



# Vegetation responses to rapid warming and to minor climatic fluctuations during the Late-Glacial Interstadial (GI-1) at Gerzensee (Switzerland)

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## ABSTRACT

High-resolution pollen analyses made on the same samples on which the ratios of oxygen isotopes were measured that provided the time scale and a temperature proxy after correlation to NorthGRIP.

- (1) A primary succession: The vegetation responded to the rapid rise of temperatures around 14,685 yr BP, with a primary succession on a decadal to centennial time scale. The succession between ca 15,600 and 13,000 yr BP included:
  - (1.1.) The replacement of shrub-tundra by woodland of *Juniperus* and tree birch (around 14,665 yr BP)
  - (1.2.) The response of *Juniperus* pollen to the shift in oxygen isotopes in less than 20 yr,
  - (1.3.) A sequence of population increases of *Hippophaë rhamnoides* (ca 14,600 yr BP), *Salix* spp. (ca 14,600 yr BP), *Betula* trees (ca.14,480 yr BP), *Populus* cf. *tremula* (ca. 14,300 yr BP), and *Pinus* cf. *sylvestris* (ca. 13,830 yr BP).
- (2) Biological processes: Plants responded to the rapid increase of summer temperatures on all organisational levels:
  - (2.1) Individuals may have produced more pollen (e.g. *Juniperus*);
  - (2.2) Populations increased or decreased (e.g. *Juniperus*, *Betula*, later *Pinus*), and
  - (2.3) Populations changed their biogeographical range and may show migrational lags.
  - (2.4) Plant communities changed in their composition because the species pools changed through immigration and (local) extinction. Some plant communities may have been without modern analogue. These mechanisms require increasing amounts of time.
  - (2.5) Processes on the level of ecosystems, with species interactions, may involve various time scales. Besides competition and facilitation, nitrogen fixation is discussed.
- (3) The minor fluctuations of temperature during the Late-Glacial Interstadial, which are recorded in  $\delta^{18}\text{O}$ , resulted in only very minor changes in pollen during the Aegelsee Oscillation (Older Dryas biozone, GI-1d) and the Gerzensee Oscillation (GI-1b).
- (4) Biodiversity: The afforestation at the onset of Bølling coincided with a gradual increase of taxonomic diversity up to the time of the major *Pinus* expansion.

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## 1. Introduction

The aim of this study is to understand better the potential responses of flora and vegetation to rapidly rising temperatures. We studied the transition from Oldest Dryas to Bølling in the sediments of Gerzensee (Switzerland) at a high sampling resolution (for both

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stable isotopes and pollen) and with a tightly constrained timescale (from NGRIP, see Rasmussen et al. (2006), applied to Gerzensee by van Raden et al., 2013–this issue).

We ask the following questions:

- (1) What were the dynamics of vegetation development under the strong and rapid climatic warming just after 14,685 yr BP?
- (2) How did climatic warming influence the vegetation responses on the levels of productivity (e.g. of pollen), plant populations, migrations, and interactions within ecosystems?
- (3) Did any vegetation changes correspond to the minor climatic oscillations recorded by oxygen isotopes within the Late-Glacial Interstadial?
- (4) How did palynological richness change under the processes of primary succession?

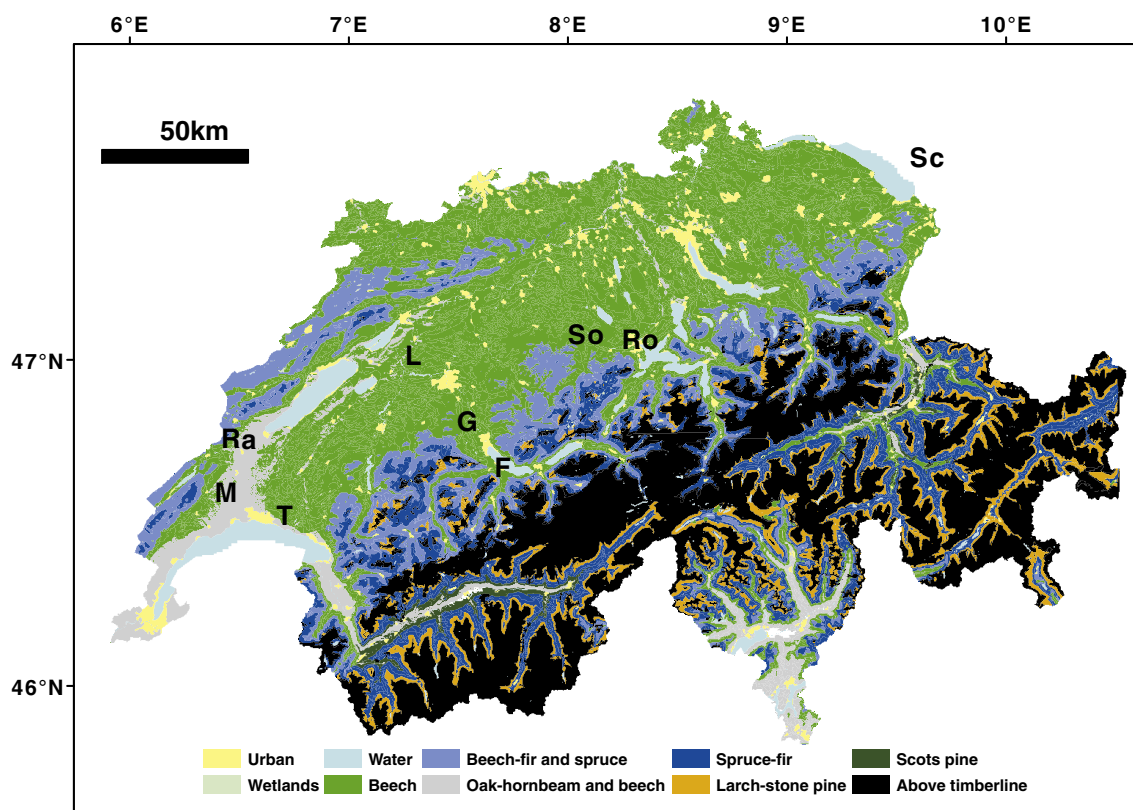
Although the Late-Glacial vegetation history on the Swiss Plateau is well known we can address these questions with the new data, which are exceptional because of the high temporal resolution and the chronological constraint, which allow us to compare the decadal- to centennial-scale variability of the pollen record with independent climatological evidence (i.e. the  $\delta^{18}\text{O}$ -record).

Even if the classical terms Oldest Dryas, Bølling, and Allerød are sometimes considered “historical baggage”, we use them here as biozones defined by Welten (1982). Provided that they are well defined, they help in communication because they are also used widely among geochemists and physicists working on ice cores or marine cores (e.g. Clark et al., 2001; Seierstad et al., 2005; Stanford et al., 2011). In addition, we use in places the Greenland terminology for late-glacial climatic events as proposed by Björck et al. (1998) and Lowe et al. (2008).

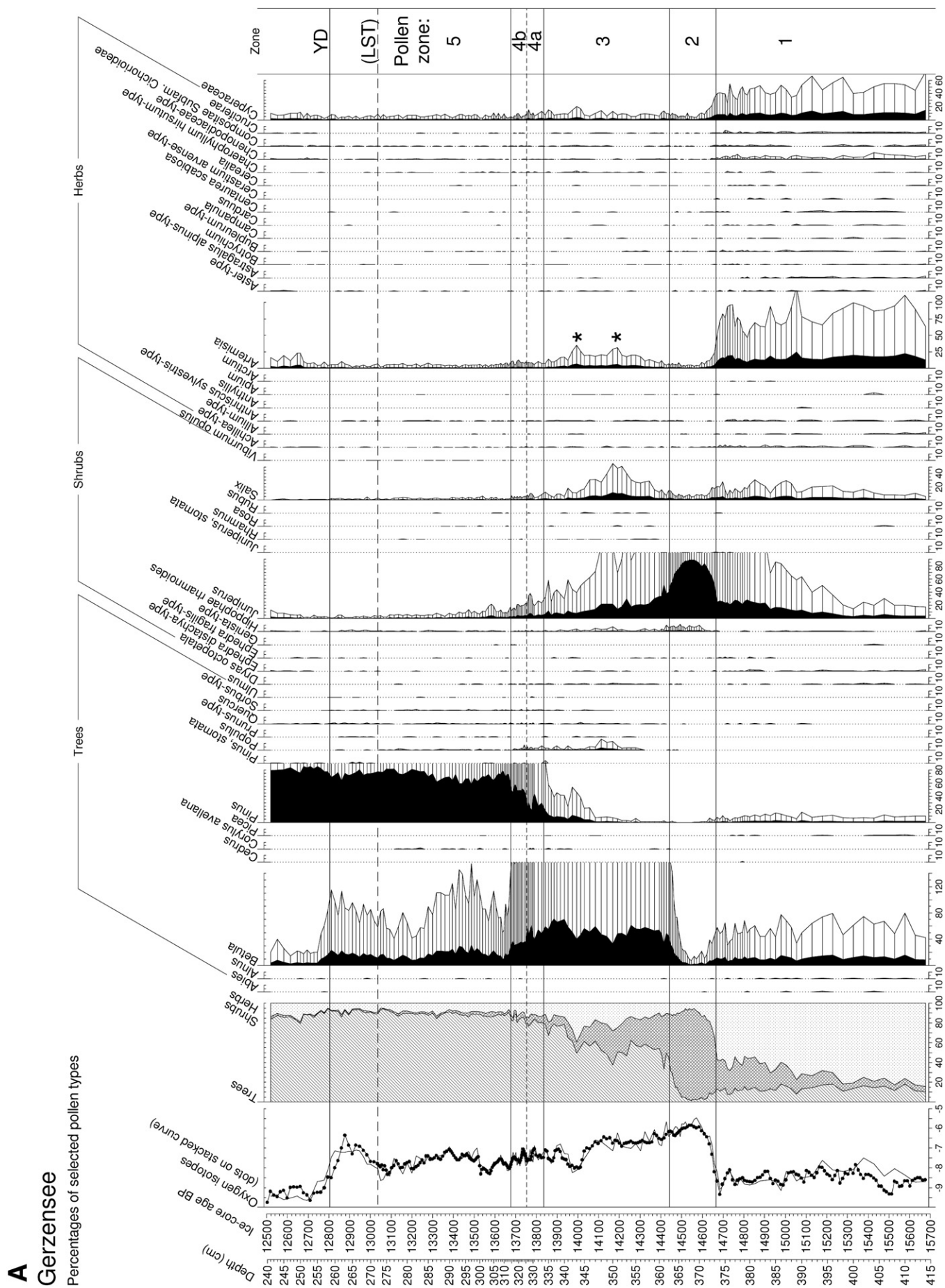
Unfortunately, plant macroremains in the sediment could not be studied because they were too scarce in the littoral lake marl examined, and for the present study we had only one core of 8 cm diameter (labelled GEJK). Early late-glacial plant macroremains elsewhere on the Swiss Plateau have been analysed either in profundal cores e.g. (Weber, 1977, 1980a,b), in delta sediments (e.g. at Vidy by Weber, 1979, 1980c) or, if on lake-marl terraces, then with very large samples either taken from open pits e.g. at Lobsigensee (Ammann and Tobolski, 1983), in 4–5 cm thick samples (e.g. at Rotsee, Lotter, 1988), or in correlated parallel cores, at Gerzensee around the Younger Dryas (Tobolski and Ammann, 2000). Such large samples were then even usable for the analysis of Coleoptera (Lemdahl, 2000). Fortunately, important features such as the shift from *Betula nana* to tree birches at the transition from Oldest Dryas to Bølling are very consistent in the macrofossil records of the Swiss Plateau (see Fig. 1: at all sites mentioned plant macroremains were studied for intervals before the Younger Dryas, except Gerzensee).

## 2. Materials and methods

The site: Gerzensee is a kettle-hole lake on the Swiss Plateau at 603 m asl (46° 49' 56.95" N, 7° 33' 00.63" E, Fig. 1). It is located on an interfluvium between the rivers Aare and Gürbe, on till of the Aare glacier deposited during the Last Glaciation. The lake surface today has an area of 25.16 ha, but it was probably double that size during the Late-Glacial (Eicher, 1979). Its maximum water depth at present is 10.7 m. It has no major inflow or outflow. The present climate is temperate-humid, with mean July temperature of 17.5 °C, mean January temperature of −1.0 °C, mean annual temperature of 8.2 °C, and an annual precipitation of about 1028 mm (data from the meteorological station of Bern-Liebfeld, 15 km from the lake). Today's

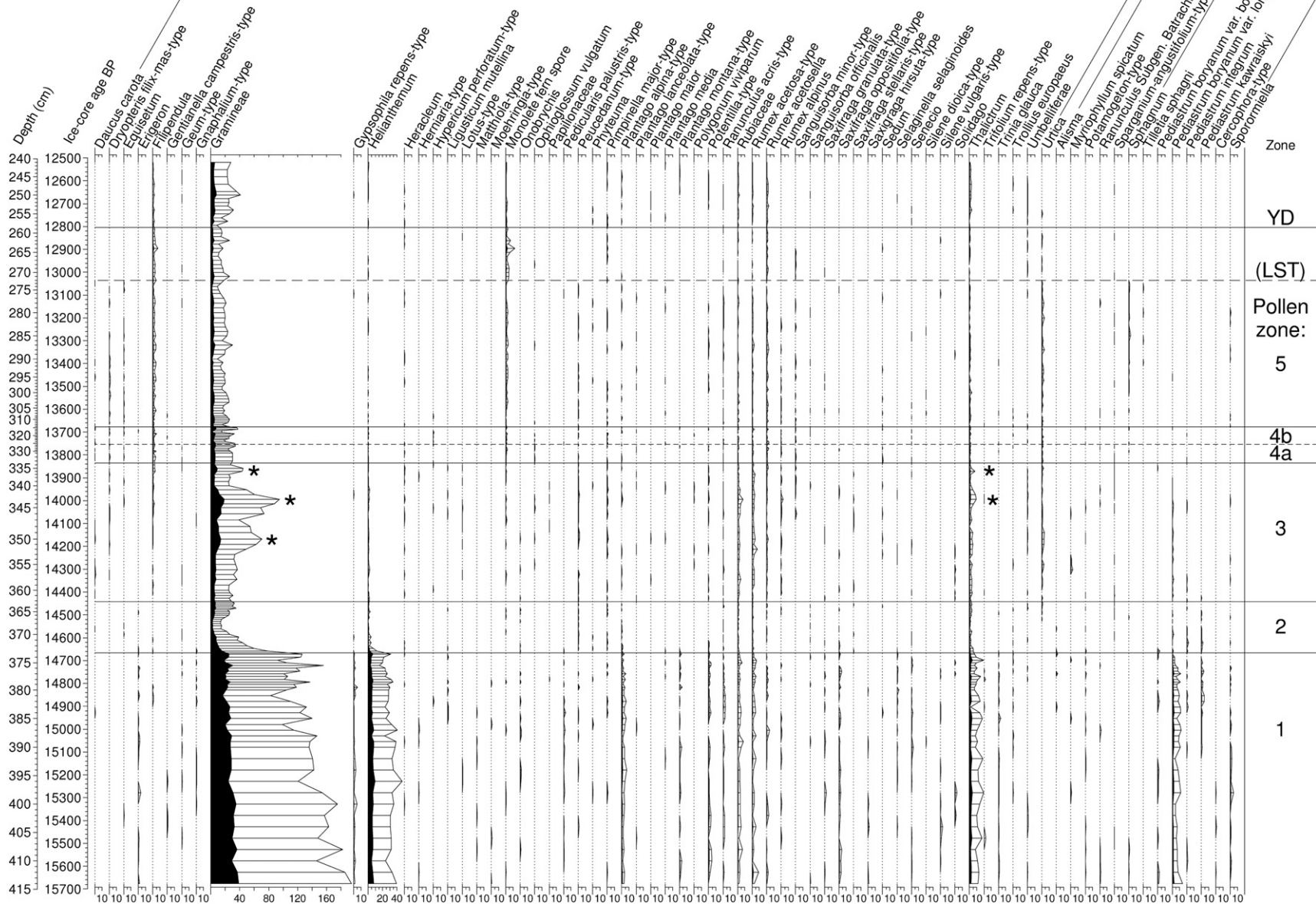


**Fig. 1.** Generalized map of the natural potential vegetation of Switzerland showing the position of Gerzensee G in the belt of the beech forest. Five other sites with high-resolution late-glacial sequences are also situated in the colline (to sub-montane) belt of beech forests: Ra for Marais de Rances, M for Grand Marais, T for Le Tronchet, F for Faulensee, L for Lobsigensee, Ro for Rotsee, S for Soppensee, and Sc for Schleinsee (Gaillard, 1984; Ammann, 1989; Lotter, 1988; Lotter et al., 1996; Lotter, 1999; Blockley et al., 2008; Müller, 1962). Map based on Brzeziecki et al., 1993: Bright green: various types of beech forests. Blue: beech-fir and spruce forests. Dark green: pine forests. Orange: Larch-stone-pine forests. Black: above timberline. Gray: various forests. Light blue: water. Yellow: urban areas. Turquoise: wetlands.





(continued)  
Pollen %



**Fig. 2.** Pollen diagram in percentages for Gerzensee: from the Oldest Dryas to the Lateglacial interstadial (Bølling and Allerød) and to the beginning of the Younger Dryas, selected pollen types only, on the time-scale of GICC-05 in BP (van Raden et al., this issue). Asterisks indicate minor peaks in non-arboreal pollen-types.

vegetation is dominated by agricultural fields and meadows, and the relict forests consist mainly of beech. The natural potential vegetation would consist of various types of beech forest (Brzeziński et al., 1993).

**Coring:** In the reed belt (*Phragmites australis*) of the littoral zone near the eastern shore of the lake and near the sites of the cores studied by Eicher and Siegenthaler (1976), two adjacent cores GEJ and GEK in metre-long segments were taken in September 2000 with a Streif modification of a Livingstone corer of 8 cm diameter (Merk and Streif, 1970). The twin cores were horizontally less than 50 cm apart and vertically shifted by 50 cm in their core sections (Wright, 1991). The linked core labelled GEJK consists of core GEK from the LST (272 cm) down to 329 cm, and the core GEJ from 330 cm down to 414 cm. The connection was checked by overlapping oxygen-isotope measurements on both cores.

**Sampling and preparation:** Samples of 1 cm<sup>3</sup> were taken at 0.5 cm intervals for the period of afforestation (380–360 cm), at 1 cm intervals before (390–380 cm) and after this (360–250 cm), and at 2 cm from 414–390 cm. Preparation followed standard procedures; *Lycopodium* tablets were added for the determination of pollen concentrations (Stockmarr, 1971).

**Pollen analysis:** A Leitz microscope under 400× magnification was used for analysis. Pollen-morphological references included the Northwest European Pollen Flora (Punt, 1976; Punt and Clarke, 1980, 1981, 1984; Punt et al., 1988, 1995; Moore et al., 1991; and Punt and Blackmore, 1991). About 200 pollen types were identified. Between 414 cm and 270 cm, 153 pollen samples were analysed. The average pollen sum is > 1000 (with a mean of 1069).

At the marker horizon of the Laacher See Tephra (LST), an additional 28 samples reaching into the Younger Dryas were added from the earlier study of Wick (2000), made on the core GEAB. The onset of the Younger Dryas has an age of 12,877 yr BP in the isotope stratigraphy and of 12,804 yr BP in the pollen stratigraphy (i.e. a decrease of *Betula*, increase of NAP; ages according to van Raden et al., 2013–this issue, for both GEJK and GEAB; see Fig. 3).

**The pollen diagram:** Pollen results are presented as percentages of the terrestrial pollen sum and as influx (grains mm<sup>-2</sup> yr<sup>-1</sup>) with use of TILIA and TILIA-Graph 2.b.0.4 and TGView 2.0.2 (Figs. 2 and 3). Loss on ignition according to Heiri et al. (2001) is shown in Fig. 4.

**Zonation:** The pollen diagram was zoned by “optimal partitioning based on partial least squares” (Birks and Gordon, 1985), as implemented in the programme ZONE, developed by Steve Juggins, and partitions were compared with the broken stick model (Bennett, 1996; Birks, 1998) to find statistically significant zones. The local pollen-assemblage zones (PAZ) are labelled GRZ for Gerzensee, with a subscript for the type of stratigraphy, i.e. GRZ<sub>pol</sub> for local pollen zones and as GRZ<sub>bulk</sub> for isotope zones (van Raden et al., 2013–this issue). To avoid too many abbreviations we use “zone” for PAZ. We also use the regional biozones Oldest Dryas, Bølling, Allerød, and Younger Dryas as defined by Welten (1982) and the regional pollen assemblage zones (RPAZ) as defined by Ammann and Lotter (1989), Ammann et al. (1994, 1996) and Lotter et al. (1992b) (see Table 1).

The chronology is based on the correlation of the oxygen-isotope ratios of bulk sediments with those of NGRIP (van Raden et al., 2013–this issue). Ages are given according to the GICC-05 time scale but as years BP (i.e. before AD 1950) in order to allow comparison with terrestrial and marine radiocarbon dates, which are expressed as years before 1950 (Rasmussen et al., 2006). We do not label the ages “cal” BP because they are not based on calibrated radiocarbon datings, and we cannot claim that we can provide “calendar years” BP in the Late-Glacial. Also, we do not round the ages, because we are primarily interested in age differences (i.e. durations of pollen changes).

**Numerical treatment:** Principal component analysis (PCA) was implemented with CANOCO (ter Braak, 1990). Percentage data were transformed to square roots, and sample distances were based on a covariance matrix between variables. PCA was determined independently for the data sets 241–414 cm and 336–414 cm (Fig. 4).

Rates-of-change estimates were implemented with RATEPOL (J.M. Line and H.J.B. Birks, unpublished software, 1994). The 100 most abundant pollen types were used, the maximum accepted in RATEPOL. Artificial sub-samples with intervals of 35 yr were created by weighted linear interpolation between adjacent pollen sub-samples. The rate of change in time periods of 70 yr was estimated, with starting times 17.5 yr apart. The results were smoothed with a weighted running mean over 5 samples (Fig. 4). For reliable results, the intervals between artificial sub-samples must be at least the maximum interval encountered among the pollen sub-samples (which is ca. 33 yr, for samples 2 cm apart), and the time periods for rate-of-change estimates must be at least twice that of the interpolated sub-samples.

As shown by Birks (2007) and Birks and Birks (2008) the amount of compositional change in pollen-stratigraphical data (species turn-over) can be estimated by detrended canonical correspondence analysis (DCCA), with sample age as the only external constraint. Percentages were transformed to square roots, rare taxa were not downweighted, detrending was done by segments, and non-linear scaling was applied. Some of the advantages of this approach are that DCCA can handle percentages, that the only constraint is sample age, and that the results are given in standard deviations, which is an ecologically interpretable unit (see Fig. 4).

Pollen richness as a proxy for plant diversity was estimated in two ways (Fig. 4): (1) based on a fixed pollen sum (here, 515), being the number of all pollen types that would have been encountered with this sum (implemented with RAREPOL based on Birks and Line (1992), and (2) based on accumulation rates, being the number of pollen types deposited each year on a fixed surface (here 10 mm<sup>2</sup>) (van der Knaap, 2009). Consecutive sub-samples were added together in a few cases in order to obtain the required surface. The results were smoothed with a weighted running mean over 5 samples.

To assess population growth, for selected taxa (*Pinus* and *Juniperus*) we scaled the influx values  $N_s(t_i)$  of taxon  $s$  at the time points  $t_i$  with their maxima and smoothed them with a temporal-distance-weighted interpolation with smoothing factor

$$\beta_s N_s(t_i) = \sum_{j=i-3}^{i+3} \frac{N_s(t_j)}{\beta |t_j - t_i| + 1} / \sum_{j=i-3}^{i+3} \frac{1}{\beta |t_j - t_i| + 1}.$$

The population change of taxon  $s$  can generally be described by the exponential growth:  $\frac{dN_s(t)}{dt} = \alpha_s(t) \cdot N_s(t)$ ,  $\alpha(t) = r_{0s} \cdot f_s(N_a(t), Env(t))$ . The intrinsic growth rate  $\alpha_s(t)$  describes the activity of the population dynamics. It comprises a fixed net reproductive rate  $r_0$  and a function that depends on the environment  $Env(t)$  and the same and other populations  $N_a(t)$ . Assuming  $\alpha$  to be constant, it can be estimated from subsequent influx values by

$$N_s(t_{i+1}) = N_s(t_i) \cdot e^{\alpha(t_{i+1}-t_i)} \Rightarrow \alpha = \ln \left( \frac{N_s(t_{i+1})}{N_s(t_i)} \right) / (t_{i+1} - t_i).$$

Changes in the resulting  $\alpha$  values indicate changes either in the environmental drivers or in the interactions with the same or other species, such as competition or facilitation. Constant positive  $\alpha$  indicates exponential growth, 0 = no change, and negative values a decrease of the population. Increasing positive  $\alpha$  indicates hyperexponential growth.

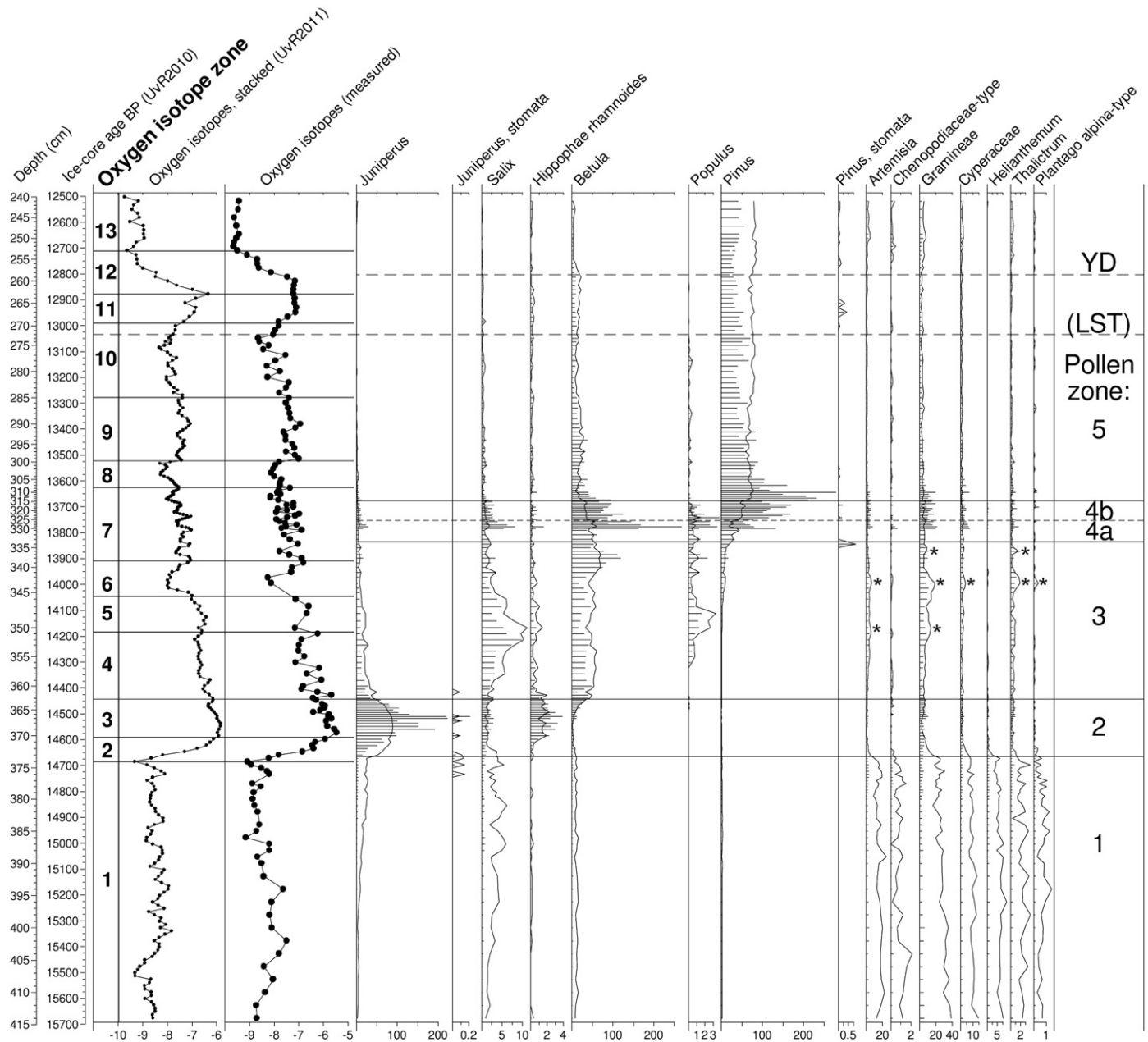
### 3. Results

#### 3.1. Lithology

The coring site lies on the former littoral terrace, where during the Late-Glacial with a higher lake level the sediment was largely lake

## Gerzensee

Pollen percentages (line) and accumulation rates (histograms; /mm<sup>2</sup>)



**Fig. 3.** Pollen diagram for Gerzensee as percentages (curves) and pollen accumulation rates (PAR, “influx”, as histograms), selected taxa, combined with the oxygen isotopes, on the time scale of GICC-05 in BP (van Raden et al., this issue). The scales for the pollen are chosen in such a way that the numbers are valid for both percentages and influx (as pollen grains per square millimetre and per year). Oxygen isotopes according to van Raden et al., this issue.

marl (not laminated); this is underlain by silt. The lithostratigraphy is as follows:

270–ca 370 cm lake marl, beige; a dark band at 272 cm is Laacher See Tephra (LST)

ca 370–415 cm lake marl with some silt, beige

415–510 cm silt with some clay, blue-grey; coarse sand with stones near the bottom (i.e. the surface of the till)

The results of loss-on-ignition (LOI) are shown in Fig. 4.

### 3.2. Temporal resolution

Sampling resolution during the afforestation period is about 8–9 yr, and before and after afforestation about 16–17 yr.

### 3.3. Pollen stratigraphy and vegetation history

The major vegetational changes are the transition from shrub-tundra to birch forest and then the immigration of pine, summarized as the following local pollen assemblage zones (Figs. 2 and 3, Table 1).

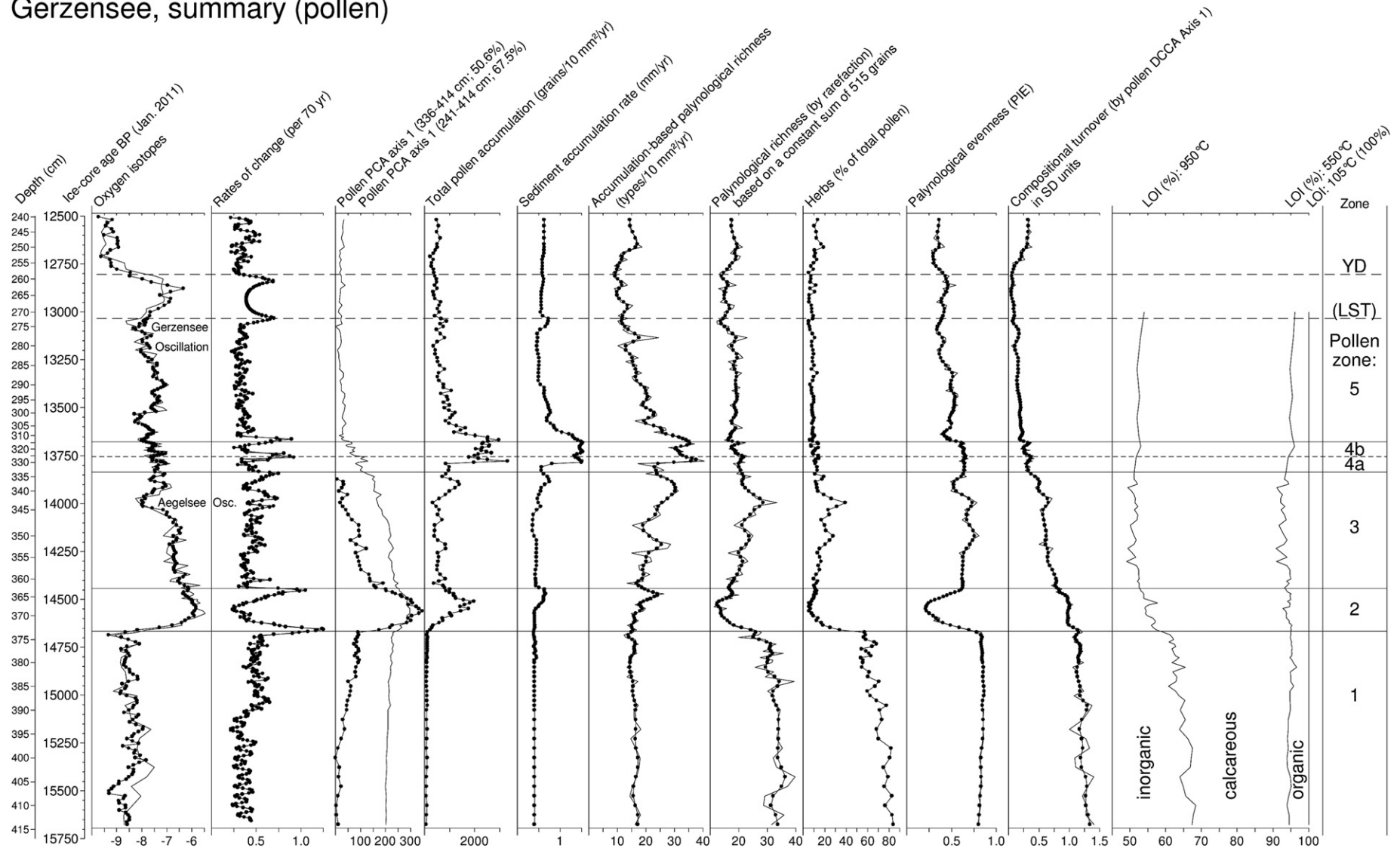
#### 3.3.1. Local Zone GRZ<sub>pol</sub>-1: Shrub-tundra

This pollen zone is equivalent to the last part of the Greenland event GS-2a or Oldest Dryas. Depth limits in the core GEJK are 414–373.25 cm, ages ca 15,676–14,665 yr BP, duration possibly 1000 yr or more.

Non-arboreal pollen (NAP) dominates, especially Poaceae, *Artemisia*, *Helianthemum*, *Thalictrum*, *Chenopodiaceae*, and *Gypsophila repens*-type.



## Gerzensee, summary (pollen)



**Fig. 4.** Quantitative estimates of palynological change from the late Oldest Dryas to the onset of the Younger Dryas. Changes in the pollen record are summarized in four ways and compared to changes in the oxygen-isotopes. From left to right: Oxygen isotopes, diamonds before 12,970 BP for stacked values, dots after 12,970 BP for measured values (see [van Raden et al., this issue](#)). Palynological changes as (1) rates of change (smoothed); as (2) scores on the first axis of a PCA (calculated separately for the whole period and for the older period of the afforestation, about 15,300 to 14,000 BP); as (3) the estimate of pollen diversity presented in two ways, i.e. as percentages and as PAR (or influx) (based on rarefaction analysis, according to [Birks and Line, 1992](#)); and finally (4) as compositional turnover estimated by DCCA and expressed in units of standard deviation. Interpretations are given in the text ([Section 4](#)).

Table 1

Chronology of the late-glacial local and regional pollen assemblage zones PAZ at Gerzensee as inferred from the correlation between the oxygen-isotope records of Gerzensee and NGRIP (van Raden et al., this issue), given on the timescale of GICC-05 in years before AD 1950 (Rasmussen et al., 2006). Asterisks at the level of the Older Dryas/Aegelsee oscillation indicate that this oscillation is more pronounced at higher altitudes.

Isotope zones						Pollen zones					Vegetation	
Isotope zones GRZ i <sub>bulk</sub>	Classical terminology used in Swiss lakes		Refined Greenland terminology	Gerz stack age (yr BP)	Gerz stack depth (cm)	GEJK depth (cm)	Limits PAZ		Assemblage zones PAZ			inferred for the Swiss Plateau
							GEJK depth	stack age	local PAZ at GRZ	Biozones Welten 1982	regional PAZ Lotter et al.1992 Ammann et al. 96	
13	Younger Dryas		GS-1	12710	273.75		256.5		G-4 in Wick 2000	Younger Dryas	CHb-4b	Open woodland Pine and Birch
12	transition						12877	262.75		314.5	13677	GRZpol-5
11	Allerød		GI-1a	12989	269.25	272						
10	Gerzensee Oscillation	LST	GI-1b	13034	272	282.75						
9	Allerød		GI-1c1	13274	282.75	285						
8			GI-1c2	13522	293.25	299						
7			GI-1c3	13624	298.25	308	314.5	13677	GRZpol-4b	Early Allerød	CHb-4a	Pine-Birch forest
							325.5	13753			GRZpol-4a	CHb-4a
6	Aegelsee Oscillation	Older Dryas	GI-1d	13908	315.25	338.5	333.5	13835	GRZpol-3	(Older Dryas very indistinct*) Late Bølling	CHb-3b*	Birch forest
5	Bølling		GI-1e1	14044	322.25	345.5						
4			GI-1e2	14183	326.25	351.5						
3			GI-1e3	14439	336.25	361.5	362.25	14443				
2	transition			14590	341.75	369.5			GRZpol-2	Early Bølling	CHb-2	Juniper-Birch forest
1	Oldest Dryas		GS-2a	14685	345.25	374	373.25	14665	GRZpol-1	Oldest Dryas	CHb-1c	Shrub-Tundra

*Ephedra distachya*-type is nearly continuous, and *Ephedra fragilis*-type is frequent after about 14,815 yr BP. The pollen richness estimated on a fixed sum is highest in this zone and decreases in the next zone with afforestation, whereas the accumulation-based pollen richness remains about constant. Among woody taxa, *Betula*, *Salix*, *Hippophaë*, and increasing values of *Juniperus* are most probably local, whereas *Pinus* and single grains of *Abies* and *Quercus* may have come by distant transport from south of the Alps. Reworking from interglacial deposits may not be the source, because reworked pollen is usually accompanied with reworked Tertiary types, which are absent here, but which are especially important at other sites near the base of the Oldest Dryas (Ammann and Tobolski, 1983; Gaillard, 1984a). This zone corresponds to the third (shrub-tundra) phase of the tripartite Oldest Dryas on the Swiss Plateau ((Ammann and Tobolski, 1983; Gaillard, 1984a; Ammann et al., 2007; Vescovi et al., 2007). In pollen records longer than Gerzensee the first phase (just above the till) contains many reworked pollen grains in the blue-grey silt, and the second phase shows many herb taxa but no shrubs (between 415 cm and 560 cm).

*Juniperus* pollen (percentages and influx) suggests a tripartition of the zone, with a tail before ca. 15,200 yr BP, an increase between 15,200 and 14,900 yr BP, and a shoulder between 14,900 and 14,685 yr BP. The first juniper stomata were found in the second half of this shoulder at 376 cm around 14,733 yr BP. This is therefore the minimum age for local presence, distinctly before the dramatic rise in pollen percentages and influx around 14,665 yr BP. Already Gaillard and Weber (1978) and Gaillard (1984a) showed that on the western Swiss Plateau juniper pollen percentages were high (8–37%) during the phase of shrub-tundra, with a few stomata findings and high values of *B. nana* pollen. By analysis of plant macroremains Gaillard (1984a) could show that besides numerous

fruits of *B. nana* a few tree birches (*B. alba*-type, i.e. *B. pubescens* and *B. pendula*) were present during the last part of the Oldest Dryas. Her sites of Grand Marais and Le Tronchet are at altitudes comparable to Gerzensee (587 m asl and 715 m asl, respectively).

The regular occurrence of spores of the coprophilous fungi *Sporormiella* and *Cercophora*-type may be a hint that large mammals used Gerzensee as a water-hole. Potential candidates are the mammals recovered from Late Palaeolithic sites on the Swiss Plateau, including horse, reindeer, wisent, deer, red deer, elk, boar, and others (Nielsen, 2013—this issue). This decrease of coprophilous spores synchronous to the shift from a herb dominated to a tree dominated vegetation resembles the findings of Jeffers et al. (2011) in south-east England around the transition from the Late-Glacial to the Holocene.

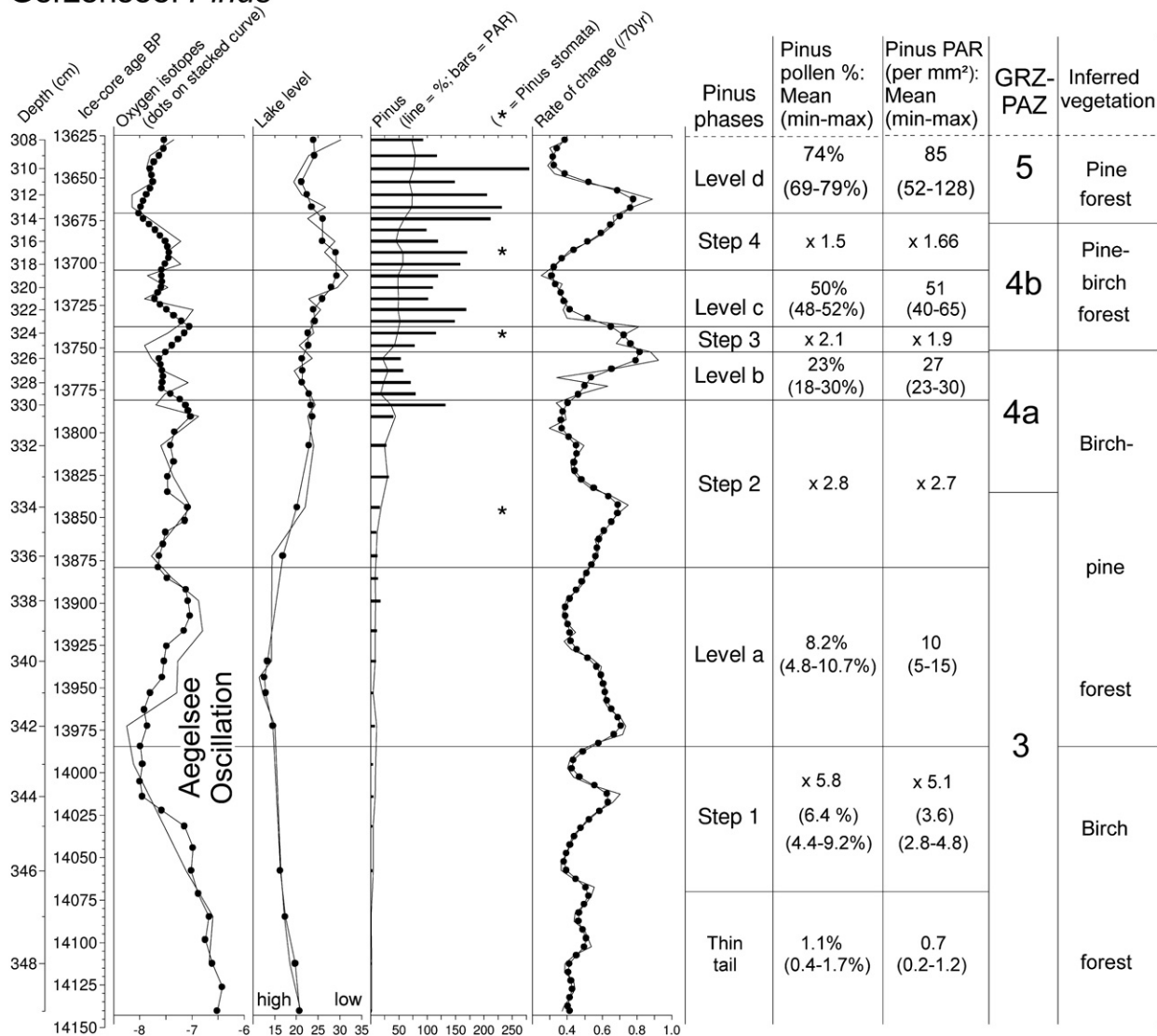
### 3.3.2. Local Zone GRZ<sub>pol</sub>-2: The juniper–birch forest of the Early Bølling

This pollen zone is approximately equivalent to the isotopic transition GRZ<sub>bulk2</sub> plus the first third of the Greenland event GI-1e, or the Early Bølling (*sensu* Welten, 1982). Depth limits in the core GEJK are 373.25–362.25 cm and ages ca 14,665–14,443 yr BP, duration about 220 yr.

The transition from Stadial GS-2 (Oldest Dryas) to Interstadial GI-1 (Bølling-Allerød) is marked by the rapid shift in oxygen isotopes (3.5‰) within about 112 yr (from about 14,672 to 14,560 yr BP) coinciding with the ecologically important process of afforestation (the “juniper jump” of Denton et al., 2006). All herb pollen types decline rapidly as percentages, but some do not as influx. Not only do the “classical” taxa of the steppe-tundra of the Oldest Dryas decrease, such as *Artemisia*, *Helianthemum*, *Ephedra*, Gramineae, Cyperaceae, and Chenopodiaceae, but also other heliophilous taxa, e.g. *Thalictrum*, *Plantago alpina*-type, Cichorioideae, Rubiaceae, *Rumex acetosa*-type, *Saxifraga oppositifolia*-type, Cruciferae, and several types of Apiaceae.



# Gerzensee: *Pinus*



**Fig. 5.** Steps and levels of the *Pinus* dynamics in relation to the record of oxygen-isotopes and to the rate-of-change in the pollen record. As in Fig. 3 the scale for *Pinus* pollen stands for both percentages and influx (per square millimetre and year).

During this transition period *Juniperus* pollen increases extremely rapidly in both percentages and influx with an intrinsic growth rate of  $\alpha = 0.012/\text{year}$  (see Fig. 6). *Hippophaë* develops after *Juniperus* with a lag of about 50 yr (onset of *Juniperus* rise at ca. 14,665 yr BP, onset of *Hippophaë* rise ca. 14,615 yr BP). The first traces of *Populus* are found towards the end of the zone. Earlier studies based on pollen percentages only suggested that the herbaceous plant cover declined rapidly during this phase due to shading-out by the forest that became rapidly denser (Iversen, 1954; Welten, 1982). But already Gaillard (1984a) and Ammann and Tobolski (1983), as well as our present data, show that influx of herb pollen did not decrease, meaning that the decline in herb percentage might be an artefact of closed data. Neither percentages nor influx can record patches free of any vegetation – and those most probably became much rarer (see decrease of minerogenic input estimated from LOI at 950 °C in Fig. 4). Moreover, the accumulation-based pollen richness indicates that the number of pollen taxa did not decrease (Fig. 4). It is therefore likely that the increasing shrubs did not form closed stands, so that sufficient light remained for the herbs. The shrubs may even have provided additional shelter against wind and excessive insolation (i.e. protection against desiccation), and also the shrub litter (and

initial soil formation) may have favoured herbs, which could grow much taller when shrubs arrived. For a possible facilitation of nitrogen-fixers by *Juniperus* see Section 4.5.5.1.

Just as with herbs, the seeming depression of *Betula* is a percentage effect not found in influx (Fig. 3). Plant macrofossils were not analysed here, but they were studied at eight other sites on the Swiss Plateau and also just north of Lake Constance. All these sites indicate a shift from predominant dwarf birch to predominant tree birches for this same transition (Lang, 1952a,b; Weber, 1977, 1980a,b,c; Ammann and Tobolski, 1983; Gaillard, 1983; Lotter, 1988). Just as with *Betula*, *Salix* percentages decrease but influx increases.

The higher sampling resolution applied in this study provides better insights into the sequence of events during this transition (starting about 50 yr before the zone limit covering about 45 yr between 14,710 and 14,665 yr BP). We can summarize the four steps of the sequence:

1. Sharp declines of *Artemisia* and *Chenopodiaceae* in both percentages and influx suggest population declines in these typical steppe taxa. Gramineae, Cyperaceae, *Thalictrum*, and *Helianthemum* percentages also decline, but their influx remains more or less constant, suggesting minor declines or stable conditions. Several

**Table 2**

Relationships between the isotopic zones GRZ<sub>bulk</sub>-1 to GRZ<sub>bulk</sub>-7 and the population dynamics of the six major woody taxa during the early Late-Glacial at Gerzensee: *Juniperus*, *Hippophaë*, *Salix*, *Betula* (tree taxa), *Populus*, and *Pinus*. Relationship between isotopic zones GRZ<sub>bulk</sub> and populations of woody taxa during the millennium of the first forests of Bølling & Allerød.

Relationship between isotopic zones GRZ <sub>bulk</sub> and populations of woody taxa during the millennium of the first forests of Bølling & Allerød												
Isotope zones	GEJK	GICC05 BP	Depth	Age	<i>Juniperus</i>	<i>Salix</i> spp.	<i>Hippophaë</i>	<i>Betula</i>	<i>Populus</i>	<i>Pinus</i> , see also Tab. 3	PAZ	
zones	Depth	Greenland	of biotic events								GRZ <sub>po</sub>	
Limit ↑	cm	yr before 1950	314.5	13677				Plateau, sub-dominance	Continuous	<b>Level d</b>		
<b>GRZ<sub>bulk</sub>-7</b>		<b>GI-1c3</b>	315.5	13684					curve ends	313 cm <b>Step 4 ↑</b> 319 cm		
			319	13708				Co-dominant with pine	Several minor fluctuations	<b>Level c</b> Co-dominant with birch	4b	Allerød
			323	13734						323 cm <b>Step 3 ↑</b> 325.5	13753 325.5	
			325	13749				Step ↓		<b>Level b</b>	4a	
					Very low values		Very low values	Third dominance		329 cm <b>Step 2 ↑</b> 337 cm	13835 333.5	
			329	13777								
			336	13872	Rel. low values		Low values					
Limit	338.5	13908	339	13916				Recovery		<b>Level a</b>		
<b>GRZ<sub>bulk</sub>-6</b>		<b>GI-1d</b> <b>Aegelsee osc</b>	342	13974	Step ↓	Step ↓	Step ↓	Step ↓	Step ↓	342 cm <b>Step 1 ↑</b> 347 cm		OD
Limit	345.5	14044		14085				Second dominance	Slope ↓			
<b>GRZ<sub>bulk</sub>-5</b>		<b>GI-1e1</b>	347 348.5									GRZ <sub>pol</sub> -3
Limit	351.5	14183	351.5	14202	plateau	Peak		Minor dip	Peak			
<b>GRZ<sub>bulk</sub>-4</b>		<b>GI-1e-2</b> <b>IBCP</b>	353	14235				First dominance				
						Increase Plateau			shoulder			
Limit	361.5	14 439	361	14416		↑ % & PAR	Step ↓		<b>Onset ↑</b>		14443 362.25	
<b>GRZ<sub>bulk</sub>-3</b>		<b>GI-1e3</b>	364	14470	Rapid ↓	Several minor fluctuations	Shoulder					GRZ <sub>pol</sub> -2
			365.5	14494			Onset of ↓	<b>Strong ↑</b>	1st grains			
			367	14519	Onset of ↓							
			368.5	14548	Peak		Peak	<b>Slight ↑</b>				
Limit	369.5	14 573	370	14585			<b>Strong onset ↑</b>					
<b>GRZ<sub>bulk</sub>-2</b>		<b>Rapid ↑↑↑ Transition</b>	373.25	14672	<b>Strong ↑</b> in % & PAR	%↓, PAR↓	<b>Slight ↑</b>				14665	GRZ <sub>pol</sub> -1
Limit	374	14 685										
<b>GRZ<sub>bulk</sub>-1</b>					1. plateau	fluctuation						
			376	14742	1. stoma							
			396	15088	Slight ↑							
			398	15104			Continuous					

other taxa (e.g. *P. alpina*-type) show a rapid decline in percentages but then a short period of stable influx after 20–30 yr, followed by decline, suggesting slightly lagged declines. Aquatic taxa such as *Pediastrum boryanum* var. *longicorne* also decline.

- Sharp rises of the oxygen-isotope ratio and *Juniperus* pollen (percentages and influx), along with a slight rise of *Betula* pollen influx but decline in percentages.
- A rise of *Hippophaë* (both percentages and influx) and *Salix* (only influx).

- A rise of *Betula* and decline of *Juniperus* (both percentages and influx).

### 3.3.3. Zone GRZ<sub>pol</sub>-3: The birch forests of the Late Bølling

This pollen zone is approximately equivalent to the Greenland events GI-1e2 and GI-1e3 plus GI-1d, or Late Bølling plus Older Dryas (*sensu* Welten, 1982). Depth limits are 362.25–333.5 cm, ages ca 14,443–13,835 yr BP, a duration of about 600 yr.

**Table 3**

Migrational lags of terrestrial plant taxa estimated from their arrival time compared to the waterplant *Myriophyllum spicatum* that has similar temperature requirements. The asterisk in Hippophaë indicates that during the ca 300 yr between 398 cm and 386 cm the pollen was regularly found (see Fig. 2), but then the record is briefly interrupted (empirical limits, just as absolute limits depend on the pollen sums counted per level). For continentality the value of 3 means suboceanic to subcontinental, and 4 means subcontinental. The various ways to estimate the temperature requirements show, that for the woody taxa the conditions would have been warm enough already with the first occurrence of *Myriophyllum spicatum*. Data from Oberdorfer (1990) and Brändli (1998).

Arrival Core depth in cm, Limits Rational, Empirical, Absolute limits	Arrival in yrs BP GICC-05 (rounded)	Taxon	Temperature requirements				Lags estimated as time since first record of <i>Myriophyllum spicatum</i>
			Minimum mean July required	Min DD growing degree days as used in models	Todays Alpine altitudinal limit in m asl as a proxy for temperatures		
					Oberdorfer 1990	Brändli 1998	
334 cm (first stomata)	13 844	<i>Pinus sylvestris</i>		610	1600 m	Max 2005 m Median 820m	1434 years
355 (rational) 356 (empirical)	14 279 14 302	<i>Populus tremula</i>		610	1300 m	rarely to 2000 m, but as a shrub to 2200 m, Median at 980 m	999 years 978 years
371 (rational) 372 (empirical) 374-370 ♂ <sup>18</sup> ♀ <sup>1</sup> 414 (absolute)	14 610 14 635 15 676	<i>Hippophaë rhamnoides</i>	10° Iversen 1954		975 m		668 years 643 (or zero*)  Earlier than <i>M.s.</i>
364.5 (rational)	14 478	<i>Betula alba</i> - type: <i>B. pendula</i>		610	<i>B. pendula</i> 1780 m, <i>B. pubescens</i> 1580	<i>B. pendula</i> Max at 2000, m Median at 990 m	800 years
374-370 ♂ <sup>18</sup> ♀ <sup>1</sup> 374 (rational) 376 first stomata	14 685 14 733	<i>Juniperus communis</i>	> 10° Iversen 1954		<i>J. communis</i> 1600m <i>J. nana</i> 2320 m		545 years 48 years
398	15 278	<i>Myriophyllum spicatum</i>	9-11°C base line		930 m asl		Baseline

Pollen data suggest that *Juniperus* declined (both percentages and influx) throughout this PAZ and that tree birches became dominant. *Hippophaë* decreased, whereas *Salix* increased. *Populus* pollen is regularly found after about 14,300 yr BP and remains important also through the next zone until about 13,700 yr BP, suggesting local presence around Gerzensee. A comparison of *Populus* occurrence with earlier pollen analyses on the Swiss Plateau, however, is difficult, as this pollen type was often overlooked or not preserved. Wick (2000) found it at Gerzensee sporadically during the Allerød and regularly during the Preboreal. On the western Swiss Plateau, Gaillard (1984a) found it already sporadically during the Bølling, Allerød, and Younger Dryas and then very consistently during the Preboreal (sites shown in Fig. 1). Gaillard and Lemdahl (1994) also found in the Bølling beetle remains characteristic for poplar. In contrast to the pollen, the plant macrofossils (bud-scales and catkin-scales) can be identified to species level. The most probable *Populus* species in this study is *P. tremula*, because its macroremains were found in Lobsigensee during the birch-dominated Bølling just before the expansion of pine (thus about coeval with the present record) and in the earlier Gerzensee core GEAB during the Allerød and Preboreal (Tobolski, 1985; Tobolski and Ammann, 2000).

In the second half of the zone, some herb pollen types show several minor peaks either only in percentages or also in influx (Figs. 2 and 3) suggesting minor transient re-expansion of herbs and steppic environments. Most prominent are three peaks of Gramineae and two peaks of *Artemisia*, marked with asterisks on Figs. 2 and 3. The second peaks (14,058–13,953 yr BP) coincide with the minimum in the oxygen-isotope ratios correlated with the cool Aegelsee Oscillation or Older Dryas (14,044–13,908 yr BP). The Aegelsee Oscillation was defined by Lotter et al. (1992b) at Aegelsee, situated 20 km south of Gerzensee at 995 m asl. Because of the very minor pollen changes in lowland sites, Welten (1982) and Lotter et al. (1992b) suggested that such a cool phase could often only be recorded at higher, more sensitive altitudes. Fig. 5 suggests that the initial population expansion of pine in the

Gerzensee area was probably between 14,000 and 13,950 yr BP. The influx of pine follows largely its percentages, with increases at the zone boundaries and less variability within the zones, i.e. within the four levels mentioned in Fig. 5. *Betula* either decreases with increasing *Pinus* both in percentages and influx, or its peaks coincide with *Pinus*-plateaux (levels a–d in Fig. 5). The early small peak of *Pinus* towards the end of the Aegelsee Oscillation supports the hypothesis of Welten (1982) and Lotter et al. (1992b) that pine actually immigrated into the Swiss Plateau during a relatively cool phase. This level is 130 yr before the first occurrence of pine-stomata just before the upper zone boundary, around 13,844 yr BP. This is therefore the minimum age for the local presence of *Pinus* at Gerzensee. As summarized in Fig. 5, already during this zone GRZ<sub>pol</sub>-3 pine shows a structure labelled as “thin tail, first step, and level a” in both percentages and influx. Our findings of stomata (as a proxy for needles) may fail to document the earliest population expansions around a site, though they are reliable as evidence of local presence. It is interesting to note that Gaillard and Lemdahl (1994) found in the core of Grand Marais a beetle characteristic for coniferous trees before the first seeds and needles of pine.

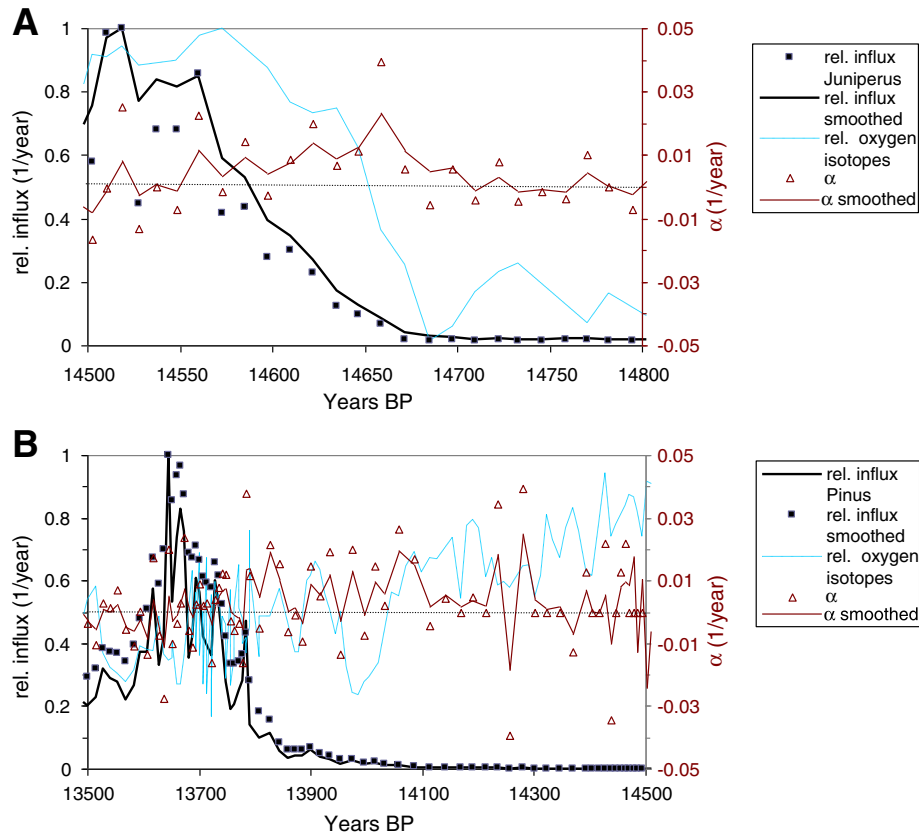
In addition the modelling results show a major increase in pine populations during “level a” of our Fig. 5, as visualized by Lischke et al. (2013–this issue) in their Fig. 8. These authors also discuss potential mechanisms for the increase of pine during a cool phase and its stepwise population growth resulting from competition and climatic oscillations.

### 3.3.4. Zone GRZ<sub>pol</sub>-4: The birch–pine forests of the Early Allerød

This pollen zone is approximately equivalent to the Greenland event GI-1c3 or the Early Allerød (*sensu* Welten, 1982). Depth limits are 333.5–314.5 cm, ages are ca. 13,835–13,677 yr BP, duration about 160 yr.

Among the steps of increasing pine populations as summarized in Fig. 5., step 1 occurred between 14,070 and 13,985 yr BP, step 2 between 13,880 and 13,780 yr BP, step 3 between 13,752 and 13,738 yr BP, and step 4 between 13,704 and 13,870 yr BP (again we emphasize





**Fig. 6.** Pollen influx (scaled between 0 and 1) and inferred intrinsic growth rate  $\alpha$  of pollen data during appearance of *Juniperus* (a) and *Pinus* (b). Dashed blue line indicates the oxygen isotopes, also scaled between 0 and 1. Zero line of  $\alpha$  in red.

that these are not absolute or calendar ages, but because age differences are important, we do not round the numbers). Thus step 1, level a and step 2 last between ca. 87 and 105 yr, and the younger steps and levels between 14 and 34 yr. Provided that our timescale is correct we may compare these durations of 85–105 yr with the slow population increase modelled by Lischke et al. (2013–this issue) and the shorter durations of 14–34 yr with the age at first flowering of pine (15–30 yr for free-standing individuals and 30–50 yr in a stand). But these suppositions need more detailed work linking palynology with ecological modelling.

The numerically determined but statistically not significant boundary between subzones GRZ<sub>pol</sub>-4a and 4b depends mainly on the change in dominance from *Betula* to *Pinus* pollen, thus probably from birch–pine forest to pine–birch forest (Fig. 2).

The upper third of subzones GRZ<sub>pol</sub>-4a and all of GRZ<sub>pol</sub>-4b (i.e. 330–310 cm) coincide with the core section that has very high sediment-accumulation rates (see Figs. 3 and 4). As shown in Table 2 by van Raden et al. (2013–this issue) the corresponding isotope zone GRZi<sub>bulk</sub>-7 (in Greenland GI-1c3) measures 17 cm in core GEM, but 30.5 cm in core GEJK. There Fig. 7, which compares four neighbouring cores, shows that to a lesser degree a higher sedimentation rate for the same period was also found in core GE-III (Eicher, 1987) for the same period. Variability in lacustrine sedimentation seems to be high on a subaquatic terrace formed by lake marl (see also Section 4.3).

### 3.3.5. Zone GRZ<sub>pol</sub>-5: The pine forests

This pollen zone is equivalent to the Greenland events GI-1c2 to GI-1a or Late Allerød (*sensu* Welten, 1982). Depth limits 314.5–270 cm, ages ca 13,677–13,000 yr BP, duration of at least 677 yr.

*Betula* pollen remains below 25% and *Pinus* pollen dominates with 60–80%, suggesting the presence of rather dense pine forests with stands of tree birch.

The Laacher See Tephra (LST) layer at 272 cm is positioned towards the end of the Gerzensee Oscillation, around 13,035 yr BP. At this level we link our new data with those of Wick (2000), who inferred from pollen of Gerzensee the vegetation during the Gerzensee Oscillation and the isotopically warmer phase of GI-1a as well as during the Younger Dryas (GS-1).

## 4. Discussion

The palynostratigraphy described above is similar to that found in numerous studies on the Swiss Plateau, which can be taken as an area typical for southern Central Europe (Welten, 1982; Ammann and Tobolski, 1983; Gaillard, 1984a; Ammann, 1989; Lotter, 1999). New in the present study are the high sampling resolution, the high taxonomic resolution (200 pollen types), and especially the close relationship with stable-isotopes (in samples at identical levels) that allowed a chronological precision that would currently not be possible with radiocarbon dating.

In the following we first consider different methods of quantifying vegetational change (Fig. 4) and then address the four questions asked in the introduction.

### 4.1. Rates of change

Rates-of-change estimates the amount of change in the pollen assemblages per unit of time. They are therefore sensitive to the precision of the timescale (Lotter et al., 1992a). Here we assume that the timescale GICC-05 developed by Rasmussen et al. (2006) and applied to Gerzensee by van Raden et al. (2013–this issue), is valid for our core (see Fig. 4). Rates-of-change is also sensitive to the proportions (percentages) of the different pollen types in the assemblages (Jacobson et al., 1987; Bennett and Humphry, 1995).

Analogous to fixed-sum estimates of pollen richness, estimates of rate-of-change are influenced by the evenness of the pollen assemblage, depending mainly on the pollen types that are dominant in the assemblage, and very little on the rare ones. Despite the clear general link between pollen and plants or vegetation, the dominance relationships (evenness) of plant taxa in the vegetation differ to some extent from that of their pollen types in the assemblages because of differential pollen productivities, dispersal, and preservation. As a result, rates of change in the pollen sequence may differ from rates of change in the vegetation reflected by the pollen. Not surprisingly, but corroborating the relation, the rates of change are generally high at or near pollen-zone boundaries derived by a different technique (optimal partitioning by least squares according to Birks and Gordon, 1985).

#### 4.2. PCA

The scores on the axes of PCA are sensitive to the gradient length, or “overall change”. We therefore calculated PCA axis 1 separately for two data sets, one including the entire period (15,676–12,500 yr BP), the other including the older section only (15,676–13,826 yr BP) (Fig. 4). Both curves have a very sharp increase with the rapid warming (14,685–14,540 yr BP). The trend of PCA axis 1 of the older section resembles strongly the juniper pollen curve (Fig. 3). The two curves are also similar for the period just before the rapid increase of juniper, where a locally present but still small juniper population is inferred from the pollen and stomata records (ca 15,200–14,685 yr BP).

#### 4.3. DCCA as an estimate of compositional change (turnover)

Pollen DCCA Axis 1, constrained on sample age presented on Fig. 4, is a relative measure of species (floristic) turnover in the landscape (Birks, 2007; Birks and Birks, 2008). With turnover is meant the appearance of new taxa and disappearance of existing taxa. Constant values on Axis 1 indicate that no floristic change took place, and shifts in values indicate turnover. The axis scores given in standard deviations (SD) show a uni-directional and gradual trend from the base up to the beginning of the Younger Dryas. Values are slightly changing in zone GRZ<sub>pol</sub>-1, somewhat more changing in zones GRZ<sub>pol</sub>-2, 3, and 4, and again slightly changing in zone GRZ<sub>pol</sub>-5 and up to the start of the Younger Dryas. The gradual character of the changes indicates that none of the major, often abrupt shifts in dominant plant species had a notable impact on the species turnover in the landscape. This implies that dominants did not matter much for presence/absence of species (see also Section 4.5.4).

#### 4.4. Dynamics of vegetation during afforestation between 14,700 and 14,400 yr BP

The transition from shrub-tundra to a juniper–birch woodland (from zone GRZ<sub>pol</sub>-1 to 2; Figs. 2, 3, 4) was surprisingly fast. Most likely this rapid change was due to (1) the rapid rise of annual temperatures (as recorded in the oxygen-isotopes: a rise of 3.6‰ in only ca 112 yr) and (2) the presence of *Juniperus* and tree birch already before the rise in temperatures, so that no migrational lag occurred for these woody taxa within this period of rapidly rising annual temperatures. Pollen productivity of juniper was discussed by Iversen (1954), Birks (1973) and Gaillard (1984a). Productivity of the prostrate *J. communis* ssp. *nana* seems to be much lower than of the tall *J. communis* ssp. *communis*. Because neither pollen nor stomata can be identified to the level of subspecies, we cannot separate them, unless we also had analyses of macroremains. On the western Swiss Plateau near Lake Geneva, Weber (1980b) found needles of *J. communis* ssp. *nana* in the sediment from the Oldest Dryas (i.e. before 14,685 yr BP) at an altitude comparable to Gerzensee.

The sequence of dominant or sub-dominant woody taxa (*Juniperus* – *Hippophaë* – *Betula* – *Salix*) is illustrated in Figs. 2 and 3 and Tables 2

and 3. This sequence forms a pattern already described by e.g. Gaillard (1984a, b), Lotter (1985, 1988, 1999), and Ammann (1989). *Salix* is ecologically difficult to interpret because many species may contribute to this pollen type. For the Late-Glacial Lang (1952a) could identify about 9 different species on the basis of macrorests in SW-Germany, and Weber (1977, 1980c) described 10 species on the western Swiss Plateau. However, all *Salix* species prefer open conditions and do usually not occur under a dense forest canopy. At Gerzensee the high temporal resolution shows that the increase of *Hippophaë* (in both percentages and influx) started about 50 yr later than that of *Juniperus* (Table 2), and peaks and declines of the two shrubs are not exactly synchronous: *Juniperus* started to decline with the very first increase of *Betula* (about at 14,520 yr BP), whereas high *Hippophaë*-values continued into the later rapid rise of *Betula* (about 14,495 yr BP). Gaillard and Weber (1978) and Gaillard (1984a) discussed the possibility that juniper became shaded out by tree-birches. Here we estimate that about 25 yr lapsed between the end of the *Juniperus* peak (about 14,520 yr BP) and the marked increase of *Betula* (about 14,495 yr BP; see Table 2).

At Gerzensee, *Larix* was not found during the Late Glacial Interstadial, but only later, during the Younger Dryas (as pollen and macrofossils; see Wick, 2000; Tobolski and Ammann, 2000). The timing of this shift from shrub-tundra to woodland at the onset of Bølling is characteristic for southern Central Europe but contrasts with other European sites. It was earlier in the foothills of the southern Alps and in Italy (Tinner et al., 1999; Vescovi et al., 2007) and later farther north in central Germany (e.g. Eifel region, (Litt and Stebich, 1999) or in The Netherlands (Hoek, 2001).

The intrinsic growth rates during afforestation are of special interest: The influx data of *Juniperus*, as the most prominent example for the dynamics of several taxa during afforestation, show a smooth increase over 100–200 yr (Fig. 6a), apparently starting at the onset of the Bølling. However, the intrinsic growth rate already fluctuated around zero for one or two centuries. After 14,680 BP it remained positive and increased steadily for about 100 yr, indicating that population growth accelerated hyperexponentially during that period. The subsequent decrease in  $\alpha$  of *Juniperus* was due to intra-specific and increasingly also inter-specific competition. Values of  $\alpha$  ranged between –0.02/year and +0.04/year. *Pinus*  $\alpha$  also shows phases with steady increases, although frequently interrupted.

#### 4.5. How did the rapid climatic warming at 14.67 ka BP influence the five levels of major biological processes?

Table 2 demonstrates that no simple relationship exists between temperature change (as recorded in oxygen isotopes) and vegetation development. But increasing temperatures obviously favoured all five (interlinked) levels of biological response:

- (1) Individual reactions (reproduction, including pollen and seed production but also growth as shown in tree rings).
- (2) Building up or decline of plant populations.
- (3) Migrations (biogeographical changes or range shifts, partly controlled by climate or by other environmental variables, such as soils, and partly by life-history traits).
- (4) Plant communities depend i.a. on species pools and therefore on the three levels mentioned above.
- (5) Processes at the ecosystem level, including species interactions such as competition or facilitation, pedogenesis, nutrient cycling.

##### 4.5.1. Level of the individual: Reproduction and pollen productivity

Changed reproduction, resulting in changed pollen production, is the fastest response to climatic change, for it may occur within a year or two (van der Knaap et al., 2010). The speed may be comparable to that of other responses on the level of the individual, such as changes in growth

expressed by tree-ring width (Friedrich et al., 2001). On the basis of numerous sites in The Netherlands Hoek (1997a,b, 2001) considered the rapid increase of *Betula* pollen around 14.7 cal ka BP primarily as a result of increased flowering, for a more-or-less closed birch forest developed only about 700 yr later. For Gerzensee, we hypothesize that every increase in pollen influx larger than an exponential population increase would be caused by the improving environmental conditions, which affected individual reproduction by more intense flowering. This could be due to faster growth, which increased also numbers of flowers and reduced time to first flowering, leading to higher reproduction (as demonstrated by increasing  $\alpha$ -values e.g. for *Juniperus*). All these individual reproduction processes also result in a larger yearly pollen production. We infer that the contribution of increasing reproduction was especially large during the very rapid increase of juniper at the transition from Oldest Dryas to Bølling (zone GRZ<sub>pol</sub>-1 to 2).

For our understanding of the temporal processes involved we need to remember that changes in pollen productivity cannot be longer than the life-span of a species and are not likely to last over more than a few years.

#### 4.5.2. Level of population: Increases or decreases of populations

Individual reproduction is an indispensable element of population dynamics, besides mortality and interactions within and between populations. Bennett (1983, 1986) showed how population dynamics can be derived from changes in pollen influx for major tree taxa. Later Birks (1989) compiled the Holocene immigration histories of several tree and shrub species over the entire British Isles by tracing the population increases. Here we study only a single site, but we can exploit the high temporal resolution for a better understanding of the processes. Lischke et al. (2013–this issue), then combine the pollen data with ecological modelling of the population dynamics.

As shown in Figs. 2 and 3 and in Tables 2 and 3, pollen data calculated both as percentages and as influx, as well as the intrinsic growth rates, help to visualize periods of near-exponential population growth in *Juniperus*, *Hippophaë*, *Salix*, *Betula*, *Populus*, and *Pinus*. The first fluctuations of intrinsic growth rates long before the rise of the pollen peaks could be due to long-distance transport or to unsuccessful establishment attempts. These attempts could have been hindered by adverse climate (*Juniperus*) but also by improved conditions for competitors (*Pinus*). The special case of arrival and population increase of *Pinus* is discussed in Section 4.5.3.

The two most heliophilous species (*Juniperus communis* and *Hippophaë rhamnoides*) exhibit not quite symmetrical curves. The increase is comparably rapid and rather short in both species (ca 75 yr), but the decreases differed to about 100 yr in *Juniperus* and 23 yr in *Hippophaë*. The simulations in Lischke et al. (2013–this issue) indicate that the decrease of the peaks is controlled by the appearance times of the competing taxa, as determined by species-specific temperature thresholds or immigration. The other woody taxa (*Salix*, *Betula*, *Populus*, and *Pinus*) did not decline so drastically after a first peak, but they remained important in the vegetation, as also shown in the simulations.

#### 4.5.3. Level of biogeography: Migrations, local arrivals and extinctions

In the earlier study at Gerzensee and three other Swiss sites that focussed on the rapid warming at the Younger Dryas/Holocene transition, Ammann et al. (2000) could exclude migrational lags because all the major taxa of the very early Holocene were already present during the Allerød and did not become extinct during the Younger Dryas. If any migrational lag occurred at the end of the Younger Dryas, it was only an altitudinal rather than a horizontal or latitudinal one: at a higher site (Leysin; 1520 m asl), trees (birch, pine, larch, and poplar) present during the Allerød had retreated during the Younger Dryas to lower altitudes and re-immigrated back a short distance in the same valley during the earliest Holocene. The immigration of thermophilous taxa such as *Corylus* or *Quercus* were not studied. Lischke et al. (2002) compared pollen data to forest model

simulations for the same period at the nearby site of Soppensee and found that cold temperatures were not sufficient to explain the absence of some tree species, such as *Abies* and *Fagus*.

Similarly, Lischke et al. (2013–this issue), found that the absence of most taxa in the present study can only be explained if very low temperatures are assumed before the onset of the Bølling. For the late appearance of pine, other causes, such as delayed immigration, had to be assumed.

We can expect such migrational lags in the present study because plants had to immigrate after the retreat of the ice. We can thus expand the population aspects: besides increases and decreases of populations one may consider the “far ends” of both, namely the onset of a local population, i.e. the immigration, and the end of a local population, i.e. the local extinction.

To estimate migrational lags, we have to (1) distinguish presence from absence of a taxon, which can be problematic especially when long-distance transport of pollen is important, such as for *Pinus*, and (2) estimate the past temperatures (based on independent proxies) to assess whether a taxon's temperature requirements were fulfilled.

The most secure way to determine presence/absence of a plant taxon is the use of plant macrofossils (Birks and Birks, 2000) or stomata (*Juniperus* and *Pinus*; Trautmann, 1953; Ammann and Wick, 1993; MacDonald, 2001). However, macrofossils and stomata can only provide positive evidence, and they may be delayed in tracing a first local presence of a taxon because of their lower production and shorter dispersal compared to pollen (i.e. no negative evidence, see Hicks, 2006). In the case of the pollen record we may use – with some caution – the classical scheme of the absolute, empirical, and rational pollen limits as a tool for taxa such as *Betula*, *Hippophaë*, and *Populus* (Firbas, 1949; Watts, 1973; Birks, 1986; Lang, 1994; Tinner and Lotter, 2006; see also Table 2). These limits designate, respectively, the first occurrences of a pollen type, the beginning of a continuous curve, and the rapid increase in percentages. Obviously, the absolute and empirical limits depend on the pollen sum, and the arrival time in relation to these limits depends on the pollen productivity. For taxa with low to medium pollen productivity such as *Hippophaë*, the latest arrival has been shown by comparison with macroremains to coincide with the empirical limit, and for high pollen producers such as pine the rational limit usually coincides with arrival, but the empirical limit can depend on long-distance transport. In compilations that aim at showing migration, percentage values as thresholds are usually selected that are proposed to show immigration and/or population expansion (e.g. Latalowa and van der Knaap, 2006; Magri et al., 2006).

To answer the question whether a taxon's temperature requirements were fulfilled, we cannot use the temperature reconstruction by Lotter et al. (2012), for this is based on the same pollen data, but we can use the aquatic indicator species *Myriophyllum spicatum*, which plays no role in Lotter et al.'s reconstruction. *M. spicatum* first occurs at ca. 15,280 yr BP. It needs a mean July temperature of at least 9–11 °C (Kolstrup, 1980) which is high enough for the five most important woody taxa of the late-glacial vegetation (see Table 3). It is not very original to use a waterplant as a baseline because already Iversen (1954), Kolstrup (1979), Birks (1981), van Geel et al. (1981), Pennington (1986) and others showed that waterplants are useful indicators of summer temperatures, because of their fast dispersal by waterbirds, short life cycles, and independence of soil development (Iversen, 1954).

*Pinus* shows the most interesting features in its record of arrival and build-up of the population, as summarized in Fig. 5: Four steps (1–4) separate four levels (a–d) in both percentages and influx. Steps (2) and (4) are partly responsible for the statistically significant boundaries of pollen zones (from GRZ<sub>pol</sub>-3 to GRZ<sub>pol</sub>-4, and from GRZ<sub>pol</sub>-4 to GRZ<sub>pol</sub>-5). The mean pine pollen percentages of the four levels are 8%, 23%, 49%, and 74%, respectively (Fig. 5). At step (2) the pine-pollen percentages are nearly tripled, at step (3) doubled, and at step (4) times 1.5, which implies an approximate tripling of the amount of pine pollen compared to the remaining pollen at each of these steps (if the non-pine pollen would be constant). The factors for percentages and



influx are quite close together: Means in influx at the four levels are 10, 27, 51, and 85 grains  $\text{mm}^{-2} \text{yr}^{-1}$  (i.e. nearly tripled, nearly doubled and times 1.66 on steps 2, 3, and 4). It needs to be checked with high-resolution sampling if a similar behaviour of *Pinus* is found at other sites. Stomata suggest that pine arrived at Gerzensee before or at the beginning of step (2); this step constitutes the rational limit, which is in agreement with Firbas (1949) as *Pinus* is a strong pollen producer, whereas in level (a) and step (1), the empirical limit, could still result from either long-distance transport or very scattered local individuals. *Pinus* is thus certainly locally present at the rational limit (possibly earlier), but not necessarily at the empirical limit as is the case with medium pollen producers (e.g. *Fagus* or *Abies*).

The intrinsic growth rate of *Pinus* fluctuated around zero for several centuries before 14,100 BP (Fig. 6b). After 14,100 BP, the growth rate remained predominantly positive as the population established. This coincides with the cold period of the Aegelsee Oscillation and with a decrease of the already established taxa *Populus* and *Betula*. However, it cannot be decided, whether *Populus* and *Betula* were suppressed by *Pinus* or by the colder climate, under which *Pinus* profited from the lighter conditions, as suggested by simulations of Lischke et al. (2013–this issue). The age of first flowering in *Pinus sylvestris* is 15–40 yr, but larger amounts of seeds are only produced at an age of 60–70 yr (Zoller, 1981). This could mean that these steps may be the expression of new generations of pine or waves in the build-up of the population 50 to 80 yr apart. This is also supported by the intrinsic growth rates, which show fluctuations with a dominant period of about 40 yr.

Migrational lags depend i.a. on the mobility of a species, which is determined by (1) dispersal vectors, e.g. ornithochorous taxa such as waterplants or *Hippophaë* often being faster than wind- or water-dispersed taxa, (2) life cycles, i.e. taxa with short life cycles being faster than taxa with long generation times, (3) competition that influences the generation times, (4) climate and soils, and (5) geographical barriers such as mountains or seas (or the lack of them). With a dynamic forest landscape model, such as TreeMig (Lischke et al., 2006) these processes and their climate dependence can be simulated in an integrated way. Potential migration rates and their dependence on climatic and competition conditions can be assessed (Meier et al., 2012). Such migration rates are consistent with the arrival of *Pinus* in the Gerzensee record from 500 km distance (Lischke et al., 2013–this issue), e.g. from the Northeastern Alps which are discussed as glacial refuges (Cheddadi et al., 2006).

A comparison of terrestrial and aquatic plants is shown in Table 3. Immigration of taxa over time affects the species pool of an area, i.e. the taxa regionally available for the formation of plant communities.

#### 4.5.4. Plant communities

Species respond individually to climatic change. Therefore the regional species pool may change over time, and past plant communities may have been non-analogous to modern ones. As shown by Jackson and Overpeck (2000), changes of two or more environmental variables through time may have caused separations or new overlaps of niche-spaces of taxa. The non-analogue climate during the early late-glacial, the incipient soil formation, and migrational lags are at least three major reasons to expect non-analogue plant communities. A prominent example is the juniper-dominated woodland with dwarf birches, willows and some tree birches during the early Bølling that may or may not be found today in high latitudes. A future study will quantify these non-analogue vegetation types for several sites on the Swiss Plateau.

The trend of species turnover in Fig. 4 has a striking similarity to the silicates in the sediment (LOI at 950 °C or residue). This resembles the findings at Kråkenes in Norway by Birks and Birks (2008), although Fig. 1a in that study represents the mineral residue at 550° because carbonates play no major role in that area. The similarity between compositional turnover and inorganic (non-calcareous) residue in our Fig. 4 is strongest in zones GRZ<sub>pol</sub>-1 and 2. Assuming that the silicates derive from eroded soils in the catchment and that soil formation led to decreased erosional input in the lake, we hypothesize that species turnover and the inorganic sediment fraction are linked by climate change triggering soil formation. This leads to the following scenario:

Soil formation during zone GRZ<sub>pol</sub>-1 must have been a slow process due to the cool climate conditions of this period. This led to a minor but clear decline of erosional sediment input, to which the vegetation responded with a gradual turnover of minor species. The (accumulation-based) floristic diversity remained about constant. This implies that the minor species turnover reflects the gradual replacement of a small number of (palynologically detected) taxa in the landscape by about the same number of different taxa. This is not necessarily only caused by local extinctions plus immigrations, for additional processes are the crossing of the palynological detection level of continually present taxa in both directions and the replacement of open ground by vegetation (i.e. a larger proportion of the area became vegetated).

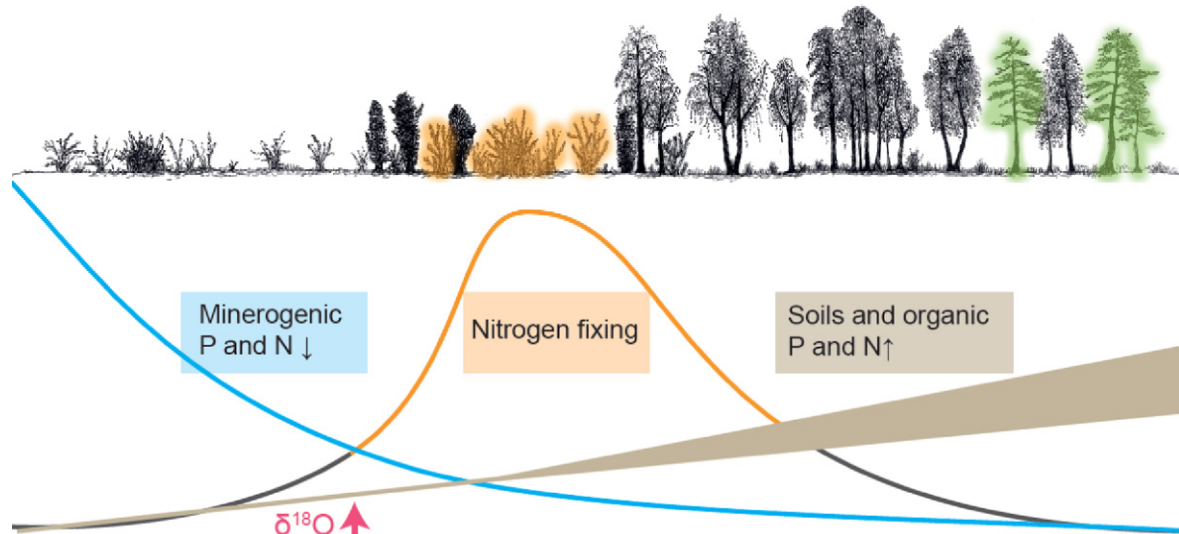
The rapid climate warming of zone GRZ<sub>pol</sub>-2 led to a marked decrease of erosional sediment input due to soil formation, whereas the species turnover was moderate. Erosional input decreased further during the first one-and-a-half century of zone GRZ<sub>pol</sub>-3 with its continued warm climate, and then it remained constant during the remainder of the zone. Species turnover, on the other hand, continued gradually through zones GRZ<sub>pol</sub>-3 and 4, and in a minor way also during zone GRZ<sub>pol</sub>-5. This may reflect the combined effect of autogenic succession, response to soil development, and immigration of new taxa. The estimated pollen richness provides hints concerning the immigration of new taxa. The gradual increase of richness during zones GRZ<sub>pol</sub>-2 and 3 implies that the number of detected taxa increased. This indicates the immigration of new taxa in the landscape and/or the increase in abundance of (presumably rare) taxa from below to above the palynological detection level.

In zones GRZ<sub>pol</sub>-4 and 5, the trend of pollen richness estimated by rarefaction starts to deviate from the pattern of the accumulation-based estimate of pollen richness. A marked maximum in the latter in and around sub-zone GRZ<sub>pol</sub>-4b (310–330 cm sediment depth) coincides with an even more marked maximum both in total pollen influx and in sediment accumulation rates, indicating variability in lacustrine sedimentation (see Sections 3.3.4. and 4.3. and van Raden et al. (2013–this issue). van der Knaap (2009) estimated the same type of accumulation-based pollen diversity by using the same pollen data but with a preliminary depth-linear time scale, and he came to a strikingly different result: neither the total pollen accumulation (named there ‘accumulation-based rarefaction sum’) nor the accumulation-based diversity shows a maximum in this depth interval (310–330 cm). Both accumulation-based variables are obviously dependent on peculiarities of the depth–age model.

During zone GRZ<sub>pol</sub>-5 the scores on axis 1 in the DCCA and the accumulation-based estimate of pollen richness decline. Several causes are possible: (1) local extinctions: the floristic diversity of the landscape decreased; (2) populations of plant species declined below palynological detection; and (3) the pollen catchment

**Fig. 7.** Primary succession, plant functional types, and nutrients during the transitions from the shrub-tundra to birch- and later pine forests as reflected in the pollen record. (A) Local and regional pollen zones. (B) Estimates of permafrost. (C) Changes in plant functional types and potential effects on evapotranspiration, lake levels, soil humidity, reduction of wind fetch. (D) Soil development: some selected taxa (recorded as pollen and plant macrofossils, the latter from neighbouring sites, Gaillard, 1984a,b) relevant for soil nutrients. (E) Comparison of potential N and P resources to the types of mycorrhiza in observed modern successions as proposed by Read, 1993. The red arrow near the bottom indicates time of the rapid increase of the  $\delta^{18}\text{O}$ . At Gerzensee this coincides with the afforestation by juniper and tree-birches.

Primary Succession on a secular scale	Oldest Dryas, last third, ca 15676–14665 cal BP	Early Bølling Ca14665–14443 cal BP	Late Bølling Ca14443–13835 cal BP	Allerød Ca14835–12710 cal BP	Younger Dryas Ca12710–11500 cal BP
(A) Pollen zones Gerzensee	GRZ <sub>pol</sub> -1	GRZ <sub>pol</sub> -2	GRZ <sub>pol</sub> -3	GRZ <sub>pol</sub> -4 and GRZ <sub>pol</sub> -5	Wick 2000, Ammann et al. 2000
Regional zones Western Swiss Plateau, Romandie (Gaillard 1984) 10 sites	<i>Artemisia–Betula nana</i>	<i>Juniperus–Hippophaë</i>	<i>Betula alba–Gramineae</i>	<i>Betula–Pinus</i>	<i>Pinus–Gramineae–Artemisia</i>
Biozones (Welten 1982, Firbas 1952)	Ia	Ib		II	III
Regional biozones Swiss Plateau (Amman et al. 1996)	CHb-1c	CHb-2	CHb-3	CHb-4a	CHb-4b
Vegetation western and central Swiss Plateau	Shrub tundra: <i>Artemisia</i> , <i>Chenopods</i> , <i>Salix</i> spp., <i>Betula nana</i>	<i>Juniper–birch</i> forest, <i>B. alba</i> -type, <i>Hippophaë</i>	Birch forests	Birch–pine forests, then pine–birch forests	More open pine–birch forests
(B) Permafrost	Probably important	Rapidly melting	Probably absent	Probably absent	?
Potential effect on lake level		Rise of lake level			
Potential effect on soils	Active layer thin	Active layer rapidly thickening			
(C) Plant functional types	Grasses, herbs, some legumes, shrubs	Trees and shrubs	Trees, some shrubs, herbs	Trees, some shrubs and herbs	Trees, some shrubs, more herbs
Evapotranspiration	Low	Rapidly increasing	increasing	Relatively high	
Potential effects on lake level and soil humidity		decreasing	decreasing		
Potential effect on wind fetch	Lakes exposed to wind	Lake sheltered between trees, wind fetch decreased, wind effects on lake and sedimentation decreased			
(D) Soil development and the presence of N <sub>2</sub> -fixers					
Pollen/Macros (Gaillard 1984) <i>Dryas octopetala</i> Leguminosae <i>Hippophaë</i>	+ + +	+ + +++	+ + +	+ + +	+ + +
Soils on western and central Swiss Plateau (Gaillard 1984)	Regosols or lithosols (patches of open ground and of vegetation)	Accumulation of organic matter ↑	Coexistence of dry and humid soils	Probably cambisols (Brown earths) of various types	



(E) Hypothetical comparison with a primary succession (Read 1993): Mycorrhizal status of plant community, direction of succession →→				
Plant–microbe mutualism	Mineral P, N ↓, Cyanobacteria on raw soils; non-mycorrhizal ruderals, AM on grasses, Legumes fixing N <sub>2</sub>	AM, and possibly maximum of N <sub>2</sub> -fixation (e.g. <i>Hippophaë</i> )	Facultatively AM or ectomycorrhiza	Ecto-mycorrhiza increasing (on <i>Pinus</i> )

decreased due to the newly established *Pinus–Betula* woodland filtering out much pollen before it could reach the lake. (1) is not unlikely due to outshading by the woodland, and (2) and especially (3) are likely. In contrast, the juniper expansion during GRZ<sub>pol</sub>-2 did not have any noticeable effect on floristic diversity if estimated by accumulation-based pollen richness (but pollen richness by rarefaction based on a constant pollen sum does show a minimum in GRZ<sub>pol</sub>-2). This indicates that the juniper shrubland remained sufficiently open for continued growth of herbs.

As all estimates of biodiversity depend on the two components of (1) species richness and (2) evenness, it is interesting to note the curve of pollen evenness calculated here as PIE (probability of interspecific encounters, according to Hurlbert, 1971; see van der Knaap, 2009) in Fig. 4: the strongest change in evenness co-occurs with the “juniper-jump”. As van der Knaap (2009) discussed the evenness of a pollen assemblage and the evenness of the vegetation may differ quite strongly due to differences in taxon-specific pollen productivity.

#### 4.5.5. Level of the ecosystem

**4.5.5.1. The example of mycorrhiza and N<sub>2</sub>-fixers.** At many sites of southern Central Europe, the late-glacial vegetation development was interpreted as a primary succession in which various species interactions occur. Well known are the competition for light and the facilitation by the accumulation of organic matter fostering pedogenesis. The sequence from pioneer taxa undemanding concerning soils to taxa requiring developed soils is well described (e.g. Iversen, 1954; Gaillard, 1984a) but hard to quantify.

Supply of nutrients is linked to at least three sources: (1) the composition of the inorganic sub-soil, (2) the accumulation of organic matter, and (3) symbioses between microorganisms and phanerogams. We hypothesize that the temporal sequence at Gerzensee (and many other sites in Central Europe) recorded in the pollen is similar to the succession derived from spatial observations and chronosequences (see Fig. 7). Read (1993) recognized four stages in space that are possibly comparable to four pollen zones in time.

- (1) In early phases of primary succession with much open ground and patchy vegetation, the minerogenic supplies of P and N may or may not be high (depending on the geological background). They decrease with closing vegetation cover. The early nitrogen-fixers may not leave any fossil trace because they are primarily cyanobacteria (both free-living and symbiotic in lichens), as found in modern studies of the primary succession in glacier forefields (Solheim et al., 1996). As van Geel et al. (1996) summarize, Cyanobacteria are so far not recorded as recognizable fossils from terrestrial sites, whereas aquatic Cyanobacteria are.
- (2) With decreasing minerogenic N-supply, major N<sub>2</sub>-fixers establish such as *Rhizobium* (bacteria) on nodulated legumes and *Frankia* (actinomycetes) on *Dryas* spp. and *Hippophaë*. After this, the succession of mycorrhiza types may open with Dark Septate Endophytes (Jumpponen and Trappe, 1998; Jumpponen, 2001), and arbuscular mycorrhiza (AM; a form of endomycorrhiza, formerly called vesicular–arbuscular or VA) on non-woody plants such as herbs, grasses, and forbs. AM provides primarily phosphorus and may go through various successional stages (Hart and Klironomos, 2002; Hart et al., 2003). In parallel, the leaf-litter increases in quantity and changes in quality.
- (3) Later, with afforestation, ectomycorrhiza become important. They are found today on taxa such as *Dryas*, *Helianthemum*, *Salix*, *B. nana*, and *Helianthemum* (all wide-spread during the shrub-tundra phase of the Oldest Dryas), on tree birches and *Populus* (important during the Bølling), and on *Pinus* (important

during the Allerød). Ectomycorrhiza provides both N and P. The temporal transition from AM to ectomycorrhiza is not sharp, as illustrated by *Salix*, a genus that includes both early and transitional species. *Salix herbacea* is one of the earliest ectomycorrhizal plants in glacier forefields (Graf and Brunner, 1997; Mühlmann and Peintner, 2008), whereas *S. repens* was observed as having abundant ectomycorrhiza but little AM (van der Heijden and Vosatka, 1999). Maximum N<sub>2</sub> fixation took place during the afforestation phase (with abundant *Hippophaë*) when *Juniperus* was dominant. For *Hippophaë* see also the modelling study of Pfeiffer et al. (2013–this issue). For *Juniperus*, endomycorrhiza are commonly reported and ectomycorrhiza occasionally (Thomas et al., 2007). In addition DeLuca and Zackrisson (2007) found enhanced soil fertility under *Juniperus* partly due to the facilitation (through shade, soil, and air humidity) of the nitrogen-fixing feather moss *Pleurozium schreberi*. Such “islands of fertility” under *Juniperus* may also be enhanced through the capability of juniper to exploit bio-available N and P through its extensive root system (DeLuca and Zackrisson, 2007). The phase of maximum N<sub>2</sub> fixation is in both the spatial (Read, 1993) and the temporal (Gerzensee) sequence intercalated between grassland (with much AM) and pioneer forest (with AM and ectomycorrhiza).

- (4) As succession proceeds, organic litter reinforces the change from mainly AM to more ectomycorrhiza and ericoid mycorrhiza, because only the latter two are adapted to litter. With soil development and its leaching, ericoid mycorrhiza start to play a major role. A modern study of a chronosequence in a glacier forefield by Cazares et al. (2005), shows this clearly, although on a much shorter time scale (60 yr).

In aquatic systems van Geel et al. (1984, 1989) found sheets of the N<sub>2</sub>-fixing pioneers of the *Gleotrichia*-type in the early Late-Glacial of Usselo.

In other parts of the world, there are some successions where it is not *Hippophaë* but *Alnus* (and *Shepherdia*), which also has nodules of *Frankia*, which plays a major role, e.g. in Glacier Bay, Alaska, where – after *Salix* and *Dryas* – *Alnus sinuata* becomes dominant (Chapin et al., 1994; Engstrom et al., 2000; Engstrom and Fritz, 2006). Also at Grandfather Lake, Alaska, where the increase of *Alnus* pollen runs parallel with increasing percentages of C and N in the lake sediment (Hu et al., 2001). But on the Swiss Plateau *Alnus* only arrived during the Holocene.

**4.5.5.2. Feedbacks on the ecosystem level.** Feedbacks on regional and global scales (including climate) are discussed in the synthesis, which reviews biotic responses to climate change in both terrestrial and aquatic ecosystems (Ammann et al., this issue). But already at a local scale and for terrestrial ecosystems we can infer feedback mechanisms. These may concern the compartments of soils, hydrology, vegetation, and their interactions. One example is given above with the hypothesis on a temporal sequence of nitrogen fixers (comparable to the spatial sequence as observed today, Fig. 7): The nitrogen enrichment in the soil by N<sub>2</sub>-fixation can be considered as a positive feedback in the ecosystem, by increasing the population of the N<sub>2</sub>-fixers and further N<sub>2</sub>-fixation. This is another potential cause for the (intermediate) increase in the intrinsic growth rate, i.e. hyperexponential growth of *Juniperus* (Lischke et al., 2013–this issue). In addition quality and quantity of the litter changed, especially also with the increase of the populations of tree birches, willows, and poplar with higher LAI than tundra plants. This in turn added organic matter to the developing soils (see decreasing values of the minerogenic residue on loss on ignition at 950 °C on Fig. 4, indicating less open ground and more vegetation cover). With increasing organic matter in the soils there the water-holding capacity improved (compared to the till rich in sand). This in turn may have



fostered many plant species, their abundances, and therefore vegetation density (delivering more litter, etc.).

#### 4.6. Impact of minor climatic oscillations on vegetation

The minor cool periods during the Late Glacial Interstadial do not seem to have reduced the vegetation cover at the altitude of 603 m asl. An interesting case is the cool period GRZ<sub>ibulk</sub>-6 (Greenland interstadial GI-1d; Older Dryas or Aegelsee Oscillation), during or at the end of which *Pinus* populations expanded on the Swiss Plateau (see Section 3.3.4. and Lotter et al., 1992b). This indicates that *Pinus* was not yet in equilibrium with climate, or, in other words, had a migrational lag (see Section 4.5.3 and Table 3). Alternatively, moisture, and soil and/or temperature conditions (incl. seasonality) may have been unsuitable for the spread of the taxon. The Scandinavian treeline vegetation today may serve as a partial analogue. In northern Fennoscandia *Betula* is able to form open forests where *P. sylvestris* is unable to grow, for the occurrence of pine is limited to latitudes about 100 km south of the treeline birch vegetation (Lang, 1994).

Oxygen isotopes show minor fluctuations during the Late Glacial Interstadial in various lacustrine cores in the Northern Hemisphere, which were correlated to records from Greenland ice cores (Lotter et al., 1992a,b; Grafenstein et al., 1999; Yu and Eicher, 2001). Table 2 presents an overview of potential correlations between minor fluctuations of oxygen isotopes of the Late Glacial Interstadial of Gerzensee and vegetation development. In *Juniperus* and *Hippophaë*, the decreases (both the onset of decrease and the rapid or stepwise decrease) occur clearly before the minor cool phase of GRZ<sub>ibulk</sub>-4 and seem to have been caused by shading-out by tree birch (Gaillard, 1984a). Interestingly, two woody taxa started a distinct increase during minor cool phases: *Populus* at the beginning of the minor minimum in the last third of isotope-zone GRZ<sub>ibulk</sub>-4, and *Pinus* within the somewhat younger and stronger minimum of the isotope-zone GRZ<sub>ibulk</sub>-6 (Aegelsee Oscillation of Lotter et al., 1992b).

The herbaceous taxa Gramineae, *Artemisia*, and *Thalictrum* show minor peaks during minima in oxygen isotopes (asterisks in Figs. 2 and 3, Section 3.3.3 on the late Bølling). In summary we can conclude that at the altitude of Gerzensee (603 m asl), these minor cool phases had only minor effects on the vegetation, even though the Aegelsee Oscillation is visible in the pollen-based reconstruction of July temperatures by Lotter et al. (2012). Sites at higher altitudes may have been ecotonal situations at that time and thus more sensitive in their vegetation, such as Aegelsee (995 m asl, 23 km south of Gerzensee in the northern Prealps (Wegmüller and Lotter, 1990) or Rotmeer (960 m asl, 125 km to the north in the southern Black Forest; Lotter and Hölzer, 1994; Lang, 2005).

The minor decreases in *Juniperus*, *Hippophaë*, *Salix*, *Betula*, and *Populus* after ca 13,760 yr BP may not necessarily be due to cooler summer temperatures but rather to competition (outshading) by *Pinus*.

## 5. Conclusions

1. Some of the vegetational changes were responses to the early rapid warming (as recorded in the oxygen-isotope ratios between 14,830 and 14,400 yr BP) within the sampling resolution (which was about 8.4 yr in this section) or up to 20 yr before and after. In other cases, recorded vegetational changes were probably triggered by the rapid warming but then took centuries to develop (e.g. migrations).
2. Afforestation (shift from shrub-tundra to a juniper–birch-woodland) was at Gerzensee the main response of regional vegetation to the rapid warming after 14,685 yr BP, as was the case at numerous sites on the Swiss Plateau and several sites in southern Central Europe.
3. The characteristic sequence of immigration and expansion of woody taxa is confirmed for southern Central Europe: *Juniperus* – *Hippophaë* – *Betula* (trees) – *Salix* – *Pinus*.

4. Population growth was hyperexponential in some cases, i.e. with positive and increasing intrinsic growth rate  $\alpha$ , e.g. in *Juniperus*.
5. In *Pinus*, four steps and four levels can be distinguished as phases of population build-up (each lasting about 35–100 yr).
6. Vegetation responded to the very rapid warming after 14,850 yr BP on all organisational levels
  - (a) Level of the individual organism, here pollen production (e.g. *Juniperus*); this is the fastest response, as it can occur within a year or two.
  - (b) Level of the population: intermediate response times, especially the building-up of populations, a process that depends heavily on generation times (e.g. annuals vs trees).
  - (c) Level of biogeography: migration can be fast or slow depending on the vectors, life-history traits such as generation times, as well as on geographical barriers.
  - (d) Level of plant communities: the species pool changed rapidly, the unvegetated surfaces decreased, or with afforestation the distribution of plant-functional types changed.
  - (e) Level of the ecosystem: response times vary, depending on species competition (e.g. for light) or facilitation (e.g. by enhanced pedogenesis), and on changing types and abundances of nitrogen-fixers.
7. The minor cool phases recorded in the oxygen-isotope record during the Late Glacial Interstadial were no more than weakly reflected in pollen stratigraphy at this altitude of 600 m asl. Even the relatively marked cool phase about 14,044–13,908 yr BP (GI-1d; Aegelsee Oscillation; Older Dryas biozone) resulted in no more than very minor peaks in a few herb taxa, which were, all the same, picked up in the reconstruction of July temperatures by Lotter et al. (2012). Sites at higher altitudes may have been ecotonal and therefore more sensitive.
8. The estimates of palynological diversity based on pollen influx (which is independent of pollen abundances) indicate that floristic diversity gradually increased during afforestation up to the time of major *Pinus* expansion.

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