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Evaluation of the regional vegetation and climate in the Eastern Alps (Austria) during MIS 3–4 based on pollen analysis of the classical Baumkirchen paleolake sequence

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Abstract

The pre-last glacial maximum paleolake sediments at Baumkirchen, western Austria, are well known in Alpine Quaternary stratigraphy as being the type locality of the Middle to Upper Würmian transition. Their location provides a rare opportunity to investigate the vegetation history of the interior of the Alps during the last glacial cycle. A recent renewed research effort involving new drilling revealed a 250-m-thick lacustrine sequence with an older, ca. Marine Oxygen Isotope Stage (MIS) 4 phase and a younger, mid- to late MIS 3 phase. Pollen analysis reveals generally poor preservation and very low pollen concentration due to very high sedimentation rates. On the basis of pollen percentages and influx rates, six pollen zones (PZ) were assigned. PZ1 and 2 correspond to the entire ca. MIS 4 section and are characterized by only scattered vegetation representing an extremely cold and dry climate. Two stadials and two interstadials were identified in the MIS 3 section. The interstadials are characterized by well-developed open vegetation with some stands of trees, with the upper PZ6 being better developed but still forest-free. On the basis of previous radiocarbon dating, this zone (PZ6) is correlated to Greenland Interstadial (GI) 7 and the lower interstadial (PZ4) tentatively to GI 8.

Keywords: Würmian; MIS 3; MIS 4; Pollen; Paleolake; Interstadial; Alps

INTRODUCTION

Thick successions of banded clayey silts, locally known as Bändertone, are present in glacially carved valleys and basins of the Alps. While the majority of these lacustrine deposits formed during the last deglaciation, some of them record earlier lake phases. One of the most interesting and best-preserved successions are the Bändertone of Baumkirchen (Tyrol, western Austria; Fig. 1), known for more than a century (Blaas, 1885; Penck, 1890). The Sub-Commission for European Quaternary Stratigraphy defined the top of these sediments in the clay pit of Baumkirchen as the stratotype of the Middle to Upper Würmian transition in the Alps (Chaline and Jerz, 1984), which corresponds approximately to the transition between Marine Oxygen Isotope Stages (MIS) 3 and 2 (e.g., Heiri et al., 2014). The clay pit was meticulously studied by Fliri and colleagues (e.g., Fliri et al., 1971; Fliri, 1973), who reported rare findings of *Pinus sylvestris* (Scots pine), *Pinus mugo* (dwarf pine), *Alnus alnobetula* (= *A. viridis*, green alder), and *Hippophae rhamnoides* (sea buckthorn). These plant remains not only provided a means to radiocarbon date these sediments (recently re-dated by Spötl et al. [2013]); they also allowed key insights into the palaeovegetation inside the Alps prior to the last glacial maximum (LGM). Pollen analysis of these sediments was first attempted by Sarnthein (1937). Later, Bortenschlager (in Fliri et al., 1970) took three samples of which he could evaluate one. The pollen content was low (<100 grains/cm^3) and preservation was poor. Markgraf (in Fliri et al., 1971) collected samples to look for seasonal patterns but did not succeed due to the low pollen content. In 1978, however, Bortenschlager and Bortenschlager succeeded through a detailed analysis of an 86-cm-long section (ca. 654 m above sea level [asl]). The pollen flora and the overall low pollen concentration correspond to a forest-free (although not tree- and shrub-free) vegetation. The authors were also able to distinguish 17 possible growing seasons in this short section. As expected, the sedimentation rate proved to be high and variable, between 3 and 8 cm/yr.

The Baumkirchen sequence corresponds to the period during the last glacial cycle dominated by Dansgaard-Oeschger cycles.

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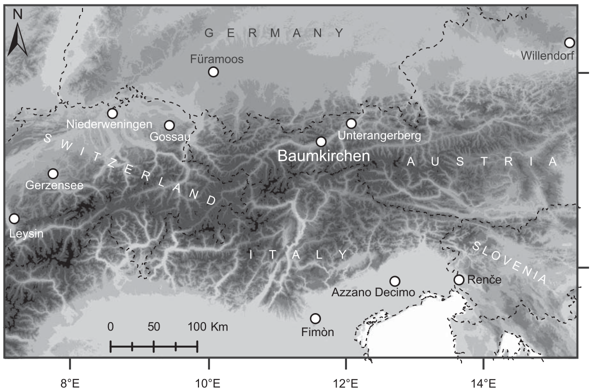

Figure 1. Map of the Eastern and Central Alps showing the location of the Baumkirchen site and other important sites mentioned in the text.

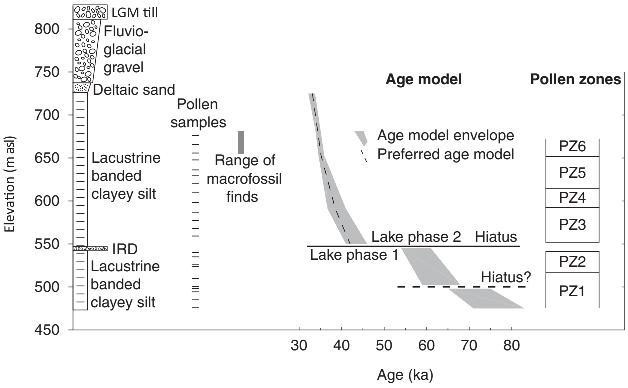

Figure 2. Simplified stratigraphic log and age model envelope based on Barrett et al. (2017). Sample locations for pollen analysis are indicated, along with the depth range of the plant macrofossils mentioned in Spötl et al. (2013). The pollen zones are also shown (see Fig. 3 and 4). IRD, ice-rafted debris.

These millennial- to centennial-scale climate events known from the Greenland ice cores (North Greenland Ice Core Project members, 2004) are also recorded by speleothems in the Eastern Alps (e.g., Spötl et al., 2006; Moseley et al., 2014). Given the scarcity of surface records, however, little is known about the impact these climatic events had on the Alpine landscape and ecosystems. Thus, the high-resolution Baumkirchen sequence provides a unique window into the response of the Alpine environment to these high-magnitude climate fluctuations. The aim of this study was to take a fresh, new look at the palynology of the Baumkirchen succession in an attempt to improve our knowledge of the paleovegetation and its response to Dansgaard-Oeschger cycles. This was made possible by a series of scientific core drillings, which provide a much longer and continuous record of these sediments than the previous (and, meanwhile, largely back-filled) clay pit.

Study site

The Baumkirchen lacustrine sequence is located in the Gnadenwald terrace on the northern rim of the Inn Valley around 12 km east of Innsbruck (Tyrol). The sediments are overconsolidated due to the overlying ice during the LGM but are uncemented and diagenetically unaltered (Köhler and Resch, 1973). The site has recently been the subject of a renewed major research effort including scientific drilling, which extended the thickness of the succession to 250 m. The latter can be divided into two lake phases chronologically constrained by luminescence dating (Barrett et al., 2017). The lower phase (LP1) is poorly constrained but extends from ca. 70–83 ka until ca. 55–63 ka, spanning MIS 4 and possibly MIS 5a, and is characterized by a low sedimentation rate. The upper phase (LP2) extends from ca. 45–33 ka with a closely spaced series of radiocarbon dates (on plant macrofossils) providing a more precise tie point of the upper part of the sequence to ca. 35 cal ka BP (Spötl et al., 2013), corresponding to mid- to late MIS 3 (Fig. 2). This upper sequence is characterized by a much higher sedimentation rate. Besides a short section (ca. 5 m) in the uppermost part of LP1 interpreted as ice-rafted debris, the majority of the paleolake sequence is interpreted as being fed by glacial streams with no direct ice contact (Barrett 2017; Barrett et al., 2017).

The central Inn Valley presently has a humid continental climate. The potential natural modern vegetation of the floor of the valley corresponds to montane riverine forests with *Alnus incana*, but is now mostly transformed into vegetable fields and meadows. At intermediate altitudes on the south-facing slopes of the Northern Calcareous Alps (Nordkette), inner-alpine pine forests (*Pinus sylvestris*) are dominant west of Innsbruck, whereas montane *Fagus-Abies* forests are present east of Innsbruck (i.e., the area immediately north of Baumkirchen). The higher altitudes are covered by dwarf pine stands (*Pinus mugo*) and alpine grassland. *Abies-Picea* forests are predominant on the north-facing slopes south of the Inn river. At higher altitudes, subalpine forests with *Larix* and *Pinus cembra* are common (Wagner, 1985). Various woodland communities have been partially transformed into spruce plantations or meadows.

Regarding the origin of the pollen embedded in the Baumkirchen sediments, three sources can be expected: (1) wind-blown grains from the vegetation of the catchment area, including the central Inn Valley, surrounding mountains, and parts of the Southern Alps and Pre-Alps due to long-distance pollen transport by strong winds (e.g., Foehn); (2) fluvially delivered grains derived from erosion of contemporaneous or older sediments; and (3) fluvially delivered grains melted out of glaciers upstream in the Inn Valley or its tributaries.

MATERIALS AND METHODS

Since the general state of the vegetation is of interest, samples for pollen analysis should include at least 10 yr. Estimates based on previous pollen analyses (Bortenschlager and Bortenschlager, 1978), radiocarbon (Spötl et al., 2013), and luminescence dating (Barrett et al., 2017) indicate high sedimentation rates of >3 cm/yr. Therefore, strips of sediment were sampled from cores of ca. 50 cm in length with a diameter of 1–1.5 cm. Thirteen samples were taken with a spacing of ca. 10 m from cores between ca. 676 and 559 m asl corresponding to LP2 (samples covering ca. 8–50 yr, spaced ca. 170–1000 yr apart). Ten samples were taken in LP1 between ca. 540 and 476 m asl with a slightly closer sample spacing of ca. 6–7 m due to the expected lower sedimentation rate (samples covering ca. 55–170 yr, spaced ca. 720–2200 yr apart).

The samples were dried and homogenized. Of this material, 6–12 cm^3 were sub-sampled and treated with cold concentrated hydroflouric acid (HF) for at least 24 hours. In some cases, the process was repeated with hot HF. As the pollen density was expected to be very low, 4–8 slides were prepared from each sample and combined to reach a minimum pollen sum of 50 pollen grains. In two samples (510 and 494 m asl) the total amount nonetheless remained lower (48 and 39 grains, respectively). *Lycopodium* pollen was added in order to obtain pollen concentration data (following Stockmarr, 1971).

Pollen counting was undertaken using a Leitz Biomed optical microscope with 400 × and 1000 × magnification. The pollen identification and nomenclature follows Beug (2004). The preservation of the pine grains partially permitted the distinction of *Pinus cembra* (semicircular form of the sacci and the presence of veruccae on the ventral part of the pollen grain) from *Pinus sylvestris/mugo*. The non-distinguished grains are included in the pollen type *Pinus* together with the *Pinus sylvestris/mugo* type. Although the macrofossils document the presence of *Alnus alnobetula* in the uppermost part of the sequence, a verification was only possible on individual grains. Therefore, they were summed up in the pollen taxon *Alnus*. The non-pollen palynomorphs (NPP) were determined on the basis of numerous reference studies listed by Miola (2012). Despite rather poor preservation, two different trilet spores of the Upper Triassic Raibl Group could be identified. They were summarized together with unidentified spores in the category "trilet pre-Quaternary spores."

In view of the general climatic situation during MIS 4–3, the growth of thermophilous trees and shrubs in the Inn Valley seems highly unlikely but not impossible. Input by long-distance transport is also unlikely, because at that time such tree species were growing only rarely on the southern slopes of the Alps. The possibility of melting out from glaciers may be negligible due to much lower pollen productivity and reduced pollen transport compared to the present-day (Festi et al., 2015). Therefore, while their origin is uncertain, the pollen grains of *Tilia*, *Ulmus*, *Fagus*, and *Corylus* were included in the pollen sum. The "Indeterminanda" may include several reworked and redeposited sporomorphs. Various extinct Pinaceae originated from the Late Pliocene and/or the Earliest Pleistocene (Draxler, I., personal communication, 2016). Within the trilet pre-Quaternary spores, two types could be distinguished: *Trilites tuberculiformis* (Cookson, 1947) frequent in the Upper Triassic, and *Paraconcavisporites sp.* with a wider stratigraphic range, but also present in the Upper Triassic (Draxler, I., personal communication, 2016). The number of reworked microfossils may be higher than presented in the results. Identification was generally difficult and the criteria "degree of compression" and "surface abrasion" (Pini et al., 2009) were not applicable due to generally poor preservation (except for *Pinus*).

The results of the analysis are presented as a reduced percentage diagram (Fig. 3) and a reduced concentration and influx diagram (Fig. 4). The pollen sum includes all pollen grains of trees, shrubs, and upland herbs (arboreal pollen

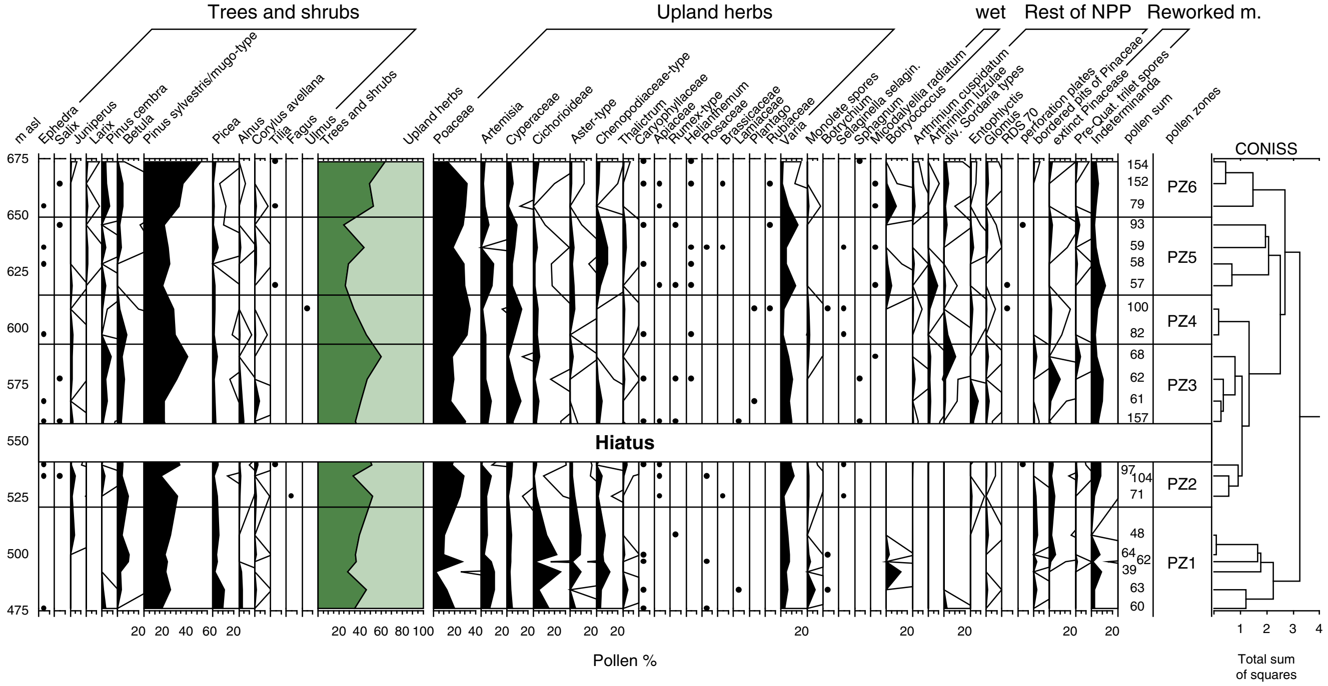

Figure 3. (color online) Pollen percentage diagram showing the most important taxa. The results of the statistical clustering analysis (CONISS) and the associated pollen zone interpretations are shown along with the pollen sums. Black lines indicate percentages multiplied by 10. Black dots indicate values less than 2%.

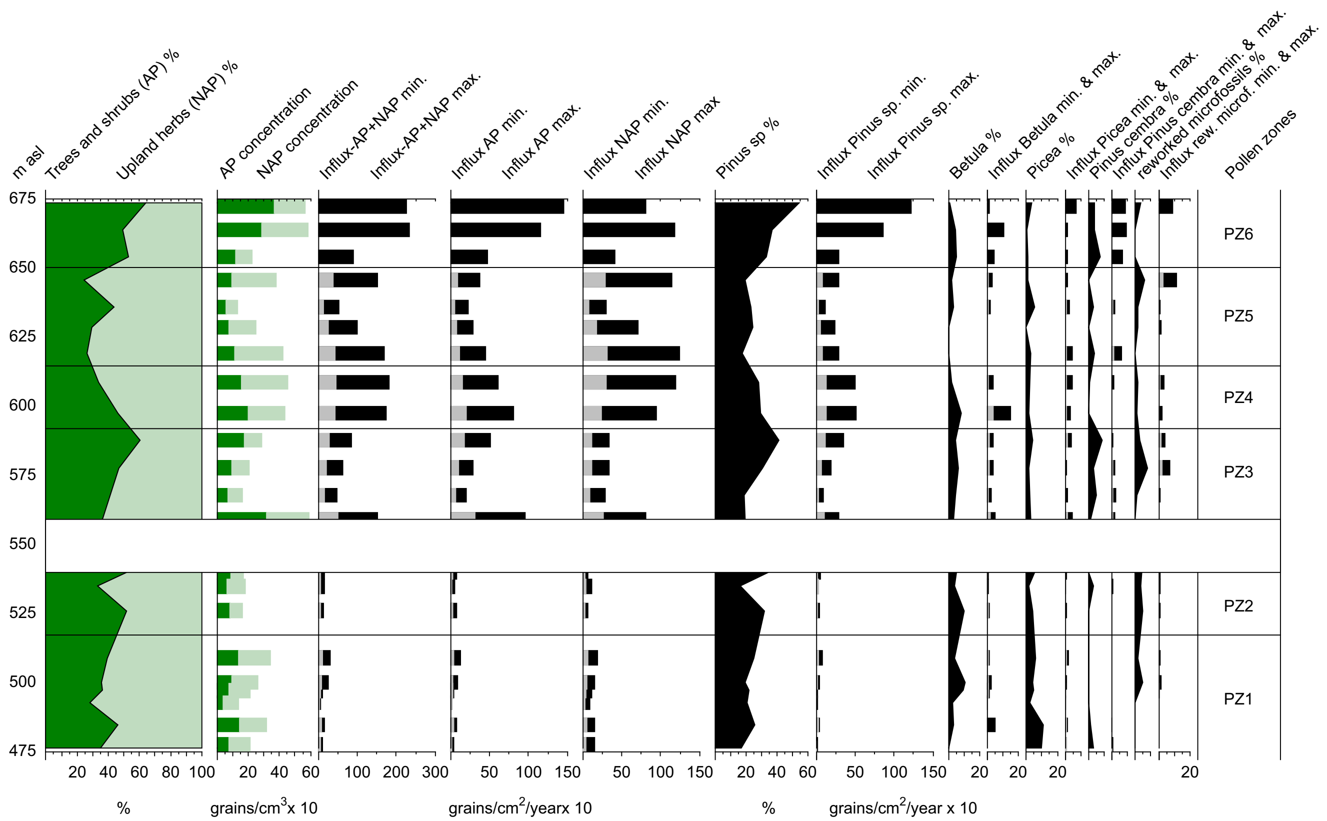

Figure 4. (color online) Pollen diagram showing percentages, concentrations, and influx of the most important taxa.

[AP] + non-arboreal pollen [NAP] = 100%) except extinct Pinaceae and pre-Quaternary spores (pollen sum + all reworked microfossils). The values for Pteridophyta and mosses were determined on the basis of the pollen sum (i.e., AP + NAP) plus Pteridophyta and mosses, and those of the NPPs as percentages of the pollen sum plus NPP.

The pollen influx rate (grains/cm^2/yr) was calculated on the basis of the sedimentation rate estimates. The degree of scatter and inherently large uncertainties of the luminescence ages (see Barrett et al., 2017) did not permit the use of a Bayesian age-modelling approach (e.g., attempts using Bacon [Blaauw and Christen, 2011] yielded unsatisfactory results). Therefore, beyond the short interval of the available radiocarbon chronology where a linear regression age model was used, an age model considering only the upper and lower bounds was produced based on the luminescence ages and the spacing of possible annual layers (for details, see Barrett, 2017; Barrett et al., 2017). This model (Fig. 2) was used to calculate generous maximum and minimum sedimentation rate estimates, which resulted in maximum and minimum pollen influx rates (Fig. 4). As the rates were estimated based on sedimentological assumptions (i.e., lack of hidden hiatuses and the nature of the presumed annual layers), these influx rates should be treated with caution.

The pollen percentage, concentration, and influx diagrams were created using TILIA and TILIA.GRAPH version 2.0.33 (Grimm, 2014). The division of six pollen zones in Figures 2–4 were established according to a stratigraphically constrained incremental sum of squares clustering method (CONISS; Grimm 1987) using percentage data for all trees, shrubs, and upland herbs. The zone division was identical when the analysis was repeated with data below 5% excluded. The concentration and influx data are shown for certain taxa only (Fig. 4).

RESULTS

The results of the pollen analysis are shown in Figures 3 and 4 (percentages and concentrations and influx, respectively). As expected, the pollen content in the slides is very low and preservation, as noted by Bortenschlager and Bortenschlager (1978), is poor. Pollen grains of herbs are often small and distorted. Since they are also flattened, identification was not always possible. The values of "Varia" (unknown pollen grains) and "Indeterminanda" (damaged and therefore indeterminable pollen grains) are hence slightly higher than is usual in late glacial or Holocene lake sediments. In general, only the pollen of *Pinus* (pine) and *Picea* (spruce), although often fragmented, lacks strong corrosion and is hence well recognizable.

Given the low pollen sums, the percentage estimates of pollen abundances below 5% are not statistically significant. Nevertheless, it is essential to include rare or generally underrepresented species (e.g., *Larix*, *Ephedra*, *Pinus cembra*, and various herb species) due to the important climatic information they provide. Excluding species with abundances below 5% has no significant effect on the pollen curves of more abundant species or on the division of the different pollen zones.

The overall pollen profile is dominated by *Pinus* (mainly *P. sylvestris/mugo* type), but its proportion remains below 50% with one exception (676 m asl). *Picea* was found in almost every horizon. The curves of *Pinus cembra*, *Betula*, and *Juniperus* are patchy, while *Ephedra*, *Hippophae*, *Salix*, and *Larix* occur only sporadically. Species demanding a more favorable climate such as *Alnus, Corylus*, *Tilia*, *Ulmus*, and *Fagus* occur irregularly and show no obvious pattern.

PZ1 and 2: 476–540 m asl (base ca. 71–83 ka; top ca. 54–61 ka)

Based on the cluster analysis (Grimm, 1987), the lower part of the sequence is divided into two pollen zones. The pollen sum in both PZ1 (476–508 m asl) and 2 (508–540 m asl) is low (39–100 grains), causing highly fluctuating pollen percentage values. On the other hand, the pollen concentration is relatively high in PZ1 (varying between ca. 150 and 350 grains/cm^2) and quite low (ca. 150 grains/cm^2) in PZ2.

Pinus dominates and is present throughout PZ1 and 2 with percentages up to 34%. Relatively high values of *Picea* (up to 13%) are recorded in the lower PZ1, whereas *Betula* and *Juniperus* are more common in PZ1 and 2. *Pinus cembra* and *Ephedra* are found irregularly or rarely. Moreover, Poaceae are represented in PZ2. Cichorioideae, Chenopodiaceae, and *Aster*-type are more frequent in upper PZ1 and *Artemisia* in lower PZ1. Among the Pteridophyta, monolete spores, *Botrychium,* and *Selaginella selaginoides* were found. The continuous presence of the extinct Pinaceae and *Glomus* in upper PZ1 and *Anthrenus* (museum and cabinet beetles) in the lower part of PZ1 is remarkable. The sum of the reworked microfossils is mostly higher than 5%.

Single microfossils not indicated in the pollen diagram are: *Plantago alpina*-type and *Geranium* in PZ1 and *Fagus*, Ranunculaceae, and *Mentha*-type in PZ2.

PZ3: 559.5–593 m asl (base ca. 46–41 ka)

The pollen concentration (ca. 160–300 grains/cm^3) is relatively low with the exception of level 559.5 m asl. This is also true for the pollen-influx values (varying between 160 and 1500 grains/cm^2/yr), but they are less reliable due to uncertainties in the chronology.

The AP rise up to 60% with *Pinus* dominating and *Betula*, *Juniperus,* and *Picea* present. *Corylus* and *Alnus* are considered reworked. Poaceae show relatively low values, and Cyperaceae are more frequent than in PZ1 and 2. *Arthrinium luzulae, Arthrinium cuspidatum*, and *Glomus* are present on a more or less regular basis. The sum of the reworked microfossils is amongst the highest in the record.

Single microfossils not represented in the diagram are *Galeopsis*-type and Lamiaceae.

PZ4: 593–625 m asl (base ca. 41–38 ka)

The pollen concentration (ca. 440 grains/cm^3 throughout) and the total influx (between 500 and 1800 grains/cm^2/yr) are relatively high. AP range from 30 to 50% and are dominated by *Pinus.* Poaceae show high percentages causing the decrease in pine, while Chenopodiaceae are absent. Some Selaginella, few *Botryococcus,* and RDS 70 (Drescher-Schneider, 2008; Huber et al., 2010) are present. The single microfossil not represented in the diagram is *Ulmus*.

PZ5: 625–650 m asl (base ca. 38–37 ka)

The pollen concentration (130–380 grains/cm^3) and total influx (between 130 and 1500 grains/cm^2/yr) are low. AP vary between 25 and 40% and are dominated by *Pinus*. *Betula* is nearly absent and Poaceae show rather low percentages. On the other hand, Chenopodiaceae, together with *Helianthemum, Artemisia, Thalictrum, Ephedra, Larix*, as well as Pre-Quaternary spores, reach maximum abundance values.

PZ6: 650– 676 m asl (base ca. 35 ka)

The pollen concentration (nearly 600 grains/cm^2) and influx (up to 2300 grains /cm^2/yr) are the highest (and the most reliable due to the well constrained chronology). AP increase slightly up to 65%. *Pinus* dominates and *Pinus* cembra is constantly present. Poaceae shows relatively high values, *Botryoccocus* is present, and the pre-Quaternary sporomorphs are mostly absent. Single pollen grains and spores not represented in the diagram are *Centaurea montana*, Ericaceae, Gentianaceae, *Pediastrum*, *Microtyrium, Ustulina deuste*, and HdV 200.

DISCUSSION

Given the limited information about the lake extent, paleogeography, and position and extent of upstream glaciers, the pollen origin and potential floating time are not well-constrained. Consequently, a high "pollen noise" with limited information about changes in climate and vegetation is to be expected. However, the analysis of an 84-cm-long sediment section with 117 individual laminae (corresponding to PZ6 of the present study) made evident that sediment layers with higher pollen concentrations (in favorable cases, seasonal pollen deposition) alternate with layers showing fewer pollen grains (Bortenschlager and Bortenschlager, 1978). On this basis, Bortenschlager and Bortenschlager (1978) concluded that sediment deposition occurred mainly in summer and ceased during winter, most probably due to freezing of the lake surface. The ability to identify seasonal pollen deposition refutes long floating periods. The uniformity of the sediments between 550 and 676 m asl (PZ3–6) suggests that the sedimentation regime did not change fundamentally. Hence, this seasonal pollen input likely also applied to the rest of the upper lake phase (LP2). The sediments of the lower lake phase (PZ1 and 2), however, are somewhat different (most notably the lower sedimentation rate), and thus the implications following from the analysis of Bortenschlager and Bortenschlager (1978) are less likely to apply there.

Vegetation development based on pollen percentages and concentrations

Throughout the profile, the total AP percentage never reaches more than 65%. Different boundaries as to what is considered forest-free vegetation are given in the literature and vary from < 45–55% (Burga, 1984) to <70–80% (Bortenschlager, 1972). Given that the majority of AP is from *Pinus*, the pollen production of which is about four times that of *Fagus* and double that of *Betula,* we consider the vegetation to be forest-free, but not free of trees throughout the profile. This interpretation is confirmed by pollen grains of herbs. The abundant grasses, sedges, *Helianthemum*, *Thalictrum*, and *Centaurea montana* suggest an open and light-demanding vegetation. Furthermore, *Artemisia* and especially Chenopodiaceae are indicative of steppe vegetation.

In PZ1 and 2, the low pollen sum giving rise to fluctuating percentages, frequently interrupted pollen curves, and the especially poor pollen preservation preclude a detailed interpretation. The possible hiatus (tentatively inferred from the chronology) between 496 and 506 m asl is not clearly indicated in the pollen curves. There are some small changes within this range, however: *Betula* increases, *Artemisia* decreases, and *Juniperus* and extinct Pinaceae start. *Betula,* Cichorioideae, and *Aster*-type, and the algae *Botryoccocus* together with relatively high concentrations of upland herbs in upper PZ1 might reflect relatively humid conditions. While *Artemisia* and pollen of mesophilic trees are slightly more abundant, the maxima of *Glomus* and extinct Pinaceae suggest a period of enhanced sediment and soil erosion due to drier conditions during PZ2. It is likely that the "bordered pits" are also reworked.

Although the pollen percentages in PZ3 do not differ substantially from PZ1 and 2, the first evidence of some microfossils of low (i.e., local) dispersal are worth mentioning: *Arthrinium luzulae* (saprophyte on *Luzula*) and *Arthrinium cuspidatum* (living symbiotically with *Juncus*; Scheuer, 1996). Nevertheless, some moist-preferring inhabitants must have existed, because *Entophlyctis* (HdV 13; van Geel, 1976; Kuhry, 1985) is a sign of nearby *Scheuchzeria palustris* bogs. The low pollen concentration, the relatively high values of Chenopodiaceae, *Artemisia*, and reworked types suggest a cold and rather dry climate with enhanced soil and sediment erosion.

The decrease of AP, mainly *Pinus,* in PZ5 is partly caused by the spread of Poaceae and Cyperaceae. Chenopodiaceae are nearly absent and the values of reworked microfossils are low. Together with a pollen concentration more than twice as high as before, this zone reflects a period of temperate, and probably rather humid, conditions with better-developed vegetation in a still woodless landscape. The small pollen proportion of woody species in PZ5 is accompanied by relatively low pollen concentrations, abundant grasses and Cyperaceae, and especially Chenopodiaceae, *Helianthemum*, and *Ephedra*: signs of a rocky semidesert. The occurrence of pre-Quaternary forms supports the interpretation of this zone as a cold period with moderate to low vegetation cover and a high input of eroded material. PZ5 represents the coldest and driest period of the PZ3–6 sequence.

Zone PZ6 shows a continuous increase in AP, *Pinus* rises, *Betula* and *Pinus cembra* are regularly above 1%, and *Larix* and *Salix* are also present. By contrast, reworked types are almost absent. This pollen zone corresponds to the previously studied part of the sequence, which contained a number of woody macro fossils (Fliri et al., 1971, 1972). Most remains were fragments of *Pinus mugo*, *Pinus sylvestris*, *Alnus alnobetula*, *Hippophae rhamnoides*, and *Salix*, including a leaf of *Dryas octopetala* (Supplementary Table 1). Their good state of preservation argues against a long-distance transport or reworking from older sediments. It is more likely that these remains were transported to the lake by either local creeks or avalanches from the northern shore. Unfortunately, the new cores lack wood fragments throughout PZ6. The only clues to the presence of trees are increasing *Pinus* percentages and concentrations and *Ustulina deusta*, a dangerous parasite on the roots of deciduous trees such as *Betula* (van Geel and Andersen, 1988; Brandstetter, 2007). High counts of Poaceae, Caryophyllaceae, Apiaceae, *Centaurea montana*, and Gentianaceae are indicators of a mostly closed vegetation cover. This was the warmest and most humid period of the complete sequence with more frequent stands of *Pinus, Betula, Pinus cembra*, *Larix*, and dwarf shrubs like *Salix* and *Dryas octopetala* in a non-forested landscape.

Vegetation development on the basis of pollen concentration and influx

Pollen-concentration values are influenced by various parameters including sediment type and composition, sedimentation rate, mode of deposition, presence or absence of high pollen producers, and changes in vegetation cover and structure (Lotter, 1985). Nevertheless, a comparison of percentage and concentration data assists in interpreting the vegetation development.

In the studied core (Fig. 4), the pollen concentration does not change significantly throughout the whole sequence. Nevertheless, the general trend of low concentrations is interrupted by two intervals of somewhat higher pollen content (PZ4 and 6).

In PZ1, concentration values vary between 160 and 343 grains/cm^3. PZ2, with ca. 160 grains/cm^2, is similar to PZ3 (with the exception of level 559.5 m, reaching 590 grains/cm^3) and the middle part of PZ5. Concentrations of ca. 440 grains/cm^3 dominate in PZ4, and about 570 grains/cm^3 are present in the two uppermost levels of PZ6. Even though the difference between PZ4 and 6, on one hand, and PZ1–3 and PZ5, on the other, is small, assuming no fundamental changes in the sedimentation regime, a trend towards denser vegetation cover and slightly more frequent tree stands is visible for PZ4 and 6. Pollen-abundance values in general are very low but confirm the observations by Bortenschlager and Bortenschlager (1978). They are also comparable to those of stadial sections at Unterangerberg 40 km downstream in the Inn Valley (Starnberger et al., 2013a) and to LGM deposits from the peri-alpine site Renče (western Slovenia; <250 grains/cm^3; Monegato et al. 2015). These values are many times lower than those in samples of the pre-Eemian glacial sediments from Niederweningen (northern Switzerland; Dehnert et al., 2012) or LGM samples from the Oglio area (Ravazzi et al., 2012) and Lake Garda (Ravazzi et al., 2014), or the MIS 3 sediments at Azzano Decimo (all Italy; Pini et al., 2009) with up to 50,000 grains/cm^3 during stadials and more than 250,000 grains/cm^3 during interstadials. They are even lower than those of the non-forested Tulppia interstadial in Finland (Bos et al., 2009) and late glacial lake sediments in the Alps prior to afforestation (Bortenschlager and Bortenschlager, 1978; Ammann, 1984; Lotter, 1985). The most likely explanation for the low pollen concentrations at Baumkirchen, as well as at Unterangerberg and Renče, is the high sedimentation rate of these paleolakes. The record of Niederweningen, showing comparable sedimentation rates in the oldest pre-Eemian section, is characterized by a high amount of reworked pollen types significantly increasing the total pollen concentration. On the other hand, Azzano Decimo is situated in a glacial refuge area of spruce and many deciduous tree species, due to increased humidity south of the Alps at that time (Florineth and Schlüchter, 2000; Pini et al., 2010). Furthermore, the late glacial sequences were deposited in lake sediments of significantly lower sedimentation rates, leading to higher pollen concentrations.

A more reliable measure of vegetation density and composition is given by the influx values, i.e., the number of pollen grains embedded per cm^2 and yr. This, however, requires reliable sedimentation rate estimates (e.g., Berglund and Ralska-Jasiewiczowa, 1986). At Baumkirchen, sedimentation rates are not precisely known. Therefore, the influx values are given as range (minimum and maximum) and provide a general trend only.

The pollen influx in PZ1 and 2, reaching values between 40 and 308 grains /cm^2/yr, is least reliable due to the highly uncertain sedimentation rate. In the other two cold-climate pollen zones (PZ3 and 5), the influx was about four times higher than in PZ1 and 2. The rate of pollen deposition in the more temperate zones (PZ4 and 6) was about twice as high as in PZ3 and 5.

Due to the highly uncertain sedimentation rates below the hiatus (LP1: PZ1 and 2), the pollen content of PZ1 and 2 will not be further discussed. Even though the calculation of pollen influx in PZ3–5 remains tentative, it is better constrained than in the older sediments. In circum-Alpine pollen records of the same time window as Baumkirchen, pollen influx values are generally not available due to the absence of a robust chronology. Values representing pollen sedimentation rates during non-forested late glacial periods are also rare. Bortenschlager (1984) estimated as few as 100 grains/cm^2/y in sediments older than 13,980 ± 240 ^{14}C yr BP at Lanser See (15 km west of Baumkirchen). Similar values (270–620 grains/cm^2/yr) were calculated in clayey sediments older than 13,300 ^{14}C yr BP at Lobsigensee, Switzerland (Ammann, 1989). Both influx estimates are comparable with PZ3 and 5 at Baumkirchen. Although it is possible that the *Pinus* grains reflect long-distance transport from south of the Alps (as also assumed for Lanser See), it is unlikely that the Inn Valley was totally devoid of trees during PZ2 and 5. *Pinus* and *Betula* may have survived in small scattered stands in climatically favorable habitats.

Concerning the two more temperate pollen zones, the pollen accumulation rates reach 1806 grains/cm^2/y in PZ4 and 2300 grains/cm^2/y in PZ6, similar to values found during the dwarf-shrub period before the *Juniperus* zone at both Lobsigensee (Ammann, 1989) and Lanser See (Bortenschlager, 1984). Furthermore, we compared our data to two deposits of Younger Dryas age in Switzerland (Wick, 2000). At Gerzensee (central Switzerland, 603 m asl), pine forests changed little between the Allerød and the Younger Dryas, with only birch trees largely disappearing. The total influx (AP + NAP) during the climatically unfavorable period at Gerzensee was about 6000–7000 grains/cm^2/y. The second location is Leysin in the Swiss Prealps (1230 m asl), which, although located above the timberline during the Younger Dryas, was not completely free of trees. In these sediments, the total influx varied between 1000 and 2000 grains/cm^2/y.

Beside the higher pollen influx rates in PZ6, the vegetation development is different in PZ4 compared to PZ6. The influx of *Pinus* increases weakly from 350 to 510 grains/cm^2/y while upland herbs rise steadily within PZ4 (from 340 to 1900 g/cm^2/y). We conclude that the tree population increased slightly due to higher humidity and probably also higher temperatures, but that the climate (and possibly the brief time span) did not permit a greater spread of trees. The steadily increasing herbs coincided with a rising variety and density of vegetation resulting in well-developed, but still not completely closed, grassland. In PZ6, however, the pollen curves indicate a different succession: the increase in the influx values is manly caused by *Pinus*, *Betula*, and *Pinus cembra*. Considering both the pollen information from this study as well as the earlier woody macro fossil finds, we infer interstadial conditions and small tree-stands on the lakeshore and in other favorable locations represented by woody species such as *Pinus sylvestris*, *Pinus mugo*, *Pinus cembra*, and the strongly under-represented *Larix* as well as by the shrubs *Alnus alnobetula*, *Hippophae*, *Juniperus*, *Salix*, and *Dryas octopetala*. Because the lacustrine Baumkirchen sequence continues for another 50 m upsection (up to 725 m asl) PZ6 may mark only the onset of a more pronounced interstadial.

Provided that the sedimentation rate estimates are broadly accurate, the interpretation of the percentage record is confirmed for the most part by the pollen influx rates. Moreover, these data allow us to refine the differences between the individual pollen zones and clarify the vegetation development and corresponding climate conditions.

The Baumkirchen pollen record in the context of other Alpine and extra Alpine records

The Baumkirchen pollen zones PZ3–6 span from ca. 45 to ca. 35 ka (i.e., mid- to late MIS 3), a period characterized by centennial- to millennial-scale Dansgaard-Oeschger oscillations. This closely corresponds to a period of occupation of caves by cave bear in the lower Inn Valley (Spötl et al., 2014). Palynological investigations of long sedimentary MIS

3 and 4 sequences from the Alps, especially those with robust chronologies, are restricted to the foreland (Füramoos, Müller et al., 2003; Azzano Decimo, Pini et al., 2009; Fimòn, Pini et al., 2010). Shorter sequences are known from Gossau (Switzerland; ca. 45–54 ka; Schlüchter et al., 1987; Preusser, 1999), Niederweningen (ca. 45 ka; Drescher-Schneider et al., 2007), and Unterangerberg (ca. 40–75/85 ka; Starnberger et al., 2013a, 2013b), the latter also being located in the Inn Valley. The vegetation pattern of the different MIS 3 interstadials in these Alpine records is still poorly chronologically constrained and thus difficult to correlate. Furthermore, the Unterangerberg and the Füramoos records both contain hiatuses from ca. 40–45 ka onwards and thus lack sediments of late MIS 3 age. Baumkirchen therefore contributes a valuable piece to the Middle Würmian puzzle.

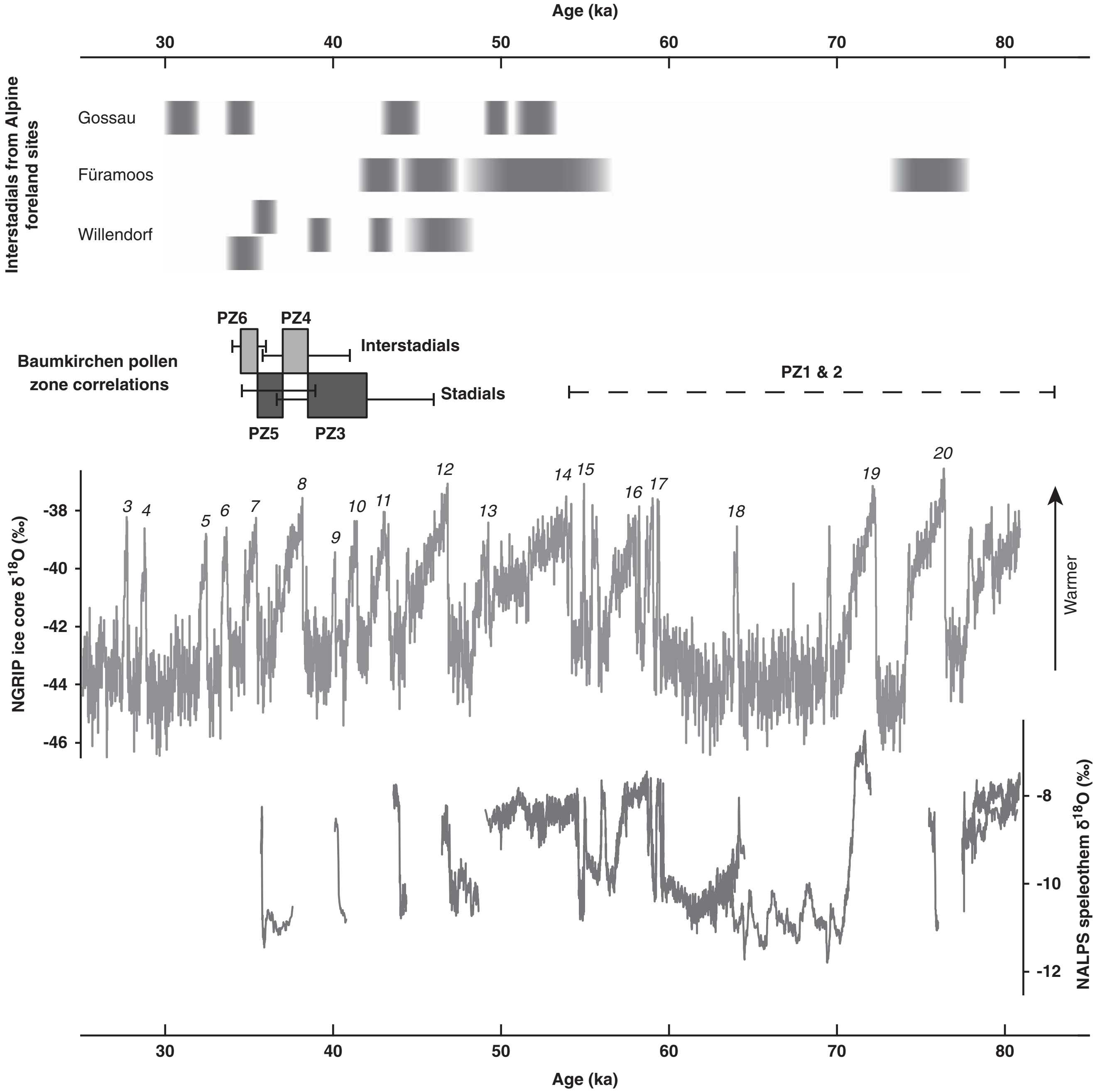

Figure 5. Comparison of Baumkirchen pollen zone age ranges with interstadials from Alpine foreland sites Füramoos (Müller et al., 2003), Gossau (Preusser et al., 2003), and Willendorf (Nigst et. al., 2014); the NGRIP $\delta^{18}O$ temperature-proxy record with interstadials numbered (GICC05modelext time scale; Seierstad et al., 2014; Rasmussen et al., 2014); and the NALPS speleothem $\delta^{18}O$ record (Boch et al., 2011; Moseley et al., 2014). For the Baumkirchen pollen zones, shaded boxes show the correlations based on the chronology and comparison of pollen results to the Greenland ice-core record, and whiskers show the full possible age range based on the chronology alone. For the interstadials from foreland sites, the faded bars schematically represent age/correlation uncertainties.

The section corresponding to the interstadial pollen zone PZ6 at Baumkirchen is well-dated to ca. 35 ka by multiple luminescence and radiocarbon dates (Spötl et al., 2013; Barrett et al., 2017), corresponding to Greenland Interstadial (GI) 7 (Fig. 5). Due to the generally poor age control of Alpine foreland sites, this is therefore the first firm correlation between an Alpine pollen record and a Greenland interstadial. On this basis, a tentative correlation can be made to the PZ6 interstadial of the Gossau section (Preusser et al., 2003) and the Schallenbach II or III interstadial at the loess section of Willendorf (Lower Austria; Nigst et al., 2014).

The onset of PZ4 is less well-constrained by luminescence dating to ca. 37–41 ka probably corresponding to GI 8. In Greenland, this interstadial was longer than GI 7 and one would expect a vegetation pattern in Baumkirchen somewhat more developed than during GI 7. Therefore, this correlation remains tentative. On the basis of the chronology, this interval may correspond to Schallenbach Ib in the Willendorf loess section (Nigst et al., 2014). The correlations of PZ6 and 4 to GI 7 and 8, respectively, and PZ5 and 3 to the respective neighboring stadials, based on the chronology and pollen data, are shown in Figure 5.

Comparison to and correlation with extra-Alpine late MIS 3 (ca. 45–35 ka) records again relies on reliable independent chronologies. With a few exceptions, however, well-dated sequences are only available from southern Europe where better climatic conditions prevailed: GI 7–9 (probably corresponding to Baumkirchen PZ6 and 4) were generally characterized by open forests (Fletcher et al., 2010). On the contrary, a dominance of Poaceae, a peak in *Betula*, and increased *Pinus* are reported for the Charbon warm period at La Grande Pile (France; ca. 40 ^{14}C yr BP; Helmens, 2014), interpreted as an increased expansion or blossoming of wood-stands or shrubs in a still open environment (de Beaulieu and Reille, 1992). Moreover, an interstadial with increased presence of *Pinus* (± 60%) and *Larix* occurs at the top of the Horoski Duźe sequence (Poland). Its chronostratigraphic position, however, is unclear and two interpretations were discussed (Helmens, 2014), a correlation with Denekamp (ca. 30 ka, a controversial interstadial, see Litt et al., 2007) or with Oerel (ca. 55 ka).

The age of the base of PZ1 and 2 is assumed to range between 75 and 85 ka (Fig. 5), a period at the end of the Early Würmian that possibly includes the interstadials during MIS 5a followed by the transition to the severe climatic deterioration of MIS 4. If this assumption is correct, the warmer interstadial conditions should be reflected in the lowermost horizons by higher percentages and influx of spruce, pine, and larch. As discussed above, however, the pollen record reflects very scarce vegetation and no evidence of former forests. Müller (2001) reported evidence of two interstadials in the Füramoos record, which he correlates to GI 20 (Dürnten) and 21 (Odderade) followed by a distinct, treeless stadial correlated to MIS 4. We therefore find it most plausible to assign PZ1 and 2 to MIS 4. Given the age uncertainties and lack of bounding pollen zones, it is not clear whether PZ1 and 2 represent the entire MIS 4 or only part of it. Therefore, no strong correlation is suggested in Figure 5.

CONCLUSIONS

Despite the very low pollen concentrations, the analysis performed on new core material from the Baumkirchen stratotype provides important new insights into the vegetation inside the Alps during the last glacial cycle prior to the LGM. These data are confirmed by pollen-influx data calculated from sediment accumulation rates based on new radiocarbon and luminescence dates. As a result, five climatic episodes could be established:

(1) An interstadial (PZ6) at around 35 cal ka BP, which is regarded as the equivalent of GI 7. This zone, which is the best developed in the sequence, is characterized by poorly developed forest stands. *Pinus sylvestris*, *P. mugo*, *Alnus alnobetula, Salix*, *Hippophae*, and *Dryas octopetala* are known from earlier wood finds, and in addition *P. cembra*, *Juniperus*, and *Larix* are documented by their pollen. This indicates relatively warm and humid conditions compared to the rest of the sequence.

(2) Framed by two cooler and drier phases (PZ5 and 3) of low pollen influx and open but not treeless vegetation, an older interstadial (PZ4) is recorded between ca. 593 and 625 m asl It differs from PZ6 by showing fewer tree stands and widespread, well-developed grassland.

(3) Based on the position below PZ6 and the presumed age of the lower boundary (ca. 41–38 cal ka BP), PZ4 may be an equivalent of GI 8 (ca. 37–38 cal ka BP). This correlation remains uncertain, because in Greenland GI 8 was longer and possibly warmer than GI 7 and one would thus expect richer vegetation and more widespread tree stands at Baumkirchen.

(4) The lowest section (PZ1 and 2) represents a period of extremely cold and dry conditions and, consequently, a treeless landscape with only a scattered vegetation cover. On the basis of the vegetation data and the luminescence age control, this interval is correlated to MIS 4.

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SUPPLEMENTARY MATERIALS

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