

The Holocene palaeolimnology of Sägistalsee and its environmental history – a synthesis

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Abstract

Multi-proxy palaeoecological and palaeolimnological studies of the sedimentary record of Sägistalsee, a small lake at the present-day timberline in the Swiss Alps, reveal distinct changes in its catchment vegetation in relation to Holocene climate change and human impact. Four phases of catchment vegetation type were defined based on plant macrofossil analyses: open *Betula-Pinus cembra* woodland, *Abies alba-Pinus cembra* woodland, *Picea abies* forest, and cultural pasture. The expansion of spruce ~ 6300 cal. BP had a major impact on all abiotic proxies, whereas the reaction of the biotic proxies to this catchment change was lagged by several centuries. During the Bronze Age (ca. 4000 cal. BP) the spruce forest was cleared and the catchment began to be used as grazing pastures. Changes in sedimentology, geochemistry, and magnetic parameters closely reflect the changes in catchment vegetation. The catchment vegetation types explain a statistically significant amount of the variance in the chironomid, cladoceran, sedimentological, and magnetic data but not in the geochemical data. The strong catchment-lake interaction masks any biotic responses to millennium-scale climatic oscillations.

Introduction

Organisms in ecotonal environments may be particularly responsive to climatic change because they are close to the physiological limits of their distribution. The physiognomically most conspicuous ecotone in mountain regions is the transition from trees to shrubs and eventually to herbs at the subalpine–alpine boundary that is often related to summer temperature and length of the growing season, as well as height and duration of snow cover (e.g., Rochefort et al., 1993; Tranquillini, 1993; Eggenberg, 1995, 2002; Körner, 1999). Palaeobotanical investigations of past changes in the location of the treeline or timberline ecotone in mire and lake deposits have traditionally been used to

reconstruct palaeotemperatures in the subarctic as well as in mountain regions of the old and new world. It is only in the past few decades that lacustrine ecosystems near such ecotones have become the focus of detailed palaeoclimatological and palaeolimnological studies (e.g., Battarbee et al., 2002). The occurrence and composition of aquatic biota are directly or indirectly related to climate (e.g., Lotter et al., 1997b; Battarbee, 2000), making mountain lakes particularly sensitive recorders of past and present climate change. The length of ice-cover and thus the duration of the open-water season determines the amount of primary production in the water column as well as the mixing regime and the amount of oxygen depletion (Livingstone, 1997), whereas the climate-dependent weathering rates of catchment soils as well as catchment vegetation can have an important influence on water chemistry (MacDonald et al., 1993; Koinig et al., 1998; Birks et al., 2000). Given not only the close interaction between vegeta-

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tion, hydrology, topography, soil, climate, and human activity, but also the link between catchment processes and physical, chemical, and biological lake responses, the catchment area of a mountain lake is an important and critical unit for study (e.g., Likens and Bormann, 1974; Birks et al., 2000) in both palaeoecological and palaeolimnological investigations. Integrated palaeoecological studies allow investigation of the behaviour of biotic and abiotic systems with regard to natural and anthropogenic disturbances. The overall aim of the study on the Holocene history of Sägistalsee was to assess the influence of climate change on the lake, thereby distinguishing between effects that influence the biota in the water column directly and effects that are mediated indirectly through catchment processes. Studying different proxies allows the estimation of leads and lags in the reaction of these proxies to disturbances and the assessment of the resilience of biota in relation to different forms of environmental change. From the outset we planned to carry out a multi-proxy study that would involve working on the same sediment core and the same samples, thereby circumventing potential ambiguities in relation to core correlation and chronology.

Sägistalsee and its Holocene history

Here, we summarize the results of the multi-proxy study at Sägistalsee, a lake within a set of mountain lakes located in different altitudinal belts in the Swiss Alps (Lotter et al. 1997a). The emphasis of this summary and synthesis is on the influence of catchment processes on the palaeolimnology of Sägistalsee. Sägistalsee is a small lake situated at 1935 m asl at the present-day treeline in the Bernese Alps (for details see Lotter and Birks, 2003a). A sediment core of 13.5 m length taken in the deepest part of the basin at 9.5 m of water depth was dated with 18 AMS radiocarbon dates on terrestrial plant remains and analysed for different biotic and abiotic parameters. The sediment record includes the past 9000 years and consists mainly of sandy silts with an organic content of between 0.8 and 1.6% dry weight and a carbonate content of between 3 and 6% dry weight (Ohlendorf et al., 2003). The catchment was covered by open *Pinus cembra* (Swiss stone pine) and *Abies alba* (fir) woodland during the early Holocene (9000–6300 cal. BP). After the expansion of *Picea abies* (spruce) approx. 6400 cal. BP, forest cover became denser and treeline rose above 2200 m asl (Wick et al., 2003). Human impact on the subalpine forests started

in the late Neolithic, at about 4400 cal. BP and extensive anthropogenic forest clearance and lowering of the treeline in the catchment of Sägistalsee occurred during the Bronze Age (3700 cal. BP). Sägistalsee was characterized throughout the entire Holocene by a low diversity of cladocera (Hofmann, 2003). The composition of the chironomid fauna reflects the successive infilling of the lake through time (Heiri and Lotter, 2003) and, together with the sediment geochemistry (Koinig et al., 2003), gives evidence of three periods of oxygen depletion due to increased human activity in the catchment.

Numerical methods

The stratigraphies of all proxies analysed from Sägistalsee (see Table 1) were numerically zoned using optimal sum-of-squares partitioning (Birks and Gordon, 1985) as implemented in the program ZONE (Lotter and Juggins, 1991) to derive a consistent stratigraphical zonation scheme for the various proxies. Because of the different numerical properties of the various stratigraphical data-sets, the data were transformed prior to the optimal partitioning in an attempt to stabilise the variances (pollen, cladocera, chironomids, plant macrofossils) or to express the variables in comparable units (magnetics, geochemistry, grain-size). The transformations used were square-root transformation of pollen and cladoceran percentages (Prentice, 1980), $\log_e(y+1)$ of chironomid concentration values (Jager and Looman, 1987), standardisation to zero mean and unit variance of magnetic, geochemical, and grain-size data (Jager and Looman, 1987), and pseudo-species coding or conjoint coding (Hill et al., 1975) with cut-levels of 1, 10, and 100 for plant macrofossil data where the various types of macrofossils of a single plant taxon had been amalgamated into one variable prior to conjoint

Table 1. Number of samples and number of variables used for the optimal partitioning and the principal component analysis or detrended correspondence analysis

Data-set	Number of samples	Number of taxa/variables
Pollen	212	203
Plant macrofossils	372	53
Chironomids	82	30
Cladocera	112	7
Geochemistry	176	14
Grain-size	294	6
Magnetics	504	5

coding. The significant number of stratigraphical zones was assessed for each proxy using the broken stick model (Bennett, 1996). Due to the different sampling strategies, the zone boundaries may include different amounts of time, as shown in Fig. 1. In an attempt to summarise the major underlying gradients in each stratigraphical data-set, the data-sets were analysed by principal components analysis (PCA; all data-sets except plant macrofossils) or detrended correspondence analysis (DCA; plant macrofossils) (ter Braak, 1987). The same data transformations were applied in these ordinations as were used in the optimal partitioning except for grain-size compositional data which were transformed by log-ratio centring (Aitchinson, 1986). PCA was used because the gradient lengths of all the data-sets, as assessed by a preliminary DCA (detrending by segments, non-linear rescaling, downweighting of rare taxa), were less than 2 standard deviations (ter Braak and Prentice, 1988), except for plant macrofossils which have a gradient length of 2.49 standard deviations. The approximate statistical significance of the first four ordination axes for each data-set was assessed by comparison with the broken-stick model (Jolliffe, 1986; Jackson, 1993; Legendre and Legendre, 1998), and only the statistically significant axes are plotted in Fig. 2. These were used as 'composite' response variables in subsequent numerical analysis and statistical modelling (see Lotter et al., 1992; Birks et al., 2001). All the PCAs were based on a covariance matrix between the transformed variables and the sample scores were scaled for Euclidian distance biplots. A series of (partial) redundancy analyses (RDA; ter Braak, 1994) were carried out to test hypotheses about the influence of known Holocene climate changes on the stratigraphy of the biological proxies (pollen, chironomids, cladocera) at Sägistalsee and about the influence of catchment vegetation type on the biological (chironomid, cladocera) and sedimentological (geochemistry, magnetics, grain-size) proxies. The statistically significant PCA axes (Fig. 2) were used as 'composite' response variables in the RDAs. The use of these axes as response variables serves to concentrate the major gradients of variation or 'signal' within the data-set to the first few major PCA axes and to relegate the minor variation or 'noise' to the later minor axes (Gauch, 1982; Lotter et al., 1992). For a detailed discussion about the use of ordination axes derived from stratigraphical data as 'composite' variables, see Lotter et al. (1992); Ammann et al. (2000); Birks et al. (2001). The predictor or 'explanatory' variables used to assess the influence of Holocene climate change are

the July insolation at 45°N (Laskar et al., 1993), the Central European (CE) cold phases defined by Haas et al. (1998, see also Tinner and Ammann, 2001), and the North Atlantic ice-rafted debris (IRD) events defined by Bond et al. (1997, 2001) (Fig. 3). To assess the influence of catchment vegetation on the aquatic biological and sedimentological proxies, we defined four major catchment vegetation types solely on the basis of the occurrence of plant macrofossils (Wick et al., 2003) and coded them then as 1/0 dummy variables for each sample (Fig. 3). The following non-exclusive catchment vegetation types were defined: *Betula-Pinus cembra* woodland (9050–7000 cal. BP); *Abies alba-Pinus cembra* woodland (8480–2900 and 1715–1600 cal. BP); *Picea abies* forest (since 6315 cal BP); and cultural pastures characterised by the occurrence of macroscopic charcoal (since 4325 cal. BP).

When statistically significant ($p < 0.05$) RDA models are found, it is important because of the strong temporal auto-correlation in fine-resolution stratigraphical data to partial out the statistical effects of stratigraphy and hence age so that the variation in a stratigraphical data-set can be assessed statistically that is uniquely attributable to a particular set of predictor variables (ter Braak and Prentice, 1988; Lotter and Birks, 1993). The statistical significance of RDA and partial RDA models was assessed by restricted Monte Carlo permutation tests for temporally ordered data (ter Braak and Smilauer, 1998). Ninety-nine permutations were used for each test. From such tests the significance level obtained is a measure of the strength of evidence against the null hypothesis of no significant climatic influence on the biotic proxies or of no significant catchment vegetation influence on the aquatic or sedimentary proxies (Lotter and Birks, 1993).

All PCA, DCA, RDA, and partial RDAs were carried out with CANOCO version 4 (ter Braak and Smilauer, 1998).

Results and discussion

Major Holocene gradients of variance

In our discussion we focus here on the longer-term trends in variation and change, whereas short-term perturbations are discussed in the individual papers in Lotter and Birks (2003b) about the different biotic and abiotic parameters. Reducing the information of all data sets to their statistically significant number of PCA or DCA axes may help to pinpoint periods of higher variability throughout the Holocene. Commonly, increased

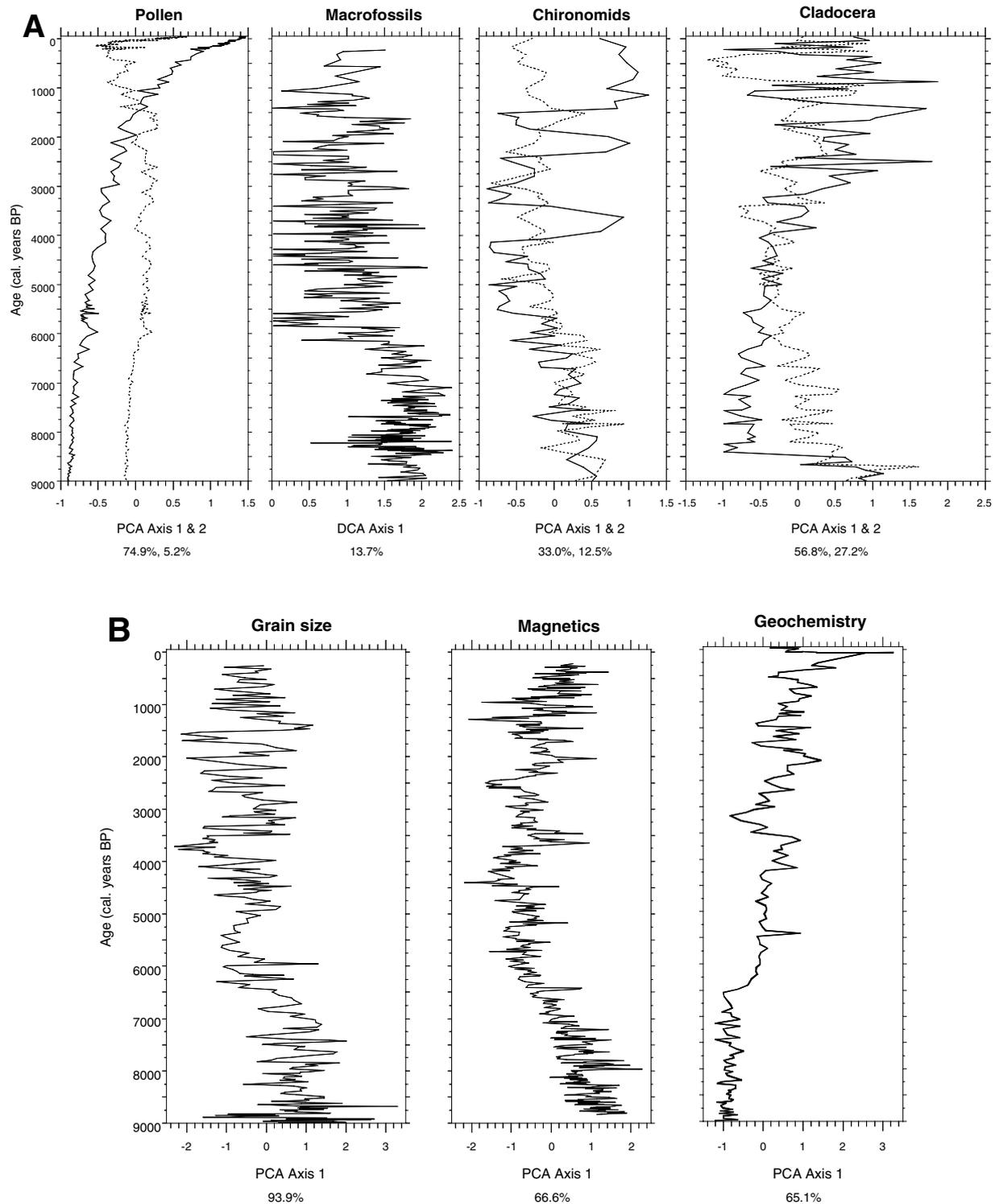


Fig. 1. Holocene sample scores on the statistically significant PCA or DCA axes of the different proxies analysed at Sägistalsee. Stippled lines indicate the second PCA axis. The percentage variance represented by the axes is also shown. (a) biotic proxies (pollen, plant macrofossils, chironomids, Cladocera); (b) abiotic proxies (grain size, magnetics, geochemistry).

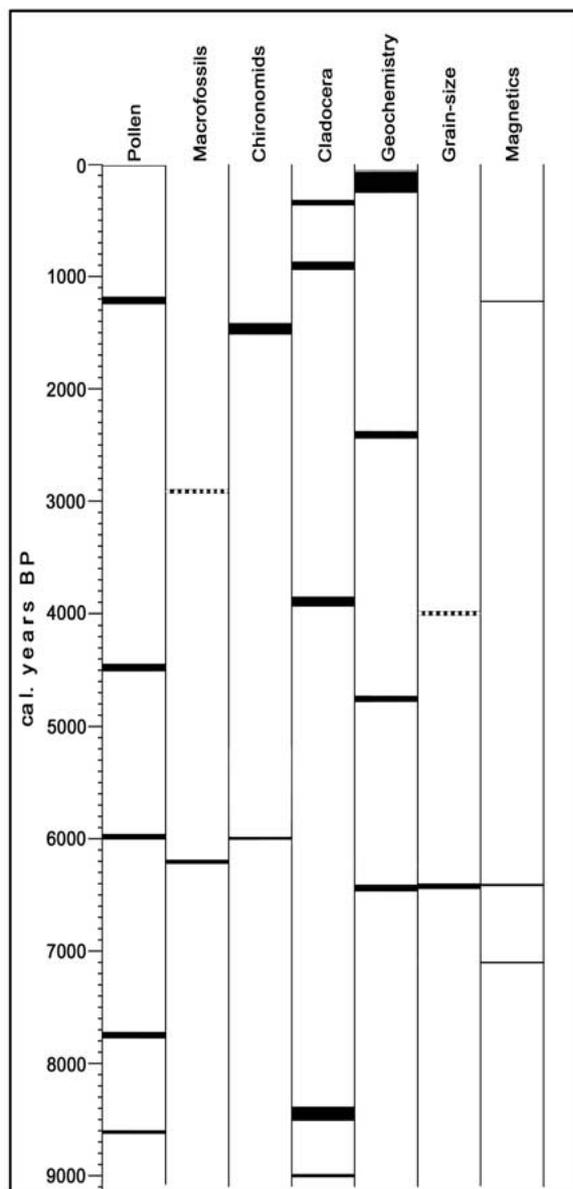


Fig. 2. Optimal sum of squares partitioning zonation of the different proxies (Birks and Gordon, 1985). The number of statistically significant zones was assessed by the broken stick model (Bennett, 1996). The dashed lines show important secondary zone boundaries that are statistically not significant.

variability in biota is considered as an indicator of ecosystem perturbation (Odum et al., 1979).

For pollen, chironomids, and cladocera, the first two PCA axes explain a statistically significant amount of the variance in the data, whereas for macrofossils, grain-size, magnetics and geochemistry only the first DCA or PCA axis was statistically significant (Fig. 1).

The pollen sample scores on the first PCA axis show a steadily increasing gradient of change, especially for the past 2000 years, mainly reflecting the increasing amounts of herb pollen (Wick et al., 2003). The pollen sample scores on the second axis primarily reflect a major change in composition and relative frequencies during the past century.

Mountainous regions such as the Alps show, over short horizontal distances, large elevational differences and thus large differences in vegetation types. Local alpine vegetation generally has a low pollen productivity with the result that regional and long-distance transported pollen from lowland vegetation suppresses the local alpine signal. This is the case at Sägistalsee (Wick et al., 2003). To assess the local catchment vegetation in arctic and alpine settings it is, therefore, necessary to combine pollen analysis with the study of stomata (Ammann and Wick, 1993; Gervais and MacDonald, 2001; MacDonald, 2001) and/or plant macrofossils (Birks and Birks, 2000; Birks, 2001). The plant macrofossil DCA sample scores from Sägistalsee show a high variability throughout the Holocene reflecting the inherent variability of plant macrofossil data (see Birks et al., 2001). Three general phases can be distinguished: a first phase of high DCA sample scores between 9000 and 7000 cal. BP corresponding to an open *Pinus cembra* – *Betula alba* – *Abies alba* woodland with dwarf willows; a second, transitional phase with gradually decreasing sample scores between 7000 and ca. 5500 cal. BP reflecting the migration and establishment of *Picea abies* into the *Pinus cembra* – *Abies alba* woodland; and a third phase with, on average, low sample scores since ca. 5500 cal. BP representing the dominance of *Picea abies* macrofossils (Wick et al., 2003).

The chironomid sample scores on the first and second PCA axes show a generally decreasing trend between 9000 and ca. 4000 cal. BP (Fig. 1). The sample scores on the first axis are then characterized by two large oscillations (ca. 4000–3500 and ca. 2300–2000 cal. BP) that correspond to phases with extremely low head capsule accumulation rates of *Stictochironomus* and *Tanytarsus lugens*-type that are attributed to hypolimnetic anoxia by Heiri and Lotter (2003).

The sample scores of the first cladocera PCA axis show a sharp decrease around 8500 cal. BP. Then they gradually increase from low values and since about 4000 cal. BP they start to oscillate. This pattern mainly reflects the absence of *Chydorus sphaericus* between 8500 and 4000 cal. BP and the increasing abundance of *Alona affinis* since ca. 8000 cal. BP (Hofmann, 2003).

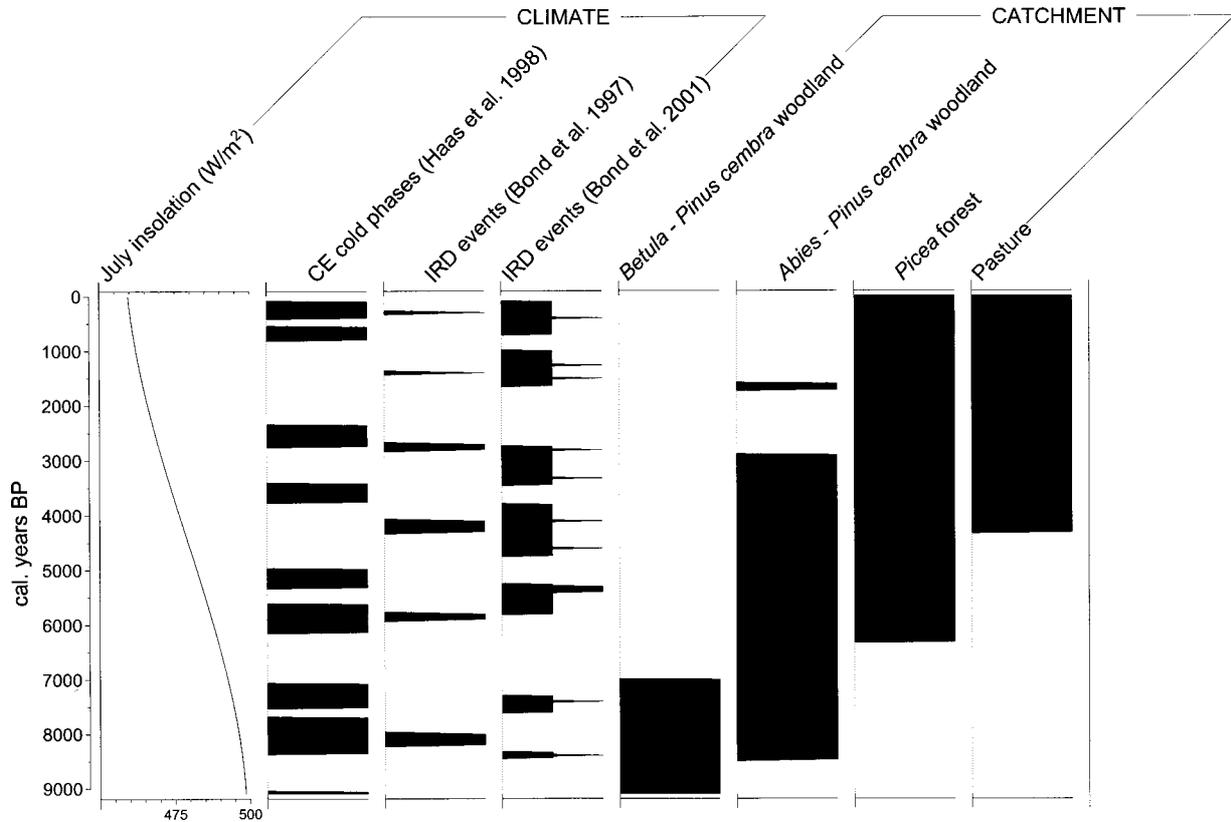


Fig. 3. Climate and catchment vegetation types used as explanatory variables in (partial) RDAs to assess their influence on the analysed proxies. July insolation values refer to 45°N (according to Laskar et al., 1993); CE refers to the Central European cold phases including the medieval cold phase and Little Ice Age (see Haas et al., 1998; Tinner and Ammann, 2001; Esper et al., 2002); the IRD event columns refer to ice-rafted debris events in the North Atlantic (Bond et al., 1997, 2001). The catchment vegetation types are defined according to the occurrence of macrofossils (Wick et al., 2003).

The PCA sample scores of the grain-size data show a first phase of more or less constant values which is followed by a transition to lower sample scores between 7000 and 6000 cal. BP (Fig. 1) reflecting the trend towards smaller fractions. Then, the sample scores stay at a lower level reflecting a lower median grain size. The major fluctuations between 4000 and 3500 and ca. 1700 and 1500 cal. BP are caused by increases in the clay-size fraction (Ohlendorf et al., 2003).

The magnetics PCA sample scores show a steady decrease until about 6000 cal. BP where they stabilize with some oscillations before they eventually start increasing again around 1500 cal. BP (Fig. 1) thus giving a mirror image of the C-ratio and T-ratio (Hirt et al., 2003). However, these ratios were not used in the numerical analyses.

The PCA sample scores of the geochemical data remain consistently low until about 6500 cal. BP when, after an initial step, they start rising gradually with some

fluctuations throughout the remaining Holocene (Fig. 1). They reflect the concentrations of elements such as Rb, As, and Zn that all show an increase around 6500 cal. BP and a major oscillation between 3500 and 3000 cal. BP. (Koinig et al., 2003).

Zones of stability and change

A consistent and comparable zonation scheme of all stratigraphies may help to distinguish between phases of stability and phases of change (Birks and Gordon, 1985). If zone boundaries of different proxies coincide, we might assume that a substantial and overriding change in a major environmental factor was the common cause. Zone boundaries occurring only in individual proxies may be the result of passing a threshold important for that individual proxy only and may thus signify environmental change at a lower level.

The numerical zonations of all the proxies show a

strong coincidence of zones between 6500 and 6000 cal. BP (Fig. 2). It is interesting to note that the magnetics, geochemical, and grain-size data show a consistent change in composition as evidenced by a synchronous zone boundary at 6400 cal. BP, whereas the biotic proxies show a lagged response or no change (cladocera) in assemblage composition. The lag is of different duration. The plant macrofossil assemblages show a change around 6200 cal. BP, whereas the pollen and chironomid assemblages change at ca. 6000 cal. BP (Fig. 2). The first *Picea abies* macrofossils indicating the local presence of this tree in the catchment of Sägistalsee occur between 6400 and 6300 cal. BP (Wick et al., 2003) and the tree may have migrated very rapidly into the catchment of Sägistalsee. The catchment reaction to this denser tree-cover seems to have been immediate through a substantial reduction of clastic input in the sand fraction (Ohlendorf et al., 2003) that also led to a reduction in sediment accumulation rate (Lotter and Birks, 2003a). The changes in the aquatic ecosystem, as seen by the biogenic silica concentration (Ohlendorf et al., 2003) and the chironomid assemblages (Heiri and Lotter, 2003), were lagged by several centuries.

Given the chronological resolution that is possible in this study, the synchronous change in the abiotic sediment properties, as well as the expansion of spruce at Sägistalsee coincides (Lotter and Birks, 2003a) with the end of a phase of distinct glacier recession in different parts of the Alps (Nicolussi and Patzelt, 2000; Hormes et al., 2001) around 6500 cal. BP. It is possible that the expansion of *Picea* that was already present at the forefield of Unteraargletscher (25 km distance) since about 9000 cal. BP (Hormes et al., 2001) into the catchment of Sägistalsee and adjacent regions was mainly triggered by climate change through a depression in treeline and not by human impact (e.g., Markgraf, 1970).

The influence of Holocene climate change

To assess the influence of Holocene climate change on the different biotic proxies, a series of (partial) RDAs was carried out using July insolation (Laskar et al., 1993), the CE cold phases (Haas et al., 1998; Tinner and Ammann, 2001), and the North Atlantic IRD events (Bond et al., 1997, 2001) as explanatory variables for the significant PCA axes of the pollen, chironomid, and cladocera proxies (see Fig. 3). July insolation explained a statistically significant part of the variance (74.8%; $p = 0.01$) in the two pollen PCA axes but, when sam-

ple age was partialled out as a covariable, the amount of variance dropped considerably and was no longer statistically significant (15.2%; $p = 0.60$). All RDA models for the chironomid PCA axes 1 and 2 and for the cladoceran PCA axes 1 and 2 and insolation were not statistically significant ($p = 0.17$ – 0.54). Neither the CE phases nor the IRD events explained statistically significant amounts of variance ($p > 0.05$) for any of the significant PCA axes of the three biological proxies. When included as predictors in conjunction with insolation, the resulting RDA models were not statistically significant except for the pollen PCA axes 1 and 2. However, when sample age was partialled out the partial RDA model was not statistically significant (15.8%; $p = 0.57$).

If we assume that the chronologies of the Sägistalsee sedimentary record are compatible and comparable with the ones of the climatic predictors used, then these millennial-scale Alpine or northern-hemispheric climatic events do not appear to have had any statistically significant impact on the biotic assemblages. The general trend of the July insolation (Fig. 3), however, is reproduced by the pollen-inferred July temperature that shows a decrease of about 3 °C throughout the Holocene (Wick et al., 2003) which is of a comparable order to that estimated from Holocene sea-surface temperature records (Calvo et al., 2002).

Catchment – lake interactions

In contrast, all RDA models based on aquatic biological and sedimentological proxies as response variables and catchment vegetation types as predictor variables (see Fig. 3) are statistically significant ($p = 0.01$) when the statistically significant PCA axes only (axis 1 only or axis 1 and 2) are used as response variables, when the first four PCA axes are used as variables, or when the full data are used as the response variables. These RDA models explained between 22.2 and 38.9% of the variance of the chironomid data, 36.3 and 42.7% of the variance of the cladocera data, 47.4 and 67.5% of the geochemical variance, 44.6 and 59.8% of the magnetic variance, and 41.0 and 43.3% of the variance in the grain-size data. When sample age is partialled out as a co-variable to allow for long-term changes and the inherent auto-correlation between samples, catchment vegetation explains between 20.1 and 49.3% of the variance (Table 2) not explained by sample age for chironomids, cladocera, grain-size, and magnetics. All these partial RDA models are statistically significant ($p = 0.01$). The partial RDA model for geochemistry is

not statistically significant ($p = 0.20$) and only explains 7.4% of the variance not explained by sample age.

Processes operating in the hydrological catchment of Sägistalsee obviously have a very strong impact on the biotic and abiotic sediment proxies. Catchment vegetation (Fig. 3) is not only influencing the amount of soil erosion as evidenced by the grain-size and magnetic proxies, but also has an important effect on the aquatic biota.

Conclusions

A major aim of the multi-proxy study of the sediments of Sägistalsee was to assess the influence of Holocene climatic change on the aquatic biota. Pollen and chironomid-inferred July temperatures (Wick et al., 2003; Heiri and Lotter, 2003) generally follow the trend of the July insolation curve (Fig. 3). They also show a Holocene thermal optimum between approximately 8000 and 6000 cal. BP with subsequently decreasing July temperatures. This feature is in accordance with results from marine studies (e.g., Calvo et al., 2002) or recent quantitative Holocene climate reconstructions from Fennoscandia (e.g., Korhola et al., 2002). Despite the location of Sägistalsee at a modern sensitive ecotone and despite a dense sampling scheme, the aquatic organisms do not show an unequivocal record of millennium-scale Holocene climatic fluctuations that have been evidenced in marine and continental climatic archives. This is likely to be the result of a combination of factors:

(i) The treeline or timberline ecotones commonly used in palaeoecological studies to trace climate change in the past are most probably not as important for aquatic organisms as for terrestrial vegetation (see e.g., Ponader et al., 2002). If environmental variables such as temperature were ecologically important for the distribu-

tion and occurrence of biota we would define a threshold situation (or 'aquatic' ecotone) where we would find the highest change in assemblage composition. Looking at modern training set from the Alps (e.g., Lotter et al., 1997b) the highest taxonomic turnover for diatoms, chironomids, or cladocera occurs at elevations that are lower than modern treeline. This suggests that Sägistalsee may be located too high (i.e., too cold in modern climatic space) for aquatic organisms to be sensitive to Holocene summer temperature change of 1–2 °C. This is not the case for terrestrial vegetation that shows some of the millennium-scale climate fluctuations through the decrease or absence of the macrofossils (see Wick et al., 2003).

(ii) Aquatic and terrestrial ecosystems are closely linked through the movement of water. The catchment of Sägistalsee apparently has an overriding effect on the lake and its biota. The establishment of spruce forest in the hydrological catchment had the strongest influence on all biota (see Fig. 2). The change from a rather open *Abies alba*–*Pinus cembra* woodland to a denser *Picea abies* forest around 6400 cal. BP had, on the one hand, an influence on the amount of soil erosion, and thus also on the accumulation rates (see Lotter and Birks, 2003a), as well as on the magnetic (Hirt et al., 2003), sedimentological (Ohlendorf et al., 2003), and geochemical properties (Koinig et al., 2003) of the sediment (see Fig. 1). If the expansion of spruce around Sägistalsee was climatically induced, the aquatic biota did not directly react to this climate change but rather indirectly to catchment-mediated processes as suggested by the lagged change in assemblage composition. Catchment processes such as tree expansion, vegetation succession, and soil development have thus been of major importance for the history of Sägistalsee in regulating and controlling critical factors for aquatic biota such as infilling, turbidity, and nutrient supply.

(iii) Human activity above treeline has been evidenced since the Mesolithic (e.g., Fedele and Wick, 1996) and forest clearance by burning has been evidenced in the Southern Alps since the Iron Age (e.g., Oeggli, 1991). At Sägistalsee there is evidence for late Neolithic and especially Bronze Age human impact in the catchment of the lake (Wick et al., 2003). At least for the past 4000 years this land-use at high altitudes in the Alps has affected terrestrial and aquatic ecosystems in different ways. Wood cutting and burning as well as grazing led not only to anthropogenic depressions of the treeline but also to nutrient enrichment of lakes. This seriously questions the concept of 'pristine' ecosystems in remote mountain regions and has important consequences

Table 2. Partial RDA results using catchment vegetation types as explanatory or predictor variables and partialling out the effect of sample age as a co-variable

Response variables	% variance explained after age is partialled out	p*
Chironomids PCA axes 1 and 2	35.8	0.01
Cladocera PCA axes 1 and 2	39.8	0.01
Geochemistry PCA axis 1	7.4	0.20 ns
Grain-size PCA axis 1	20.1	0.01
Magnetics PCA axis 1	49.3	0.01

*As assessed by 99 restricted Monte Carlo permutations; ns: not significant.

for nature conservation and management of aquatic systems in the Alps. Moreover, the impact of forest clearance and grazing makes the interpretation of the influence of climate and other natural environmental factors on mountain ecosystems difficult to assess. It is only in very few cases that we can disentangle the influence of climate and of human impact on mountain lakes (see, e.g., Hausmann et al., 2002).

The study of Sägistalsee illustrates the critical role of the hydrological catchment in climate-change studies (see also Birks et al., 2000). More such integrated studies are needed to better understand catchment–lake interactions, which may under certain circumstance override the effects of climate change.

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