A multi-proxy Late-glacial palaeoenvironmental record from Lake Bled, Slovenia

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Abstract This study investigates the palaeoecological record (δ^{18}O, δ^{13}C, pollen, plant macrofossils, chironomids and cladocera) at Lake Bled (Slovenia) sedimentary core to better understand the response of terrestrial and aquatic ecosystems to Late-glacial climatic fluctuations. The multi-proxy record suggests that in the Oldest Dryas, the landscape around Lake Bled was rather open, presumably because of

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the cold and dry climate, with a trend towards wetter conditions, as suggested by an increase in tree pollen as well as chironomid and cladocera faunas typical for well-oxygenated water. Climatic warming at the beginning of the Late-glacial Interstadial at ca. 14,800 cal yr BP is suggested by an increase in the δ^{18}O value, the appearance of *Betula* and *Larix* pollen and macrofossils, and a warmth-adapted chironomid fauna. With further warming at ca. 13,800 cal yr BP, broad-leaved tree taxa (*Quercus, Tilia, Ulmus*), *Artemisia*, and *Picea* increase, whereas chironomid data (*Cricotopus B*) suggest lowering of lake levels. After 12,800 cal yr BP (and throughout the Younger Dryas), the climate was colder and drier, as indicated by lower δ^{18}O values, decline of trees,

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increase of microscopic charcoal, xerophytes and littoral chironomids. A warmer climate, together with the spread of broad-leaved tree taxa and a deeper, more productive lake, mark the onset of the Late-glacial/Holocene transition. These results suggest that terrestrial and aquatic ecosystems at Lake Bled were very dynamic and sensitive to Late-glacial climatic fluctuations.

Introduction

A new interest has developed in the rapid climatic shifts of the Late glacial of the last glaciation because these shifts were so rapid and of so large amplitude. Even if conditions were very different from the present in several respects, and if direct analogues to future climatic warming may not be correct in detail, we may learn about the behaviour of the systems from the past. This includes both the climatic system and various ecosystems. These data on past changes may also be useful to test models.

The study area is situated at a crossroad between south-central Europe, the southeastern Alps and the Balkan Peninsula. Several biogeographically important issues may therefore be tackled from a detailed study of the Late glacial, e.g. biogeographical questions about the position of refugia of plants and invertebrates and their migration routes. Palaeobotanical and genetic studies suggest that glacial refugia

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for coniferous and some deciduous trees were located in the Iberian, Italian and Balkan Peninsulas and in parts of central and eastern Europe (e.g. east of the Alps, Hungarian Plain and River Danube), with Slovenia being located in the vicinity or in central part of the suggested refuge areas (e.g. Willis et al., 2000; Petit et al., 2003; Willis & van Andel, 2004). For example, it has been suggested that eastern Alps was one of the most important refugia for *Fagus sylvatica* (Magri et al., 2006), and it is interesting that the study site lies between ranges of two distinctive haplotypes of *Pinus sylvestris* (Cheddadi et al., 2006).

Previous palynological research in Slovenia suggests that at the beginning of the Late glacial, the vegetation of Slovenia consisted of predominantly herbaceous steppe with few pine trees, but with the climatic warming in the Late glacial, Interstadial woodlands (*Pinus, Betula, Picea, Quercus, Corylus, Fagus, Tilia,* and *Ulmus*) were expanding (Culiberg, 1991). However, despite intensive palynological research in the area, studies including radiocarbon-dated multi-proxy analysis of the sediment are very rare. This article presents the results of such multi-disciplinary palaeoecological research on Late-glacial sediment at Lake Bled (Slovenia) to better understand changes of Late-glacial vegetation, climate and hydrology.

Earlier research at Lake Bled focused on studies of the modern carbon budget (e.g. $\delta^{13}C$ and $\delta^{15}N$ analyses) and pollen records from short (ca. 45 cm) cores (Molnar et al., 1978; Dolenec et al., 1984; Ogrinc et al., 1997, 1998, 2002; Lojen et al., 1997, 1999). The results of pollen analysis for the last ca. 400 years indicate a forest dominated by *Fagus* and increasing evidence of human pressure (grazing and agriculture, suggested by *Fagus* decline and an increase of cereals, buckwheat and maize), followed by diminished human impact indicated by an increase of tree pollen, especially *Pinus* (Molnar et al., 1978).

In 1982, a 675-cm-long sediment core was taken from the deepest (eastern) part of the basin (Fig. 1), and a multi-proxy study was carried out. Results from analysis of Ostracoda, mosses, sedimentary pigments and pollen (Löffler, 1984; Schultze, 1984, 1988) suggested a Late-glacial age (from the bottom to 550 cm), with a pollen assemblage dominated by *Artemisia, Pinus* and *Betula*. Subsequently, the vegetation shifted to a mixed oak forest, with *Fagus* showing up at the beginning of the Holocene. The
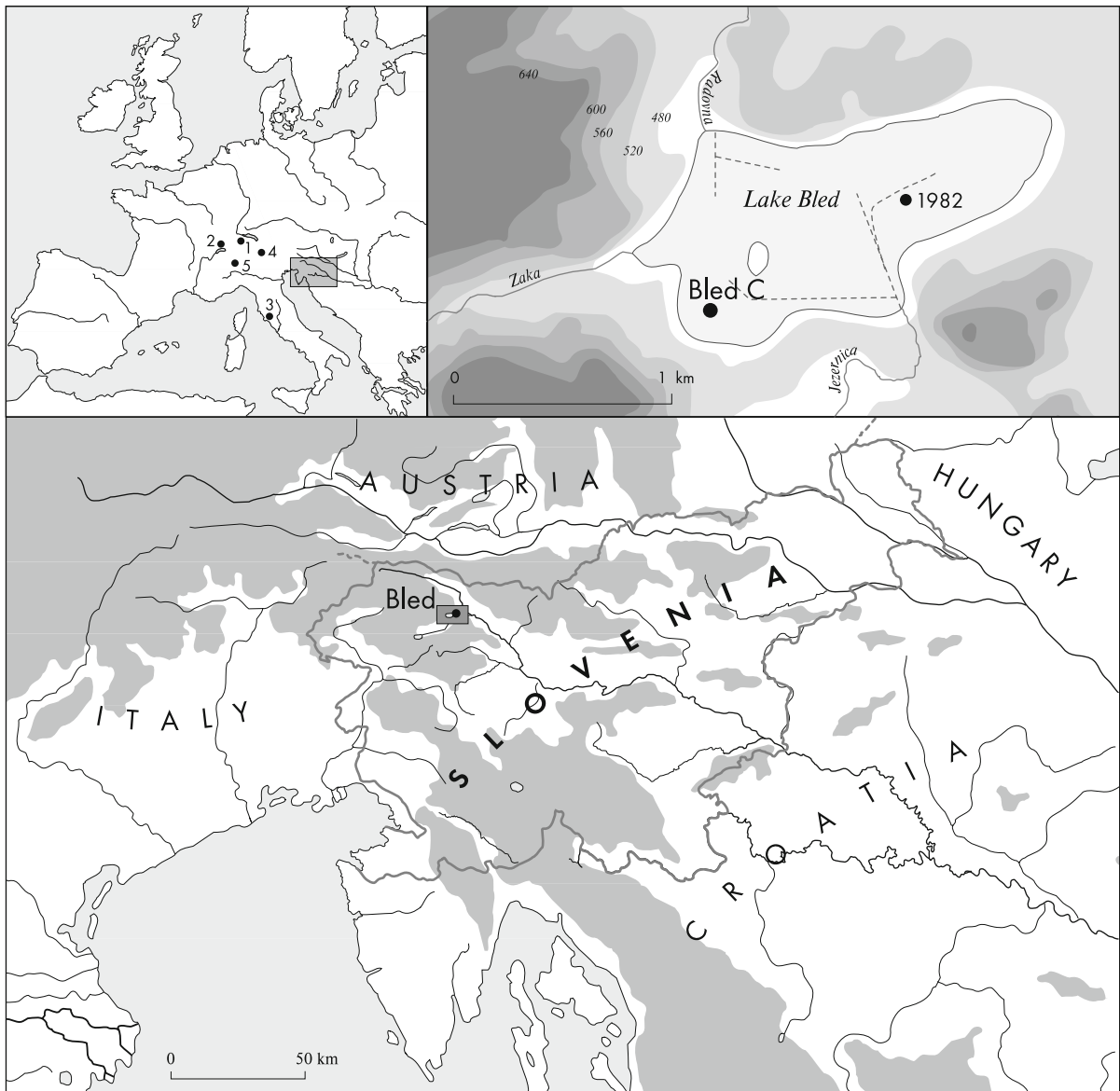
Fig. 1 The geographical position of Lake Bled (Slovenia) and the sediment core. The location of Olszewski tubes is marked by *dotted lines*. • 1982 marks the position of the sediment core collected by Schultze (1984). Study sites, mentioned in Table 3 are as follows: 1—Gerzensee, 2—Lake Lautrey, 3— Lake Accesa, 4—Lago di Origlio, 5—Lago Piccolo di Avigliano (study sites on map)

information about the vegetation during the Holocene at Lake Bled is vague, because sampling resolution in the upper section of the core was rather low (10-cm interval, no pollen was analysed above 470 cm), and the sequence was not radiocarbon dated. Despite the attempt to reconstruct Lake Bled environmental history using a multi-proxy approach, the lack of high sampling resolution and chronological control made it unfeasible. Hence in 2002, to complement the previous study, a new 521-cm sediment core was collected in the southwestern part of the lake and studied to determine the history of the vegetation, hydrology and climate. An age model was constructed using AMS radiocarbon dating and analysis of loss-on-ignition (LOI), stable isotopes (δ^{18}O, δ^{13}C), geochemistry ($CaCO_3$), plant macrofossils, mosses, pollen, chironomids and cladocerans. Results of this research are presented in this article.

Lake Bled lies in limestone and dolomite bedrock at 475 m a.s.l. in northwestern Slovenia (46°22′ N, 14°06′ E, Fig. 1). Its maximum depth is 30 m, and covers an area of 1.45 km² (Grimšičar, 1955; Geological Map of Slovenia, 1993). The lake is surrounded by ground and marginal moraines, with last glacial maximum terminal moraines located to the east of the lake (Grimšičar 1955). The whole valley of the Sava River, where the lake is positioned, is surrounded by high mountains (some of them higher than 2500 m) on the west, north and south, and open only to the east. The climate of the area is temperate (average of the coldest month between 0 and −3°C, and average of the warmest month between 15 and 20°C), with a submediterranean precipitation regime (1300–2800 mm annual precipitation with a maximum in autumn) (Ogrin, 1996). In Lesce, ca. 8 km east of Lake Bled, mean July temperature is 18°C, mean annual temperature 8.4°C and annual precipitation 1541 mm (Pak, 2001). Forest of predominant beech (*Fagus sylvatica*) grows to the west and north of the lake, whereas patchy woodlands of hornbeam (*Carpinus betulus*) and willow (*Salix* sp.) are located to the east (Čarni et al., 2003). Meadows and agricultural fields are also located in the vicinity of the lake.

Dimictic Lake Bled developed in a depression shaped by a glacier (Radinja et al., 1987). Today, the lake receives water from small natural tributaries (e.g. Zaka River) and artificial inflows (e.g. Radovna River) as well as precipitation. At the beginning of the twentieth century and especially after the Second World War, the lake experienced an increase of nutrient loading from sewage and agriculture, triggering blooms of blue-green algae *Oscillatoria rubescens*, which threatened the tourist industry. As a consequence, in 1964, clean water from the Radovna River was artificially diverted to the lake (2000 l s⁻¹), and later on in 1980 and 1982, the basin was drained by Olszewski tubes, and domestic sewage was rerouted from the lake (Fig. 1; Radinja et al., 1987). Pumping of hypolimnetic cold water from the bottom of the lake resulted in decrease of nutrients in the water column, and finally in the disappearance of *Oscillatoria rubescens* (Vrhovšek et al. 1982, 1984, 1985). After several years of anoxic conditions below a depth of 15–18 m during thermal stratification in late summer and late winter, oxygen conditions improved. Nowadays, only short-lasting anoxic events occurred from time to time.

Materials and methods

Fieldwork

Sediment core Bled C (521-cm-long) was collected from a coring platform in the southwestern part of the lake (Fig. 1) with a Livingstone piston corer (modification after Merkt & Streif, 1970) with a tube of 4.8 cm diameter. A single core with 1-m-long core sections was analysed. Water depth at the coring location was 9.6 m. Immediately after extrusion, the core sections were wrapped in thick plastic and stored in the dark at +4°C. Subsamples of 1 to 20 cm³ of the sediment (depending on the type of analysis) were analysed with the following techniques: LOI, stable isotope analysis (δ¹⁸O and δ¹³C), Chironomidae, Cladocera, pollen and plant macrofossils. AMS radiocarbon measurements were made on selected sections (see below).

Radiocarbon dating, LOI and stable isotope analyses

The age was determined by AMS radiocarbon dating of terrestrial plant macrofossils and bulk organic carbon, extracted from the sediment at 40, 60 and 210 cm depths (Table 1). Conventional ages were calibrated using CALIB Rev 5.0.1 (CALIB 5.0 Website; Stuiver and Reimer, 1993) on IntCal 04 calibration dataset (Reimer et al., 2004). Median cal yr BP values (as recommended by Telford et al., 2004) were used to construct the age-depth model (linear interpolation; Fig. 2). The percentage of organic material and carbonate in the sediment was determined by LOI at 550°C and 950°C (Bengtsson and Ennell, 1986). The isotopic composition of oxygen (δ¹⁸O) and carbon (δ¹³C) on bulk carbonate was measured following the conventional method described by Siegenthaler & Eicher (1986).

Plant macrofossil and moss analyses

For macrofossil analysis, 2.5-cm sediment slices with volume of approximately 20 cm³ were taken with 10-cm sampling resolution. After brief soaking (5–10 min) in 10% KOH, the samples were washed through 400- and 160-μm sieves in two fractions. The material was sorted and identified under stereomicroscope with magnification up to 56×. For determination

Table 1 Radiocarbon dating in Lake Bled core

Sample no. (material dated, pre-treatment)	Depth (cm)	Conventional radiocarbon age (BP)	13C/12C ratio (‰)	2 Sigma calibration (Intcal 04) (BP)	Median (BP)
Beta-222472	60	9340 ± 40	−26.9	10679–10426	10555
(*Larix* leaves, part of cone scale and wings of coniferous seeds, acid/alkali/acid)					
Beta-217805	210	11930 ± 40	−28.2	13908–13699	13790
(*Larix* twig and needles, acid/alkali/acid)					
Beta-189953	40	13860 ± 100	−33.8		
(organic sediment, acid washes)					
Poz-3123	40	15430 ± 80	/		
(organic sediment, acid washes)					

The two dates based on terrestrial plant macrofossils (Beta-222472 and Beta-217805) are in good agreement with palynological events in Northern Italy (Vescovi et al., 2007)

The two dates based on organic sediments (Beta-189953 and Poz-3123) are too old and inconsistent with regional events and were not used for age-depth modelling (see text)
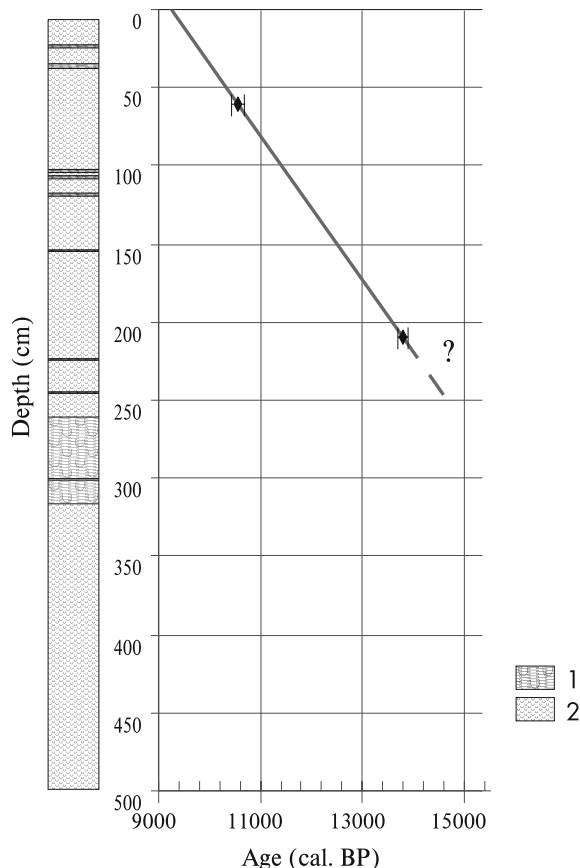

Fig. 2 Age-depth model (linear interpolation). The estimated age of Lake Bled sediment (cal yr BP) is plotted against depth (cm). Details of radiocarbon measurements are presented in Table 2. Lithology: 1—moss layers and 2—calcareous clay (lake marl)

of macrofossils, the reference collection from the Herbarium of Sofia University and specialised literature was used (Beijerinck 1947; Katz et al., 1977; Tobolski, 2000). Plant macrofossil concentrations (number of macrofossils in 20 cm^3 of the sediment) were integrated in the pollen diagram (Fig. 4). The sample volume was much smaller than that recommended for plant macrofossil analysis (Birks, 2002), and this could affect the results to some extent.

Samples for moss analysis were collected from distinct moss layers at 315, 299, 269, 244, 225, 153, 104, 36.5 and 24.5 cm and identified under light microscope at 600× magnification. Keys of Nyholm (1954–1969) and Smith (2004) were used for taxonomic identification.

Pollen analysis

For pollen analysis, 1 cm^3 of the sediment was used following standard laboratory procedures (Bennett & Willis, 2002). Two tablets with a known number of *Lycopodium* sp. spores were added prior to laboratory preparation to determine the pollen concentration (Stockmarr, 1971). A minimum of 500 pollen grains of terrestrial plants and spores was counted in each sample, with a sampling resolution of 8 cm. Pollen identification was carried out under a Nikon Eclipse E400 light microscope at (400× magnification) using a reference collection of the Institute of Archaeology from Ljubljana and ID keys by Moore et al., 1991 and

Reille, [1992], [1995]. Microscopic charcoal particles and estimation of past fire activity in the area were counted according to the method of Clark ([1982]). Pollen data were analysed and plotted with the PSIMPOLL 3.00 program (Bennett, [1998]; http://chrono.qub.ac.uk/psimpoll/psimpoll.html). The pollen diagram was divided into five statistically significant pollen zones by the method of optimal splitting by information content (Bennett, [1996], [1998]).

Chironomid analysis

Subfossil chironomid analysis was carried out on 29 samples. Subsamples of 3–4 cm^3 wet weight (WW) were deflocculated in 10% KOH and heated to 70°C for 20 min. The sediment was subsequently passed through 212- and 95-μm mesh sieves. Chironomid larval head capsules were picked out from a Bogorov sorting tray with fine forceps under a stereo microscope at 25–40× magnification. Larval head capsules were mounted in Euparal, ventral side up, under a 6 mm diameter coverslip. Larvae were identified with reference to Cranston ([1997]) and Wiederholm ([1983]). Chrionomid data were processed, analysed and graphed with TILIA v. 1.12, TILIAGRAPH (Grimm [1991]) and C2 software (Juggins, 2001, unpublished). The chironomid percentage diagram was created with TILIAGRAPH and C2 graphic tools. In order to detect zones of similar chironomid assemblages within the core, both stratigraphical-constrained cluster analysis with CONISS and optimal partitioning (Birks & Gordon, [1985]) with ZONE v. 1.2 (Juggins, 1991, unpublished) were used.

Cladocera analysis

Cladoceran analysis was carried out on 1-g wet weight sediment on the same 29 depths as for chironomid analysis. Samples were washed under a 50-μm sieve to remove fine mineral and organic particles. The material left on the mesh was analysed for Cladocera remains (for details see Korhola & Rautio, [2001]). Most of the samples were screened under stereomicroscope at magnification of 40 or 100×. Due to the very low concentration of Cladocera remains, the whole sample was analysed, and only qualitative results can be presented.

Results

Radiocarbon dates, LOI and stable isotopes

The results of radiocarbon measurements are presented in Table [1]. Radiocarbon dates of organic sediment at 40 cm (Beta-189953 and Poz-3123; Table [1]) were not used in the age-depth model due to the errors presumably caused by the reservoir effect (i.e. hard-water effect). Linear interpolation between median values of radiocarbon dates at 210 cm and 60 cm was used for age-depth modelling (Fig. [2]), suggesting that most of the Holocene sediment is missing. Conversely, Late-glacial and early-Holocene sediments deposited between 13,790 ca. and 10,555 cal yr BP show an average sedimentation rate of 0.046 cm yr^{-1}. The Holocene sediment is often absent on subaquatic (littoral) terraces and is usually explained by either non-sedimentation or erosion due to wave action (Digerfeldt, [1986]), lower lake levels (Scholz, [2001]) and movement of sediment from littoral to profundal zone following breakdown of thermocline (Davis, [1976], after Dearing & Foster, [1986]) during the early Holocene and/or after the basin was drained by Olszewski tubes.

The amount of organic material, carbonate and the remaining (after burning at 950°C) inorganic residue was obtained by LOI and was calculated as a percentage of the sediment dry weight (Fig. [3]). LOI shows that below 310 cm, there is a high percentage of inorganic material (65–75%) remaining. The percentage of organic material stays low throughout the core, whereas carbonate increases to 40% (and the remaining inorganic material decreases to 55%) above 270 cm.

The samples below 400 cm show positive δ^{13}C values (+1‰), whereas δ^{18}O values are ca. −5‰ and CaCO$_3$ 40–45% (Fig. [3]). At about 300 cm, carbonates increase to ca. 80%, δ^{13}C values are negative and a decrease of δ^{18}O to ca. −10.50‰ is observed between 300 and 262 cm. The δ^{18}O values decrease sharply between depths of 168- and 152-cm, and the values remain at these low values until 102 cm but with a slightly increasing trend towards shallower depth. The upper part of the profile from 102 cm up to 50 cm (some sediment is missing due to coring problems) exhibits a step-like increase by 0.8‰. Towards the core surface, the values remain relatively high at −8.1‰.
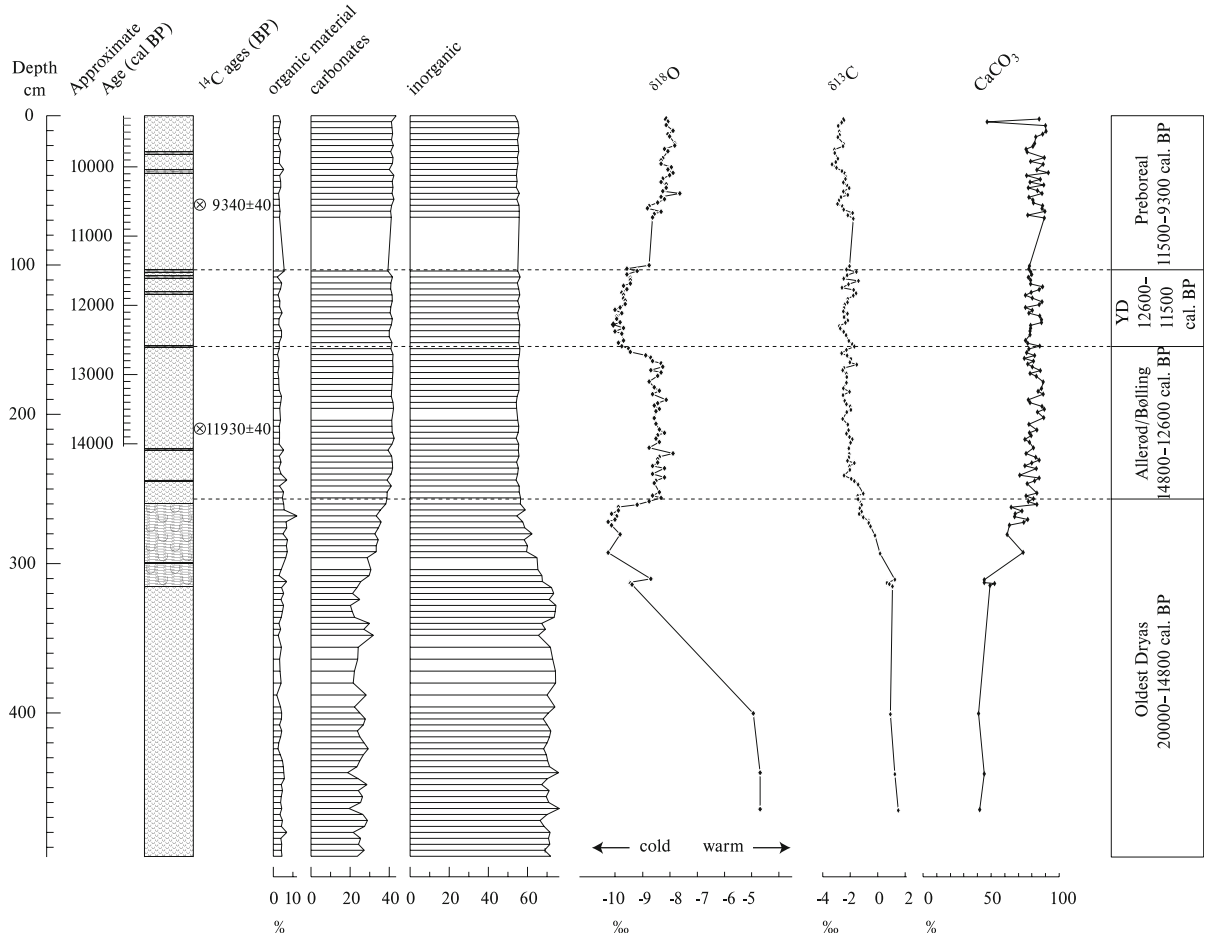
Fig. 3 Chronology and physical and chemical characteristics (loss-on-ignition: organic material, carbonates, inorganic residue; stable isotopes: $\delta^{18}O$, $\delta^{13}C$; $CaCO_3$) of a sediment core Bled C

Plant macrofossils and moss

Moss layers were found between 315 and 223 cm, 155 and 107 cm, and 29 and 24 cm, with a thick moss layer between 315 and 260 cm, (indicated as dark horizontal lines in sedimentary column of Figs. 3, 4a, b, 5, 6). Moss species recovered belong to the genera *Scorpidium* (*S. scorpioides*), *Pseudocalliergon* (*P. trifarium*) and *Calliergon* (*Calliergon* cf. *C. cordifolium—giganteum*). Plant macrofossils appear only in the upper part of the sequence (from ca. 320 cm upward), and the dominant assemblages are a combination of needles of *Larix* and *Betula* catkins. *Picea* (and *Populus* in B-5) macrofossils appear in the last two pollen zones (Fig. 4a).

Pollen

Due to the poor preservation and low concentration of pollen in pollen zones B-1 and B-2 (496–390, 390–315 cm) (ca. 500 pollen grains per 1 cm³ of wet sediment, with more than 20% of degraded pollen grains, Fig. 4b), the pollen sum in most of the samples was below the statistically required minimum (300 grains per count). The main taxa present are *Pinus* and herbs. In pollen zone B-3 (315–200 cm), pollen concentration increases to ca. 2000–30,000 pollen grains cm^{-3}, with high percentage of *Pinus* (ca. 75–95%) and much lower percentage of herbs than in the previous two zones. At the beginning of pollen zone B-4 (200–115 cm), the percentage of *Pinus* starts to
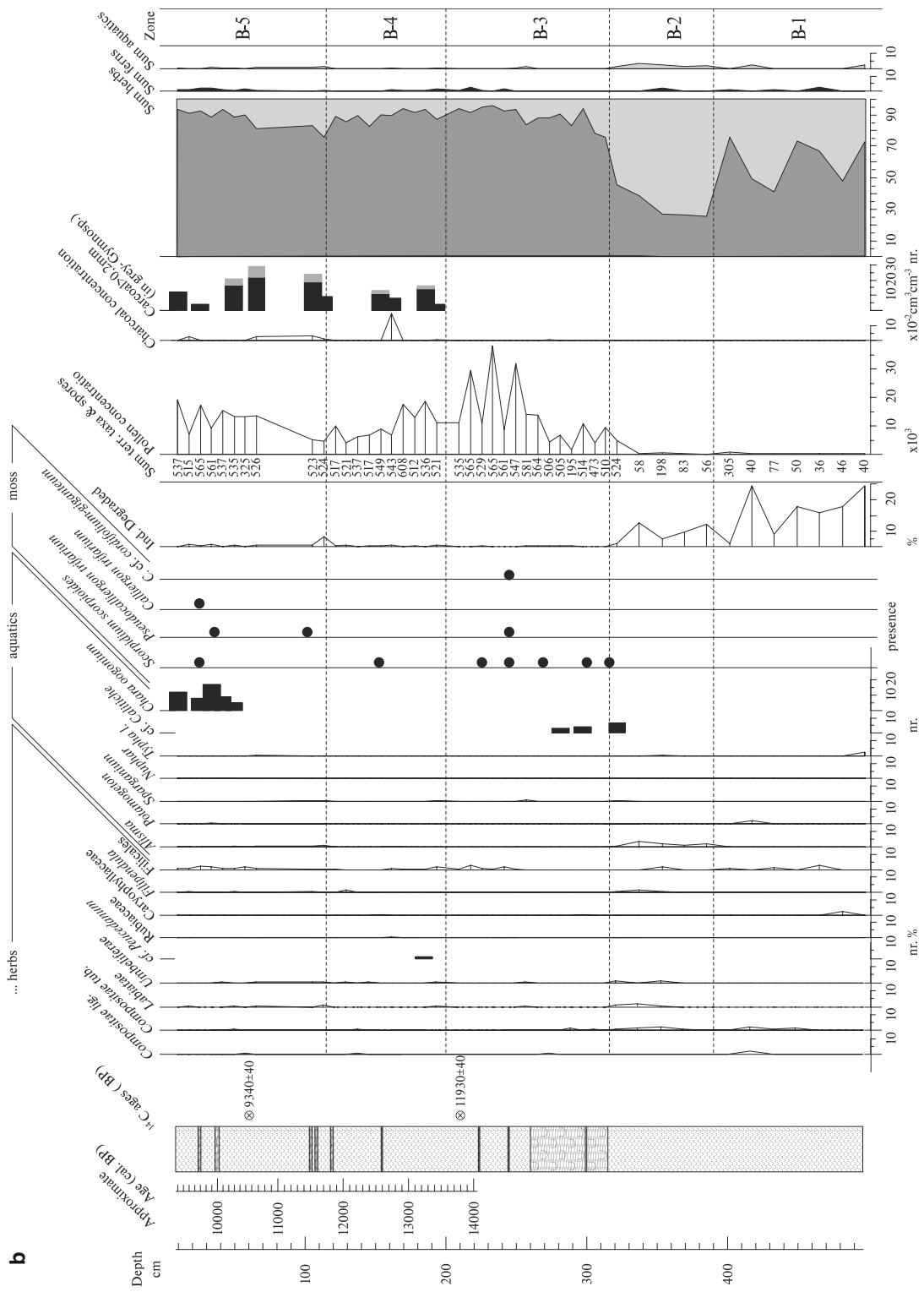
Fig. 4 Pollen and plant-macrofossil diagram of selected taxa. Pollen is presented as percentage data. Macrofossils are presented as number of macrofossils per 20 cm³ of sediment (*black columns*)

Fig. 4 continued

decline, whereas other tree taxa (*Picea, Larix, Tilia, Ulmus, Quercus, Corylus*) increase with short tree taxa declining in the upper half of the zone (160–115 cm). Finally, at the beginning of zone B-5 (115–0 cm), tree taxa start to increase again. In pollen zones B-4 (192 and 160 cm) and especially B-5 (104, 64, and 16 cm), charcoal peaks occur more frequently than in the lower part of the core.

Chironomids

A total of 28 chironomid taxa were identified in the Lake Bled sediment sequence (for taxonomic notes, see Electronic supplementary material), and the distribution of selected taxa is shown in Fig. 5. Optimal partitioning and CONISS analysis allowed us to recognise six zones along the core: Zone Ch-1 (496–312 cm) was devoid of chironomids below 336 cm. At the top of this zone, head-capsule concentrations were very low, and in most samples, not more than 20 head capsules were counted. Cold stenohermic taxa such as *Paracladius* and *Heteotrissocladius* were present. At the top of the zone, warm-adapted *Chironomus antracinus* and *Tanytarsus* B appear. Zone Ch-2 (312–264 cm) is characterised by the increase of *Micropsectra radialis* and the appearance of *Paratanytarsus penicillatus* and several species of the cold stenothermic *Heterotrisocladius*. At the beginning of the zone Ch-3 (264–200 cm), a decline in *M. radialis* coincides with an increase in *P. penicillatus*. Appearing for the first time are *Chironomus plumosus* and *Arctopelopia*. Zone Ch-4 (200–168 cm) is characterised by the decrease of *M. radialis* and *Ch. antracinus,* and the increase of *Cricotopus* B, and specially *Arctopelopia* and *Parakiefferiella*. In zone Ch-5 (168–120 cm), *Cricotopus* B reaches its maximum value. In Zone Ch-6 (120–90 cm), there is a decrease in the number of head capsules. The zone is characterised by the increase of *M. radialis* and the decease of *P. penicillatus, T. chineyensis, Arctopelopia* and *Cricotopus* B. In zone Ch-7 (90–0 cm), there is a marked drop in *M. radialis* mirrored by the increase of *P. penicillatus*.

Cladocera

Very few remains of Cladocera (always >10 remains g^{-1}) were found in the sediment, and only head shields and valves were used to identify them to the species level. In total, only four taxa of Cladocera (all species are benthic) were detected along the core: *Acroperus harpae*, *Alona affinis*, *Alonella nana* and *Chydorus sphaericus* (Table 2). No Cladocera remains were present below the depth of 272 cm, and neither Ostracoda nor Mollusca were found below 320 cm. The most common species recovered in most of the samples up to the depth of 272 cm was *Alona affinis,* found in 10 samples (out of 13). The section between 48 cm and the top of the core is characterised by very poor Cladocera assemblage, with no remains or very low concentrations of *A. affinis* and *A. harpae*.

Discussion

Oldest Dryas, undated, presumably > ca. 14,800 cal yr BP (496–260 cm)

The isotope values from the deepest part of the core below ca. 300 cm are influenced by micritic, allochtonous carbonates, transported into the lake from the surrounding watershed; therefore, they cannot be used to determine temperature (Lister 1988; Finsinger et al., 2008). Below 336 cm, no biological remains were found, except for pollen in very low concentrations. This absence of fauna could be related to the low percentage of organic matter and extremely cold waters, making insufficient food for animals to survive. Soon after, at 325 cm, macrofossil remains of *Callitriche* indicate very shallow water at the coring point. A rather high percentage of herbaceous pollen (e.g. Poaceae) and xerophytes (∼10–50%, e.g. Chenopodiaceae and *Artemisia, Pinus* stays around 50%, *Picea* goes up to almost 10%, Fig. 4a and 6) suggests that the landscape was rather open, presumably due to cold and dry climate. Sporadic pollen (but no macrofossils) of broad-leaved tree taxa such as *Quercus, Ulmus, Tilia, Carpinus, Acer* and *Fagus* probably does not reflect local vegetation and can be linked to two possible sources: either long-distance transport or reworking from older sediment. If we compare Lake Bled palaeoecological record with other study sites in northern Italy and southern Switzerland (e.g. Lago di Origlio, Lago Piccolo di Avigliano and Lago della Costa with local presence of Larix and Betula in LGM, Kaltenrieder et al., in press a), a similar silty clay is visible above glacial
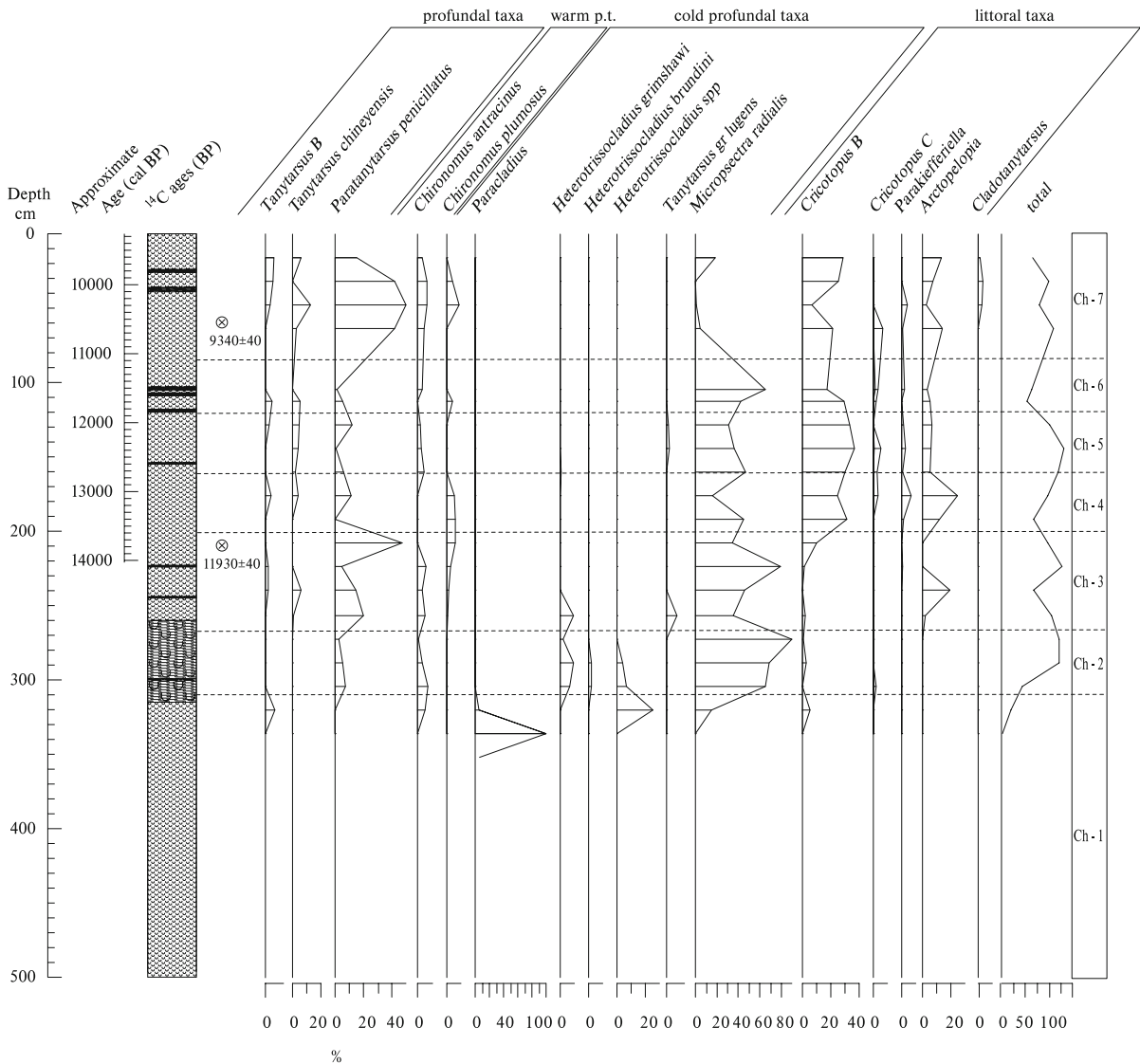
Fig. 5 Chironomid stratigraphy. Data are presented as percentage of relative abundance plotted against depth (cm). Only selected taxa are shown

till (at ca. 18,000 cal yr BP), after glacial retreat. Pollen, stomata and plant-macrofossil data from those study sites suggested that before 16,000 cal yr BP, the lowlands of northern Italy and southern Switzerland were not yet covered by dense forest vegetation (Vescovi et al., 2007, Table 3). A similar vegetation, namely an herb-dominated steppe tundra, probably with some shrubs of *Salix* and *Betula*, was growing also around Lake Bled. The presence of *Pinus* and *Picea* trees cannot be completely ruled out, although

plant macrofossils, proving that they were growing in the vicinity of the lake, were not found.

Results from the Lake Bled core during the Oldest Dryas are in accordance with palaeoclimatic research based on a simple glacier-flow model and statistical glacier-climate models of the Gschnitz glacier (Ivy-Ochs et al., 2006b) suggesting that during the Gschnitz cold period (from 19,000 to 18,000 cal yr BP, coinciding with Heinrich 1 ice rafting event), the precipitation was about one-third of modern-day
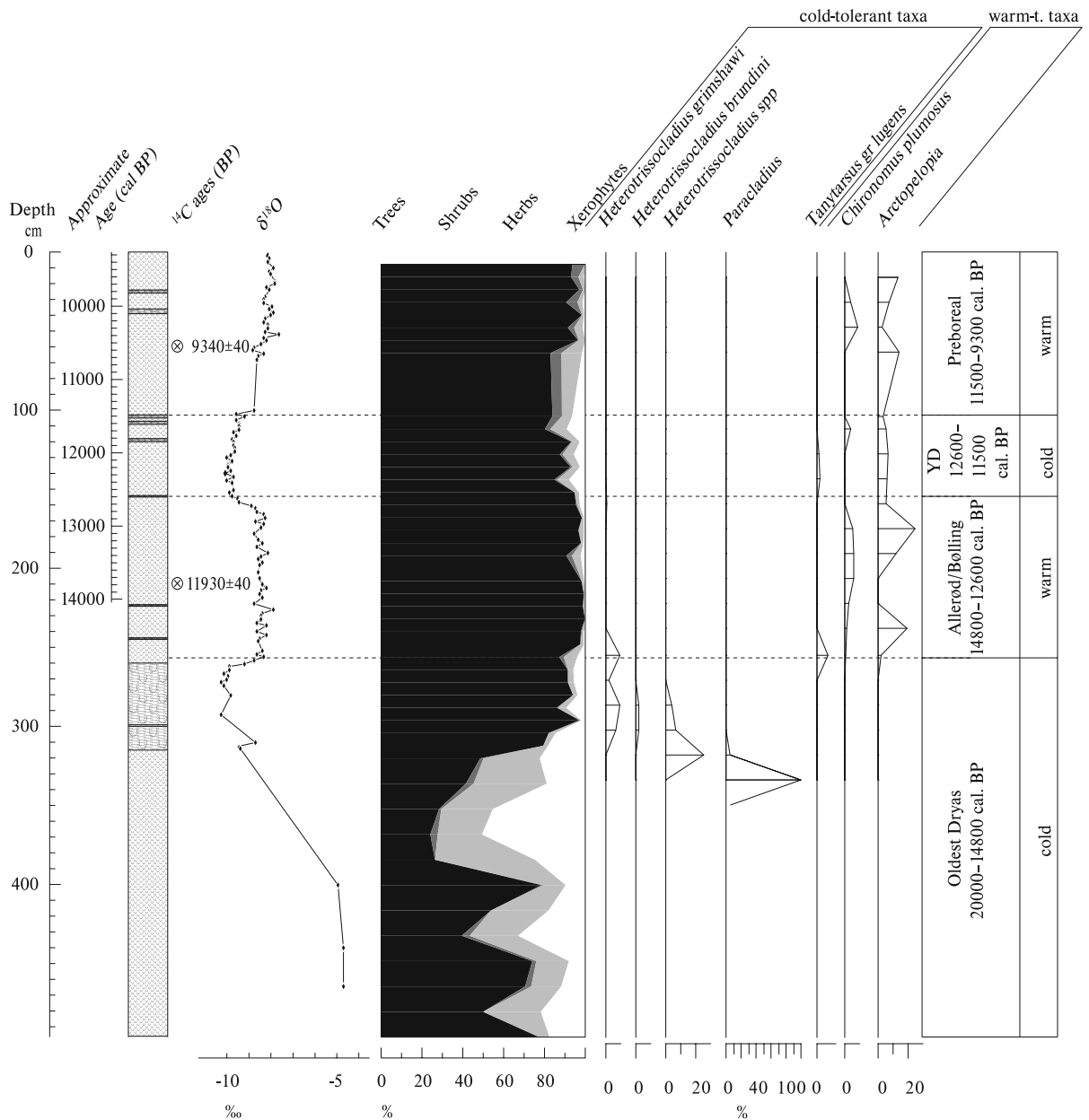
Fig. 6 Comparison of selected multi-proxy data (stable isotopes-$\delta^{18}O$, pollen and chironomid—in percentages) plotted against depth and estimated age

values, and summer temperatures were around 10°C lower than today (Ivy-Ochs et al., 2006a; Kerschner & Ivy-Ochs, 2008). Also, pollen- and chironomid-inferred reconstructions of Oldest Dryas episode for Lake Lautrey (E France) suggest a 3.0–5.5°C lower temperature of the warmest month than today and a drier climate (Peyron et al., 2005, Table 3). Similarly,

drier Late-glacial climate was suggested for eastern-central Europe by quantitative, pollen-based methods (Feurdean et al., 2008).

Later on (at 315 cm depth), the palaeoecological record of Lake Bled changes significantly with negative $\delta^{13}C$ values, and $CaCO_3$ (most probably of biogenic origin, as suggested by the appearance of

Table 2 Cladocera remains (presence/absence analysis) and some other groups of organisms (mollusca, ostracoda) from Lake Bled

No. of sample	Depth (cm)	Acroperus harpae	Alona affinis	Alonella nana	Chydorus spahericua	Ostracoda	Mollusca	Mosses
1	16	X	X			X		
2	32					X		
3	48					X	X	
4	64	X	X	X	X	X	X	
5	112	X	X			X	X	
6	128	X	X			X		
7	144		X			X		
8	160	X	X	X		X		
9	176	X	X			X		
10	192		X			X		
11	208		X			X		
12	224					X		X
13	240	X	X			X		
14	256		X			X		
15	272		X			X		X
16	288							X
17	304					X		X
18	320					X		
19	336							
20	352							
21	368							
22	384							
23	400							
24	416							
25	432							
26	448							
27	464							
28	480							
29	496							

ostracoda and *Callitriche* macrofossils) increases to 80%. Low $\delta^{18}O$ values (−10.5‰) indicate low temperatures. However, climate conditions were rather favourable (increased availability of moisture) and supported the growth of macrophytes, as suggested by the presence of a 55-cm thick *Scorpidium scorpidioides* moss layer at a depth of 315–260 cm, which was most probably growing 'in situ'. In Slovenia today, this moss grows in marshy areas on wet soil or in shallow (<1 m depth) permanent wet pools (Martinčič, 1996). However, from the literature, it is also known that *Scorpidium* spp. can grow in shallow lakes up to 20-m depth (Light & Smith

1976). All moss taxa discovered in Lake Bled tolerate various climatic conditions, and can be found from subarctic to southern Europe today (with the exception of the Mediterranean), at 250–1200 m a.s.l. The chironomid assemblage consists of a typical cold-profundal fauna represented by *Micropsectra radialis* and several species of genera *Heterotrissocladius* and *Paracladius*, typical for well-oxygenated waters. All Cladocera remains are present in a much lower concentration than in present-day samples from other Slovenian lakes (Brancelj et al., 2002). All are benthic and very eurytopic (ubiquitous), tolerant of high oscillations of physical and chemical

Table 3 Comparison of environmental change at Lake Bled with some other European lakes

	Lake Bled (Slovenia) this study 475 m a.s.l.	Lake Gerzensee (Switzerland) Schwander et al. (2000), Wick (2000), von Grafenstein et al. (2000) and in prep., Lotter et al. (2000) and in prep. 603 m a.s.l.	Lake Lautrey (E France) Heiri and Millet (2005), Peyron et al. (2005) 877 m a.s.l.	N Italy, S Switzerland Vescovi et al. (2007)	Lake Accesa (Italy) Magny et al. (2006)
Preboreal After 11,500 cal yr BP (105–0 cm)	Warmer and wetter Mixed pine-broad-leaved forest High water levels with abundant vegetation, mesotrophic/ eutrophic lake and lower oxygen concentrations	Rapid warming, summer temperature 11.5–15°C Immigration of *Corylus*, *Ulmus*, *Quercus*	Warmer and wetter, summer temperatures: 14–17.5°C, annual precipitation: >450 mm, *Betula-Pinus* forest	Thermophilous tree taxa expanded	Warmer, deciduous *Quercus-Corylus*-NAP zone, first cold and low lake levels, later highstand
Younger Dryas 12,600–11,500 cal yr BP (155–105 cm)	Cold and dry Slightly more open landscape (Chenopodiaceae and *Artemisia* increase) Low water levels, but still well-oxygenated water	Depression in the oxygen isotopes of bulk sediments and of ostracods, as well as in tree pollen. Summer temperatures 9–10°C	Onset colder, later warmer, drier, summer temperatures: 12–14°C, annual precipitation: 300–450 mm, increase of NAP (*Artemisia*, Poaceae)	Cooling, forest cover diminished, herbs, xerophytes increase	Colder, Poaeceae-*Artemisia*-Chenopodiaceae zone, after 12,150 cal yr BP drier, increased microcharcoal
Late-glacial interstadial (Allerød, Bølling) 14,800–12,600 cal yr BP (260–155 cm)	Warmer Mixed woodland (*Betula*, *Larix*, *Picea*, *Quercus*) warm, well-oxygenated water, rich in vegetation Towards the end of this time period, climate gets colder and dryer	Very rapid warming at 14670 cal yr BP, then minor fluctuations Summer temperatures 12–16°C Open woodlands of juniper, sea-buckthorn and then tree birches Immigration of pine 14,000 cal yr BP. Minor lake-level fluctuations	Warmer, summer temperatures: 16°C, annual precipitation: 800 mm, increase of *Juniperus* and *Betula*, later also *Pinus*	Ca. 14,800–14,400 cal yr BP change of forest structure and density due to warming. Palughetto: expansion of *Pinus*, *Betula*, *Larix*, *Picea*, *Quercus*, mixed oak forest at 13,000–12,600 cal yr BP	Warmer, deciduous oak zone, colder and lower lake levels at 14,300–14,200 and 13,900–13,700 cal yr BP, cold and high lake level at 13,400–13,100 cal yr BP
Oldest Dryas 20,000–14,800 cal yr BP (496–260 cm)	Cold and dry, becoming wetter after 16,000 cal yr BP Open, predominantly herbaceous vegetation. Well-oxygenated lake water, rich in vegetation and increase of trees after 16,000 cal yr BP	Cold and dry, shrub tundra: summer temperatures ≤11°C.	Cold and dry, summer temperatures: 10–12.5°C, annual precipitation: 200–300 mm, open, herbaceous landscape (*Artemisia*, Poaceae)	Herb-dominated steppe tundra, open woods and shrublands (*Juniperus*, *Betula*, *Larix*, *Pinus cembra* from 17,500 cal yr BP, 16,000 cal yr BP: afforestation (*Pinus*, *Betula*) in lowlands, treeline ascended to 800–1000 m a.s.l.	Cold, *Artemisia*-Poaceae-*Juniperus* zone

parameters. *Alona affinis* is common in different types of stagnant water, but it prefers an environment rich in vegetation, either algae or macrophytes (e.g. dense moss stands growing in the lake). This suggests that although climatic conditions were still cold, lake water was well oxygenated and warm enough to support the growth of macrophytes.

Better pollen preservation, as well as, an increase of *Pinus* and decline of herbaceous taxa indicate moist conditions. Arboreal pollen (mostly *Pinus*) starts to increase above 315 cm, but the first tree macrofossils (*Betula* catkins, demonstrating that *Betula* was present close to the lake margin) occur only at 270 cm. Although the percentage values for *Pinus* are rather high (75–95%, >14,000 cal yr BP), surprisingly no macrofossils were discovered in the core. It is possible that either only very few pine trees were growing in the vicinity of the lake, or pine pollen came from long-distance transport. Local absence of plants cannot be proved by the absence of macrofossils for taphonomic reasons, as they have much more limited dispersal than pollen, and macrofossils of terrestrial taxa tend to be under-represented in fossil assemblages (Birks, 2003; Jackson & Booth, 2007). *Pinus* pollen accumulation rates (PAR) in dated section of the core (with exception of 13,300–12,800 cal yr BP interval) are, namely, below the threshold value for the presence of local pine (= 500 pollen grains $cm^{-2} yr^{-1}$) according to the modern PAR studies in the Alps and in Scandinavia (van der Knaap et al., 2001; Seppä & Hicks, 2006). Taphonomic reasons for the absence of *Pinus* macrofossils are not excluded, especially in the depth between 315 and 260 cm characterised by a moss layer. Such moss vegetation, if growing in very shallow water, can also play a role of 'filter' for the macrofossils. No pine wood or charcoal was found in the vicinity of the lake, but *Pinus* wood, discovered in Late-glacial sediment of the Soča River valley ca. 50 km to the west, was radiocarbon dated to 12,450 ± 70 BP (14,205–14,959 cal yr BP) (Culiberg, 1991). A similar change in vegetation composition at 16,000 cal yr BP is noticeable in northern Italy, with pollen, stomata, and plant-macrofossil data indicating afforestation by *Pinus* and *Betula* (and termophilous taxa at Lago della Costa, Kaltenrieder et al., in press b) between 16,000 and 15,800 cal yr BP, and the treeline shifted to 800–1000 m a.s.l. due to an increase in temperature (Vescovi et al., 2007).

Late-glacial interstadial, undated before 13,790 cal yr BP, presumably ca. 14,800–12,600 cal yr BP (260–155 cm)

Climatic warming at the beginning of the Late-glacial interstadial is suggested by $\delta^{18}O$ increase by 1.5–2‰ to ca. −8.5‰ (Fig. 3). Warmer condition is also suggested by the pollen and plant-macrofossil record (Figs. 4a, b). Pollens of tree taxa (e.g. *Betula*) and *Larix* increase, whereas plant-macrofossil records suggest that *Larix* and *Betula* (after 13,000 cal yr BP also *Picea*) were growing on the lakeshore. The cold-adapted chironomid *Micropsectra radialis* and *Heteroterissocladius* spp. disappear and warm-adapted fauna, such as the representatives from the Pentaneurini tribe, appear. A mixed warm-adapted chironomid fauna including *Arctopelopia, Dicrotendipes, Chironomus pulmosus* and *Tanytarus chineyensis* appears, indicating that although the lake became warmer and probably more productive, it was still well oxygenated. Also, the presence of littoral-dweller cladoceran *Acroperus harpae*, together with *Alona affinis*, which is a common inhabitant in modern littoral vegetation, suggests warm water. Similar environmental change was also detected in northern Italy and southern Switzerland between 14,800 and 14,400 cal yr BP, when abrupt changes in forest composition and density were associated with climatic warming (von Grafenstein et al., 2000; Lowe et al., 2001; Heiri & Millet, 2005; Vescovi et al., 2007), which is also in accordance with northern-hemispheric reconstructions (Björck et al., 1998; Lowe et al., 2008). Besides, pollen- and chironomid-inferred temperatures for the Lake Lautrey suggest strong climatic warming and increase of precipitation by that time (Peyron et al., 2005). Also pollen-based climate estimations for northwestern Romania suggest summer temperatures close to modern values (Feurdean et al., 2008). Further in south east, the increasing moisture availability is recorded by the palynological and plant macrofossil assemblages of the Rila, Pirin Mountains (Bozilova et al., 1996; Stefanova & Ammann, 2003) and Thracian Plain (Magyari et al., 2008). At Lake Bled, the local presence of *Picea* in the late Alleröd, as indicated by macroremains, demonstrates the more easterly position of refugia in the southeastern Alps and southwestern Carpathians, as indicated by van der Knaap et al. (2005), Latałowa & van der Knaap (2006), Ravazzi et al. (2006), Vescovi et al. (2007) and Feurdean et al. (2007).

A change in vegetation composition also occurs at ca. 13,800 cal yr BP. The decrease of *Pinus* and the increase of *Quercus*, *Tilia*, *Ulmus*, as well as *Artemisia* (drier) and *Picea* could be linked to warmer conditions, although stable isotope record at Lake Bled does not show significant increase of δ^{18}O. A sharp increase of chironomid larvae of *Cricotopus* B at the same time suggests that the lake levels decreased. Again, similar vegetation change and lowering of lake levels occurred over a wider area on the southern side of the Alps (Vannière et al., 2004; Magny et al., 2006; Vescovi et al., 2007).

After 12,800 cal yr BP, δ^{18}O started to decrease, suggesting climatic cooling. Climate was possibly also getting drier, as suggested by the increase of microcharcoal concentrations, the decline of pollen of tree taxa, the increase of xerophytes and the presence of littoral chironomids *Parakiefferiella*, *Arctopelopia* and *Cricotopus*.

Younger Dryas, 12,600–11,500 cal yr BP (155–105 cm)

Oxygen-isotope records indicate that both the onset and termination of Younger Dryas as recorded in the presented Lake Bled record are remarkably sharp (Fig. 3). Climatic conditions during the Younger Dryas were cold (δ^{18}O −9.7‰) and dry, as suggested by the increase of Chenopodiaceae and *Artemisia*, and the recurrent presence of moss layers. Chironomid taxa are mostly littoral, suggesting that throughout the YD the lake was probably shallow. The presence of *Alonella nana*, which is common in the environment rich in organic debris and well oxygenated water, is also an indication of cold and dry conditions. Among the trees, *Larix* (cold and drought adapted species, also present at other sites in central and eastern Europe, e.g. Willis et al., 2000; Feurdean et al., 2007) is more abundant than *Quercus*, as in northern Italian pollen records (Vescovi et al., 2007). The palaeoecological records at Lake Lautrey (Peyron et al., 2005) and Gerzensee (von Grafenstein et al., 2000; Lotter et al., in prep.) also suggest colder and drier climate, although lake level at Gerzensee was 1.7 m higher than today (0.4 m higher than during the Alleröd). This is probably due to less vegetation and longer season of frozen soils, causing reduced percolation of water to groundwater and increased direct runoff into the lake. The palaeoecological record of Lake

Kremensko-5, Pirin Mountains covering YD show also increasing aridity and remarkable retreat of the *Pinus, Picea* and *Betula* curves related to colder climatic conditions (Atanassova & Stefanova, 2003; Stefanova et al., 2006). Also, palaeoclimatic modelling based on simple glacier-flow model and statistical glacier-climate models of Egesen maximum advance (ca. 12,400–12,300 cal yr BP) suggest that after 12,700–12,600 cal yr BP, summer temperature was ca. 3.5°C lower, with 20–30% less precipitation in the interior of the Alps. Winters were cold and dry, but summers were presumably only moderately drier or even wetter than today (Kerschner & Ivy-Ochs, 2008).

Preboreal, 11,500–9300 cal yr BP (105–0 cm)

Climatic warming at the Late-glacial–Holocene transition is inferred from a sharp increase of δ^{18}O to ca. −8‰. Tree taxa including *Betula, Fagus, Tilia, Quercus, Carpinus betulus, Carpinus orientalis/Ostrya, Alnus, Acer, Fraxinus excelsior* type, *Ulmus, Salix, Corylus* and *Abies* started to increase, whereas Chenopodiaceae and *Artemisia* declined. The increase of profundal chironomids *Micropsectra radialis* and the decrease of littoral *Cricotopus* at the beginning of the zone may indicate an increase of water level. However, at 11,200 cal yr BP, *Micropsectra radialis* decreases sharply, and all the fauna typical for well-oxygenated water disappears. Both species of *Chironomus* reach their maximum values. This is the typical situation in a mesotrophic/eutrophic lake that only support *Chironomus*, and other species adapted to survive under low oxygen concentrations (Hofmann, 1986; Walker, 2001). At ca. 10,400 cal yr BP, the conditions must have been favourable for cladocera, as it is the only interval when all the four taxa (*Allona affinis, Acroperus harpae, Allonella nana* and *Chydorus spahericus*) coexist. This assemblage is quite different from present-day cladoceran assemblages at Lake Bled, which are more planktonic (*Daphnia hyalina*, *D. hyalina* × *galeata*, *Bosmina longispina, Diaphanosoma brachyurum* and *Scapholeberis kingi*) (Brancelj, 1991), whereas benthic Cladocera are reduced due to the eutrophic condition of the lake. *Allonella nana*, which is present in the core, has not yet been found in the present-day fauna of Lake Bled (Brancelj, unpublished). The species is quite common in the littoral zone of oligotrophic–mesotrophic coldwater lakes. This conditions are no more existing in

Lake Bled, which is mesotrophic–eutrophic warm water. Palaeoecological research at Lakes Gerzensee and Lautrey suggest a temperature rise of ca. 3°C at the Holocene transition in less than 50 years (Lotter et al., 2000; Lotter et al., in prep.; Schwander et al., 2000; von Grafenstein et al., 2000; Peyron et al., 2005).

In summary, at the beginning of Preboreal, the climate became warmer and wetter, with a mixed pine-broad-leaved forest around the lake. The water level increased, and the lake became deep again, holding favourable conditions for Cladocera and profundal chironomid assemblages.

Conclusions

Late-glacial terrestrial and aquatic ecosystems at Lake Bled were very dynamic, and several proxies responded to climatic change simultaneously, enabling more detailed reconstruction of environmental changes. Both ecosystems, i.e. terrestrial and aquatic, responded to changes of temperature, precipitation and hydrological conditions; therefore, our assumptions about past climate (e.g. temperature) are affected also by local (e.g. lake level) conditions.

Whereas in the Oldest Dryas the climate was cold and dry, later a trend towards wetter and warmer climate occurred, with the beginning of the precipitation of biogenic carbonates, suggested by the appearance of ostracods and an increase of aquatic plant macrofossils (e.g. *Callitriche*). By that time, Lake Bled water was well oxygenated and rich in vegetation (e.g. *Callitriche, Scorpidium scorpidioides*), and the lake was probably surrounded by predominantly herbaceous vegetation, with only very small populations of shrub and tree taxa. The climate became warmer, with an increase of tree cover (*Betula, Larix*) and warmer chironomid fauna, suggesting a well-oxygenated, more productive lake. Further climatic warming at 13,800 cal yr BP led to increase of broad-leaved tree taxa (*Quercus, Tilia, Ulmus*) and *Picea* and lower lake levels, as indicated by Chironomid record.. Towards the end of this interstadial, the climate became colder and drier, as suggested by the δ^{18}O record, increase of xerophytes and microcharcoal and lower lake levels (presence of littoral chironomids) after 12,800 cal yr BP. A warmer and wetter Preboreal climate after 11,500 cal yr BP enabled the spread of broad-leaved

tree taxa, whereas the lake became deeper (increase of profundal Chironomids) and mesotrophic/eutrophic, with lower oxygen content.

The local presence of a wide variety of tree taxa is not a surprise, given the proximity of Slovenia to full-glacial refugia (e.g. Willis & van Andel, 2004; Cheddadi et al., 2006). Plant macrofossils suggest the local presence of *Betula* (probably from ca. 15,000 cal yr BP), *Larix* (probably ca. 14,500 cal yr BP), *Picea* (ca. 13,000 cal yr BP), *Populus* (ca. 12,000 cal yr BP) and *Ephedra* (probably ca. 14,700 cal yr BP), but surprisingly, no *Pinus* macrofossils were found. Although general vegetation development at Lake Bled is comparable to that of the neighbouring regions (e.g. northern Italy; Vescovi et al., 2007, Hungary; Willis et al., 1995, 2000), the stable-isotope record, in contrast to many lakes south of the Alps (Eicher, 1987), shows a distinct negative Younger Dryas δ^{18}O signal (colder climate). A similar stable-isotope record is characteristic only for Lago Piccolo di Avigliana (Finsinger et al., 2008).

Future research should focus also on multi-proxy studies of Late-glacial and Holocene environmental change and human versus climatic impact on the environment at Lake Bled and other study sites in the region to better understand the present and future environmental changes.

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