

# Vegetational and agricultural dynamics at Burgäschisee (Swiss Plateau) recorded for 18,700 years by multi-proxy evidence from partly varved sediments

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**Abstract** Little is known about the timing and the vegetation dynamics shortly after the Last Glacial Maximum (LGM) on the Swiss Plateau 19,000–15,000 cal BP. Subsequent Late Glacial and Holocene vegetation changes are better known; however, it is unclear if the few available palynological and macrofossil records are able to capture the entire vegetation variability of the region. A new palaeoecological multi-proxy study using pollen, spores, charcoal and X-ray fluorescence (XRF) from Burgäschisee (Swiss Plateau, 465 m a.s.l.) is applied to reconstruct vegetation, fire and land use for the past 19,000 cal years. Steppe tundra vegetation established at c. 18,700 cal BP only c. 300 years after the end of the LGM and deglaciation. A shift from steppe tundra (*Artemisia*, *Helianthemum*) to shrub tundra (*Betula nana*, *Salix*, *Juniperus*) with sporadic tree *Betula* stands occurred around 16,000 cal BP, most likely in response to climate warming after the end of Heinrich event 1. Abundant spores of coprophilous fungi (*Sporormiella*, *Cercophora*) may reflect the presence of Pleistocene large herbivores (e.g. *Mammuthus primigenius*, *Bison bonasus*, *Rangifer tarandus*). Afforestation started more than 2,000 years later with *Juniperus* and tree *Betula* around 14,500 cal BP. Mixed

*Betula* and *Pinus sylvestris* forests persisted until 10,800 cal BP, when mixed elm forests expanded into the region in response to climate warming. Around 8,200 cal BP, mesophilous *Fagus sylvatica* and *Abies alba* partly replaced more heliophilous species in the forests, when climate became less continental and more moist. Pollen of *Cerealia*, *Plantago lanceolata* and other crops and weeds suggest that agricultural activities became significant during the Neolithic around 6,500 cal BP (4550 cal BC). Archaeological findings from Neolithic pile dwellings around 5,950 cal BP (4000 cal BC) indicate local settlements around the lake. The lake sediments are laminated for most of the last c. 6,800 years. With two independent proxies (XRF and pollen), we can demonstrate that these laminations are annual, suggesting short-term mixing of the lake water due to a more open landscape in response to land use. Our study shows that the annually laminated (varved) sediments from Burgäschisee have a great potential for high-resolution multi-proxy analyses covering the past c. 6,800 years. They can provide accurate ages of cultural phases that might be compared with dendrochronologically dated evidence from lake dwellings.

**Keywords** Fire history · Heinrich event 1 · Human impact · LGM · Varves · Vegetation history

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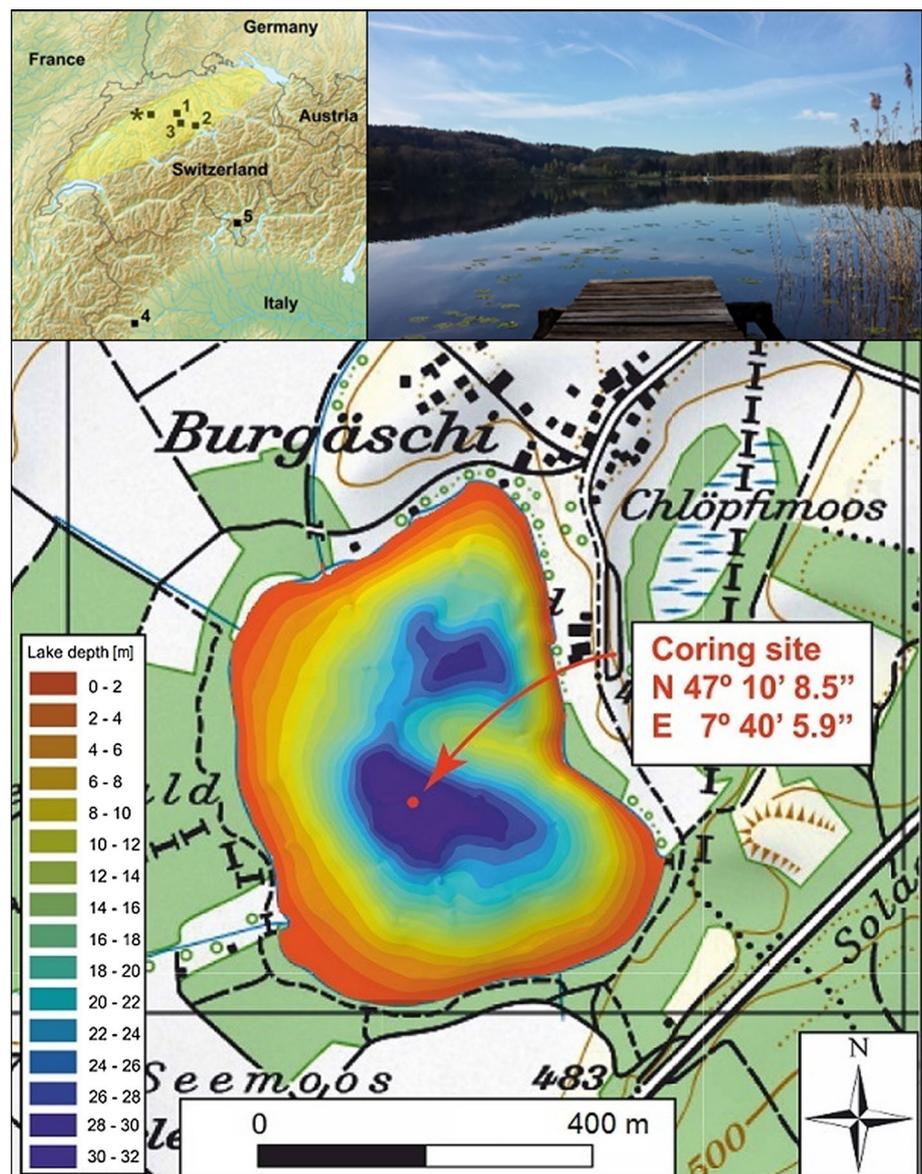
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## Introduction

The Swiss Plateau is a densely populated area that stretches from Lake Constance in the East to Lake Geneva in the West. It forms a complex mosaic of forests, agricultural lands, lakes, rivers and settlements. This lowland region with its rather favourable climate for agriculture is also at the origin of early Neolithic farming societies in Switzerland with more or less permanent settlements. Many archaeological

**Fig. 1** Overview map (top left) with the location of the Swiss Plateau (yellow area), Burgäschisee (asterisk) and study sites for oldest radiocarbon dates in sediment records: 1 Wauwilermoos (Beckmann 2004), 2 Rotsee (Lotter and Zbinden 1989), 3 Soppensee (Lotter 1999), 4 Lago Piccolo di Avigliana (Larocque and Finsinger 2008), 5 Lago di Origlio (Tinner et al. 1999). Photograph of Burgäschisee (top right). Seismic map of the study site with the coring location (bottom). Green areas around the lake forests, green empty circles single trees (topographic maps: © swisstopo)



findings across the whole Swiss Plateau show that it has been successively populated ever since (Hafner and Suter 2003; Stöckli 2016), emphasizing the importance of the lowlands for past civilizations.

Palaeobotanical and palaeoecological studies on the Swiss Plateau have a long tradition (e.g. Welten 1946; Ammann 1989; Lotter 1999; Wehrli et al. 2007). Many of these studies focused on the Late Glacial environmental history (e.g. Ammann and Tobolski 1983; Ammann et al. 1994) but also the Holocene has been intensely investigated (e.g. Ammann et al. 1996; Haas and Hadorn 1998; Tinner and Lotter 2006; Gobet et al. 2017). The temporal evolution of the vegetation in the Late Glacial and the Holocene is well established for the Swiss Plateau (Ammann and Lotter 1989; Lotter 1999; Wehrli et al. 2007). However, the timing and onset of the deglaciation and the initial vegetation development north of

the Alps is still unclear (Eicher 1987). In the Southern Alps and their forelands *Juniperus* shrublands (pollen, stomata finds) established c. 18,000–17,500 cal BP in the formerly glaciated areas, c. 3,000 years before a similar expansion occurred north of the Alps (Vescovi et al. 2007). Similarly, afforestation in the Southern Alps and their forelands preceded that in the Northern Alps and the Swiss Plateau by about 2,000 years (e.g. Vescovi et al. 2007; Pini et al. 2016). While north of the Alps forest vegetation established in response to the Bølling warming, south of the Alps similar vegetation dynamics were caused by warming after Heinrich event 1 (Samartin et al. 2012). We assume that pre-Bølling warming (e.g. at 19,000–17,000 and 16,500–16,000 cal BP) also had an impact on the vegetation north of the Alps, but this issue has not been investigated so far.

Burgäschisee lake sediments are an exceptional archive in Central Europe covering more than 18,700 years of vegetation history including most of the settlement phases during the last c. 6,800 years. In the 1940s, the site was palynologically investigated by Max Welten, resulting in a more than 15,000 years long vegetation reconstruction (Welten 1946). The lake shore settlements were investigated intensively in the middle of the last century including an on-site palynological transect through one of the settlements (Welten 1955, 1967).

Annually laminated sediments are rare (Geyh et al. 1971; Zolitschka 1998; Swierczynski et al. 2013). For the Swiss Plateau, only very few annually laminated sediment sequences are known and the laminated parts usually end before the onset of the Neolithic or cover only the last few decades (Welten 1944; Lotter 1999; Monchamp et al. 2016). New subaquatic coring devices allowed for the coring of the deep centre of Burgäschisee offering the unique opportunity to retrieve sediments with annual layers and therefore to investigate human impact with high chronological precision and resolution. In this study we present a modern multi-proxy environmental reconstruction from Burgäschisee on the Swiss Plateau. The aims of the study are (1) to better understand the deglaciation timing and the vegetation dynamics during the Oldest Dryas (19,000–15,000 cal BP), (2) to compare the vegetation and fire history of the last 19,000 years with other lowland sites north and south of the Alps to provide novel well-dated information, and (3) to prove the annual structure of the sediments with pollen and XRF data.

## Study site

Burgäschisee is a small eutrophic lake at 465 m a.s.l. (47°10'8.5"N, 7°40'5.9"E) on the Swiss Plateau which geologically belongs to the generally carbonatic-rich molasse region with abundant sandstones between the Jura mountains and the Alps (Schmid et al. 2004, Fig. 1). The lake is named after the village Burgäschi which is located on the north western lake shore. It has a surface area of 21 ha, a maximum water depth of 31 m and a hydrological catchment area of 319 ha (Guthruf et al. 1999). Four small inflows feed the lake in the southwest and one outflow leaves the lake in the north (Müller-Beck 2005a). In 1943, the lake level was lowered by up to 2 m to drain the wetlands in the surroundings and create agricultural land (Arn 1945). Since 1977, deep water has been mixed with oxygen to improve water quality (Ambühl and Stumm 1984). The climate at Burgäschisee is oceanic. The mean annual temperature is 9.1 °C and the annual rainfall averages out at 1,088 mm (data from Koppigen c. 6 km from Burgäschisee, © MeteoSchweiz). The warmest month is July with a mean temperature of

18.6 °C and the wettest months are May–August with more than 100 mm of precipitation per month.

Black alder (*Alnus glutinosa*) and common ash (*Fraxinus excelsior*) grow along the lake shores. Mixed beech (*Fagus sylvatica*) forests are dominant on the more elevated surroundings. The rest of the landscape is intensively shaped by agricultural activities. The lake, the shores and the wetlands around (e.g. Chlöpfmoos) are under nature protection and are partly used for leisure activities. About 18,500 years ago, the lake surface was c. six times larger than today (von Burg et al. 2011). Several findings from hunters' camps located along the former lake shores (e.g. Fürsteiner) can be attributed to the Magdalenian and the Late Palaeolithic c. 18,500–11,600 cal BP (16550–9650 cal BC; Wyss 1952; von Burg et al. 2011). In addition, Mesolithic sites from hunter-gatherers are known in the region (Wyss 1953). The first main archaeological excavation activities started in 1877 and 1902. After the lake level lowering in 1943, wooden piles from Neolithic settlements emerged. All of them were partly excavated in the middle of the last century (Müller-Beck 2005b; Wey 2012). New excavations devoted to the recovery of material culture and wood for dendrochronological dating are currently running at Burgäschisee within the interdisciplinary project "Beyond Lake Villages" (Swiss National Science Foundation, CR20IIL\_152862). So far, at least five settlements sites are known from Burgäschisee. One of these sites ("Burgäschisee-Ost") is part of the UNESCO World Heritage "Prehistoric pile dwellings around the Alps". Early and Middle Bronze Age archaeological findings are rare; however, Late Bronze Age settlements point to increased human activity in the region (Hodel et al. 2011). From the Iron Age onwards until today, the Burgäschisee region has always been occupied as shown by many finds, including Iron Age and Roman artifacts at the nearby Inkwilersee, a Roman storage building close to Burgäschisee and the remains of a church from the Early Middle Ages (Hodel and Bachmann 2011; Marti 2011).

## Materials and methods

### Seismic survey and coring

A high-resolution (3.5 kHz) reflection seismic survey was performed in July 2009 to find the most suitable spot for coring (avoidance of subaquatic landslides) and to understand the topographic structure of the lake basin (Fig. 1). In September 2009, three parallel sediment cores (Burg A–C), reaching a coring depth of 15 m, were retrieved from the deepest part of the lake with an UWITEC piston corer with a diameter of 60 mm. Since it was not possible to create a complete composite sediment core, a second coring

campaign was successfully performed in April 2014 to fill the gap (Burg I).

### Chronology

Sixteen radiocarbon dates on terrestrial plant macrofossils (Table 1), the Laacher See Tephra (LST) at 806.5 cm and the sediment surface (year 2009) were used for the age-depth model. The radiocarbon content of terrestrial plant remains was measured at the Laboratory of Ion Beam Physics at ETH Zurich, the Poznan Radiocarbon Laboratory and the Laboratory for the Analysis of Radiocarbon at Bern University using accelerator-mass-spectrometry (AMS). The radiocarbon dates were calibrated with the program Calib 7.1 (Stuiver and Reimer 1993) using the IntCal13 calibration curve (Reimer et al. 2013). A smooth-spline curve (smoothing 0.23) was calculated with the program clam 2.2 (Blaauw 2010) to assess the definite age-depth model (Fig. 2). The modelled curve runs within the  $2\sigma$  error range of the calibrated radiocarbon ages and the  $2\sigma$  confidence envelope of a generalized mixed-effect regression that includes sample depth and age uncertainties (Birks and Heegaard 2003; Heegaard et al. 2005).

### XRF and LOI analyses

XRF core scanning with an Avaatech core scanner was performed at a continuous 1 mm resolution. An area of 1 mm down-core and 12 mm cross-core was measured for 20 s per measurement with 10 kV (1500  $\mu$ A, no filter) and 30 kV (2,000  $\mu$ A, Pd-thick filter). In the end, the measurements for each sediment core segment were compiled to one composite record with a total length of 940.5 cm.

To determine the organic matter and the carbonate content, loss-on-ignition (LOI) on 108 samples was performed. 1 cm<sup>3</sup> of sediment every 8 cm were taken and treated following Heiri et al. (2001).

### Pollen and charcoal analyses

105 samples for pollen and microscopic charcoal analysis were retrieved from the sediment core from 11.4 m to the top. The standard sampling was 1 cm<sup>3</sup> every 8 cm. For the three lowest samples, 2 cm<sup>3</sup> were taken due to low pollen concentrations. The samples were treated with HCl, KOH, HF, acetolysis, sieved with a 0.5 mm sieve and mounted in glycerine, following standard methods (Moore et al. 1991). *Lycopodium* tablets were added before the chemical treatment for estimating microscopic charcoal, pollen and spore concentrations (Stockmarr 1971). Pollen and spores were identified using palynological keys (Moore et al. 1991; Beug 2004), photo atlases (Reille 1992) and the reference collection at the Institute of Plant Sciences at Bern University.

*Betula nana* pollen was separated from tree *Betula* pollen following Birks (1968) and Clegg et al. (2005). A total number of 212 terrestrial pollen types were identified. A pollen sum of > 500 terrestrial pollen grains per sample was counted. Pollen are presented in percentages calculated on the terrestrial pollen sum excluding *Cannabis sativa* pollen.

To test whether the laminations were varves, five light brown and four dark brown layers between 333.6 and 332.5 cm were scraped off under a binocular microscope following Welten (1944) and Lotter (1989) and were treated separately with the above mentioned standard methods. A pollen sum of >400 terrestrial pollen grains per sample was counted. These samples are presented in percentages of the terrestrial pollen sum according to their flowering season (Lauber et al. 2014). Microscopic charcoal particles >10  $\mu$ m were analysed and counted following Tinner and Hu (2003) and Finsinger and Tinner (2005).

The main diagram (Fig. 3) was separated into six local pollen assemblage zones (LPAZ) identified by the use of optimal sum-of-squares partitioning (Birks and Gordon 1985) with the program ZONE 1.2 (Juggins 1991). The statistically significant zones were determined with the program BSTICK following the broken-stick method (Bennett 1996). For a better separation of the lowest part, LPAZ Burg-1 was split up into two sub-zones (Burg-1a and Burg-1b) that were not statistically significant.

## Results and interpretation

### Seismic survey and bathymetry

The seismic signal could not penetrate the sediments probably due to gas accumulation. The bathymetry shows two c. 30 m deep basins separated by an east–west oriented ridge (Fig. 1). The slopes of the lake basin are steep with some slightly shallower parts in the east. The coring in 2009 (Burg A-C) and in 2014 (Burg I) took place in the deepest part of the southern basin at a water depth of 31 m.

### Sedimentation and lithology

The lowermost part of the sediment core (1,500–1,037 cm, 18,700 cal BP and older) consists of clay and sand layers. According to the age-depth model (Fig. 2), sedimentation rates are relatively constant between 18,700–4,000 cal BP. From 1,037–846 cm (18,700–14,500 cal BP), the sediment consists of silt without sandy layers. Probably as a consequence of the smooth topography and the absence of major inflows and big streams from melting glaciers (Müller-Beck 2005a), stable soil conditions were established shortly after deglaciation. From 846 cm (14,500 cal BP) upward, the sediment consists of fine detritus gyttja, partly laminated

**Table 1** Radiocarbon dates and calibrated ages from the Burgäschisee record

Lab. code	Depth (cm)	Material	$^{14}\text{C}$ age (BP) <sup>a</sup>	Age (cal BP) <sup>b</sup>	Age 2 $\sigma$ range (cal BP) <sup>b</sup>	Modelled age (cal BP) <sup>c</sup> in diagrams
ETH-43940 <sup>e</sup>	154	Deciduous tree leaf	445 ± 25	504	479–529	503
ETH-43941 <sup>e</sup>	267–268	Deciduous tree leaf	1,340 ± 25	1,245	1,187–1,303	1,250
ETH-43942 <sup>e</sup>	338–341	<i>Betula</i> leaf	2,145 ± 30	2,156	2,008–2,303	2,148
ETH-43943 <sup>e</sup>	448–450	<i>Betula</i> leaf; <i>Fagus sylvatica</i> bud scale	3,080 ± 25	3,294	3,225–3,363	3,287
ETH-43944 <sup>e</sup>	498–499	<i>Abies alba</i> needle	3,675 ± 30	3,999	3,908–4,089	4,013
ETH-43945 <sup>e</sup>	556–558	<i>Betula</i> leaf; bud scale deciduous	4,745 ± 30	5,457	5,330–5,584	5,458
ETH-43946 <sup>e</sup>	576–578	<i>Betula</i> leaf	5,290 ± 35	6,066	5,948–6,184	6,019
ETH-43947 <sup>e</sup>	615–617	<i>Betula</i> fruit, leaf fragments	6,190 ± 35	7,108	6,978–7,237	7,232
BE-2549.1.1 <sup>f</sup>	644–647	Leaf fragments	7,760 ± 25	8,525	8,456–8,593	8,480
BE-2550.1.1 <sup>f</sup>	659–662	<i>Betula</i> fruit, anthers, leaf fragment	8,230 ± 130	9,148	8,780–9,516	9,052
BE-2551.1.1 <sup>f</sup>	689–692	<i>Betula</i> fruit scales	8,710 ± 130	9,832	9,504–10,160	10,008
ETH-43948 <sup>e</sup>	716–719	<i>Pinus sylvestris</i> short shoot, needles, bud scale; leaf fragments	9,565 ± 35	10,915	10,739–11,090	10,846
	806.5	Laacher See Tephra (LST)		13,034 <sup>d</sup>	12,884–13,184 <sup>d</sup>	13,071
BE-2552.1.1 <sup>f</sup>	835.5–838.5	<i>Betula</i> fruits, fruit scale	12,050 ± 130	13,997	13,579–14,414	13,997
ETH-43949 <sup>e</sup>	886.5–892.5	<i>Betula nana</i> fruit scales, fruits; periderm deciduous, leaf fragments deciduous, bud scales deciduous, twiglet, bark	13,000 ± 50	15,540	15,316–15,764	15,447
BE-2553.1.1 <sup>f</sup>	947.5–952.5	Twiglet	13,440 ± 200	16,140	15,512–16,767	16,321
Poz-60131 <sup>g</sup>	1,042.5–1,047.5	Twiglet	15,400 ± 70	18,665	18,512–18,817	18,650

<sup>a</sup>Stuiver and Polach (1977)<sup>b</sup>Stuiver and Reimer (1993); Reimer et al. (2013)<sup>c</sup>Blaauw (2010)<sup>d</sup>van Raden et al. (2013)<sup>e</sup>Laboratory of Ion Beam Physics, ETH Zurich, Switzerland<sup>f</sup>Laboratory for the Analysis of Radiocarbon, Bern University, Switzerland<sup>g</sup>Poznan Radiocarbon Laboratory, Poland

at 836–823 cm (around 13,900 cal BP), at 812–739 cm (13,250–11,450 cal BP) and from 604 cm (6,800 cal BP) to the top with only minor gaps. The uppermost 500 cm (from c. 4,000 cal BP onward) are marked by an increase of sedimentation rates, most likely due to more erosional input in response to anthropogenic disturbance close to the lake shore (Figs. 3, 4).

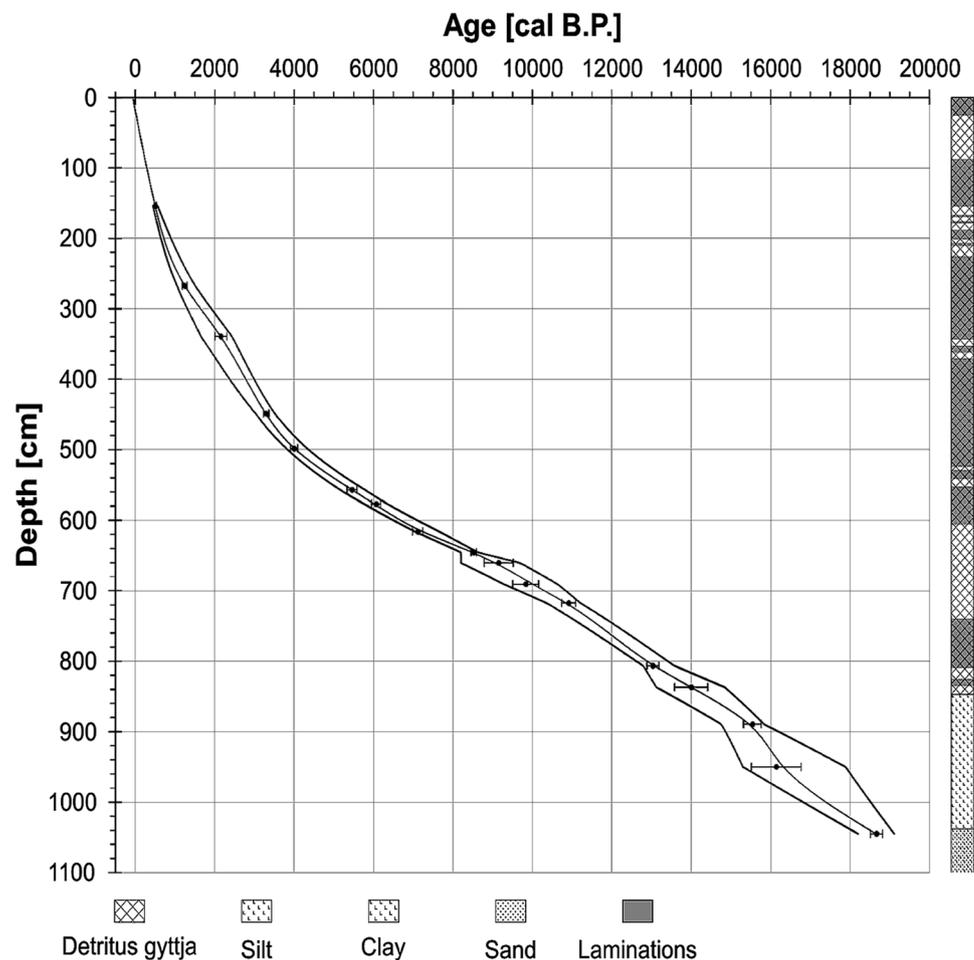
Loss-on-ignition (LOI) inferred organic content is low (<5%) for the bottom part of the sediment (Fig. 4) but steadily increases to values of just below 10% at 922–842 cm (15,950–14,200 cal BP). This trend is interpreted as an increase of lake productivity and/or soil stabilization under warming environmental conditions. Organic content increases after 842 cm (14,200 cal BP), when values reach up to 50%. At 809–744 cm (13,150–11,550 cal BP) the organic content drops again below 35%. This falls in the second laminated sequence with increased XRF-inferred Fe, Ti and Mn elements (Fig. 4). Chronologically, this shift falls in the Younger Dryas cooling. Subsequently at the onset of the Holocene, the organic

content is increasing again and stays at around 55% until c. 500 cm (4,050 cal BP). Afterwards, organic values are continuously decreasing to below 15% in the uppermost sediments. This shift is probably due to more erosional input as a consequence of human activities (e.g. open soils). The third laminated part (6,800 cal BP–present) again shows increased Fe- and Mn values. The carbonate content of the sediment is generally low (LOI 950, XRF Ca), reaching c. 5% on average. Only in the bottom part and in the uppermost part, the values are slightly increased (10–20%) possibly due to inwash of allochthonous carbonates.

### Varve identification

The pollen percentages of the most abundant taxa in the seasonal layers (dark vs. bright) at 333.6–332.5 cm show that *Corylus avellana* and *Alnus glutinosa*-type pollen have higher relative values in the dark brown layers (Fig. 5). These two taxa are mainly flowering early on the Swiss Plateau from February to March (Lauber et al. 2014). On

**Fig. 2** Age-depth-model and lithology of Burgäschisee. *Black dots* show calibrated ages of terrestrial plant macrofossils with  $2\sigma$  error bars (IntCal13, Reimer et al. 2013). The *black line* is the modelled chronology (smooth-spline with the program clam 2.2, Blaauw 2010). The *grey lines* indicate the 95% confidence envelope of the generalized mixed effect regression (GAM, Heegaard et al. 2005)



the other hand, herb pollen such as Poaceae, Cyperaceae, Cerealia-type, *Secale*, *Plantago lanceolata* and *Rumex*-type, generally flowering from April to September, have their highest values in the light brown layers. Some pollen types like *Betula*, *Fagus sylvatica*, *Quercus* and *Abies alba* show no clear signal due to their intermediate and overlapping flowering season from March to May. Thus, dark layers correspond to late autumn-early spring, while bright layers correspond to the summer season, confirming earlier studies from the Swiss Plateau and lowland Alps (Welten 1944; Lotter 1989).

The XRF data of the laminated sequence at 332.2–333.3 cm show that the laminated couplets consist of two main layers with a distinct elemental signature (Fig. 6). The dark brown layers are dominated by fine organic matter with low concentrations of Mn and Ca, while the light brown layers are enriched in these elements. Rhodochrosite ( $\text{MnCO}_3$ ) as an authigenic Mn-rich mineral is mainly found in these light brown layers (van Raden 2012). This is probably related to redox reactions occurring in the lake water and the pore water of the sediment (Stevens et al. 2000; Wetzel 2001). During the mixing of Mn enriched bottom

waters and oxygen enriched surface waters, authigenic Mn is formed from Mn oxides. A stable Mn-rich layer is only preserved when anoxic conditions with no bioturbation are re-established and the reducing process is slower than the sedimentation process (Davison 1993; Stevens et al. 2000). Thus the XRF analyses confirm and refine the palynological results with dark layers formed during late autumn-early spring and the light layers during late spring-early autumn.

### Vegetation and fire history

The pollen diagram (Fig. 3) is subdivided into six statistically significant local pollen assemblage zones (LPAZ) and two subzones Burg-1a und 1b. LPAZ Burg-1a (18,700–16,000 cal BP) is dominated by herbaceous pollen (values over 80%) such as Poaceae, Cyperaceae, *Artemisia*, *Helianthemum*, *Thalictrum*, Chenopodiaceae, Rubiaceae and *Rumex acetosa*-type. These pollen results point to the establishment of open steppe/tundra vegetation shortly after deglaciation (c. 19,000 cal BP, Beckmann 2004). Some pollen grains of *Betula nana*, *Ephedra distachya*-type and *Juniperus* are present, indicating that these shrubs were growing

in the area. The presence of shrub vegetation is underlined by the finding of two woody twiglets that provided radiocarbon dates at the onset and towards the end of this subzone (Table 1). Charcoal influx values are very low, pointing to rare regional fire activity due to a sparse vegetation cover that mainly consisted of herbs.

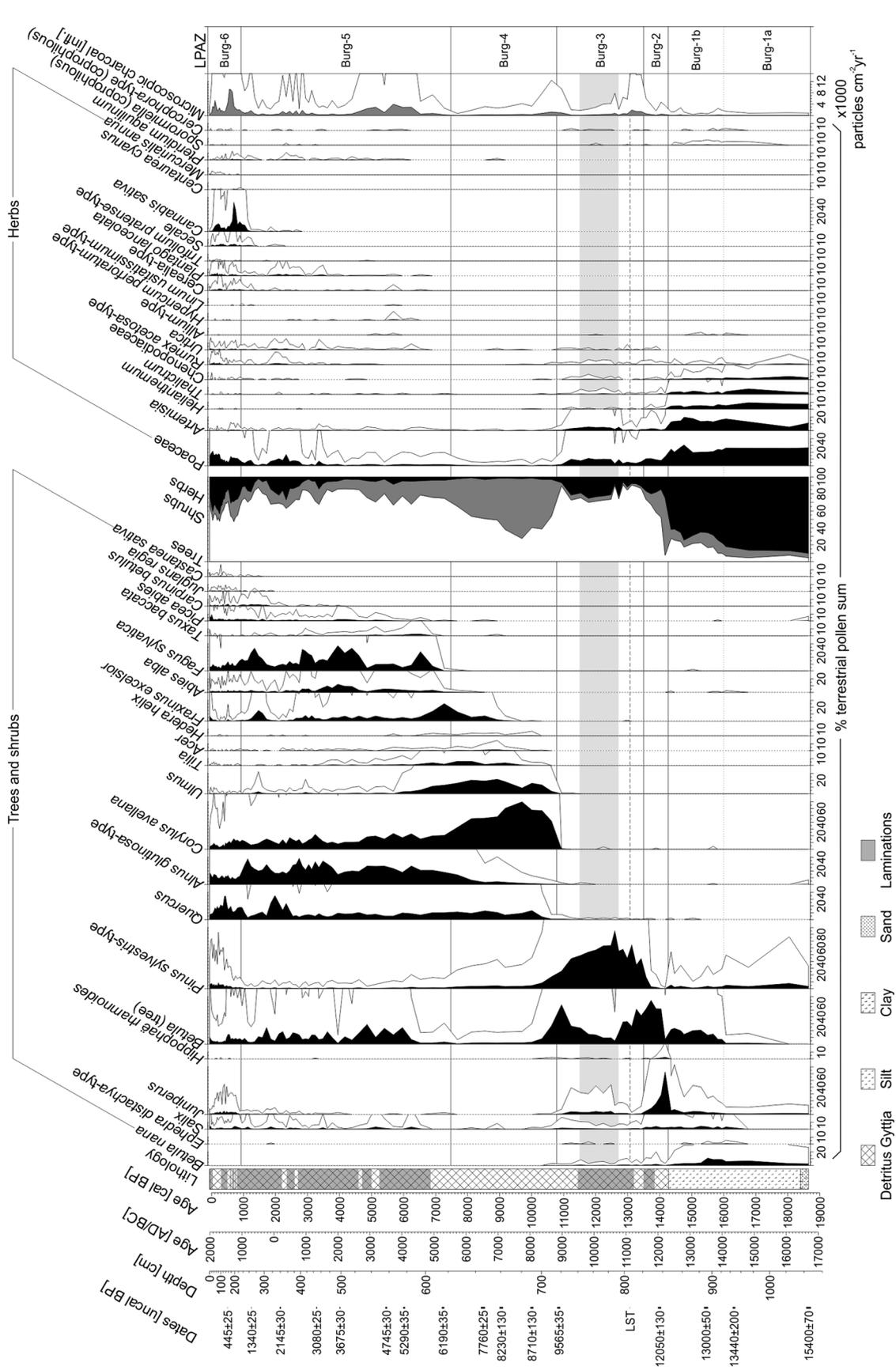
The beginning of the next subzone (LPAZ Burg-1b: 16,000–14,300 cal BP) is marked by an increase of tree *Betula* pollen percentages to values of up to 15%. This shift is accompanied by the highest *Betula nana* pollen percentages (up to 10%) of the entire record. Additionally, other shrub pollen such as *Ephedra distachya*-type and *Salix* are found. Fruit scales and fruits of *Betula nana* used for radiocarbon dating (Table 1) and the increase of arboreal pollen point to a spread of shrub tundra with *Betula nana* and *Salix* around Burgäschisee. Tree *Betula* could have grown as small shrubs or krummholz as they do today at the tree-line in the Alps. The high non-arboreal values (>60% with abundant *Artemisia*, Chenopodiaceae, *Helianthemum*), show that steppic environments were prevailing, pointing to the presence of steppe tundra. The highest percentage (up to 1%) and influx values (up to 70 spores/cm<sup>2</sup>yr, not shown) of *Sporormiella* as well as the occurrence of *Cercophora* coprophilous fungal spores, point to large herbivores close to the lake shore (van Geel 2006). These spores are normally interpreted as evidence for pastoral farming from the Neolithic onward (e.g. Rey et al. 2013). Their marked presence in the Oldest Dryas steppe tundra can be ascribed to the presence of Pleistocene megafauna such as *Mammuthus primigenius* (woolly mammoth), *Bison bonasus* (bison) and *Rangifer tarandus* (reindeer), typical of the steppic environments at that time and fits well with the presence of Palaeolithic hunting camps on the former lake shore attributed to this period (Wyss 1952). A small charcoal peak at the beginning of the subzone around 16,000 cal BP suggests a minor increase of fire activity, possibly due to more fuel availability and/or warming climate.

Afforestation (LPAZ Burg-2, 14,300–13,500 cal BP) and the gradual replacement of the steppe tundra started with a short-term mass expansion of shrubs (*Juniperus* pollen percentages >60%, *Salix* and *Hippophaë rhamnoides* pollen percentages increase) during the Bølling warming period (onset c. 14,600 cal BP, van Raden et al. 2013). This juniper shrubland phase lasted c. 200 years, and was followed by a sharp rise in tree *Betula* pollen, suggesting the formation of birch forests. The latter vegetational change marked the final collapse of the steppic tundra environments (decline of *Betula nana*, *Artemisia*, Chenopodiaceae). At the same time, around 14,300 cal BP, the organic content of the sediment rises sharply, showing increased organic productivity in the lake. Herb, shrub and tree pollen concentrations remain more or less constant (Fig. 4), suggesting stable sedimentary

conditions. Fires were still rare as shown by low charcoal influx values.

Pollen results suggest that mixed birch and pine forests established around 13,500 cal BP (LPAZ Burg-3, 13,500–10,800 cal BP). This vegetation type persisted through the Allerød period (13,900–12,900 cal BP, van Raden et al. 2013) as indicated by the pollen assemblages. *Quercus* pollen is regularly found, possibly as a result of long distance transport from the adjacent region south of the Alps, where oak stands grew at that time (Finsinger et al. 2006; Monegato et al. 2007). Given that the empirical limit (closed curve, Birks and Tinner 2016) is almost reached, these stands could, however, have been located closer to the site, perhaps in the nearby Rhone valley (c. 90 km distance), which opens onto the Mediterranean Sea. Around 12,800 cal BP, *Pinus sylvestris*-type pollen becomes dominant, followed by a marked increase of herb pollen (c. 25%, e.g. Poaceae, *Artemisia*), a minor increase of *Juniperus* pollen (c. 5%) and a decrease of *Betula* pollen (below 20%) in the upper part of the zone (c. 12,600–11,200 cal BP). We interpret this opening of the forests as a result of climate cooling during the Younger Dryas (12,710–11,500 cal BP; Vescovi et al. 2007; van Raden et al. 2013). Shortly after the onset of the Holocene, after c. 11,500 cal BP, closed mixed birch-pine forest re-established as indicated by high arboreal pollen percentages (from 80 to 95%). Continuous curves of *Quercus*, *Ulmus*, *Tilia* and *Alnus glutinosa*-type pollen suggest the establishment of temperate forest stands in response to rapid climate warming at the onset of the Holocene (Heiri et al. 2015). Charcoal influx values increase temporarily (c. 1,200 particles/cm<sup>2</sup>year) at the onset of the Allerød and at the onset of the Holocene, suggesting increased burning during these transition periods.

Pollen of temperate trees and shrubs such as *Ulmus*, *Quercus*, *Tilia*, *Acer*, *Corylus avellana* and *Hedera helix* increases during LPAZ Burg-4 (10,800–7,500 cal BP), suggesting a further expansion of temperate deciduous forests at the expense of boreal forests (tree *Betula* and *Pinus sylvestris*-type pollen declines). After c. 9,000 cal BP, *Fraxinus excelsior* pollen percentages and *Alnus glutinosa*-type percentages increase and *Abies alba* and *Fagus sylvatica* reached their empirical limit (at 8,100 and 7,700 cal BP respectively), suggesting that these trees expanded locally (Birks and Tinner 2016). At the same time, *Corylus avellana* pollen percentages start to decrease, indicating that heliophilous hazel shrublands were gradually reduced by more mesophilous vegetation. Regional fire activity was moderate during the first half of the zone (10,800–9,000 cal BP) as indicated by intermediate charcoal influx values. After c. 9,000 cal BP, charcoal influx values decrease, suggesting less burning. This decline of regional fire activity and the spread of mesophilous trees can be attributed to a decline in summer insolation



**Fig. 3** Percentages of selected pollen types, fern spores and coprophilous fungal spores and charcoal influx values of Burgäschisee. Empty curves are the 10× exaggerations. LPZ local pollen assemblage zones, LST Laacher See tephra (dashed line). Light grey bar Younger Dryas (van Raden et al. 2013)

(Wanner et al. 2008) and a shift towards a more oceanic climate reflected by higher lake levels (Magny et al. 2011).

Pollen data suggest that during LPAZ Burg-5 (7,500–900 cal BP), *Fagus sylvatica* became the dominant tree species together with *Abies alba*, forming dark mesophilous beech–fir forests that gradually replaced the previously prevailing mixed elm–lime–maple–oak forests. At c. 6,500 cal BP (4550 cal BC), the first pollen grains of Cerealia-type and *Plantago lanceolata* appear in the pollen sequence, marking the onset of conspicuous agricultural activities around Burgäschisee. The occurrence of *Linum usitatissimum*-type pollen, *Allium*-type pollen, *Hypericum perforatum*-type pollen, Cerealia-type pollen and *Plantago lanceolata* pollen suggest Neolithic arable and pastoral farming close to the lake at around 5,750 cal BP (3800 cal BC, Cortailod Culture). Towards the upper part of the zone, herbaceous pollen becomes more frequent indicating that open land increased. *Betula* trees, a typical successional pioneer tree, spread again. *Tilia* pollen disappears (temporarily) during this LPAZ, suggesting that *Tilia* trees became very rare or even locally extinct during the Bronze Age c. 3,500 cal BP (1550 cal BC) (Tinner et al. 2005). Remarkable transient closings of forests (AP > 95%) occurred during the Bronze Age and during the Late Roman to Early Medieval period. Charcoal influx shows moderate to high values, suggesting higher regional fire activity that peaked around 6,500–5,000 cal BP (4550–3050 cal BC) and 3,000–2,000 cal BP (1050–50 cal BC), most likely in response to human activities such as slash-and-burn.

Land-use intensified during the Middle Ages and later, as shown by herb pollen percentages of up to 40% (LPAZ Burg-6,900 cal BP–present). Typical for this time is the spread of *Cannabis sativa*, an important fibre plant, reaching maximum values around 800 cal BP (cal AD 1150). The high pollen percentage values of *Cannabis sativa* are due to retting of the entire plant in the lake (Ranalli and Venturi 2004) and are therefore a good biostratigraphic marker (Gobet and Tinner 2012). Charcoal influx values show two major peaks. At the same time, herb pollen percentages are highest, indicating massive regional forest burnings to expand agricultural land.

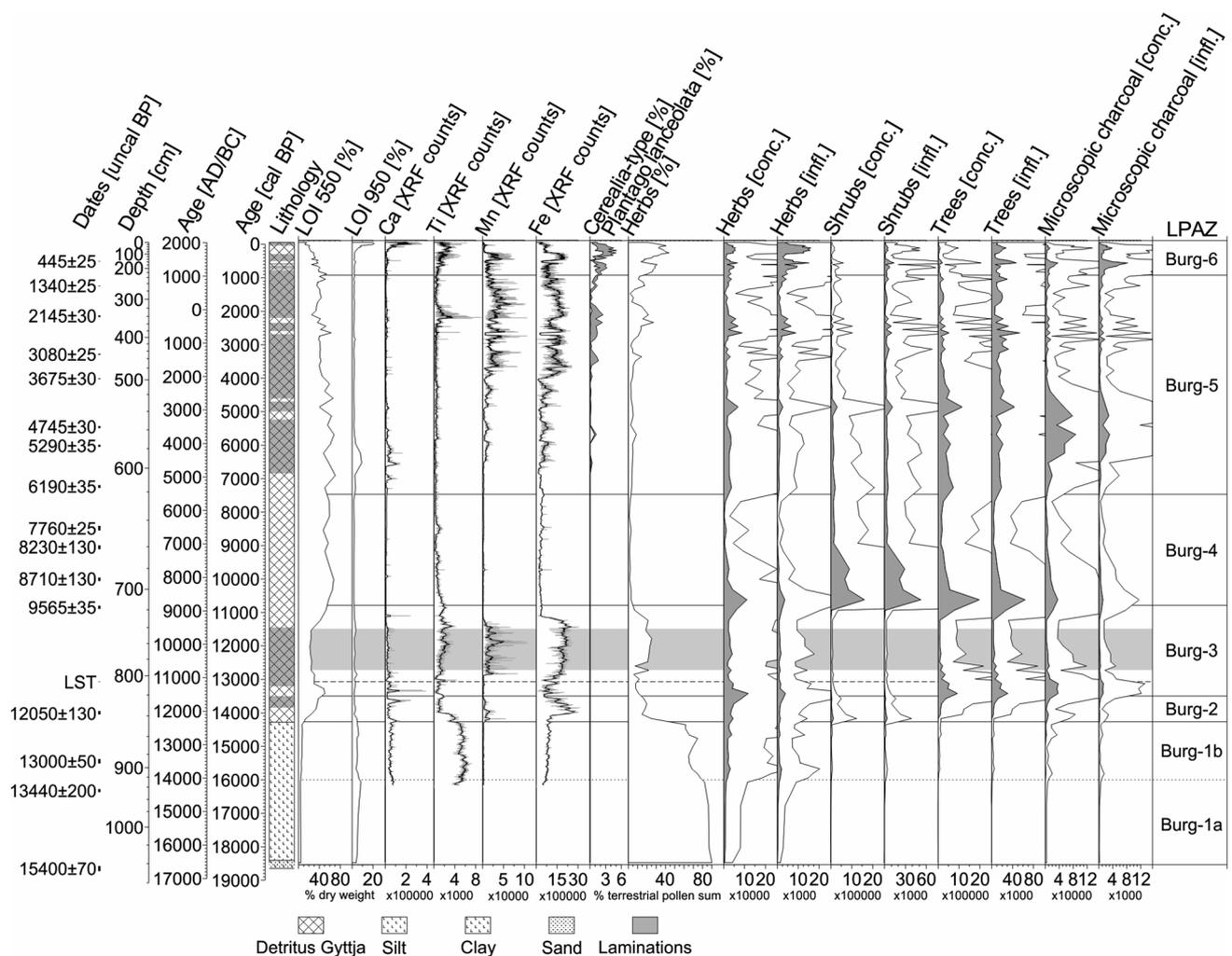
## Discussion

### Deglaciation and vegetation dynamics during the Oldest Dryas north and south of the Alps

The glacier extent during the Last Glacial Maximum (LGM) has been intensively investigated by analysing the distribution and age of moraines and glacial landforms (Jäckli 1962; Bini et al. 2009). Recently, the dating of moraines with the

$^{10}\text{Be}$  method has become established in the Alps and their forelands (e.g. Ivy-Ochs et al. 2004; Gianotti et al. 2008; Reuther et al. 2011; Federici et al. 2012; Reber et al. 2014). All these studies suggest an age for the LGM ranging from 24,000–18,000 cal BP, which is in agreement with palaeoecological and palaeoclimatic records from radiocarbon-dated sites close to the Alps that had never been glaciated (e.g. Kaltenrieder et al. 2009; Samartin et al. 2016; LGM c. 23,000–19,000 cal BP). However, the error of the  $^{10}\text{Be}$  surface exposure dating is substantial (usually  $\pm 1,000$ – $2,000$  years) and thus the assessment of local deglaciation dynamics is only preliminary. Here, independent radiocarbon dating of terrestrial macrofossils deposited in lake sediments from sites located within the margin of the former ice sheet might help to date the spatial deglaciation patterns more precisely. Earliest dates on terrestrial plant remains for lowland sites in the Alpine region that were ice-covered during the LGM are available from south and north of the Alps (Table 2). Burgäschisee, Wauwilermoos (Beckmann 2004) and Lago Piccolo di Avigliana (Larocque and Finsinger 2008) are all located at the margins of the LGM ice cover (Ehlers and Gibbard 2004; Bini et al. 2009) and have radiocarbon dates that are all older than 18,000 cal years. The radiocarbon dates from Rotsee (Lotter and Zbinden 1989), Soppensee (Lotter et al. 1997; Lotter 1999) and Lago di Origlio (Tinner et al. 1999) are slightly younger (around 17,500 cal BP). These lakes were located below rather thick ice sheets (800–1,000 m) and 15–20 km away from the glacier front. The rather small age difference between these lakes suggests that the deglaciation process in the lowlands was fast (within <1,000 years). This sudden retreat of the glaciers and the reduction of ice mass may have been triggered by increasing summer insolation (Berger and Loutre 1991) and increasing  $\text{CO}_2$  concentrations (Smith et al. 1999). Similar patterns are evident from  $^{10}\text{Be}$  exposure dated boulders and bedrock on nunataks in the Inner Alps (Wirsig et al. 2016).

The change in the lithology (Figs. 3, 4) suggests that pioneer plants colonized the glacier forelands at Burgäschisee and the pollen evidence shows that a species rich steppe tundra established, stabilizing the soils rapidly after deglaciation at 19,000 cal BP. Arboreal plants, dwarf shrubs and shrubs, formed thickets (e.g. dated macrofossils of Ericaceae and other shrubs; Beckmann 2004; this study). Other sites in the Swiss Plateau lowlands such as Murifeld (Welten 1982), Faulenseemoos (Welten 1944, 1982), Lobsigensee (Ammann and Tobolski 1983; Ammann 1989), Rotsee (Lotter and Zbinden 1989), Le Loclat (Hadorn 1992), Soppensee (Lotter 1999) and Wauwilermoos (Beckmann 2004) show similar pioneer vegetation patterns in the deepest parts of the analysed section. However, only Rotsee, Soppensee and Wauwilermoos have radiocarbon dates for this early phase prior to 16,000 cal BP. South of the Alps, *Juniperus* stands expanded as early as 18,000–17,500 cal BP in the formerly



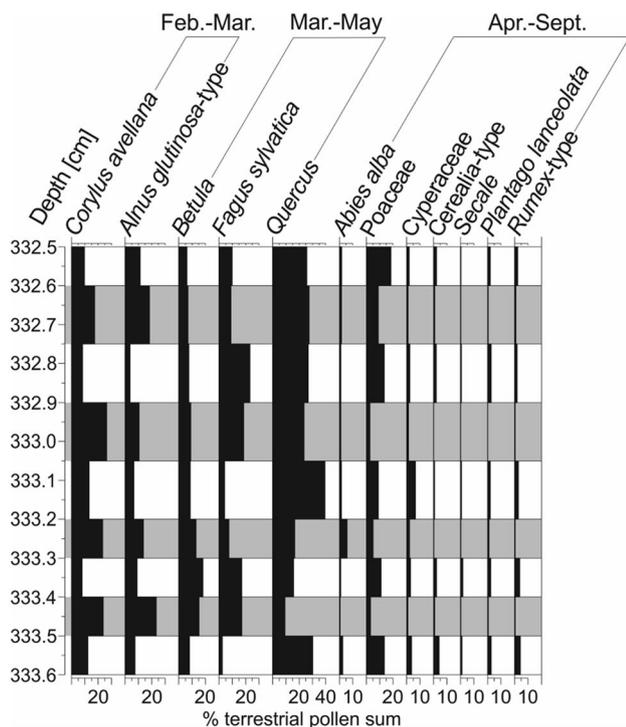
**Fig. 4** Composite of lithology, loss on ignition at 550 °C (LOI 550) and 950 °C (LOI 950), XRF counts of selected elements per area (0.2×12 mm, van Raden 2012) (left part). The grey lines of the XRF data show the original counts, the black lines are the moving averages (period=19). Pollen percentages of selected pollen types, pollen concentrations (particles/cm<sup>3</sup>) of herbs, shrubs and trees, pollen influx

(particles/cm<sup>2</sup>/year) of herbs, shrubs and trees, microscopic charcoal concentrations and microscopic charcoal influx (right part). Empty curves are the 10× exaggerations. LPAZ local pollen assemblage zones, LST Laacher See tephra (dashed line). Light grey bar Younger Dryas (van Raden et al. 2013)

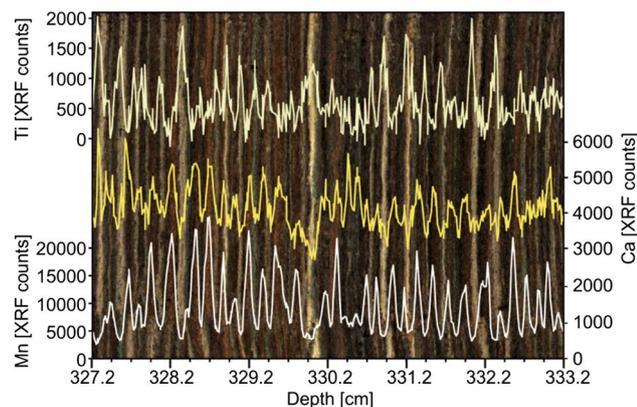
glaciated areas of the Ticino area (e.g. Origlio, Tinner et al. 1999; Vescovi et al. 2007). Stomata and macrofossil findings at e.g. Lago di Rognona (Monegato et al. 2007) in eastern Italy, at Lago Piccolo di Avigliana (Finsinger et al. 2006) in western Northern Italy suggest that *Larix decidua*, tree *Betula* and *Pinus* sp. occurred between 17,500–16,000 cal BP, after having expanded from their unglaciated refugial sites (e.g. Euganean Hills in the Eastern Po Plain, Kaltner et al. 2009). It is likely that these early post-LGM vegetation dynamics resulted from climate warming of around 3 °C after c. 19,000 cal BP (Samartin et al. 2016).

Vegetation changed around 16,000 cal BP at Burgäschisee with an expansion of shrub tundra (pollen of tree *Betula*, *Betula nana*, *Salix*, *Juniperus*). First macrofossils of *Betula*

*nana* show that dwarf birch thickets were wide-spread in the landscape. This vegetational re-organization is well documented at many lowland sites north of the Alps (e.g. Welten 1982; Lotter 1999). We assume that *Betula humilis* (shrubby birch) and *Betula* trees (e.g. *Betula pubescens*) were growing in the most favourable habitats; however, their local presence has not been confirmed by radiocarbon-dated macrofossil finds so far. At around 16,700–16,000 cal BP, forests expanded (e.g. *Pinus cembra*, *Larix decidua*) at lowland sites south of the Alps (e.g. Wick 1996; Tinner et al. 1999; Hofstetter et al. 2006; Vescovi et al. 2007; Pini et al. 2016), long before the onset of the Bølling period and sites above 1,000 m a.s.l. became ice-free, e.g. Palughetto at 1,040 m a.s.l. (Vescovi et al. 2007) and Pian di Gembro at 1,350 m



**Fig. 5** Pollen analysis of seven consecutive sediment layers (*five light layers and four dark layers*) from 333.6 to 332.5 cm. The selected pollen types are ordered by the general timing of their flowering (Laubert et al. 2014)



**Fig. 6** XRF curves showing the correlation of Mn and Ca and the occurrence of sporadic Ti-rich (erosional) layers from 333.2 to 327.2 cm. The y-axes represent the concentrations for each element (van Raden 2012, modified)

a.s.l. (Pini 2002). These major vegetation and environmental changes are likely the response to Late-Glacial warming of c. 2.5 °C higher summer temperatures after Heinrich event 1 (Samartin et al. 2012).

The great abundance of coprophilous spores (*Sporormiella*, *Cercophora*) at Burgäschisee during the Late Glacial

period from 17,000–14,300 cal BP during the steppe-tundra vegetation phase is striking. In North America, coprophilous fungal spores in the Late Glacial were connected to the presence of the last Pleistocene large herbivores such as *Mammuthus primigenius* (woolly mammoth), *Bison bison* (American bison) and *Rangifer tarandus* (reindeer) (Robinson et al. 2005; Davis and Shafer 2006; Gill et al. 2012). In Siberia, an excavation revealed high numbers of *Sporormiella* spores next to a mammoth carcass (Mol et al. 2006). Findings of mammoth, reindeer and bison remains are abundant in Switzerland until c. 14,000 cal BP (Fahlke 2009; Nielsen 2013). Numerous flints were found at the hunting camps of Fürsteiner (Wyss 1952) that existed at the same time as the Pleistocene herbivores on the former Burgäschisee lake shore and were assigned to the Magdalenian [18,000–14,000 cal BP (16050–12050 cal BC), Le Tensorer and Niffeler 1993; von Burg et al. 2011].

### Vegetation and fire dynamics on the Alpine Foreland during the last 14,500 years

The mass expansion of *Juniperus* followed by the establishment of *Betula* woodlands occurred at c. 14,300 cal BP. This is c. 200–250 cal BP later than at Gerzensee (van Raden et al. 2013) and the difference is probably due to calibration uncertainties attributed to the radiocarbon plateau at the onset of the Bølling (Reimer et al. 2013). This initial afforestation is well documented in many lowland records north of the Alps (e.g. Ammann and Tobolski 1983; Lotter 1999; Beckmann 2004) including a pioneer land core from Burgäschisee (Welten 1946). Montane to subalpine sites in the Alps became ice-free up to 1,800 m a.s.l. (Welten 1982; Ilyashuk et al. 2009; Rey et al. 2013) and dense boreal forests (e.g. *Pinus sylvestris*, tree *Betula*) established south of the Alps (Tinner et al. 1999; Hofstetter et al. 2006). South of the Alps forests expanded from elevations of about 800 m to at least 1,350 m a.s.l. (Pini 2002; Vescovi et al. 2007), showing that the Bølling warming released an upslope movement of about 500–600 m. Forest expansions in Southern and Central Europe followed a rapid 3–4 °C warming, as e.g. recorded in stable isotopes and chironomid records (Heiri and Millet 2005; Heiri et al. 2007; Larocque and Finsinger 2008; Larocque-Tobler et al. 2010; Lotter et al. 2012).

Subsequently fairly dense mixed *Pinus sylvestris* and *Betula* forests formed during the Allerød period (c. 13,500 cal BP) at Burgäschisee. This spread of boreal forests occurred across the entire Swiss Plateau (e.g. Lotter 1999; Wick 2000) and elsewhere in Central Europe (e.g. Becker et al. 2006; Kleinmann et al. 2015). Closed forests in combination with stable and warm summer temperatures (Heiri et al. 2015) possibly led to an increase of regional fires. South of the Alps temperate trees (e.g. *Tilia*, *Quercus*, *Ulmus*, *Fraxinus excelsior*) invaded the Allerød

**Table 2** Oldest radiocarbon dates in sediment sequences from lowland regions around the Alps

Site name	Altitude (m a.s.l.)	Reference	<sup>14</sup> C age (BP) <sup>a</sup>	Age (cal BP) <sup>b</sup>	Age 2σ range (cal BP) <sup>b</sup>	Depth (cm)	Total core length (cm)
Burgäschisee	465		15,400 ± 70	18,665	18,512–18,817	1,045	1,500
Wauwilermoos	500	Beckmann (2004)	15,300 ± 130	18,548	18,263–18,832	690	c. 795
Rotsee	419	Lotter and Zbinden (1989)	14,600 ± 200	17,764	17,254–18,274	915	c. 1,250
Soppensee	595	Lotter et al. (1997); Lotter (1999)	14,200 ± 120	17,272	16,917–17,627	680	c. 800
Lago Piccolo di Avigliana	365	Larocque and Finsinger (2008)	14,900 ± 80	18,120	17,902–18,337	909	c. 1,490
Lago di Origlio	419	Tinner et al. (1999)	14,500 ± 80	17,684	17,453–17,915	1,398	1,955

<sup>a</sup>Stuiver and Polach (1977)

<sup>b</sup>Stuiver and Reimer (1993); Reimer et al. (2013)

boreal forests (Tinner et al. 1999; Vescovi et al. 2007), as also unambiguously documented by macrofossils (Monegato et al. 2007; Finsinger et al. 2006).

During the Younger Dryas cooling (c. 12,710–11,500 cal BP), steppe-tundra vegetation including *Artemisia*, Chenopodiaceae, Poaceae and others temporarily recovered. Forest disruption with a decline of short-lived tree *Betula* and the dominance of long-lived *Pinus sylvestris* is typical for Central Europe and is confirmed by macrofossil analysis (Lotter 1999). South of the Alps forest disruption was less marked, however, temperate trees such as *Quercus* markedly declined (Finsinger et al. 2006). After 11,400 cal BP, at the onset of the Holocene, mixed *Pinus sylvestris* and *Betula* forests recovered quickly in both regions. Chironomid-based summer temperature reconstructions suggest a rapid warming of c. 3 °C at the onset of the Holocene (e.g. Heiri et al. 2015). However, forest composition changed significantly after 10,800 cal BP when boreal forests were gradually replaced by temperate forests consisting of *Tilia*, *Ulmus*, *Acer*, *Hedera helix* and *Corylus avellana*. These species characterized the forests over 4,000 years in Central Europe (e.g. Clark et al. 1989; Hadorn 1992; Richoz 1998; Lotter 1999; Litt et al. 2009) and reflect natural forest composition under warm but rather continental conditions (maximum summer and minimum winter solar insolation; Kutzbach and Webb 1993).

Continental forests around Burgäschisee remained stable until c. 8,500–8,000 cal BP when *Alnus* and *Fraxinus* increased and *Abies alba* as well as *Fagus sylvatica* established. *Alnus* and *Fraxinus* are still growing at the lake shore today. Both trees can cope with wet soil conditions and generally grow in moist forests (Lauber et al. 2014). *Fagus sylvatica* and *Abies alba* are both shade-tolerant mesophilous late-successional trees species. The shift to mixed beech forests was found at many sites on the Swiss Plateau (e.g. Ammann 1989; Lotter 1999) and the reasons for this change have been controversially discussed for many years (e.g. Tinner and Lotter 2006). In fact, regional differences can be substantial. For instance, on the Western Swiss Plateau close to the Jura Mountains *Fagus sylvatica* was

co-dominant with *Quercus* (Ammann 1989; Hadorn 1992; Richoz 1998). *Abies alba* was less abundant possibly due to drier conditions in the shade of the Jura Mountains. At Burgäschisee, *Abies alba* was locally present (Table 1) but its abundance was moderate and corresponds to that at other sites in Western Switzerland. Higher *Abies alba* abundances (values > 15%) occurred in the lowland areas of Central and Eastern Switzerland, e.g. at Wauwilermoos, Bibersee and Zürichsee (Beckmann 2004; Gobet et al. 2017). A general trend to increasing *Abies alba* abundances is also evident with increasing altitude (Lotter 1999; van der Knaap et al. 2004; Wehrli et al. 2007; Gobet and Tinner 2012), probably also reflecting a moisture gradient, given that the species is more competitive under mesophilous conditions, particularly if exposed to excessive anthropogenic disturbance (e.g. fire, browsing, Tinner et al. 1999, 2013; Henne et al. 2013; Ruosch et al. 2016).

The onset of noticeable agricultural activities around Burgäschisee dates to c. 6,500 cal BP (4550 cal BC) in our pollen record. This inference is in good agreement with the archaeological evidence, with single Neolithic archaeological finds dated to the period after 6,250 cal BP (4300 cal BC) and by the existence of local settlements after c. 5,950 cal BP (4000 cal BC; Wey 2012). The expansion of arable and pastoral farming (e.g. Cerealia-type, *Plantago lanceolata*, *Linum usitatissimum*-type) as well as of disturbance-adapted *Fagus sylvatica*, *Corylus avellana* and *Betula* is typical for the lowland in Central Europe. It may generate successional cycles that might be recognized depending on the temporal resolution of the records (e.g. Kleinmann et al. 2015; Rösch and Lechterbeck 2016). Forest disruptions and land use phases were associated with increasing fire activity (Clark et al. 1989; Tinner et al. 2005), suggesting that fire was intensely used to gain open land and contributed to the reduction of fire sensitive trees and lianas (e.g. *Tilia*, *Ulmus*, *Fraxinus*, *Acer*, *Abies alba*, *Hedera helix*). Interestingly, at Burgäschisee this first Neolithic forest disruption coincided with the onset of the formation of varves in the sediment. This may indicate changes in the mixing system

of Burgäschisee, probably due to a more open landscape because of forest clearance and therefore increased windiness as a trigger for short-term mixing (Davison 1993; Stevens et al. 2000; van Raden 2012).

Land use intensified during the Mid Bronze Age (around 3,500 cal BP, 1550 cal BC) and the Iron Age (after 2,800 cal BP, 850 cal BC) when fire-sensitive trees such as *Tilia* (Tinner et al. 2005) collapsed completely. Most of the Neolithic log boats were built out of *Tilia* trunks (Hafner et al. 2012) whereas the Bronze Age log boats were mainly made of harder oak trunks (Mainberger 2009) that are more difficult to work on. This depletion of the preferentially used lime trees can be considered a prehistoric example of inadequate handling of natural resources. Similar intensifications of land-use during the Bronze and Iron Age have been reconstructed at Lobsigensee (Ammann 1989) and at Le Loclat (Hadorn 1992) documenting the importance of the Swiss Plateau lowlands (<600 m a.s.l.) for crop production. In contrast to that, more remote study sites e.g. Soppensee (Lotter 1999), Schwantenua (Gobet and Tinner 2012), Egelsee (Wehrli et al. 2007) only experienced strong openings of the forests during the Middle Ages (c. 800 cal BP, cal AD 1150), when less fertile areas (colder, moister) also became intensively used.

## Conclusions

We reconstruct vegetation, fire and land use dynamics over the past 18,700 years at a novel site. We can demonstrate the sediments of Burgäschisee are varved over millennia. A radiocarbon age of a twiglet provided a calibrated age of c. 18,700 cal BP, which is one of the earliest absolute dates for the establishment of vegetation after the LGM on the Swiss Plateau. Late Glacial vegetation dynamics at c. 19,000–18,000, 16,000, 14,500, 11,600 and 8,200 cal years ago were closely connected to climate changes, in particular warming and/or increase of moisture availability. Frequently found coprophilous spores (*Sporormiella*, *Cercophora*) suggest the presence of Pleistocene large herbivores (e.g. *Mammuthus primigenius*) during the non-forested Late Glacial, c. 17,000–14,000 cal BP. After the onset of the Neolithic c. 7,500 years ago, vegetation changes were primarily controlled by human activities, including fire disturbance. These societally induced changes, specifically deforestation, likely initiated the formation of varved sediments that are unique for the Swiss Plateau. As varved sediments allow a precise chronology comparable to that of tree rings, the Burgäschisee record has a great potential for further multiproxy high-resolution studies. Such investigations would offer the possibility of reconstructing short-term vegetation changes, responses to climate shifts and/or anthropogenic disturbance. Specifically, the ecological and environmental

consequences of short-lived Neolithic lake shore settlements (lasting less than 30 years, Bleicher and Burger 2015) might be investigated and linked to the tree ring records from prehistoric villages. Complex linkages between climate, vegetation, fire and land use might be explored with sufficient time resolution and precision, an endeavour which has not been achieved so far for the Swiss Plateau and adjacent areas of Central Europe.

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