

Encyclopedia of Quaternary Science

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Hardcover: 3576 pages

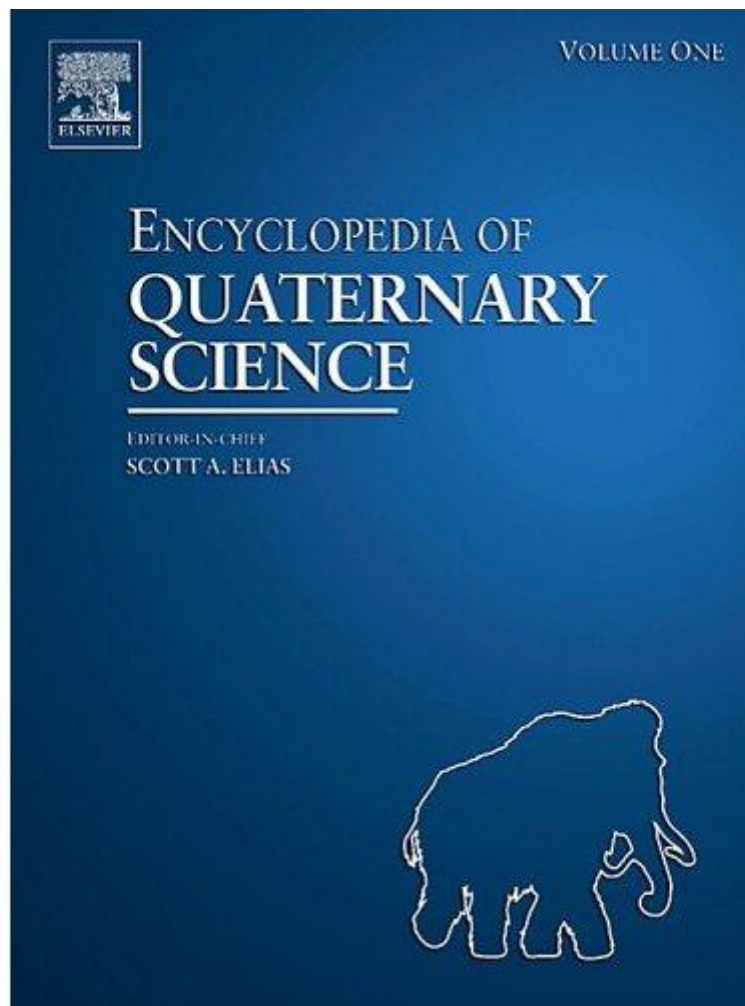
Publisher: Elsevier Science; 1 edition (December 14, 2006)

Language: English

ISBN-10: 044451919X

ISBN-13: 978-0444519191

Product Dimensions: 12 x 9.8 x 9.4 inches



The quaternary sciences constitute a dynamic, multidisciplinary field of research that has been growing in scientific and societal importance in recent years. This branch of the Earth sciences links ancient prehistory to modern environments. Quaternary terrestrial sediments contain the fossil remains of existing species of flora and fauna, and their immediate predecessors. Quaternary science plays an integral part in such important issues for modern society as groundwater resources and contamination, sea level change, geologic hazards (earthquakes, volcanic eruptions, tsunamis), and soil erosion.

With over 360 articles and 2,600 pages, many in full-color, the Encyclopedia of Quaternary Science provides broad ranging, up-to-date articles on all of the major topics in the field. Written by a team of leading experts and under the guidance of an international editorial board, the articles are at a level that allows undergraduate students to understand the material, while providing active researchers with the latest information in the field.

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Late Glacial Multidisciplinary Studies

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Abiotic and biotic variables can reflect ecological processes and their changes on several temporal and spatial scales. The reconstruction of environmental changes in the Late Glacial period is of special interest because the changes in climate and hence in climate-dependent responses of these variables were both rapid and of large amplitude.

Organisms and environmental gradients show interesting relationships. Therefore, biostratigraphies providing qualitative and quantitative changes of taxa are time series of the behavior of various types of organisms and also of environmental change. Generally, species show responses to ecological gradients by exhibiting optima and tolerances that reflect population size or productivity or some other measure of fitness. They are often unimodal. We use three examples to illustrate how these relationships can be reconstructed in three different ways: qualitative reconstruction of past environmental changes; quantitative reconstruction of past climatic changes; and estimation of the biotic response to climate change, which is possible only if an independent line of evidence for the climate change is available.

Time control is essential for all estimates of rates of change. However, in the Late Glacial period (ca. 16,000–11,500 cal yr BP) time control can be hampered by (1) the absence of organic material suitable for radiocarbon dating, (2) the presence of reworked organic material, (3) plateaus of constant radiocarbon ages, and (4) problems of calibrating the radiocarbon timescale. Dating techniques other than radiocarbon (e.g., several geophysical techniques) may have large errors or are applicable only at special sites (e.g., annual sediment layers or varves).

Among terrestrial ecosystems, the vegetation (i.e., the primary producers) may provide the best reconstruction of the past climate. Aquatic ecosystems may be of special interest because water plants and aquatic invertebrates (e.g., insects or Cladocera) can respond rapidly to climatic warming or cooling for at least three reasons: Their dispersal of propagules (seeds, fruits, resting stages, or adults) may be fast because of the high mobility of the main vector (e.g.,

water fowl); their life cycles are relatively short; and they have no special requirements, such as mature soils.

The complementarity of pollen and plant macrofossil analyses may be especially useful for the reconstruction of past environments. Identification of plant macrofossils can often go to the species level (instead of only the genus or family level; see the example of dwarf birch and tree birches), and local presence can be assumed if heavy macroremains are found, whereas pollen may be more easily transported from a long distance. Both aspects may apply to terrestrial and aquatic plants.

Qualitative Reconstruction of Past Environments

Multidisciplinary studies are most precise if all analyses can be made on a single core. Some studies, however, need relatively large volumes of sediment per sample (e.g., beetle analysis); in such cases,

several cores and their correlation may be needed. Alternatively, open exposures may provide large sample volumes. Beetles may offer additional information, such as habitat structure or openness of vegetation.

We present two examples of the qualitative reconstruction of past Late Glacial environments, one indicating primarily changes in temperatures and the other indicating changes in both effective moisture (lake level) and temperature.

The Late Glacial in Switzerland

The biostratigraphic changes during the Late Glacial on the Swiss Plateau (the lowland between the Jura Mountains and the Alps) are summarized in Figure 1 and Table 1. Two phases of strong and rapid warming occur at approximately 14,500 and 11,500 cal yr BP (i.e., at the beginning of the Bolling and beginning of the Holocene). They reflect global or hemispheric pulses of climatic warming. The Oldest Dryas on the

Multidisciplinary studies in the Late Glacial of the Swiss Plateau

Several sites on the Swiss Plateau						Lobsigensee on the Swiss Plateau								
Cal years BP	Bio zones	Regional Pollen zone	Plant macro fossils	Inferred vegetation	$\delta^{18}\text{O}$ Lit.4	Sediment	Chironomids & Chaoborus	Cladocera	Coleoptera & Trichoptera	Mollusca	Ostracods & pigments: O_2 strictly anoxic			
	Preboreal	Pinus-Corylus, QM		Birch-Pine forest, hazel										
11 500					T↑					T↑				
12 000	Younger Dryas	Pinus-Gramineae-Artemisia (some Ephedra)	Less Pinus, Betula dominant	open Pine forest with Birch, Larch, Poplar		Lake marl	chironomid assemblage dominated by littoral taxa, no taxa indicative of oligotrophic conditions	Bosmina longispina ↓, Bosmina longirostris	No faunal changes but lower abundances	Number of individuals ↑	meromixis and/or temporarily anoxic			
12 500														
12 850														
13 000	Allerød	Pinus-Betula	Pinus sylvestris Betula "alba"	Pine Birch forests	T↓				Temperate fauna 14-16°C mean July temperature	Number of individuals ↓				
13 500														
13 600														
14 000	Belling	B. "alba" Salix-Artemisia	Betula pubescens B. pendula Pop. tremula	Birch forests	T↑		cold-stenotherm species absent	sub-arctic species absent	Temperate fauna	maximum number of individuals				
14 500														
15 000	Oldest Dryas 3 rd phase	Artemisia-Betula nana	Betula nana Salix sp.	Shrub-tundra Salix, B. nana	T↑	transit	Faunal change	Faunal change	Faunal change	T↑				
15 500?														
16 000														
16 500?	Oldest Dryas 2 nd phase	Artemisia-Helianthemum Cyperaceae	Selaginella selaginoides, Gypsophila repens, Potentilla, Onobrychis....	Steppe-tundra, species-rich		Silt & clay	many cold-stenotherm species present	sub-arctic species present	boreal & boreo-montan fauna, 10-12°C mean July	Valvata piscinalis ↑, Pisidium ↓	no meromixis			
17 000?														
17 500?	Oldest Dryas 1 st phase	Artemisia-Pinus & reworked pollen		open ground, some pioneers								transit Sand, Till	***** ?first occur	***** ?first occur
18 000?														

Figure 1 Overview of bio- and isotope stratigraphies of the Late Glacial on the Swiss Plateau. Ecologically, the most remarkable change from the shrub-tundra in the Oldest Dryas to a juniper-birch forest in the early Bolling (i.e., a shift in dominance from dwarf birches to tree birches) coincides with the rapid shift in oxygen isotopes of at least 3 around 14,500 cal yr BP. It is accompanied by changes in the assemblages of insects (chironomids, Chaoborus, Coleoptera, and Trichoptera) and Cladocera as well as a change in abundances among mollusks. The subdivision of the Oldest Dryas based on pollen and plant macrofossils (see text for details) is also reflected in the biostratigraphies of the invertebrates: First occurrences coincide with the stepwise development of the vegetation. The rapid cooling at the beginning and the rapid warming at the end of the Younger Dryas are recorded in the oxygen isotope ratios and all biostratigraphies. Data from Ammann (1989), Gaillard (1984, 1994), Lotter *et al.* (1992), and Richoz (1997); the references for Lobsigensee are given in Table 1.

Table 1 Multidisciplinary studies at Lobsigensee included in **Figure 1** for the environmental reconstruction of the Late Glacial periods

Ammann, B. (1985) Introduction and Palynology: vegetation history and core correlation at Lobsigensee (Swiss Plateau). <i>Dissertationes Botanicae</i> 87 : 127–135.
Ammann, B. (1989) Late-Quaternary palynology at Lobsigensee – Regional vegetation history and local lake development. <i>Dissertationes Botanicae</i> 137 : 1–157.
Ammann, B., Chaix, L., Eicher, U., Elias, S.A., 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). <i>Revue de Paléobiologie</i> 2 : 221–227.
Ammann, B., Tobolski, K. (1985) Vegetational development during the Late-Würm at Lobsigensee (Swiss Plateau). <i>Revue de Paléobiologie</i> 2 : 163–180.
Chaix, L. (1985) Malacofauna at Lobsigensee. <i>Dissertationes Botanicae</i> 87 : 148–150.
Elias, S.A., Wilkinson, B. (1983) Lateglacial fossil insect assemblages from Lobsigensee (Swiss Plateau). <i>Revue de Paléobiologie</i> 2 : 189–204.
Elias, S.A., Wilkinson, B. (1985) Fossil assemblages of Coleoptera and Trichoptera at Lobsigensee. <i>Dissertationes Botanicae</i> 87 : 157–162.
Gaillard, M.-J. (1983) On the occurrence of <i>Betula nana</i> L. pollen grains in the Late-glacial deposits of Lobsigensee (Swiss Plateau). <i>Revue de Paléobiologie</i> 2 : 181–188.
Hofmann, W. (1985) Developmental history of Lobsigensee: subfossil Cladocera (Crustacea). <i>Dissertationes Botanicae</i> 87 : 150–153.
Hofmann, W. (1985) Developmental history of Lobsigensee: subfossil Chironomidae (Diptera). <i>Dissertationes Botanicae</i> 87 : 154–156.
Löffler, H. (1986) An early meromictic stage in Lobsigensee (Switzerland) as evidenced by ostracods and Chaoborus. <i>Hydrobiologia</i> 143 : 309–314.
Siegenthaler, U., Eicher, U. (1985) Stable isotopes of carbon and oxygen in carbonate sediments of Lobsigensee. <i>Dissertationes Botanicae</i> 87 : 162–164.
Tobolski, K. (1985) Plant macrofossils from Lobsigensee. <i>Dissertationes Botanicae</i> 87 : 140–143.
Züllig, H. (1985) Carotinoids from plankton and phototrophic bacteria in sediments as indicators of trophic changes: evidence from the Late-Glacial and the early Holocene of Lobsigensee. <i>Dissertationes Botanicae</i> 87 : 143–147.

Swiss Plateau can usually be subdivided into three phases. At the base, the pollen concentration is low, plant macroremains are absent, and many reworked pollen grains are present, indicating the dominance of open ground and scarce vegetation after deglaciation. The second phase reflects a species-rich steppe-tundra (sometimes subdivided into two subphases) (Gaillard, 1984). Then a marked increase in the birch pollen curve can be attributed to a higher abundance of dwarf birch (*Betula nana*); the species identification is based primarily on plant macrofossils (a few remains of tree birches are also found). The sharpest transition for the entire Late Glacial occurs at approximately 14,500 cal yr BP at the beginning of the Late Glacial interstadial (Bølling). The plant macrofossils show a change from dominant dwarf birch to dominant tree birch (the last remains of dwarf birch are found within the *Juniperus-Hippophaë* regional pollen zone; the Linnean species *Betula 'alba'* includes several species of tree birches). At the same time as this ecologically important period of afforestation, the assemblages of all groups of aquatic organisms change (Fig. 1). Most inferences of biotic changes involve steps in climate warming (and cooling at the beginning of the Younger Dryas). However, related, climate-induced conditions are important, such as pedogenesis, trophic state, and seasonal circulation patterns in lakes (affecting oxygen conditions). The forested Late Glacial is first dominated by tree birches (Bølling) and then by

pine and tree birches (Allerød). Minor fluctuations within this Late Glacial interstadial can only be traced if the sites are at sensitive altitudes and if the sampling resolution is sufficiently high. The Younger Dryas cool period is reflected in the lowland by an opening of the forests, when heliophilous taxa such as *Larix* and *Populus* are recorded as plant macrofossils, as well as pollen of *Artemisia* and *Ephedra*. At higher altitudes, a lowering of the timberline was registered.

The Pleniglacial and Late Glacial in Lake Zeribar, Zagros Mountains, Iran

Paleoecological changes between ca. 18,000 and 6,000 cal yr BP in the Mediterranean climate area of western Iran are illustrated by different proxy data obtained from a single sediment core from Lake Zeribar, Zagros Mountains, Iran (Fig. 2). A pollen diagram (van Zeist and Bottema, 1977) illustrates the dominance of *Artemisia*-Chenopodiaceae steppe-like vegetation in the Pleniglacial and Late Glacial until ca. 12,000 cal yr BP. Trees were absent or limited to a few sheltered places until ca. 15,400 cal yr BP (Heinrich 1 cool oscillation). Their number increased slightly in the Bølling/Allerød interstadial, but it was reduced again during the Younger Dryas stadial. A slight increase in humidity approximately 12,000 cal yr BP favored the expansion of Poaceae-dominated steppe-like vegetation, but the climate was still too dry for an extensive spread of trees. Until

approximately 7,000 cal yr BP, the drought-resistant *Pistacia* was the major tree; between ca. 7,000 and 6,000 cal yr BP the climate became sufficiently humid for oak woodland to become established.

Evidence of fluctuations in water levels and in salinity is obtained from various proxies in the lake (Fig. 2). In the macrofossil record (Wasylikowa, 2005), peaks of *Chenopodium rubrum*, which typically expands on seasonally exposed lakeshores, indicate episodes of fluctuating and/or low lake water levels. Two cold episodes (Heinrich 1 and Younger Dryas) were also characterized by increased salinity, as indicated by the presence of halophytic macrophytes, *Ruppia maritima*, *Salicornia europaea*, and *Suaeda* sp. (Wasylikowa 2005); by peaks of brackish water and marine diatoms (Fig. 2; Wasylikowa *et al.*, 2006); and by high conductivity values (Snyder *et al.*, 2001). Among the submerged aquatics, *Potamogeton pectinatus* expanded. It tolerates brackish water. It can also withstand short-lasting emergence and it became abundant at the same time as *C. rubrum* (Wasylikowa, 2005). The cause of the lower lake levels was probably dry climate, as indicated by elevated $\delta^{18}\text{O}$ values (Stevens *et al.*, 2001). Higher lake water levels during the Bolling/Allerød interstadial are indicated by the disappearance of *C. rubrum* and the spread of *Najas marina*, which tolerates brackish conditions but, unlike *P. pectinatus*, is sensitive to desiccation. A slight increase in temperature is suggested by the appearance of *Ceratophyllum demersum*, a relatively thermophilous aquatic species. In the Holocene, a series of low lake level episodes occurred between ca. 10,000 and 6,300 cal yr BP, but unlike the earlier episodes, the water was fresh and salinity indicators were absent. The curve of the noncombustible mineral fraction in the loss-on-ignition diagram indicates that this was the time of intensified catchment erosion (Stevens *et al.*, 2001). The replacement of the dominant *Najas marina* by *N. minor* approximately 11,000 cal yr BP could reflect the increase in temperature and decline of salinity.

Quantitative Reconstruction of Climate Change in the Late Glacial: The Role of Plant Macrofossils

Analog or Indicator Species Approaches

If the ecological and environmental tolerances of a taxon are well-known, either through observation or experiment, the past ecological and environmental conditions can be inferred if the taxon is found as a fossil or subfossil; it can thus be used as an indicator species. Similarly, the environmental tolerances of an assemblage can be inferred from a modern analogue;

the analog assemblage approach applies particularly well to vegetation reconstruction. If types of vegetation can be reconstructed from fossil plant assemblages, past habitats and past temperature and humidity can be reconstructed. Plant macrofossils are well suited to the analogue approach to environmental and climatic reconstruction. Past vegetation can be reconstructed in some detail, mainly because of the rather local deposition of plant macrofossils and the possibility of identifying many plant macrofossils to a detailed taxonomic level, often to species.

When pollen data were used to reconstruct the spatial and temporal distribution of vegetation types and the ecotones between them in the Late Glacial of western Norway (Birks, 1994), a southern and western distribution of birch trees was inferred during the interstadial. The ability of macrofossils to refine pollen data was then used to distinguish between tree birch (e.g., *Betula pubescens*) and dwarf birch (*B. nana*). The macrofossil record indicated that the Late Glacial interstadial of western Norway lacked birch trees. All the *Betula* pollen was derived from trees to the south by long-distance transport, or it came from *B. nana*, which was shown by macrofossil records to be present in some abundance inland but absent along the Norwegian coast (Birks, 2003). Therefore, temperature and ecotone reconstructions made on the basis of the pollen-inferred occurrence of tree birch had to be revised. Late Glacial assemblages of plant macrofossils in western Norway closely resemble the modern sub-Alpine and Alpine vegetation. The mean July temperature ranges of these modern vegetation zones are known and can thus be inferred for the past. The new interpretations are supported by the entire macrofossil assemblages, which indicate a treeless low-Alpine or mid-Alpine vegetation (Birks, 1993, 2003).

A special case of the analog approach is the mutual climate range method, used especially with Coleoptera data. By overlapping the modern climate ranges of species within a fossil assemblage, the most likely climate envelope for that assemblage is narrowed down. This approach has been applied with greater mathematical rigor to plant assemblages, particularly macrofossil assemblages with species determinations (probability density functions) (Kühl *et al.*, 2002). It has not been applied to Late Glacial plant assemblages, but it shows promise as an alternative approach to modern analogs and transfer functions.

Multivariate Approach to Climate Reconstruction

This approach to climate reconstruction involves the use of large modern data sets of organisms that are

related to their present environment by a transfer function. The transfer function is applied to fossil data to reconstruct past environments and climates. In the Late Glacial, climate transfer functions are most often used to reconstruct mean July (T_{jul}) or summer temperatures. They have been applied in Late Glacial studies in North America (Levesque *et al.*, 1994) and Europe (Lotter, 2000; Brooks and Birks, 2000).

Temperature Reconstructions in the Late Glacial at Kråkenes, Western Norway: An Example of a Multiproxy Climate Reconstruction

At Kråkenes, western Norway, all of the previously discussed approaches were applied to several data sets from the same Late Glacial sediment core to reconstruct mean July temperature (T_{jul}). The transfer function approach was used on pollen, chironomid, and Cladocera data; the MCR method was applied to the Coleoptera data (but the data were too sparse to make a continuous curve); and the analog approach was used on the plant macrofossil data. The results are compared in Figure 3 (Birks and Ammann, 2000).

The shapes of the temperature curves are all similar. The Allerød interstadial temperatures were cool,

ca. 3–6°C below the present T_{jul} . All the proxies show a decrease into the Younger Dryas of 1 or 2°C. This small decrease, probably combined with increased precipitation and snow accumulation in the cirque behind the lake, was sufficient to lead to the formation and advance of a cirque glacier that drained directly into the lake, forming glaciolacustrine sediments. The proxies all show a rapid temperature rise into the early Holocene, reaching modern temperatures after approximately 1,000 years (Fig. 3).

A more detailed comparison of the results in Figure 3 shows that the absolute temperature values differ between proxies. The transfer function reconstructions (pollen, chironomids, and Cladocera) differ largely because of features of the modern data sets. Modern pollen assemblages from arctic or alpine situations contain long-distance transported pollen of trees with high pollen productivity and dispersal (*Betula*, *Pinus*, and *Alnus*) that was largely absent in the Late Glacial. Modern chironomid assemblages have lower taxonomic diversity below approximately 9°C T_{jul} (e.g., on Svalbard) and therefore cannot easily differentiate cold temperatures. The cladoceran modern data set was compiled for Switzerland, where the reconstructions from Cladocera showed overall higher temperature (Birks

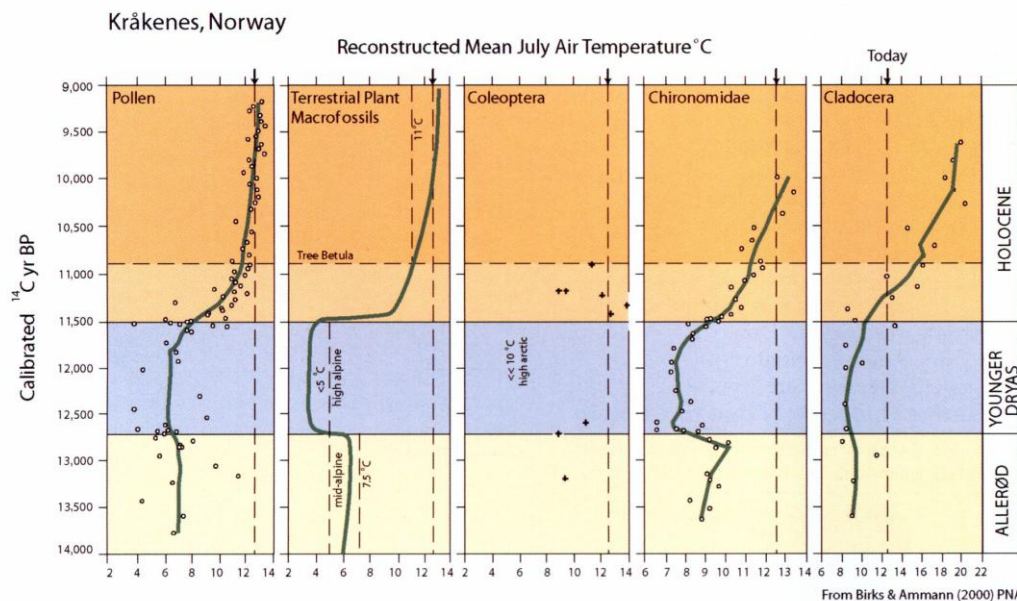


Figure 3 Comparison of mean July air temperature reconstructions at Kråkenes, western Norway. Pollen, chironomids, and Cladocera reconstructions were made with transfer functions. Coleoptera reconstructions were made with the MCR method. The plant macrofossil reconstructions were made by comparison with modern analog assemblages. From Birks HH, and Ammann B (2000) Two terrestrial records of rapid climatic change during the glacial–Holocene transition (14,000–9,000 calendar years B.P.) from Europe. *Proceedings of the National Academy of Sciences, USA* 97:1390–1394.

and Ammann, 2000). The analog reconstructions from the plant macrofossil data are probably the most reliable, although they are ranges rather than single values for each sample, representing the ranges of the low Alpine (10–7.5°C), the mid-Alpine (7.5–5°C), and the high Alpine (<5°C) vegetation zones of today.

The vegetation reconstructions from the macrofossil data are clear; all taxa conform to the proposed modern analog, and none disagrees. Within each vegetation zone, communities can be differentiated—for example, those related to snow beds or winter exposure, snow meltwater flushes, unstable stony ground, grassland, and dwarf-shrub heath. These mosaics also conform to present-day vegetation community mosaics in the Alpine zones of western Norway. Mosses contributed to these reconstructions (Jonsgard and Birks, 1995), and terrestrial oribatid mites were also valuable habitat indicators (Solhøy and Solhøy, 2000).

Timing and rates of climate changes at Kråkenes
Terrestrial plant macrofossils, mostly *Salix herbacea* leaves, were used to obtain a high-resolution series of AMS ^{14}C dates between 12,700 and 10,000 ^{14}C BP. A calendar-year chronology for the upper Late Glacial and early Holocene was reconstructed by wiggle matching against the Hohenheim tree-ring data that dated the Younger Dryas–Holocene transition to 11,530 ± 40 –60 cal yr BP (Gulliksen *et al.*, 1998). In the older Late Glacial, a calendar chronology was constructed by comparison with ^{14}C -dated laminated lake sediment series. Rates of change could then be calculated for the various groups of organisms (Birks *et al.*, 2000). The rates of T_{Jul} change shown in Figure 3 are summarized in Table 2. All the proxies show a rate of decrease from Allerød to Younger Dryas of 0.7–1°C per 25 years. Although the actual temperature drop was small, it occurred very rapidly. The rate of temperature change during the first 500 years of the Holocene was 0.2–0.3°C per 25 years. After the initial very rapid responses to the Holocene temperature rise, rates of change

decreased as communities and soils developed and internal successional processes started, thus reducing the sensitivity of the ecosystem to large temperature changes (Birks *et al.*, 2000). These results all hinge on the use of terrestrial plant macrofossils to obtain a high-resolution series of radiocarbon dates.

Biotic Response to Climate Change

The Concept

Two conditions need to be fulfilled if the estimation of biotic responses to climate change is the goal: Some independent line of evidence for climatic change is needed to avoid circular reasoning, and the temporal resolution must be high enough to capture the relevant biological processes.

Various groups of organisms have different life cycles, including generation times and rates of response to environmental changes (e.g., speeds of migration). If we combine several groups of organisms that provide different life histories, we may be able to separate biological processes on several time-scales. The precondition is that our time control is good enough for recording these processes.

For example, the transition from the Late Glacial to the Holocene as one of the most rapid periods of warming was studied on the Swiss Plateau and in the western Alps at two sites with a record of oxygen isotopes (Gerzensee and Leysin) and three site without carbonates (one of them presented here; Ammann, 2000; Ammann *et al.*, 2000; Brooks, 2000; Schwander *et al.*, 2000; Tobolski and Ammann, 2000; von Grafenstein *et al.*, 2000; Wick, 2000).

The Responses of Flora, Fauna, and Vegetation to Rapid Climatic Changes

Figure 4 presents a comparison between the pollen and plant macrofossil records at the transition from the Late Glacial to the Holocene at three sites at different altitudes in the western Swiss Alps: Gerzensee at 603 m a.s.l., Leysin at 1,230 m a.s.l.,

Table 2 Comparison of Late Glacial mean July temperature (T_{Jul}) reconstructions using different proxies and methods, the temperature changes between the Late Glacial periods, and the rates of these temperature changes at Kråkenes, western Norway.

	Mean T_{Jul} , AL (°C)	AL–YD drop (°C)	Rate per 25 years (°C)	Mean T_{Jul} , YD (°C)	Holocene T_{Jul} after 500 years (°C)	Rate per 25 years (°C)
Pollen	7	1	0.7	6	6	0.25
Chironomids	9–10	1.5–2.5	0.7	7.5	3.5	0.2
Cladocera	9	1		8	6	0.3
Macrofossils	~6	1	~1	<5	6	0.25
Coleoptera	9.6	~2		<<10	~5	

AL, Allerød; YD, Younger Dryas.

and Zeneggen at 1,530 m a.s.l. At Gerzensee and Leysin, the oxygen isotopes of the bulk carbonates reflect the changes in the summer temperatures at this transition from the Younger Dryas to the Preboreal (independent from biostratigraphies). These isotope changes were correlated with the ones in the GRIP ice core, from which the timescale was then transferred (Schwander *et al.*, 2000). At Zeneggen, however, no autochthonous carbonates occurred in the sediment, so the organic matter of the sediment (expressed as loss on ignition at 550°C) was used as a proxy for productivity and thus indirectly for summer temperatures. During the cooling of the Younger Dryas, the lowest site remained forested (some opening of the forest is indicated by somewhat higher percentages of *Ephedra*, *Artemisia*, *Selaginella selaginoides*, and other heliophilous herbs, along with lower concentrations of macrofossils from trees). At the two sites at higher altitudes, forests were virtually absent and only a few trees survived during the Younger Dryas. Although Zeneggen is situated nearly 300 m higher, plant macrofossils from trees are richer than at Leysin. This may be explained by the special climate in the central Alps at Zeneggen/Valais, which has a very high insolation and high continentality. Zeneggen is only 30 km from Zermatt and 40 km from Goullé Rion, where the modern timberline reaches a maximum elevation of 2,400 m, with single *Pinus cembra* specimens currently up to 2,500 m a.s.l. (i.e., 500–700 m higher than the timberline made by spruce on the northern slope of the Alps, including Leysin).

Placing the results of pollen and macrofossil analyses into a broader context, Figure 5 demonstrates the biotic responses of groups of organisms other than plants. Changes in species composition and abundances (i.e., qualitative and quantitative changes) are summarized as the scores on the first axes of either PCA or CA (depending on the gradient length). At Zeneggen, the highest site (without a GRIP timescale), there seems to be the following sequence of responses: Cladocera first, pollen second, and plant macrofossils third. The rise in organic matter seems to last longer than the overall changes in the biota recorded in the PCA (axis 1). This is an indication that the changes in species composition in vegetation and cladoceran fauna as recorded in the PCA/CA lasted shorter than the increase in productivity as recorded in the LOI. At the two sites where the transition from the Late Glacial to the Holocene is recorded by oxygen isotopes, the biotic responses are quite complex. First, several changes had already occurred in the last third of the Younger Dryas, especially among the Cladocera. Second, several groups of organisms show two or three steps of

overall changes. Some of these changes are associated with both the beginning and the end of the transition as recorded by oxygen isotopes (e.g., plant macrofossils at Gerzensee). Other biotic changes may then be controlled by succession, which was triggered by climatic change.

Conclusions on Biotic Responses

On the basis of not only pollen and plant macrofossils but also groups of aquatic invertebrates, the general conclusions about biotic responses to rapid climatic warming in southern central Europe from the Swiss study are the following (Ammann *et al.*, 2000):

(1) Biotic lags to the isotope record of temperature increase of organisms with various life cycles were less prominent than expected for both aquatic and terrestrial taxa. Responses occur within approximately 4–16 years, often within the sampling resolution.

(2) The duration of the biotic response can last longer (or shorter) than the period of the climatic shift recorded in the isotopes. This depends on species-specific environmental thresholds and on biogeographical features such as range limits and the process of succession.

(3) Altitudinal differences in sites are useful to capture fine-scale changes. Large climatic shifts such as the Younger Dryas are recorded at all altitudes but small-scale changes only at sensitive altitudes (i.e., near the ecotones of the taxa present).

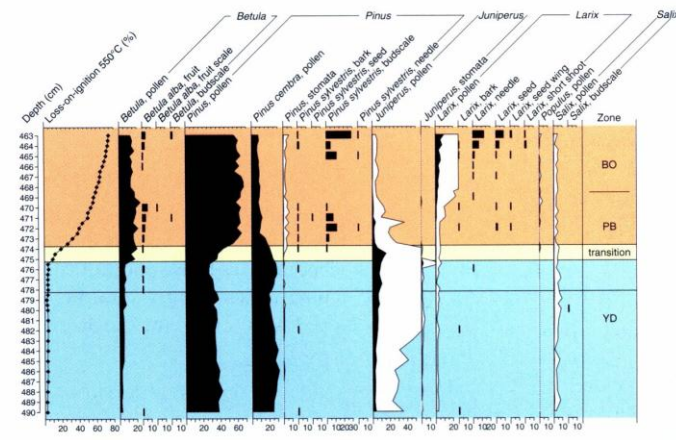
(4) The nature of the biotic response to climatic change involves at least four groups of processes acting on different timescales:

(i) Biogeographical changes include local (or global) extinction as well as immigration. Species migration is the slowest of the three processes; migration velocity depends, among other things, on generation times and the maximum distances of dispersal jumps. Migration (i.e., the shift of range limits) may occur in less than 1 year (e.g., algae, microorganisms, and some insects) or it may take millennia (e.g., trees). Species migration also depends on the distances involved and on barriers (e.g., mountains or oceans).

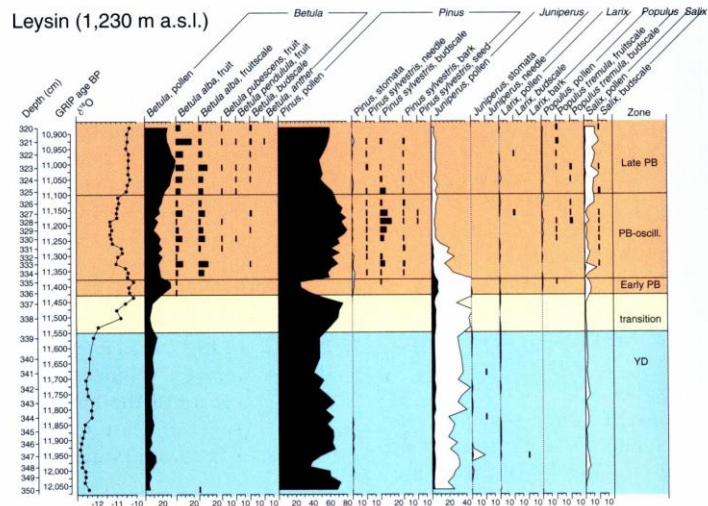
(ii) Population dynamics after arrival of a species in an area involve the building up of populations. The time needed for this depends, among other things, on age of first reproduction and generation time. Population changes occur at an intermediate rate.

(iii) Productivity (e.g., pollen production per year or tree ring width): This is the fastest type of response and can occur within 1 year.

Zeneggen (1,510 m a.s.l.)



Leysin (1,230 m a.s.l.)



Gerzensee (603 m a.s.l.)

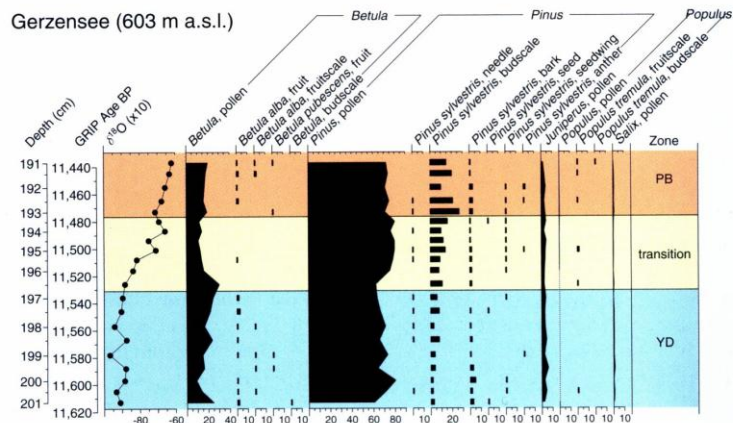


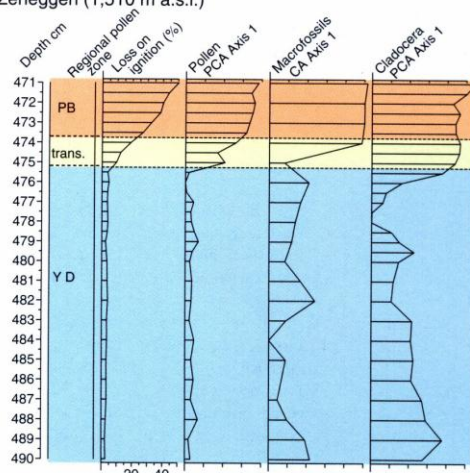
Figure 4 (Continued on next page)

Figure 4 Altitudinal transect of pollen (curves) and plant macrofossils (histograms) as stratigraphies covering the transition from the Younger Dryas to the early Holocene (preboreal); Gerzensee and Leysin presented on a GRIP timescale. At Gerzensee, the forest did not disappear during the Younger Dryas but was more open than before and after. At Leysin and Zenegggen, only a few trees survived the cool period of the Younger Dryas. Timescale after Schwander *et al.* (2000), and botanical results combined from Wick (2000) and Tobolski and Ammann (2000).

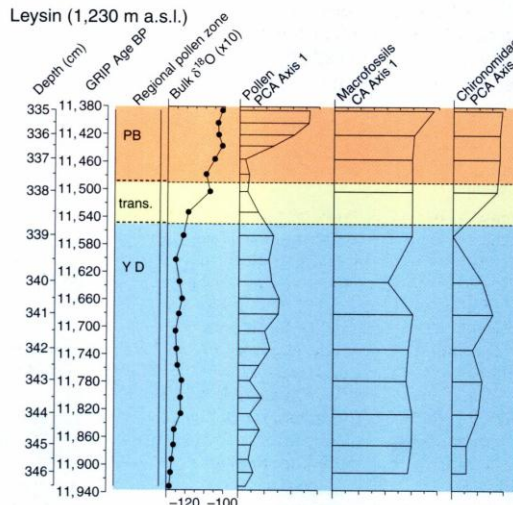
(iv) Genetic variability within populations may lead to adaptation. Processes of population genetics (including phenomena such as bottle necks, founder effects, and drift) occur on all timescales and are related to the groups of processes mentioned under (i) and (ii). Both, paleo-records (e.g., for spruce

Latalowa and van der Knaap, 2006) and phylogeography (e.g., for spruce Scotti *et al.*, 2000; Sperisen *et al.*, 2001) provide complementary information on tree migration (as an integrated example see for beech Magri *et al.*, 2006). Again, the results of plant macrofossils may be important here for the

Zenegggen (1,510 m a.s.l.)



Leysin (1,230 m a.s.l.)



Gerzensee (603 m a.s.l.)

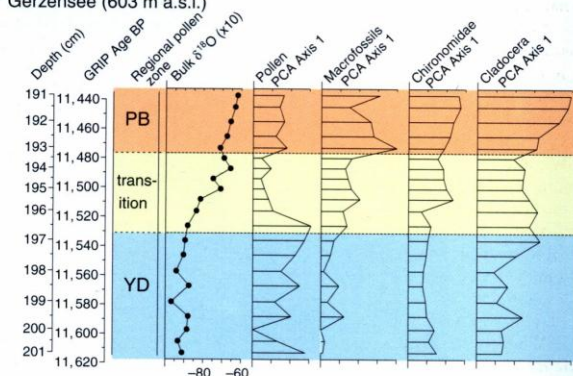


Figure 5 Biotic responses to the rapid warming at the end of the Younger Dryas in the same sites as in **Figure 4**. The qualitative and quantitative changes in species composition and abundances are summarized as scores of the first axis of a PCA of one or two groups of invertebrates and as a CA for plant macrofossils. Cladocera seem to respond first; pollen, plant macrofossils, and chironomids respond in complex ways and usually in two steps. Responses often occur within the sampling resolution. Modified from Ammann B, Birks HJB, Brooks SJ, *et al.* (2000) Quantification of biotic responses to rapid climatic changes around the Younger Dryas—A synthesis. *Palaeogeography Palaeoclimatology, Palaeoecology* 159:313–347.

taxonomic and spatial distinctions (i.e., the distinction between tree species within a genus and the distinction between presence and absence in the past). An important bridge between paleoecology and phylogeography may develop if the analysis of ancient DNA becomes less problematic, provided that DNA degradation is not too serious. In this context, the analysis of plant macrofossils will become even more important by providing species-specific samples.

See also: Chironomid Overview. Oribatid Mites.

Paleoclimate Reconstruction: Approaches.

Paleoclimate Relevance to Global Warming.

Paleolimnology: Cladocera. Plant Macrofossil

Introduction. Plant Macrofossil Methods and Studies:

Tree-line Studies; Validation of Pollen Studies.

Radiocarbon Dating: Conventional Method.

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Plate Tectonics *see* **Glacial Landforms**: Glacitectonic Structures and Landforms; **Glaciation, Causes**: Tectonic Uplift-Continental Configurations; **Glaciations**: Late Quaternary in North America

Pliocene Environments *see* **Paleoclimate Reconstruction**: Pliocene Environments

POLLEN ANALYSIS, PRINCIPLES

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Introduction

Pollen analysis, the study of fossil pollen and spores, is the principal technique for long-term (10^2 – 10^5 yr) vegetation reconstructions. Pollen-stratigraphical results have greatly shaped the development of ideas on the nature of vegetation and climate during the Quaternary glacial–interglacial cycles. They have provided unique insights into long-term ecological patterns and processes such as dispersal dynamics and distribution changes of tree species, the ancestry, development, and continuity of modern plant communities and biomes, and the sensitivity and response mechanisms of plants and vegetation to climate changes. They have also shed light on the origin and spread of early agriculture and the role of humans in influencing vegetation.

Plants liberate enormous quantities of pollen into the air, the production of pollen grains in one forest hectare rising into the billions (Pohl, 1937). In the atmosphere, pollen is efficiently transported and integrated by wind. Pollen is therefore widely and evenly spread, and fossil pollen records are available from various sedimentary environments such as seas, lakes, ponds, peatlands, soils, and humus layers. The pollen

concentration of sediments is usually high, in lake sediment often of a magnitude of 10^3 – 10^5 grains cm^{-3} , and pollen analysis can often be carried out from sediment samples smaller than 1.0 cm^3 in volume. The sedimentary pollen records are therefore unique in their stratigraphic completeness and detail. This is one of the major advantages of pollen analysis, namely, a methodological flexibility permitting adjustment of the technique according to the time dimensions relevant for the study. Consequently, the applications of pollen analysis can vary from investigations of the vegetation dynamics of the continents during the glacial–interglacial cycles to studies of annual to subdecadal patterns of the secondary plant succession after a local forest disturbance.

The spread of airborne pollen by wind also results in methodological complexities, some of which constitute the most important limitations and pitfalls of the method. The crux of the problem is that many different patterns of plant abundance can yield the same flux densities of pollen types (Prentice, 1988). The reason for this is that the pollen dispersal mode from a singular source such as a single tree is typically leptokurtic; most of the pollen is deposited within 10^1 – 10^3 m from the source, but a small proportion of pollen is transported in the atmosphere over longer, theoretically indefinite distances. It is therefore difficult for a paleoecologist to know whether small proportions of given taxa in sediment reflect a