrofossils represent different but indeterminate spatial scales. The regional pollen rain reflects vegetation at a regional scale, but pollen may also be derived more locally, such as from lake-side and aquatic vegetation (Birks 2005). Plant macrofossils are usually not dispersed far from their source. However, they can be carried long distances by water and by wind. For example, it has been difficult to determine the local significance of isolated *Betula* fruits and small fragments of *Pinus* bark in sites above the tree-line (Eide et al. 2006). Within a lake, aquatic macrofossils are usually related closely to the parent vegetation. Consequently, they are better represented in shallow water where the macrophytes were growing (Birks 2001). Thus a core from deep water in the centre of a lake, ideal for pollen, is not always so suitable for macrofossil representation. Central cores appear to contain a good representation of the chironomid community (Heiri 2004), whereas marginal cores can give a biased record of chironomids (Brooks 2000). Central cores contain diatoms from all the available lake habitats (plankton, mud, sand, stones, macrophytes). However, few comparisons have been made of central and littoral cores in multi-proxy studies, mainly because of the large amount of work involved (e.g. Digerfeldt 1971, 1986; Anderson et al. 2005). The multi-proxy study at Lobsigensee led by Brigitta Ammann is an impressive example of using both central and littoral cores to study a wide range of late-glacial proxies and their responses to climatic changes (Ammann et al. 1983, 1985; Ammann and Tobolski 1983; Chaix 1983; Eicher and Siegenthaler 1983; Elias and Wilkinson 1983; Hofmann 1983; Ammann 1989b).

Recent examples of multi-proxy studies

The Kråkenes Project (Birks and Wright 2000) is an example of how a variety of proxies can be used to reconstruct the lake ecosystem, including the catchment, and climate changes over the Late-glacial and early Holocene. Plots of DCA sample scores on axis 1 of the groups together with the % LOI and *Pediastrum* curves, all showed synchronous changes at the end of the Allerød interstadial, the inception of the glacier in the catchment during the Younger Dryas stadial, and its melting and the temperature rise at the beginning of the Holocene. A similar synchroneity was observed at Pine Ridge Pond in eastern Canada (Levesque et al. 1994), indicating that temperature changes were the over-riding forcing factor in late-glacial ecosystem change. During the early Holocene at Kråkenes, however, major changes in turnover of the various groups were not synchronous and different groups reached compositional stability at different times. This suggests that internal ecosystem factors were playing an important role, such as the development of macrophyte communities, cessation of mineral inwash from the catchment, natural acidification and reduction of nutrients in the lake water, and catchment vegetation and soil development culminating in the immigration of birch trees and the development of birch forest (Birks et al. 2000).

A good chronology can be used to estimate rates of biotic change, as at Kråkenes (e.g. Birks et al. 2000). Here, rapid rates of change in the Late-glacial coincided with the major temperature changes. In the early Holocene rates of change were variable among proxies, reflecting major stages in the successions of the different groups, related particularly to catchment vegetation and soil development and to lake nutrient status. In contrast, the chronology of the recent sediment sequences in the CASSARINA project in North Africa was often poor because of low ^{210}Pb accumulation (Appleby et al. 2001). However, all the sequences covered about 100–150 years. Plots of the DCA sample scores on axis 1 of the organism groups (aquatic and terrestrial macrofossils, pollen, zooplankton, diatoms; Birks and Birks 2001) showed very large amounts of compositional turnover, quantifying the enormous changes in aquatic ecosystems that had occurred within decades under strong forcing imposed by human activity, in this case freshwater withdrawal or continuous freshwater supply in the Nile Delta.

When palaeolimnological data are available from many sites and for the same time period (e.g. last 150 years), the amount of compositional change or biotic turnover for the time interval of interest can be estimated for each site and compared between sites (Smol et al. 2005). This approach was applied to 55 palaeolimnological records from lakes in the circumpolar Arctic and it demonstrated widespread changes in algal and invertebrate communities that are consistent with recent climate warming (Smol et al. 2005). The observed palaeolimnological changes in diatoms, chrysophytes, chironomids, and cladocera are interpreted as reflecting increases in arctic lake primary production (Smol et al. 2005). This hypothesis has been tested for six lakes on Baffin Island by using reflectance spectroscopy to infer changes in lake sediment chlorophyll *a* concentrations and hence change in lake primary productivity (Michelutti et al. 2005). The inferred changes in chlorophyll *a* are paralleled by changes in total organic carbon reflecting the balance between the production and decomposition of organic carbon, in biogenic silica, and in C:N ratios. The changes in these four biogeochemical proxies are all consistent with the hypothesis of increased primary production since A.D. 1850. Similarly, a multi-proxy study of Svalbard lakes has illustrated how lake development has responded to climate change over the last century (Birks et al. 2004).

A similar multi-proxy approach involving a range of biological, biogeochemical, and stable isotope variables, and numerical techniques has been used to test hypotheses about recent (last 100 years) changes in diatom assemblages in alpine lakes in the Colorado Front Range. The changes appear to be a response to anthropogenic nitrogen deposition from agricultural and industrial sources to the east of the Rockies (Wolfe et al. 2001, 2002, 2003; Das et al. 2005). The effects of recent human impact have also been demonstrated by a multi-proxy study of Upper Klamath Lake, USA (Bradbury et al. 2004) and the impact of lake pollution and subsequent recovery were traced by Hynynen et al. (2004). Human impact has also been studied in an archaeological context (Davies et al. 2004).

A recent development in multi-proxy studies is the statistical testing of alternative hypotheses about the causes of the observed or reconstructed changes. This has already been mentioned at Sägistalsee (Lotter and Birks 2003). There is great potential for developing this approach more specifically in future multi-proxy studies (Lotter and Birks 1997; Birks 1998, 2003) as a means of evaluating multiple alternative hypotheses.

Future directions

Multi-proxy studies are making major contributions to palaeoecology and palaeolimnology. Our knowledge about the history of past climate change and past ecosystem development and lake ontogeny is steadily increasing. Each proxy reflects the environment at its own spatial scale, taking its place in the network of interactions that comprise an ecosystem, thus providing insights into different facets of an ecosystem.

New proxies are continually being recognised, applied and evaluated. Some of the most promising and diverse include biogeochemistry (e.g. Meriläinen et al. 2001; Fisher et al. 2003; Hynynen et al. 2004; Das et al. 2005; Sayer et al. 2006) and stable isotopes (e.g. Finney et al. 2000, 2002; Hammarlund et al. 2002; Veski et al. 2004; Wooller et al. 2004; Seppä et al. 2005). As well as the development of under-utilised fossil proxies (e.g. animal hairs Hodgson et al. 1998, phytoliths Carnelli et al. 2004, fish scales Davidson et al. 2003), well-known proxies are being used in new ways, using newly developed analytical techniques and improved chronologies to estimate amounts and rates of change through time, and using new approaches to detect morphological or genetic changes in response to environmental change (e.g. Weider et al. 1997; Kerfoot et al. 1999; Cattaneo et al. 2004; Hairston et al. 2005).

An important new direction in multi-proxy studies is a shift in the approaches to the interpretation of palaeolimnological data. Many multi-proxy studies today are focusing on palaeoecological questions as well as environmental reconstructions, invoking ecological indicator species and assemblages to provide new insights into past ecosystem functioning and pushing proxies further in interpretations of possible causal processes and driving factors. Data interpretation used to be primarily descriptive in terms of the reconstruction of past populations, communities, environments, and ecosystems (Birks and Birks 1980) but it can become more ecologically focused on the potential causes of the observed patterns of change or stability (Bennett and Willis 2001). It is here that well-designed multi-proxy studies can make a great contribution in the future because they can provide several potentially independent lines of evidence that can help to evaluate and resolve alternative competing hypotheses set up as explanations for a given stratigraphical pattern in the data (Bennett and Willis 2001). Multi-proxy studies can thus explore 'the geological record of ecological dynamics' (NRC 2005) and use 'the geological record as an ecological laboratory' (NRC 2005) to study critical research problems concerning biological diversity, community structure, the role of biogeochemistry, ecological impacts of climatic variability, habitat alteration, and the dynamics of biotic invasions. The resolution of such problems requires the fourth dimension of time that can only be provided by palaeolimnological or other palaeoecological data. Carefully designed and rigorously implemented multi-proxy studies have the potential to provide unique records of ecological dynamics over time and thus to contribute to our understanding of the natural variability of populations, communities, and environments, and of the responses of biological assemblages to a range of different environmental changes and forcing functions. Statistical techniques that take account of the inherent properties of multi-proxy data (Birks 1993b, 1996, 1998) can play an important role in testing competing hypotheses concerning possible causal factors and will allow a fuller exploitation of 'the geological record as an ecological laboratory' (NRC 2005). Deevey (1964) proposed over 40 years ago the idea of 'coaxing history to conduct experiments' as a way of exploiting the palaeoecological record as a long-term ecological experiment. The available analytical and statistical tools have expanded greatly and become increasingly more refined and will no doubt continue to do so. They can be used in the future to focus multi-proxy studies on ecological interpretations and causal factors and to exploit the palaeolimnological record as a unique source of information on biotic changes and responses over a wide range environmental changes at many temporal scales.

A further exciting development in multi-proxy studies is the involvement of ecological dynamic models. For example, a forest succession model has been used to simulate tree-line dynamics and forest composition over long time periods. Climatic parameters derived from palaeolimnological proxies that are independent of the vegetation proxies (e.g. chironomid-inferred temperatures) were used to drive the model (Heiri et al. 2006). In this elegant study the model results were compared with pollen and plant macrofossil reconstructions of the catchment vegetation, making it possible to disentangle the effects of climate and human impact on long-term vegetation dynamics. The combination of ecological models and palaeolimnological proxies (e.g. Keller et al. 2002; Lischke et al. 2002; Heiri et al. 2006) is a powerful means of interpreting observed patterns of ecological changes and dynamics in terms of several causal processes, and highlights the future potential of multi-proxy studies in the modelling and understanding of palaeoecological patterns and processes.

Conclusions

Multi-proxy studies are deceptively simple, highly seductive, and seemingly full of promise. In practice, they are a huge amount of work, they are never simple, they are full of surprises, even shocks, and they are rarely neat, tidy, or simple to interpret. In terms of multi-proxy reconstructions of past climates, we may be near the resolution of current data and predictive abilities of our transfer-function models. The sample-specific errors of prediction estimated by bootstrapping or some form of statistical cross-validation of about 0.8–1.5°C for July temperatures (Birks 2003) encompass the likely range of summer temperature change within the Holocene. In Norway the major changes in glaciers during the Holocene appear to be a response to changes in winter precipitation rather than to changes in summer temperature (e.g. Bjune et al. 2005). Reconstruction of the full picture of Holocene climate change here thus requires a major multi-proxy combination of biological, geological, and sedimentological data (e.g. Dahl et al. 2003; Bakke et al. 2005a, b; Bjune et al. 2005). Multi-proxy studies are not really 'safe' science. It is relatively easy and 'safe' to develop modern organism-environment calibration data-sets and associated transfer functions. However, complexities can and do arise when these transfer functions are applied to stratigraphical data in multi-proxy studies (e.g. Rosén et al. 2003; Velle et al. 2005a, b).

Despite these problems, multi-proxy studies are important research activities as they provide the means to study lake and biotic responses to environmental change which may have social implications. For example, the CASSARINA project in North Africa (Birks and Birks 2001; Birks et al. 2001; Flower 2001) revealed alarming amounts of biotic change in the last 100 years in response to human impacts. In the Egyptian Nile delta lakes, hydrological and salinity modifications resulted from the year-round inflow of fresh irrigation water controlled by the Nile dams and the rise in the freshwater table due to inadequate drainage in the flat delta. *Azolla nilotica* recently became extinct in these lakes (Birks 2002), probably as a result of eutrophication and salinity changes. Without the evidence provided by the analysis of plant macrofossils, pollen, diatoms, mollusca, foraminifera, ostracods, and other animal remains from the same cores, the extinction of *A. nilotica* would not have been recorded and the likely causes would have remained obscure.

Multi-proxy studies are challenging. Projects are usually expensive because of the labour involved, so they have to be carefully designed and coordinated and suitable sites must be chosen to provide the maximum amount of useful information in relation to the aims of the project. It is a major challenge to synthesise the large amount of diverse data and to prepare it for publication. Although we now have vast computing resources, a diverse range of numerical techniques, and large numbers of modern calibration data-sets and transfer functions, the real challenge is to improve on the classical pioneer studies and to argue as logically and as rigorously as was done in the early multi-proxy studies (e.g. Livingstone 1957; Livingstone et al. 1958; Cowgill et al. 1966; Wright 1966; Hutchinson 1970; Deevey 1984; Likens 1985). There has been a tendency in some aspects of palaeolimnology to get too pre-occupied with the minutiae of reducing modern prediction errors from 0.91 to 0.89°C when the environmental data themselves have inherent variability of 1 or 2°C, or with the details of a particular ordination or time-series technique. As a result there is a danger that we can lose sight of the important research questions, of the research hypotheses we are trying to test, of the long-term trends we are trying to detect, and of the limitations of our data, methods, and approaches. Carefully designed and critically implemented multi-proxy studies have the potential to contribute greatly to our understanding of how lakes and their biota respond to internal and external forcing, and to our appreciation of the sensitivities, strengths, and weaknesses of different proxies. They will enable us test specific hypotheses about lake development and biotic responses to specific factors. The interpretation of multi-proxy data raises many important research questions involving new approaches such as ecological modelling and statistical testing. Much has been achieved in such studies, much more remains to be done.

Acknowledgements We dedicate this essay to Brigitta Ammann on the occasion of her retirement from the University of Bern, in appreciation of her friendship, support, and scientific collaboration, and in recognition of her many contributions to Quaternary vegetation history, palaeoecology, and multi-proxy studies.

We are indebted to the many colleagues who have stimulated our interest in multi-proxy studies, in particular Brigitta Ammann, John Anderson, Rick Battarbee, Emily Bradshaw, Steve Brooks, Svein Olaf Dahl, Roger Flower, Viv Jones, Steve Juggins, Andy Lotter, Atle Nesje, Bent Odgaard, Heikki Seppä, John Smol, Richard Telford, Gaute Velle, and Herb Wright. We are grateful to Feng

Sheng Hu, John Smol, and Pim van der Knaap for their comments on the manuscript, and to Cathy Jenks for her help in preparing the manuscript. This is publication A126 from the Bjerknes Centre for Climate Research, Bergen.

References

Alley RB, Mayewski PA, Sowers T, Stuiver M, Taylor KC, Clark PU (1997) Holocene climate instability: a prominent widespread event 8200 yr ago. Geology 25:483–486

Ammann B (1989a) Late-Quaternary palynology at Lobsigensee—Regional vegetation history and local lake development. Diss Bot 137, Cramer, Stuttgart

Ammann B (1989b) Response times in bio- and isotope stratigraphies to Late-Glacial climatic shifts–an example from lake deposits. Ecologae Geologicae Helvetiae 82:183–190

Ammann B (2000) Biotic responses to rapid climatic changes: introduction to a multidisciplinary study of the Younger Dryas and minor oscillations on an altitudinal transect in the Swiss Alps. Palaeogeogr Palaeoclimatol Palaeoecol 59:191–201

Ammann B, Tobolski K (1983) Vegetational development during the late-Würm at Lobsigensee (Swiss Plateau). Studies in the late Quaternary of Lobsigensee 1. Revue de Paléobiologie 2:163–180

Ammann B, Chaix L, Eicher U, Elias SA, Gaillard M-J, Hofmann W, Siegenthaler U, Tobolski K, Wilkinson B (1983) Vegetation, insects, molluscs, and stable isotopes from Late Würm deposits at Lobsigensee (Swiss Plateau). Studies in the late Quaternary of Lobsigensee 7. Revue de Paléobiologie 2:221–227

Ammann B, 18 other authors (1985) Lobsigensee–late-glacial and Holocene developments of a lake on the Central Swiss Plateau. Diss Bot 87:127–170

Ammann B, Birks HJB, Brooks SJ, Eicher U, Grafenstein U von, Hofmann W, Lemdahl G, Schwander J, Tobolski K, Wick L (2000) Quantification of biotic responses to rapid climate changes around the Younger Dryas–a synthesis. Palaeogeogr Palaeoclimatol Palaeoecol 159:313–347

Anderson L, Abbott MB, Finney BP, Edwards ME (2005) Palaeohydrology of the Southwest Yukon Territory, Canada, based on multiproxy analyses of lake sediment cores from a depth transect. The Holocene 15:1172–1183

Anderson NJ (2000) Diatoms, temperature, and climate change. Eur J Phycol 35:307–314

Anderson NJ, Renberg I, Segerström U (1995) Diatom production responses to the development of early agriculture in a boreal forest lake-catchment (Kassjön, northern Sweden). J Ecol 83:809–822

Anderson NJ, Odgaard BV, Segerström U, Renberg I (1996) Climate-lake interactions recorded in varved sediments from a Swedish boreal forest lake. Global Change Biol 2:399–405

Andersson C, Risebrobakken B, Jansen E, Dahl SO (2003) Late Holocene surface ocean conditions of the Norwegian Sea (Vøring Plateau). Palaeoceanography 18:1044, doi: 10.1029/2001PA000654

Appleby PG (2004) Environmental change and atmospheric contamination on Svalbard: sediment chronology. J Paleolimnol 31:433–443

Appleby PG, Birks HH, Flower RJ, Rose N, Peglar SM, Ramdani M, Kraïem MM, Fathi AA (2001) Radiometrically determined dates and sedimentation rates for recent sediments in nine North African wetland lakes (the CASSARINA project). Aquatic Ecol 35:347–364

Atkinson TC, Briffa KR, Coope GR (1987) Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. Nature 325:587–592

Bakke J, Dahl SO, Nesje A (2005a) Late-glacial and early Holocene palaeoclimatic reconstruction based on glacier fluctuations and equilibrium-line altitudes at northern Folgefonna, Hardanger, western Norway. J Quat Sci 20:179–198

Bakke J, Lie Ø, Nesje A, Dahl SO, Paasche Ø (2005b) A high-resolution glacial reconstruction based on physical sediment parameters from pro-glacial lakes at northern Folgefonna, western Norway. The Holocene 15:161–176

Bartlein PJ, Whitlock C (1993) Paleoclimatic interpretation of the Elk Lake pollen record. Geol Soc Am Spec Paper 276:275–293

Battarbee RW (2000) Palaeolimnological approaches to climate change, with special regard to the biological record. Quat Sci Rev 19:107–124

Battarbee RW, Cameron NG, Golding P, Brooks SJ, Switsur R, Harkness D, Appleby P, Oldfield F, Thompson R, Monteith DT, McGovern A (2001) Evidence for Holocene climate variability from the sediments of a Scottish remote mountain lake. J Quat Sci 16:339–346

Battarbee RW, Grytnes J-A, Appleby PG, Catalan J, Korhola A, Birks HJB, Heegaard E, Lami A (2002) Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years. J Paleolimnol 28:161–179

Bennett KD (1994) Confidence intervals for age estimates and deposition time in late-Quaternary sediment sequences. The Holocene 4:337–348

Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. New Phytologist 132:155–170

Bennett KD (2002) Comment: the Greenland 8200 cal yr BP event detected in loss-on-ignition profiles in Norwegian lacustrine sediment sequences. J Quat Sci 17:97–99

Bennett KD, Willis KJ (2001) Pollen. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments. Terrestrial, algal, and siliceous indicators, vol 3. Kluwer Academic Publishers, Dordrecht, pp 5–32

Bennion H, Wunsam S, Schmidt R (1995) The validation of diatom-phosphorus transfer functions: an example from Mondsee, Austria. Freshwater Biol 34:271–283

Bigler C, Larocque I, Peglar SM, Birks HJB, Hall RI (2002) Quantitative multi-proxy assessment of long-term patterns of Holocene environmental change from a small lake near Abisko, northern Sweden. The Holocene 12:481–496

Birks HH (2000) Aquatic macrophyte vegetation development in Kråkenes Lake, western Norway, during the late-glacial and early Holocene. J Paleolimnol 23:7–19

Birks HH (2001) Plant macrofossils. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments. Terrestrial, algal, and siliceous indicators, vol 3. Kluwer Academic Publishers, Dordrecht, pp 49–74

Birks HH (2002) The recent extinction of *Azolla nilotica* in the Nile Delta, Egypt. Acta Palaeobot 42:203–214

Birks HH, Ammann B (2000) Two terrestrial records of rapid climate change during the glacial–Holocene transition (14,000–9000 calendar years BP) from Europe. Proc Nat Acad Sci 97:1390–1394

Birks HH, Birks HJB (2001) Recent ecosystem dynamics in nine North African lakes in the CASSARINA project. Aquatic Ecol 35:461–478

Birks HH, Birks HJB (2003) Reconstructing Holocene climates from pollen and plant macrofossils. In: Mackay A, Battarbee RW, Birks HJB, Oldfield F (eds) Global change in the Holocene. Hodder Arnold, London, pp 341–357

Birks HH, Wright HE (2000) Introduction to the reconstruction of the late-glacial and early aquatic ecosystems at Kråkenes Lake, Norway. J Paleolimnol 23:1–5

Birks HH, Whiteside MC, Stark D, Bright RC (1976) Recent paleolimnology of three lakes in northwestern Minnesota. Quat Res 6:249–272

Birks HH, 23 others (1996) The Kråkenes late-glacial palaeoenvironmental project. J Paleolimnol 15:281–286

Birks HH, Battarbee RW, Birks HJB (2000) The development of the aquatic ecosystem at Kråkenes Lake, western Norway, during the late glacial and early Holocene–a synthesis. J Paleolimnol 23:91–114

Birks HH, Peglar SM, Boomer I, Flower RJ, Ramdani M (2001) Palaeolimnological responses of nine North African lakes in the CASSARINA project to recent environmental changes and human impact detected by plant macrofossil, pollen, and faunal analyses. Aquatic Ecol 35:405–430

Birks HJB (1993a) Quaternary palaeoecology and vegetation science–current contributions and possible future developments. Rev Palaeobot Palynol 79:153–177

Birks HJB (1993b) Impact of computer-intensive procedures in testing palaeoecological hypotheses. INQUA Commission for the Study of Holocene Working Group on Data-Handling Methods Newsletter 9:1–5

Birks HJB (1995) Quantitative palaeoenvironmental reconstructions. In: Maddy D, Brew JS (eds) Statistical modelling of Quaternary science data. Quaternary Research Association, Cambridge, pp 161–254

Birks HJB (1996) Achievements, developments, and future challenges in quantitative Quaternary palynology. INQUA Commission for the Study of Holocene Sub-Commission on Data-Handling Methods Newsletter 14:2–8

Birks HJB (1998) Numerical tools in palaeolimnology–progress, potentialities, and problems. J Paleolimnol 20:307–332

Birks HJB (2003) Quantitative palaeoenvironmental reconstructions from Holocene biological data. In: Mackay A, Battarbee RW, Birks HJB, Oldfield F (eds) Global change in the Holocene. Hodder Arnold, London, pp 107–123

Birks HJB (2005) Fifty years of Quaternary pollen analysis in Fennoscandia 1954–2004. Grana 44:1–22

Birks HJB, Birks HH (1980) Quaternary palaeoecology. Edward Arnold, London

Birks HJB, Gordon AD (1985) Numerical methods in Quaternary pollen analysis. Wiley, London

Birks HJB, Line JM (1994) Sequence-splitting of pollen accumulation rates from the Holocene and Devensian late-glacial of Scotland. Diss Bot 234:145–160

Birks HJB, Jones VJ, Rose NL (2004) Recent environmental change and atmospheric contamination on Svalbard, as recorded in lake sediments–synthesis and conclusions. J Paleolimnol 31:531–546

Bjune AE, Bakke J, Nesje A, Birks HJB (2005) Holocene mean July temperature and winter precipitation in western Norway inferred from palynological and glaciological lake-sediment proxies. The Holocene 15:177–189

Booth RK, Jackson ST (2003) A high-resolution record of late-Holocene moisture variability from a Michigan raised bog, USA. The Holocene 13:863–876

Booth RK, Jackson ST, Gray CED (2004) Paleoecology and high-resolution paleohydrology of a kettle peatland in Upper Michigan. Quat Res 61:1–13

Boyle JF (2004) A comparison of two methods for estimating the organic matter content of sediments. J Paleolimnol 31:125–127

Braak CJF ter (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179

Bradbury JP, Dean WE (eds) (1993) Elk Lake, Minnesota: Evidence for Rapid Climate Change in the North-Central United States. Geological Society of America Special Paper 96

Bradbury JP, Colman SM, Reynold RL (2004) The history of recent limnological changes and human impact on Upper Klamath Lake, Oregon. J Paleolimnol 31:151–165

Bradshaw EG (2001) Linking land and lake. The response of lake nutrient regimes and diatoms to long-term land-use change in Denmark. Doctoral thesis, University of Copenhagen, Copenhagen

Bradshaw EG, Anderson NJ (2001) Validation of a diatom-phosphorus calibration set for Sweden. Freshwater Biol 46:1035–1048

Bradshaw EG, Jones VJ, Birks HJB, Birks HH (2000) Diatom responses to late-glacial and early-Holocene environmental change at Kråkenes, western Norway. J Paleolimnol 23:21–34

Bradshaw EG, Rasmussen P, Odgaard BV (2005a) Mid- to late-Holocene land-use change and lake development at Dallund Sø, Denmark: synthesis of multiproxy data, linking land and lake. The Holocene 15:1152–1162

Bradshaw EG, Rasmussen P, Nielsen H, Anderson NJ (2005b) Mid- to late-Holocene land-use change and lake development at Dallund Sø, Denmark: trends in lake primary production as reflected by algal and macrophyte remains. The Holocene 15:1130–1142

Breemen N van, Wright RF (2004) History and prospect of catchment biogeochemistry: a European perspective based on acid rain. Ecology 85:2363–2368

Broderson KP, Anderson NJ (2002) Distribution of chironomids (Diptera) in low arctic West Greenland lakes: trophic conditions, temperature and environmental reconstruction. Freshwater Biol 47:1137–1157

Brodersen KP, Odgaard BV, Vestergaard O, Anderson NJ (2001) Chironomid stratigraphy in the shallow and eutrophic Lake Søbygaard, Denmark: chironomid–macrophyte co-occurrence. Freshwater Biol 46:253–267

Broderson KP, Pederson O, Lindegaard C, Hamburger K (2004) Chironomids (Diptera) and oxy-regulatory capacity: an experimental approach to palaeolimnological interpretation. Limnol Oceanography 49:1549–1559

Brooks SJ (2000) Late-glacial fossil midge stratigraphies (Insecta: Diptera: Chironomidae) from the Swiss Alps. Palaeogeogr Palaeoclimatol Palaeoecol 159:261–279

Brooks SJ (2003) Chironomid analysis to interpret and quantify Holocene climate change. In: Mackay A, Battarbee RW, Birks HJB, Oldfield F (eds) Global change in the Holocene. Hodder Arnold, London, pp 328–341

Brooks SJ, Birks HJB (2001) Chironomid-inferred air temperatures from Late-glacial and Holocene sites in north-west Europe: progress and problems. Quat Sci Rev 20:1723–1741

Buck CE, Millard AR (eds) (2004) Tools for constructing chronologies—Crossing disciplinary boundaries. Lecture Notes in Statistics 177, Springer, London

Carnelli AL, Theurillat J-P, Madella M (2004) Phytolith types and type-frequencies in subalpine-alpine plant species of the European Alps. Rev Palaeobot Palynol 129:39–65

Cattaneo A, Couillard Y, Wunsam S, Courcelles M (2004) Diatom taxonomic and morphological changes as indicators of metal pollution and recovery in Lac Default (Québec, Canada). J Paleolimnol 32:163–175

Chaix L (1983) Malacofauna from the late glacial deposits of Lobsigensee (Swiss Plateau). Studies in the late Quaternary of Lobsigensee 5. Revue de Paléobiologie 2:211–216

Chambers FM, Charman DJ (2004) Holocene environmental change: contributions from the peatland archive. The Holocene 14:1–6

Charman DJ, Chambers FM (eds) (2004) Peatlands and Holocene environmental change. The Holocene 14:1–143

Chaudhuri P, Marron JS (1999) SiZer for exploration of structure in curves. J Am Stat Assoc 94:807–823

Clark JGD (1954) Excavations at Star Carr. An early Mesolithic site at Seamer, near Scarborough, Yorkshire. Cambridge University Press, Cambridge

Clark JS (2005) Why environmental scientists are becoming Bayesians. Ecol Lett 8:2–14

Cohen AS (2003) Paleolimnology–the history and evolution of lake systems. Oxford University Press, Oxford

Cowgill WM, Goulden CE, Hutchinson GE, Patrick R, Racek AA, Tsukada M (1966). The history of Laguna de Petenxil. Memoirs of the Connecticut Acad Arts Sci 17:1–126

Crawley MJ (1993) GLIM for ecologists. Blackwell Scientific Publications, Oxford

Cushing EJ, Wright HE (1965) Hand-operated piston corers for lake sediments. Ecology 46:380–384

Dahl SO, Bakke J, Lie Ø, Nesje A (2003) Reconstruction of former glacier equilibrium-line altitudes based on pro-glacial sites: an evaluation of approaches and selection of sites. Quat Sci Rev 22:275–287

Das B, Vinebrooke RD, Sanchez-Azofeifa A, Rivard B, Wolfe AP (2005) Inferring sedimentary chlorophyll concentrations with reflectance spectroscopy: a novel approach to reconstructing historical changes in the trophic status of mountain lakes. Can J Fisheries and Aquatic Sci 62:1067–1078

Davidson TA, Sayer CD, Perrow MR, Tomlinson ML (2003) Representation of fish communities by scale sub-fossils in shallow lakes: implications for inferring percid-cyprinid shifts. J Paleolimnol 30:441–449

Davidson TA, Sayer CD, Bennion H, David C, Rose N, Wade MP (2005) A 250 year comparison of historical, macrofossil and pollen records of aquatic plants in a shallow lake. Freshwater Biol 50:1671–1686

Davies SJ, Metcalfe SE, MacKenzie AB, Newton AJ, Endfield GH, Farmer JG (2004) Environmental changes in the Zirahuén Basin, Michoacán, Mexico, during the last 1000 years. J Paleolimnol 31:77–98

Davis BAS, Brewer S, Stevenson AC, Guiot J, Data Contributors (2003) The temperature of Europe during the Holocene reconstructed from pollen data. Quat Sci Rev 22:1701–1716

Davis JC (2002) Statistics and data analysis in geology. Wiley, New York

Dean WE (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss-on-ignition: comparison with other methods. J Sedimentary Petrol 44:242–248

Deevey ES (1964) Coaxing history to conduct experiments. Bioscience 19:40–43

Deevey ES (1984) Stress, strain, and stability of lacustrine ecosystems. In: Haworth EY, Lund JWG (eds) Lake sediments and environmental history. University of Leicester Press, Leicester, pp 203–229

Delcourt HR, Delcourt PA (1991) Quaternary ecology—a paleoecological perspective. Chapman & Hall, London

Digerfeldt G (1971) The post-glacial development of the ancient lake of Torreberga, Scania, south Sweden. Geologiska Föreninger i Stockholm Förhandlingar 93:601–624

Digerfeldt G (1986) Studies on past lake-level fluctuations. In: Berglund BE (ed) Handbook of Holocene palaeoecology and palaeohydrology. Wiley, Chichester, pp 127–143

Douglas MSV, Hamilton PB, Pienitz R, Smol JP (2004) Algal indicators of environmental change in Arctic and Antarctic lakes and ponds. In: Pienitz R, Douglas MSV, Smol JP (eds) Long-term environmental change in Arctic and Antarctic lakes. Springer, Dordrecht, pp 117–157

Duigan CA, Birks HH (2000) The late-glacial and early-Holocene palaeoecology of cladoceran microfossil assemblages at Kråkenes, western Norway, with a quantitative reconstruction of temperature changes. J Paleolimnol 23:67–76

Eicher U, Siegenthaler U (1983) Stable isotopes in lake marl and mollusc shells from Lobsigensee (Swiss Plateau). Studies in the late Quaternary of Lobsigensee 6. Revue de Paléobiologie 2:217–220

Eide W, Birks HH, Bigelow NH, Peglar SM, Birks HJB (2006) Holocene tree migrations in the Setesdal Valley, southern Norway, as reconstructed from macrofossil and pollen evidence. Veget Hist Archaeobot 15:65–85

Elias SA (1994) Quaternary insects and their environments. Smithsonian Institution Press, Washington

Elias SA (1997) The mutual climatic range method of palaeoclimate reconstruction based on insect fossils: new applications and inter-hemispheric comparisons. Quat Sci Rev 16:1217–1225

Elias SA (2001) Mutual climatic range reconstructions of seasonal temperatures based on Late Pleistocene fossil beetle assemblages in Eastern Beringia. Quat Sci Rev 20:77–91

Elias SA, Wilkinson B (1983) Late-glacial insect fossil assemblages from Lobsigensee (Swiss Plateau). Studies in the late Quaternary of Lobsigensee 3. Revue de Paléobiologie 2:189–204

Elias SA, Andrews JT, Anderson KH (1999) Insights on the climatic constraints on the beetle fauna of coastal Alaska, USA, derived from the mutual climatic range method of paleoclimate reconstruction. Arctic Antarctic Alpine Res 31:94–98

Ellison AM (2004) Bayesian inference in ecology. Ecol Lett 7:509–520

Engstrom DR, Hansen BCS (1985) Postglacial vegetational change and soil development in southeastern Labrador as inferred from pollen and chemical stratigraphy. Can J Bot 63:543–561

Ewing HA (2002) The influence of substrate on vegetation history and ecosystem development. Ecology 83:2766–2781

Ewing HA, Nater EA (2002) Holocene soil development on till and outwash inferred from lake-sediment geochemistry in Michigan and Wisconsin. Quat Res 57:234–243

Finkelstein SA, Peros MC, Davis AM (2005) Late Holocene paleoenvironmental change in a Great Lakes coastal wetland: integrating pollen and diatom datasets. J Paleolimnol 33:1–12

Finney BP, Gregory-Evans I, Sweetman J, Douglas MSV, Smol JP (2000) Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. Science 290:795–799

Finney BP, Gregory-Evans I, Sweetman J, Douglas MSV, Smol JP (2002) Fisheries productivity in the northeastern Pacific Ocean over the last 2200 years. Nature 416:729–733

Fisher E, Wake R, Oldfield F, Boyle J, Wolff GA (2003) Molecular marker records of land use change. Organic Chem 34:105–119

Flower RJ (2001) Change, stress, sustainability and aquatic ecosystem resilience in North African wetland and lakes during the 20th century: an introduction to integrated biodiversity studies within the CASSARINA Project. Aquatic Ecol 35:261–280

Ford MS (1990) A 10,000-year history of natural ecosystem acidification. Ecol Monographs 60:57–89

Fritz SC (1989) Lake development and limnological response to prehistoric and historic land-use in Diss, Norfolk, U.K. J Ecol 77:182–202

Fritz SC (2003) Lacustrine perspectives on Holocene climate. In: Mackay A, Battarbee RW, Birks HJB, Oldfield F (eds) Global change in the Holocene. Hodder Arnold, London, pp 328–341

Fritz SC, Engstrom DR, Haskell BJ (1994) “Little Ice Age” aridity in the North American Great Plains: a high-resolution reconstruction of salinity fluctuations from Devils Lake, North Dakota, USA. The Holocene 4:69–73

Gardiner FP, Haedrich RL (1978) Zonation in the deep benthic megafauna. Application of a general test. Oecologia 31:311–317

Gehrels WR, Roe HM, Charman DJ (2001) Foraminifera, testate amoebae, and diatoms as sea-level indicators in UK saltmarshes: a quantitative multiproxy approach. J Quat Sci 16:210–220

Gordon AD (1982) Numerical methods in Quaternary palynology V. Simultaneous graphical representation of the levels and taxa in a pollen diagram. Rev Palaeobot Palynol 37:155–183

Goslar T, Knaap WO van der, Hicks S, Andric M, Czernik J, Goslar E, Räsänen S, Hyotyla H (2005) Radiocarbon dating of modern peat profiles: pre- and post-bomb ^{14}C variations in the construction of age-depth models. Radiocarbon 47:115–134

Grimm EC (1991–2004) TILIA, TILA.GRAPH, and TGView. Illinois State Museum, Research and Collections Center, Springfield, USA (http://demeter.museum.state.il.us/pub /grimm/)

Gulliksen S, Birks HH, Possnert G, Mangerud J (1998) A calendar age estimate of the Younger Dryas–Holocene boundary at Kråkenes, western Norway. The Holocene 8:249–259

Hairston NG, Kearns CM, Demma LP, Effler SW (2005) Species-specific *Daphnia* phenotypes: a history of industrial pollution and pelagic ecosystem response. Ecology 86:1669–1678

Hammarlund D, Barnekow L, Birks HJB, Buchardt B, Edwards TWD (2002) Holocene changes in atmospheric circulation recorded in the oxygen-isotope stratigraphy of lacustrine carbonates from northern Sweden. The Holocene 12:339–351

Haug G, Ganopolski A, Sigman DM, Rosell-Mele A, Swann GEA, Tiedemann R, Jaccard SL, Bollmann J, Maslin MA, Leng MJ, Eglington G (2005) North Pacific seasonality and the glaciation of North America 2.7 million years ago. Nature 433:821–825

Heegaard E, Birks HJB, Telford RJ (2005) Relationships between calibrated ages and depth in stratigraphical sequences: an estimation procedure by mixed-effect regression. The Holocene 15:612–618

Heegaard E, Lotter AF, Birks HJB (2006) Aquatic biota and the detection of climate change: are there consistent aquatic ecotones? J Paleolimnol 35:507–518
Heiri C, Bugmann H, Tinner W, Heiri O, Lischke H (2006) A model-based reconstruction of Holocene treeline dynamics in the Central Swiss Alps. J Ecol 94:206–216
Heiri O (2004) Within-lake variability of subfossil chironomid assemblages in shallow Norwegian lakes. J Paleolimnol 32:67–84
Heiri O, Lotter AF, Lemcke G (2001) Loss-on-ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J Paleolimnol 25:101–110
Heiri O, Wick L, Leeuwen JFN van, Knaap WO van der, Lotter AF (2003) Holocene tree immigration and the chironomid fauna of a small Swiss subalpine lake (Hinterburgsee, 1515 m a.s.l). Palaeogeogr Palaeoclimatol Palaeoecol 189:35–53
Hill MO, Gauch HG (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58
Hodgson DA, Johnston NM, Caulkett AP, Jones VJ (1998) Palaeolimnology of Antarctic fur seal *Arctocephalus gazella* populations and implication for Antarctic management. Biol Conservation 83:145–154
Hodgson DA, Verleyen E, Sabbe K, Squier AH, Keely BJ, Leng MJ, Saunders KM, Vyverman W (2005) Late Quaternary climate-driven environmental change in the Larsemann Hills, East Antarctica, multi-proxy evidence from a lake sediment core. Quat Res 64:83–99
Hofmann W (1983) Stratigraphy of subfossil Chironomidae and Ceratopogonidae (Insecta: Diptera) in late glacial littoral sediments from Lobsigensee (Swiss Plateau). Studies in the late Quaternary of Lobsigensee 4. Revue de Paléobiologie 2:205–209
Hofmann W (1996) Empirical relationships between cladoceran fauna and trophic state in thirteen northern German lakes: analysis of surficial sediments. Hydrobiologia 318:195–201
Hofmann W (2000) Response of the chydorid faunas to rapid climatic changes in four alpine lakes at different altitudes. Palaeogeogr Palaeoclimatol Palaeoecol 159:281–292
Huang Y, Shuman B, Wang Y, Webb T (2004) Hydrogen isotope ratios of individual lipids in lake sediments as novel tracers of climatic and environmental change: a surface sediment test. J Paleolimnol 31:363–375
Hughen KA, Eglington TI, Xu L, Makou M (2004) Abrupt tropical vegetation response to rapid climate changes. Science 304:1955–1959
Hutchinson GE (1970) Ianula: an account of the history and development of the Lago di Monterosi, Latium, Italy. Trans Am Philosophical Soc 60
Hynynen J, Palomäki A, Meriläinen JJ, Witick A, Mäntyoski K (2004) Pollution history and recovery of a boreal lake exposed to a heavy bleached pulping effluent load. J Paleolimnol 32:351–374
Iversen J (1954) The late-glacial flora of Denmark and its relation to climate and soil. Danmarks Geologiske Undersøgelse Series II 80:87–109
Jackson DA (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74:2204–2214
Jackson RB, Hedin LO (2004) Terrestrial and freshwater biogeochemistry. Ecology 85:2353–2354
Jolliffe IT (2002) Principal component analysis, 2nd edn. Springer, New York
Juggins S (1996) The PALICLAS database. Memorie del l'Istituto Italiano di Idrobiologia 55:321–328
Juggins S (2002) Palaeo Data Plotter Version 1.0. University of Newcastle, Newcastle upon Tyne, UK (http://www.staff.ncl.ac.uk/stephen.juggins)
Juggins S (2003) C2 A program for analysing and visualising palaeoenvironmental data Version 1.0. University of Newcastle, Newcastle upon Tyne, UK (http://www.staff.ncl.ac.uk/stephen.juggins)
Keller F, Lischke H, Mathias T, Möhl A, Wick L, Ammann B, Kienast F (2002) Effects of climate, fire, and humans on forest dynamics: forest simulations compared to the palaeological (sic) record. Ecol Model 152:109–127
Kerfoot WC, Robins JA, Weider LJ (1999) A new approach to historical reconstruction: combining descriptive and experimental limnology. Limnol Oceanography 44:1232–1247
Korhola A, Weckström J, Holmström L, Erästö P (2000) A quantitative Holocene climatic record from diatoms in northern Fennoscandia. Quat Res 54:284–294
Korhola A, Vasko K, Toivonen HTT, Olander H (2002) Holocene temperature changes in northern Fennoscandia reconstructed from chironomids using Bayesian modelling. Quat Sci Rev 21:1841–1860
Korsman T, Segerström U (1998) Forest fire and lake-water acidity in a northern Swedish boreal area: Holocene changes in lake-water quality at Makkassjön. J Ecol 86:113–124
Kovach WL (1993) Multivariate techniques for biostratigraphical correlation. J Geol Soc, Lond 150:697–705
Kühl N (2003) Die Bestimmung botanisch-klimatologischer Transferfunktionen und die Rekonstruktion des bodennahen Klimazustandes in Europa während der Eem-Warmzeit. Diss Bot 375
Kühl N, Litt T (2003) Quantitative time series reconstruction of Eemian temperature at three European sites using pollen data. Veget Hist Archaeobot 12:205–214
Kühl N, Gebhardt C, Litt T, Hense A (2002) Probability density functions as botanical–climatological transfer functions for climate reconstruction. Quat Res 58:381–392
Larsen E, Stalsberg MK (2004) Younger Dryas glaciolacustrine rhythmites and corrie glacier variations at Kråkenes, western Norway: depositional processes and climate. J Paleolimnol 31:49–61
Last WM, Smol JP (eds) (2001a) Tracking environmental change using lake sediments. Basin analysis, coring, and chronological techniques, vol 1. Kluwer, Dordrecht
Last WM, Smol JP (eds) (2001b) Tracking environmental change using lake sediments. Physical and geochemical methods, vol 2. Kluwer, Dordrecht
Levesque AJ, Cwynar LC, Walker IR (1994) A multiproxy investigation of late-glacial climate and vegetation change at Pine Ridge Pond, southwest New Brunswick, Canada. Quat Res 42:316–327
Likens GE (ed) (1985) An ecosystem approach to aquatic ecology. Mirror lake and its environment. Springer-Verlag, New York
Lischke H, Lotter AF, Fischlin A (2002) Untangling a Holocene pollen record with forest model simulations and independent climate data. Ecol Model 150:1–21
Livingstone DA (1957) On the sigmoid growth phase in the history of Linsley Pond. Am J Sci 255:364–373
Livingstone DA, Bryan K, Leahy RG (1958) Effects of an arctic environment on the origin and development of freshwater lakes. Limnol Oceanography 3:192–214
Livingstone DM, Lotter AF (1998) The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. J Paleolimnol 19:181–189
Livingstone DM, Lotter AF, Walker IR (1999) The decrease in summer surface water temperature altitude in Swiss alpine lakes: a comparison with air temperature lapse rates. Arctic Antarctic Alpine Res 31:341–352
Lotter AF (1998) The recent eutrophication of Baldeggersee (Switzerland) as assessed by fossil diatom assemblages. The Holocene 8:395–405
Lotter AF (1999) Late-glacial and Holocene vegetation dynamics as shown by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee, central Switzerland. Veget Hist Archaeobot 8:165–184
Lotter AF (2001) The palaeolimnology of Soppensee (central Switzerland) as evidenced by diatom, pollen, and fossil-pigment analyses. J Paleolimnol 25:65–79

Lotter AF (2003) Multi-proxy climatic reconstructions. In: Mackay A, Battarbee RW, Birks HJB, Oldfield F (eds) Global change in the Holocene. Hodder Arnold, London, pp 373–383

Lotter AF, Birks HJB (1997) The separation of the influence of nutrients and climate on the varve time-series of Baldeggersee, Switzerland. Aquatic Sci 59:362–375

Lotter AF, Birks HJB (2003) The Holocene palaeolimnology of Sägistalsee and its environmental history–a synthesis. J Paleolimnol 30:333–342

Lotter AF, Ammann B, Sturm M (1992) Rates of change and chronological problems during the late-glacial period. Clim Dynamics 6:233–239

Lotter AF, Birks HJB, Zolitschka B (1995) Late Glacial pollen and diatom changes in response to two different environmental perturbations: volcanic eruption and Younger Dryas cooling. J Paleolimnol 14:23–47

Maberly SC, King L, Gibson CE, May L, Jones RI, Dent MM, Jordan C (2003) Linking nutrient limitation and water chemistry in upland lakes to catchment characteristics. Hydrobiologia 506–509:83–91

Mackay AW, Jones VJ, Battarbee RW (2003) Approaches to Holocene climate reconstruction using diatoms. In: Mackay A, Battarbee RW, Birks HJB, Oldfield F (eds) Global change in the Holocene. Hodder Arnold, London, pp 274–309

Mackereth FJH (1965) Chemical investigation of lake sediments and their interpretation. Proc R Soc Lond B 161:295–309

Mackereth FJH (1966) Some chemical observations on post-glacial lake sediments. Proc R Soc Lond B 250:165–213

Mann ME. (2002) The value of multiple proxies. Science 297:1481–1482

Maslin MA (2004) Ecological versus climatic thresholds. Science 306:2197–2198

McCarroll D, Jalkanen R, Hicks S, Tuovinen M, Gagen M, Pawelleck F, Eckstein D, Schmitt U, Autid J, Heikkinene O (2003) Multiproxy dendrochronology: a pilot study. The Holocene 13:829–838

Meiri S, Dayan T, Simberloff D (2004) Carnivores, biases and Bergmann's rule. Biol J Linnean Soc 81:579–588

Meriläinen JJ, Hynynen J, Palomäki A, Veijola H, Witick A, Mäntyloski K, Granberg K, Lehtinen J (2001) Pulp and paper mill pollution and subsequent ecosystem recovery of a large boreal lake in Finland: a palaeolimnological analysis. J Paleolimnol 26:11–35

Michelutti N, Wolfe AP, Vinebrooke RD, Rivard B, Briner JP (2005) Recent primary production increases in arctic lakes. Geophys Res Lett 32:L19715, doi: 10.1029/2005GL023693,205

Mighall TM, Lageard JGA, Chambers FM, Field MH, Mahi P (2004) Mineral deficiency and the presence of *Pinus sylvestris* on mires during the mid- to late-Holocene: palaeoecological data from Cadogan's Bog, Mizen Peninsula, Co Cork, southwest Ireland. The Holocene 14:95–109

Milecka K, Szeroczyńska K (2005) Changes in macrophytic flora and planktonic organisms in Lake Ostrowite, Poland, as a response to climatic and trophic fluctuations. The Holocene 15:74–84

Moine O, Rousseau D-D, Jolly D, Vianey-Liaud M (2002) Paleoclimate reconstruction using Mutual Climatic Range on terrestrial mollusks. Quat Res 57:162–172

Möller AP, Jennions MD (2001). Testing and adjusting for publication bias. Trends in Ecol Evol 16:580–586

Nesje A (1992) A piston corer for lacustrine and marine sediments. Arctic Alpine Res 24:357–359

Nesje A, Dahl SO (2001) The Greenland 8200 cal yr BP event detected in loss-on-ignition profiles in Norwegian lacustrine sediment sequences. J Quat Sci 16:155–166

Nesje A, Matthews JA, Dahl SO, Berrisford MS, Andersson C (2001) Holocene glacier fluctuation of Flatebreen and winter precipitation changes in the Jostedalesbreen region, western Norway, based on glaciolacustrine records. The Holocene 11:267–280

NRC (National Research Council) (2005) The geological record of ecological dynamics—understanding the biotic effects of future environmental change. National Academies Press, Washington, DC

Odgaard BV, Rasmussen P (2001) The occurrence of egg-cocoons of the leech *Piscicola geometra* (L) in recent lake sediments and their relationship with remains of submerged macrophytes. Archiv für Hydrobiologie 152:671–686

Oldfield F (1996) The PALICLAS Project: Synthesis and Overview. Memorie del l'Istituto Italiano di Idrobiolgia 55:329–357

Oldfield F, Asioli A, Accorsi CA, Mercuri AM, Juggins S, Langone L, Rolph T, Trincardi F, Wolff G, Gibbs Z, Vigliotti L, Frignani M, Post K van der, Branch N (2003a) A high-resolution late Holocene environmental record from the central Adriatic Sea. Quat Sci Rev 22:319–342

Oldfield F, Wake R, Boyle J, Jones R, Nolan S, Gibbs Z, Appleby P, Fisher E, Wolff G (2003b) The late-Holocene history of Gormire Lake (NE England) and its catchment: a multiproxy reconstruction of past human impact. The Holocene 13:677–690

Pace ML, Cole JJ, Carpenter SR, Kitchell JF, Hodgson JR, Bogert MC van de, Bade DL, Kritzberg ES, Bastviken D (2004) Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427:240–243

Pancost RD, Baas M, Geel B van, Damsté JSS (2003) Response of an ombrotrophic bog to a regional climate event revealed by macrofossil, molecular and carbon isotopic data. The Holocene 13:921–932

Pienitz R, Douglas MSV, Smol JP (eds) (2004) Long-term environmental change in Arctic and Antarctic lakes. Springer, Dordrecht

Pross J, Klotz S, Mosbrugger V (2000) Reconstructing palaeotempertures for the Early and Middle Pleistocene using the mutual climatic range method based on plant fossils. Quat Sci Rev 19:1785–1799

Racca JMJ, Wild M, Birks HJB, Prairie YT (2003) Separating wheat from chaff: diatom taxon selection using an artificial neural network pruning algorithm. J Paleolimnol 29:123–133

Ralska-Jasiewiczowa M, Goslar T, Madeyska T, Starkel L (eds) (1998) Lake Gościąż, Central Poland. A Monographic Study Part 1. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków

Ralska-Jasiewiczowa M, Goslar T, Różański K, Wacnik A, Czernik J, Chróst L (2003) Very fast environmental changes at the Pleistocene/Holocene boundary, recorded in laminated sediments of Lake Gościąż, Poland. Palaeogeogr Palaeoclimatol Palaeoecol 193:225–247

Reimer PJ, 28 others (2005) IntCal04 terrestrial radiocarbon age calibration, 0–26 Cal K yr BP. Radiocarbon 46:1029–1058

Renberg I, Hultberg H (1992) A palaeolimnological assessment of acidification and liming effects on diatom assemblages in a Swedish lake. Can J Fisheries and Aquatic Sci 49:65–72

Risebrobakken B, Jansen E, Andersson C, Mjelde E, Hevrøy K (2003) A high-resolution study of Holocene palaeoclimatic and palaeoceanographic changes in the Nordic Seas. Palaeoceanography 18 doi: 10.1029/2002PA000764

Rosén P, Dåbakk E, Renberg I, Nilsson M, Hall R (2000) Near-infrared spectrometry (NIRS); a new tool to infer past climatic changes from lake sediments. The Holocene 10:161–166

Rosén P, Segerström U, Eriksson L, Renberg I, Birks HJB (2001) Holocene climatic change reconstructed from diatoms, chironomids, pollen and near-infrared spectrometry at an alpine lake (Sjuodjijaure) in northern Sweden. The Holocene 11:551–562

Rosén P, Segerström W, Eriksson L, Renberg I (2003) Do diatom, chironomid, and pollen records consistently infer Holocene July air temperature? A comparison using sediment cores from four alpine lakes in northern Sweden. Arctic Antarctic Alpine Res 35:279–290

Sayer CD, Roberts N, Sadler J, David C, Wade PM (1999) Biodiversity changes in a shallow lake ecosystem: a multi-proxy palaeolimnological analysis. J Biogeography 26:97–114

Sayer CD, Jackson MJ, Hoare DJ, Simpson GL, Appleby PG, Boyle JF, Henderson ACG, Jones II, Liprot ER, Waldock MJ (2006) TBT causes ecosystem collapse in freshwater lakes. Environ Sci Technol (in press)

Selby KA, O'Brian CE, Brown AG, Stuits I (2005) A multi-proxy study of Holocene lake development, lake settlement, and vegetation history in central Ireland. J Quat Sci 20:147–168
Seppä H, Birks HJB (2001) July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. The Holocene 11:527–539
Seppä H, Weckström J (1999) Holocene vegetational and limnological changes in the Fennoscandian tree-line area as documented by pollen and diatom records from Lake Tsuolbmajarvi, Finland. Ecoscience 6:621–635
Seppä H, Nyman M, Korhola A, Weckström J (2002) Changes of treelines and alpine vegetation in relation to post-glacial climate dynamics in northern Fennoscandia based on pollen and chironomid records. J Quat Sci 17:287–301
Seppä H, Hammarlund D, Antonsson K (2005) Low-frequency and high-frequency changes in temperature and effective humidity during the Holocene in south-central Sweden: implications for atmospheric and oceanic forcings of climate. Clim Dynamics 25:285–297
Shuman B (2003) Controls on loss-on-ignition variation in cores from two shallow lakes in the north-eastern United States. J Paleolimnol 30:371–385
Shuman B, Newby P, Huang Y, Webb T (2004) Evidence for the close climatic control of New England vegetation history. Ecology 85:1297–1310
Sinka KJ, Atkinson TC (1999) A mutual climatic range method for reconstructing palaeoclimate from plant remains. J Geol Soc, London 156:381–396
Smith AG (1965) Problems of inertia and threshold related to post-glacial habitat changes. Proc R Soc Lond B 161:331–342
Smith SV, Bradley RS, Abbott MB (2004) A 300 year record of environmental change from Lake Tuborg, Ellesmere Island, Nunavut, Canada. J Paleolimnol 32:37–48
Smol JP (2002) Pollution of lakes and rivers–a paleoenvironmental perspective. Arnold, London
Smol JP, Birks HJB, Last WM (eds) (2001a) Tracking environmental change using lake sediments. Terrestrial, algal, and siliceous indicators, vol 3. Kluwer, Dordrecht
Smol JP, Birks HJB, Last WM (eds) (2001b) Tracking environmental change using lake sediments. Zoological indicators, vol 4. Kluwer, Dordrecht
Smol JP, Wolfe AP, Birks HJB, 23 others (2005) Climate-driven regime shifts in the biological communities of arctic lakes. Proc Nat Acad Sci 102:4397–4402
Telford RJ, Birks HJB (2005) The secret assumption of transfer functions: problems with spatial autocorrelation in evaluating model performance. Quat Sci Rev 24:2173–2179
Telford RJ, Andersson C, Birks HJB, Juggins S (2004a) Biases in the estimation of transfer function prediction errors. Palaeoceanography 19:PA1404, doi: 10.1029/2004PA001072
Telford RJ, Heegaard E, Birks HJB (2004b) All age–depth models are wrong: but how badly? Quat Sci Rev 23:1–5
Teranes JL, McKenzie JA, Lotter AF, Sturm M (1999) Stable isotope response to lake eutrophication: calibration of a high-resolution lacustrine sequence from Baldeggersee, Switzerland. Limnol Oceanography 44:320–333
Thompson R, Berglund BE (1976) Late Weichselian geomagnetic 'reversal' as a possible example of the reinforcement syndrome. Nature 263:490–491
Thompson R, Clark RM (1989) Sequence slotting for stratigraphic correlation between cores: theory and practice. J Paleolimnol 2:173–184
Vélez MI, Berrio JC, Hooghiemstra H, Metcalfe S, Marchant R (2005) Palaeoenvironmental changes during the last ca. 8590 calibrated yr (7800 radiocarbon yr) in the dry forest ecosystem of the Patía Valley, Southern Columbian Andes: a multiproxy approach. Palaeogeogr Palaeoclimatol Palaeoecol 216:279–302
Velle G, Larsen J, Eide W, Peglar SM, Birks HJB (2005a) Holocene environmental history and climate at Råtåsjøen, a low-alpine lake in south-central Norway. J Paleolimnol 33:129–153
Velle G, Brooks SJ, Birks HJB, Willessen E (2005b) Chironomids as a tool for inferring Holocene climate: an assessment based on six sites in southern Scandinavia. Quat Sci Rev 24:1429–1462
Verschuren D, Tibby J, Sabbe K, Roberts N (2000) Effects of depth, salinity, and substrate on the invertebrate community of a fluctuating tropical lake. Ecology 81:164–182
Veski S, Seppä H, Ojala AEK (2004) Cold event at 8200 yr BP recorded in annually laminated lake sediments in eastern Europe. Geology 32:681–684
Walker D, Pittelkow Y (1981) Some applications of the independent treatment of taxa in pollen analysis. J Biogeography 8:37–51
Walker D, Wilson OR (1978) A statistical alternative to the zoning of pollen diagrams. J Biogeography 5:1–21
Wasylikowa K, Starkel L, Niedziałkowska E, Skiba S, Stworzerwicz E (1985) Environmental changes in the Vistula valley at Pleszów caused by Neolithic man. Przegld Archeologiczny 33:19–55
Watkins ND (1971) Geomagnetic polarity events and the problem of "the reinforcement syndrome". Comments on Earth Sciences: Geophysics 2:36–43
Watts WA (1978) Plant macrofossils and Quaternary palaeoecology. In: Walker D, Guppy JC (eds) Biology and Quaternary environments. Australian Academy of Science, Canberra, pp 53–67
Weedon G (2003) Time-series analysis and cyclostratigraphy. Cambridge University Press, Cambridge
Weider LJ, Lampert W, Wessels M, Colbourne JK, Lamburg P (1997) Long-term genetic shifts in a micro-crustacean egg bank associated with anthropogenic changes in the Lake Constance ecosystem. Proc R Soc Lond B 264:1613–1618
Wick L, Leeuwen JFN van, Knaap WO van der, Lotter AF (2003) Holocene vegetation development in the catchment of Sägistalsee (1935 m a.s.l.), a small lake in the Swiss Alps. J Paleolimnol 30:261–272
Willis KJ, Braun M, Sümegi P, Tóth A (1997) Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. Ecology 78:740–750
Willemse NW, Törnqvist TE (1999) Holocene century-scale temperature variability from West Greenland lake records. Geology 27:580–584
Wolfe AP, Baron JS, Cornett RJ (2001) Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). J Paleolimnol 25:1–7
Wolfe AP, Kaushela SS, Fulton JR, McKnight DM (2002) Spectrofluorescence of sediment humic substances and historical changes of lacustrine organic matter provenance in response to atmospheric nutrient enrichment. Environ Sci Technol 36:3217–3223
Wolfe AP, Gorp AC van, Baron JS (2003) Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition. Geobiology 1:153–168
Wooller MJ, Francis D, Fogel MK, Miller GH, Walker IR, Wolfe AP (2004) Quantitative palaeotemperature estimates from $\delta^{18}O$ of chironomid head capsules preserved in arctic lake sediments. J Paleolimnol 31:267–274
Wright HE (1966) Stratigraphy of lake sediments and the precision of the palaeoclimatic record. In: Sawyer JJ (ed) World climate from 8000 to 0 B.C. Royal Meteorological Society, London, pp 157–173