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ORIGINAL ARTICLE

Holocene vegetation change at Grosssee, eastern Swiss Alps: effects of climate and human impact

Allison R. Dwileski[1] · Fabian Rey[1] · Marina A. Morlock[2] · Nicole Glaus[3] · Sönke Szidat[4] · Hendrik Vogel[3] · Flavio S. Anselmetti[3] · Oliver Heiri[1]

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Abstract

Pollen, spores, and microscopic charcoal from the sediments of Grosssee (1,619 m a.s.l.), a small lake in the lower subalpine vegetation zone of the Glarus Alps, Switzerland, were analysed to reconstruct vegetation patterns and land use over the past ca. 12,300 calibrated ^{14}C years BP (cal BP). Pollen data revealed an open landscape covered with grasses and herbs such as *Artemisia* during the Late Glacial Period. The catchment was likely initially afforested with *Betula* and *Pinus cembra* or *Pinus sylvestris* during the Early Holocene. Thermophilous taxa such as *Ulmus*, *Tilia*, and *Alnus glutinosa*-type expanded from ca. 11,000–9,200 cal BP, and mesophyllic *Picea abies* and *Fagus sylvatica* followed, and expanded beginning from ca. 8,000–7,600 cal BP. Interestingly, *Alnus viridis* (synonym: *A. alnobetula*) expanded about 2,000 years earlier than at comparable sites in the northern Swiss Alps. Its expansion was profound and persistent, and percentages > 15% were already achieved by ca. 7,000 cal BP. Local erosion events that followed are well explained by vegetation changes and inferred human land use activities at Grosssee. In particular, this led to a more open landscape, and land uses (e.g. grazing) intensified from the Mid- to Late Holocene. Indicators of environmental disturbance including persistently high levels of *A. viridis*, monolete fern spores, and microscopic charcoal were pronounced after ca. 4,000 cal BP. At that time, high influxes of spores from coprophilous fungi and the consistent presence of cultural indicators (Cerealia-type, *Plantago lanceolata*) indicate increased grazing and high levels of human impact. Land use and grazing activities seemed to have been particularly pronounced and to have promoted diversity in the vegetation over the past 1,000 years.

Keywords Pollen · Vegetation change · Erosion · *Alnus viridis* · *Alnus alnobetula* · Human impact

Introduction

Lake sediments serve as valuable archives to better understand patterns of regional environmental development and change over the course of a lake's history (Bennett and Willis 2001; Smol et al. 2001). Investigations using multiple proxies from a single site can be overlapped to form a valuable picture of environmental dynamics (Birks and Birks 2006). For example, lithological and geochemical studies of sediments as well as their structures and chronostratigraphy can be used to better understand soil and hydrological patterns in watersheds, trends in sediment deposition, and to identify large-scale events including floods and landslides (Koinig et al. 2003; Gilli et al. 2013; Glur et al. 2013; Wirth et al. 2013; Perret-Gentil et al. 2024). Plant macrofossils, pollen, and spores, on the other hand, can be used to reconstruct the history of terrestrial vegetation of a region, looking at patterns of plant migration and succession (Rey et al. 2019), shifts

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✉ Oliver Heiri
oliver.heiri@unibas.ch

[1] Geoecology, Department of Environmental Sciences, University of Basel, Basel, Switzerland

[2] Department of Ecology and Environmental Sciences, Umeå University, Umeå, Sweden

[3] Institute of Geological Sciences and Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

[4] Department of Chemistry, Biochemistry and Pharamaceutical Sciences & Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

between open tundra and open pasture to shrubland and forest communities, and signs of human-associated land-use from agriculture to grazing to large-scale clearing (Moore et al. 1991). In addition, charcoal can be used to reconstruct fire histories (Tinner and Hu 2003; Conedera et al. 2009). It is when different types of proxies are combined that a clearer picture of the abiotic and biotic environment over the course of time can be made, and ideas about future environmental responses to climatic and land-use changes can be developed (Rull et al. 2018).

Montane to alpine environments are locations of high diversity (e.g. habitats, species) (Garcés-Pastor et al. 2022). They are fragile and fragmented, often steep and exposed, affected by extremes (i.e. in temperature), and susceptible (with increasing altitude) to low growing season temperatures limiting tree growth (Körner 1999, 2004; Paulsen and Körner 2014). They are also highly sensitive to change (Körner 1999). It is the combination of these aspects that places high-altitude environments as suitable locations for the study of climatic and vegetation patterns during the Late Glacial period and the Holocene.

Grosssee, a subalpine lake in the Walensee region of the Glarus Alps of eastern Switzerland, is suitable for the use of pollen to reconstruct vegetation history and to look for connections between patterns of vegetation, climate change, and land use. The first pollen-based studies of the greater region have investigated the eastern central Swiss Alps (e.g. Müller 1972; Perret 1993; Perret and Burga 1994) using a combination of the Russian borer and Dachnowsky sampler to retrieve cores from peats and near-shore lake sediments. One of these studies (Seebenalp) is located very close to Grosssee (Perret 1993). These studies are highly valuable in that they investigated multiple nearby sites in parallel, however, the aspect of the sampling technique (littoral lake sediments) resulted in very local signals for use in vegetation reconstruction compared to cores retrieved from the centre of lake basins (Bennett and Willis 2001). Recent advances in coring technology now allow sampling of sediment records from the centre of lakes, where sediments better integrate the extra-local to regional pollen deposition. Furthermore, recent developments of accelerator mass spectrometry (AMS) ^{14}C analysis now allow the development of more highly resolved and constrained radiocarbon chronologies than was possible for many of these earlier studies (e.g. Rey et al. 2023; Heiri et al. 2024).

Several recent pollen studies of the upper montane and subalpine vegetation belts of the central Swiss Alps have focused on lakes in western and southwestern (Wick et al. 2003, Sägistalsee; Rey et al. 2013, Lauenensee; Schwörer et al. 2014, Iffigsee; Thöle et al. 2016, Lac de Bretaye; Rey et al. 2022, Lac de Champex) and southeastern (Gobet et al. 2003) Switzerland. Such studies have identified the development of Holocene vegetation and patterns of change in the Alps and have connected them to variations in climate as well as human-driven impacts such as land clearance by logging and/or fire to create summer pastures (Gobet et al. 2003; Heiri et al. 2003; Rey et al. 2013; Schwörer et al. 2015).

Massive soil mobilization and erosive runoff of denuded slopes in the catchment was observed at Grosssee during a heavy rainstorm in June 2016, which lead to the idea of coring the lake and an initial study on erosion and sediment flux at this site (Glaus 2018; Morlock et al. 2023). This study reported increases in the frequency and intensity of erosion from the Mid- to Late Holocene, raising questions about the extent to which changing vegetation cover combined with climate and particularly human impact have affected erosion in the Grosssee catchment. Moreover, recent studies have found links between increases in erosion in the European Alps and climate change during the Holocene (e.g. Glur et al. 2013; Wirth et al. 2013; Arnaud et al. 2016). The present study provides a detailed vegetation reconstruction for this site shown to be strongly affected by increasing erosion during the Holocene (Glaus 2018). This will contribute to a better understanding of the extent of both climate and human impacts at sites like Grosssee and will therefore also be of relevance to climate science.

This study aims to (1) use pollen from lake sediments retrieved at Grosssee as a proxy to investigate Holocene vegetation change and see how it compares to other Alpine sites of similar altitude, (2) assess factors affecting overall vegetation patterns including past influences of climate and early human activities (e.g. agriculture, pasturing/alpine transhumance, fire) using pollen as a proxy for vegetation change and selected pollen and non-pollen palynomorph (NPP) types as well as microscopic charcoal as indicators for early human impact, and (3) examine indications of regional land clearance and disturbance to investigate how historical vegetation is related to sedimentation rates, past erosion, and flood events in and around Grosssee.

Materials and methods

Study site

Grosssee is a small lake of the lower subalpine vegetation belt (Roth 1912; Perret 1993; Landolt 2003) on the northern slopes of the Glarus Alps (Canton St. Gallen) (Fig. 1). The lake (47°04’44”N, 9°14’47”E), at an elevation of 1,619 m a.s.l., has a surface area of 0.05 km^2 and a maximum depth of 11.5 m (Lotter et al. 1997). It is the middle and largest of a group of three small connected lakes. Grosssee receives inflow from one of these via a narrow inlet (Roth 1912).

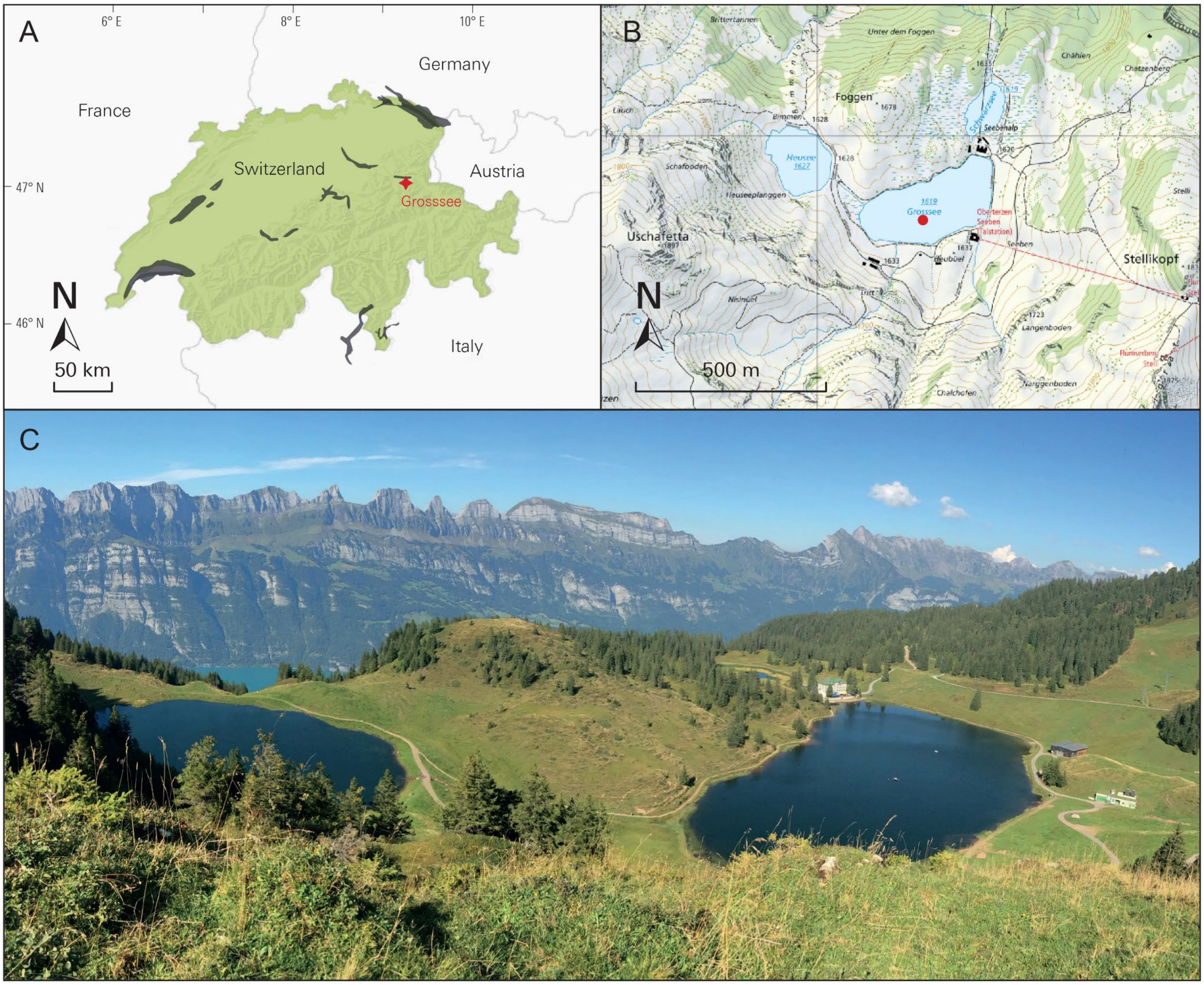


Fig. 1 Location of **A** the study site Grosssee (red diamond), **B** the coring location (red dot), **C** Photo of Grosssee (centre right) and its surroundings. (image credits: **A**, **B** from Bundesamt für Landestopografie swisstopo (©swisstopo), modified; **C**, A. Dwileski)

Three small rivulets lead into Grosssee from the southern slope but only carry water during snowmelt and rainstorms (Roth 1912).

Grosssee has a total catchment of 2.2 km^2 (Glaus 2018) and is part of the Mürtschen Nappe of the Helvetic Alps (Pfiffner 2009; Glaus 2018). The bedrock is composed predominately of acidic purple to reddish-brown Permian Verrucano formations to the north and west of Seebenalp overlain by a succession of highly erodible Triassic-to-Liassic siliceous (57%, e.g. sandstones and Quarten schists) and carbonate (43%, e.g. dolomite) sediments (Lotter et al. 1997).

Mean annual temperature for the period AD 1960–1990 was indicated to be 2.9 °C with mean summer and winter temperatures of 10.3 and −4.5 °C, respectively (Lotter et al. 1997). Since then, mean temperatures have risen steadily due to global warming with more pronounced increases in recent years (2018). Lotter et al. (1997) have further reported mean annual precipitation of 1,824 mm distributed across the year with the highest amounts falling from June to August. During periods of heavy rain, the southeastern slopes above Grosssee are at highest risk of erosion (BAFU 2022). Glaus (2018) has reported Holocene flooding and erosion events, with distinct turbidite layers visible in the sediment core. The first onset of such events began around 8,000 cal BP, they were increasingly present at a continuous but low level of occurrence starting around 6,000 cal BP, and they strongly increased in both frequency and magnitude after 4,000 cal BP (Glaus 2018).

At present, the area around Grosssee bears floral elements from the colline to subalpine vegetation zones (Landolt 2003; Delarze et al. 2008). The area immediately around the lake has been strongly modified and converted to summer cattle pastures (Lotter et al. 1997). In winter, the southeast slopes are used for skiing, forming part of the Flumserberg ski region. Forest and unwooded green surfaces are present to a limited extent in the catchment (Lotter et al. 1997). Northern downslope areas below the lake are forested to a much greater degree. Forested areas are dominated by *Picea abies*, with individual *Pinus cembra* occasionally present on the forest margins. Deciduous subalpine *Sorbus aucuparia* and *Acer pseudoplatanus* are present to a much lesser degree. Understorey shrubs include *Alnus viridis* (synonym: *A. alnobetula*) and *Salix appendiculata* as well as *Vaccinium myrtillus* and *Rhododendron ferrugineum*.

Coring and chronology

Percussion piston coring (UWITEC GmbH, Mondsee, Austria) of lake sediments at Grosssee was performed in June 2017 as part of an effort to study Holocene sediment flux and flood events (Glaus 2018). Piston coring was performed in the deepest part of the basin (11.5 m) to recover a set of partly overlapping 3 m sections used to establish a composite core of 773 cm length. Flood layers (turbidites) distinctly visible to the naked eye were used to line up various core sections, and layers ≥ 2 mm were measured and counted to quantify flood and erosion events (Glaus 2018). Coring and core correlation are described in detail in Glaus (2018) and Morlock et al. (2023).

The original age-depth model of Glaus (2018) was based on a limited number of four radiocarbon dates. For the present study, additional layers were dated resulting in 17 radiocarbon dates from terrestrial plant macrofossils (Table 1). All samples were measured at the Laboratory for the Analysis of Radiocarbon with AMS (LARA), University of Bern (Szidat et al. 2014). Radiocarbon dates were calibrated with 2σ confidence according to the IntCal 20 calibration curve using the online application CALIB 8.2 (Reimer et al. 2020). To obtain a more accurate background sedimentation rate, all turbidite layers ≥ 2 mm were removed from the core (Glaus 2018), and this formed the basis for the event-free age-depth scale (cm_{ef}), which is used throughout this manuscript. An age-depth model was then calculated with Clam 2.2 using linear interpolation between dates to provide age estimates for this revised depth scale. Linear interpolation between the bottommost ^{14}C sample and a pollen-based age estimate was used to provide coarse age estimates below the bottommost ^{14}C sample. For this, the following time points were applied: (a) the known oldest

Table 1 Radiocarbon dates from the sediment record from Grosssee

Code	Composite core depth [cm]	Event-free[a] depth [cm]	Material	^{14}C age [BP][b]	Med. age [cal BP][c]	Age 2σ range [cal BP][c]	Model. age [cal BP][d]
GS17-1[e]	96–98	73.3	Terr. macrophyte W	985 ± 70	870	730–1,055	875
BE-14246.1.1	149.5–151.5	112.6	*Picea abies* N	1,300 ± 25	1,225	1,175–1,290	1,230
BE-14245.1.1	172–174	126.5	*P. abies* N	1,530 ± 25	1,395	1,350–1,515	1,405
GS17-10.C[e]	228.6	165.5	Terr. macrophyte W	1,980 ± 20	1,910	1,835–1,990	1,915
BE-14244.1.1	247–249	181.9	*Abies alba* N	2,275 ± 15	2,320	2,080–2,345	2,285
BE-14243.1.1	262–264	196.2	*P. abies* N + S; conifer BS	2,465 ± 15	2,605	2,430–2,705	2,580
GS17-11B[e]	387.4	263.6	Terr macrophyte W	3,580 ± 25	3,880	3,775–3,975	3,880
BE-14242.1.1	397–399	274.2	*P. abies* N + BS	3,740 ± 15	4,105	3,990–4,150	4,085
BE-14241.1.1	406.5–408.5	283.5	*P. abies* N + BS + SW; conifer BS	3,825 ± 20	4,205	4,100–4,350	4,200
BE-14240.1.1	456.5–458.5	325.5	*P. abies* N + T + S	4,530 ± 20	5,155	5,050–5,310	5,175
BE-14239.1.1	467.5–469.5	333.5	*P. abies* N + BS	4,860 ± 20	5,590	5,490–5,650	5,585
BE-14238.1.1	505.2–507.2	371.6	*A. alba* N, *Betula* F, *P. abies* N	5,660 ± 20	6,435	6,310–6,435	6,440
BE-14237.1.1	516.7–518.7	382.9	*Juniperus*, *P. abies*, *P. cembra* N	5,975 ± 20	6,810	6,740–6,885	6,810
BE-14236.1.1	533–535	397.1	*A. alba*, *Juniperus*, *P. cembra* N	6,885 ± 20	7,710	7,670–7,780	7,710
BE-14235.1.1	546–548	409.0	Indet T	7,890 ± 20	8,680	8,595–8,850	8,685
GS17-12A[e]	555.5–555.7	418.5	Terr macrophyte indet	8,620 ± 60	9,600	9,485–9,745	9,610
BE-14234.1.1	574–578	438.0	Caryophyllaceae F; indet L + FS	10,035 ± 40	11,540	11,325–11,750	11,540

[a] Event-free depths are plotted on the pollen diagram (Fig. 3)

[b] Stuiver and Polach (1977)

[c] Reimer et al. (2020)

[d] Blaauw (2010)

[e] Core section samples prepared and dated as described in Glaus (2018)

Terr terrestrial, *W* wood, *N* needles, *S* seed, *BS* bud scale, *SW* seed wing, *T* twig, *F* fruit, *indet* indeterminable, *L* leaf fragment, *FS* infructescence, *model* modelled

Samples with the prefix BE were prepared by F. Rey

^{14}C age and corresponding depth (11,540 cal BP at 438 cm$_{ef}$, Table 1), (b) the known date attributed to the midpoint of the Late Glacial to Early Holocene increase in percent of *Pinus sylvestris* at a comparable site to Grosssee (i.e. 11,900 cal BP = midpoint date of *P. sylvestris* peak at Lac de Champex (Rey et al. 2022), and (c) the known midpoint depth (i.e. 520 cm$_{ef}$) for the corresponding *P. sylvestris* peak at Grosssee. This resulted in the age of ca. 12,335 cal BP for the oldest sediment sample at 619 cm$_{ef}$.

The composite core consisted of three main lithological units (Glaus 2018): Clays comprised the bottommost core succession ranging from 619 to 435 cm$_{ef}$ with the corresponding age of 12,335–11,243 cal BP. Diatom-rich gyttja consisting of at least 56% biogenic silica occurred at 435–261 cm$_{ef}$ with a corresponding age of 11,243–3,833 cal BP. A total of 17 flood layers occurred within this lithological unit. The transition to the uppermost lithological unit consisting of organic-rich gyttja occurred at 261.2 cm$_{ef}$ at 3,833 cal BP. This lithological unit extended to the surface (AD 2017) and had > 107 flood layers.

Pollen, spores, NPPs, and microscopic charcoal analysis

Eighty, 1-cm thick subsamples of 1 cm^3 volume were retrieved for analysis of pollen, spores, NPPs, and microscopic charcoal. Care was always taken to avoid turbidite layers. When these were encountered, subsamples were retrieved from the adjacent turbidite-free area above the layers. For estimation of concentrations, *Lycopodium* tablets (University of Lund batch no. 140119321 with 19,855 spores per tablet) were added to the samples prior to chemical processing (Stockmarr 1971).

All subsamples were chemically processed with 10% HCl, 10% KOH, 40% HF, acetolysis, sieved through a mesh size of 0.5 mm, and suspended in glycerine according to standard protocols for pollen processing (Moore et al. 1991). One sample was lost during chemical processing, leaving 79 for analysis. Slides prepared with the resulting pollen samples were stained with either fuchsine or safranin and sealed with a mixture of 50% paraffin and 50% bee wax.

Pollen and NPPs (including e.g. spores from coprophilous fungi and fungal wood parasites (i.e. *Ustulina deusta*)) were identified under a light microscope (Leica, Germany) using 400x magnification according to standard palynological keys for northwestern Europe (Punt and Clarke 1984; Reille 1992; Beug 2015). A target of at least 500 terrestrial pollen was identified per sample. Sums and percentages of terrestrial pollen were calculated for subalpine trees, lowland trees, subalpine shrubs, lowland shrubs, and herbs (including *Cannabis sativa* given its infrequency). Pollen of aquatic plants was excluded from the pollen sum. Cyperaceae were retained in the pollen sum, since this group contains many fully terrestrial species that are not restricted to wetlands. Tree *Betula* refers to *Betula* pollen excluding *B. nana*-type, which was very rare in our record. Influxes (particles cm^{-2} yr^{-1}) were calculated for all NPPs. Stomata of conifers were identified based on Trautmann (1953) and following Finsinger and Tinner (2020), which together with biogeographical knowledge on the main tree species occurring in Switzerland, allowed an identification to the level of species or genus (for *Pinus*). Microscopic charcoal (> 10 µm) was counted under 400x magnification following Tinner and Hu (2003) and Finsinger and Tinner (2005) and charcoal influx (particles cm^{-2} yr^{-1}) was calculated to serve as a proxy for regional fire activity. Plant macrofossils in the samples prepared for ^{14}C analysis were identified using appropriate keys (e.g. Schoch et al. 1988) and based on comparison to reference collections.

Numerical analyses

Optimal sum of squares partitioning (Birks and Gordon 1985) was used to determine local pollen assemblage zones (LAPZ) using the program Zone 2.1 (Juggins 1991). The broken-stick model was performed in BSTICK (Bennett 1996) to determine the number of statistically significant zones. Palaeoecological diversity of terrestrial pollen types as a proxy for species richness was assessed using rarefaction (Birks and Line 1992) in the program Past 4.03 (Hammer et al. 2001; https://past.en.lo4d.com/windows) to account for different count sizes and to determine palynological richness (PRI) of individual samples. Rarefaction was based on the lowest count of 504 pollen grains.

Percentage data for terrestrial pollen together with aquatic plants and all NPPs were analysed using an unconstrained detrended correspondence analysis (DCA) with a gradient length of the first axis of 2.2 standard deviation units using square-root transformed data, and down-weighting of rare response variables. Analyses were performed using CANOCO (version 5.2, 2017) (Šmilauer and Lepš 2014; ter Braak and Šmilauer 2018).

Results

Age-depth relationship

^{14}C dates from Grosssee covered the interval of 11,540 to 875 cal BP with no major age reversals (Table 1). The additional pollen-inferred age further suggests significantly higher sedimentation rates in the lowest section of the record preceding 11,540 cal BP than in later sections. According to the age-depth model (Fig. 2), sedimentation rates were

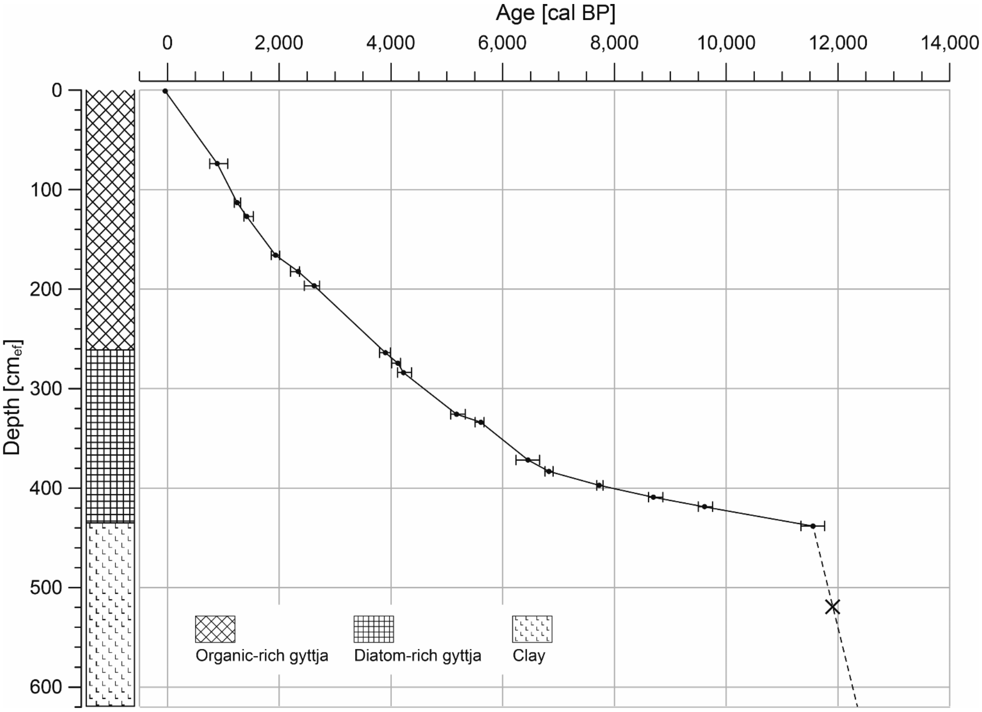


Fig. 2 Event-free age-depth model (cm$_{ef}$) and lithology from Grosssee. Dots indicate calibrated ^{14}C ages with 95% probabilities (2σ). The X at 11,900 cal BP marks the age of the appearance of *P. sylvestris* at sites of comparable altitude in the central Alps (Rey et al. 2021), and the resultant dashed line is a linear interpolation based on this date

highest in the lowest section of the record, predating the first ^{14}C date. This was followed by moderate to low sedimentation rates until ca. 6,800–6,400 cal BP. Afterwards, the sedimentation rate increased further and was highest from ca. 1,910 cal BP to the surface.

Vegetation history

The pollen diagram (Fig. 3) for Grosssee is divided into five statistically significant local pollen assemblage zones (LPAZ GS-1 to 5) based on optimal zonation and testing of significance using the broken-stick model. Zone 4 is further divided into two non-significant subzones (GS-4a and b) for discussion. This subzone boundary just precedes a key transition in lithology from diatom-rich gyttja to organic-rich gyttja as well as a profound increase in floods and major erosion events (Glaus 2018). Pollen counts as well as the influx values of key taxa are given in ESM 1.

GS-1 (ca. 12,340–11,900 cal BP), *Pinus*-Poaceae-*Artemisia* LPAZ

The oldest zone began during the Late Glacial period when the landscape was predominately open with herbs at abundances of 55–65%. This zone was dominated by Poaceae (up to 35%), *Artemisia* (10–20%), and Cyperaceae (~ 5%). Of the woody plants, subalpine taxa including *Juniperus* and tree *Betula* were present in percentages of 5–20% and up to 10%, respectively. Lowland *P. sylvestris*-type pollen was also present in abundances ranging between 5 and 30%. No plant macrofossils for dating were found, and microscopic charcoal influx was consistently low (< 680 particles cm^{-2} yr^{-1}) throughout this subzone.

GS-2 (11,900–10,550 cal BP), *Pinus*-Poaceae-*Artemisia*-*Corylus avellana* LPAZ

This zone is marked by the closing of the landscape, with herbs ranging from 10 to 50% and showing a clear decline to values around 10% at the end of this zone. *P. sylvestris*-type became the dominant taxon, with abundances ranging from about 50% to nearly 75%. Tree *Betula* remained at stable low abundances, similar to but slightly lower than in GS-1. *P. cembra*-type pollen made its first appearance at the start of this zone but never achieved abundances > 5%. Towards the end of this zone at around 10,750 cal BP, thermophilous *Ulmus* (10%) and *C. avellana* (10%), and to a lesser extent *Tilia* and *Quercus* made their first appearances. *Juniperus* declined to < 1% by 11,200 cal BP and remained at such low levels for several thousand years only to show a slight increase in the most recent samples. Microscopic charcoal had two very low peaks with values up to ca. 1,340 particles cm^{-2} yr^{-1} until around ca. 10,000 cal BP. Afterwards, it strongly decreased and was hardly detectable (values ca. 60–140 particles cm^{-2} yr^{-1}). Around the same time, peaks in the influx of trilete fern spores (< 245 spores cm^{-2} yr^{-1}) and spores from coprophilous fungi (< 235 spores cm^{-2} yr^{-1}), particularly *Sordaria* and *Sporormiella*, were apparent.

GS-3 (10,550–6,840 cal BP), *Corylus avellana-Ulmus-Alnus glutinosa*-type LPAZ

Herbs strongly declined to 5–10% throughout this zone, and thermophilous tree taxa including *C. avellana*, *Ulmus*, and *Alnus glutinosa*-type were in strong abundance. *C. avellana* was dominant particularly during the first third of this zone from around 10,550 cal BP with percentages ranging from 40 to 55% followed by a steady decline to 10% by about 6,850 cal BP. Percentages of *Ulmus* pollen were at a Holocene peak with percentages of around 20% from the onset of this zone until around 7,850 cal BP. Afterwards, *Ulmus* declined steadily over the next 1,000 years to around 10%. Appearing with percentages < 5% at the very start of this zone and increasing to nearly 20% at around 9,025 cal BP, abundance of *A. glutinosa*-type pollen was also at its overall highest. Similar to *Ulmus*, it declined towards the end of this zone, when it fluctuated between 10 and 15%.

P. abies and *A. viridis* were both present at very low abundance at the beginning of this zone. *P. abies* sharply increased to 10% by around 7,450 cal BP and neared 20% by the end of the zone. The first *P. abies* macrofossils in the samples analysed for ^{14}C dating also appeared around this time (6,810 cal BP). *A. viridis* increased markedly over roughly 250 years from < 5% to < 15% by about 7,000 cal BP. Pollen of other trees including *Betula*, *P. cembra*, *Salix*, *Sorbus*, *Acer*, *Tilia*, and *Quercus* showed a continued presence or made their first appearance (i.e. *Abies alba*, *Fraxinus excelsior*, and *Fagus sylvatica*), but all were present in abundances of < 10%. The first stomata of *Pinus* (presumably *P. cembra*, as *P. mugo* and *P. sylvestris* were not present as macrofossils), *A. alba*, and *P. abies* appeared together at around 7,875 cal BP, and the first macrofossils of *P. cembra*, *A. alba*, and *Juniperus* at 7,710 cal BP.

Influx of microscopic charcoal fragments and spores from coprophilous fungi was low (< 495 particles cm^{-2} yr^{-1} and < 25 spores cm^{-2} yr^{-1}, respectively) throughout this entire zone.

GS-4a (6,840–4,050 cal BP), *Alnus viridis-Picea abies-Alnus glutinosa*-type-*Fagus sylvatica* LPAZ

Low presence of herbs continued throughout this subzone with percentages around 5% at the beginning and increasing to 10% around 4,745 cal BP. The subalpine shrub *A. viridis* represented the single-most dominant species (25–50%). The declining trend of previously abundant *Ulmus* was already < 5% at the start of this subzone and continued to decline to < 2% by the end. Further downward-trending tree taxa included *Acer*, *A. alba*, *P. abies*, *Tilia*, and *C. avellana*. Conversely, both *Quercus* and *F. sylvatica* showed slight upward trends. In this subzone, pollen of *C. avellana* had also declined to around 10% and lower, a trend which continues to the present day.

This subzone shows the first clear Late Holocene presence of NPPs including monolete and other fern spore taxa (not shown) as well as the spores from coprophilous fungi (ca. 10–160 spores cm^{-2} yr^{-1}) (i.e. *Delitschia*, *Sordaria*, *Sporormiella*) and of the saprophytic wood parasite *Ustulina deusta* (ca. 10–70 spores cm^{-2} yr^{-1} where it was present). Influx of microscopic charcoal was also consistently higher with two peaks around 6,200–6,025 cal BP and 5,750–5,600 cal BP (ca. 1,820 and ca. 1,135 particles cm^{-2} yr^{-1}, respectively).

GS-4b (4,050–900 cal BP), *Alnus viridis-Picea abies-Alnus glutinosa*-type-*Fagus sylvatica* LPAZ

This subzone shows a clear reopening of the landscape with an increase in herbs from upwards of 10% at the beginning to abundances over 20% and as high as almost 30% by 1,325 cal BP. Towards the end of this subzone, the landscape reclosed with herbs dropping to 10–13% for about 100 years from ca. 1,130–1,010 cal BP. *A. viridis* continued as the dominant pollen type but declined towards the end. In addition, there were steady simultaneous declines in *P. cembra*, *Sorbus*, *A. alba*, *P. abies*, *C. avellana*, and *Ulmus*; the latter to generally below 1%. *Juniperus* conversely showed slight gains in this subzone, though its abundance was rarely above 1%.

Towards the end of this subzone, the first indications of cultivated trees were observed. *Castanea sativa* appeared around 1,555 cal BP and *Juglans regia* around 1,440 cal BP. There was an increase and more regular appearance of Cerealia-type pollen. In addition, *Cannabis sativa* made its first appearance around 1,320 cal BP, and there was an increase in grassland/pasture indicators (Behre 1981) including *Plantago lanceolata*, *Rumex acetosa*, *Ranunculus acris*, together with Asteraceae (*Achillea*-type, *Artemisia*, *Gnaphalium*) and Apiaceae (*Ligusticum mutellina* and *Peucedanum*-type) taxa. Nutrient indicator *Urtica* had likewise increased in this subzone.

Influxes of NPPs in this subzone remained high. Influx of monolete spores was particularly high (maximum influx, ca. 16,955 spores cm^{-2} yr^{-1}), and microscopic charcoal influx profoundly increased especially during the latter half of this subzone with maximum values reaching ca. 4,725 particles cm^{-2} yr^{-1}.

GS-5 (900 cal BP to present), *Alnus viridis*-Cyperaceae-Poaceae LPAZ

This final zone marks roughly the last 1,000 years of vegetation history at Grosssee. In general, it marks a reopening

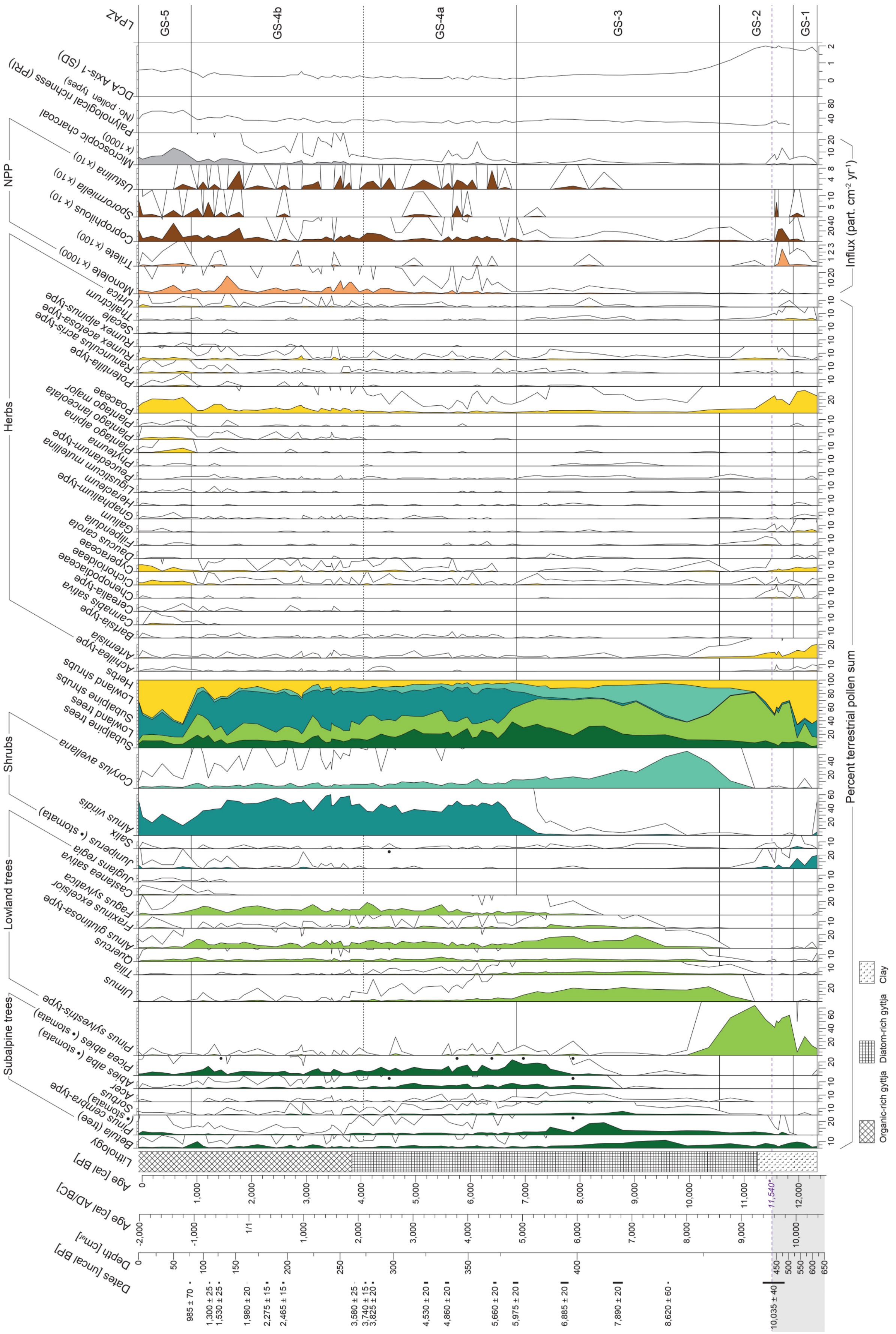

LPAZ
GS-5
GS-4b
GS-4a
GS-3
GS-2
GS-1
DCA Axis-1 (SD)
Palynological richness (PRI) (No. pollen types)
Microscopic charcoal (x 1000)
Ustulina (x 10)
Sporormiella (x 10)
Coprophilous (x 100)
Trilete (x 100)
Monolete (x 1000)
NPP
Urtica
Thalictrum
Secale
Rumex alpinus-type
Rumex acetosa-type
Ranunculus acris-type
Potentilla-type
Poaceae
Plantago major
Plantago lanceolata
Plantago alpina
Phyteuma
Peucedanum-type
Mutellina
Ligusticum
Heracleum
Gnaphalium-type
Galium
Filipendula
Daucus carota
Cyperaceae
Cichorioideae
Chenopodiaceae
Cerealia-type
Cannabis sativa
Bartsia-type
Artemisia
Achillea-type
Herbs
Herbs
Lowland shrubs
Subalpine shrubs
Lowland trees
Subalpine trees
Corylus avellana
Shrubs
Alnus viridis
Salix
Juniperus (• stomata)
Juglans regia
Castanea sativa
Fagus sylvatica
Fraxinus excelsior
Alnus glutinosa-type
Quercus
Tilia
Ulmus
Lowland trees
Pinus sylvestris-type
Picea abies (• stomata)
Abies alba (• stomata)
Acer
Sorbus
Pinus cembra-type (• stomata)
Betula (tree)
Subalpine trees
Lithology
Age [cal BP]
Age [cal AD/BC]
Depth [cm$_{sed}$]
Dates [uncal BP]
Influx (part. cm^{-2} yr^{-1})
Percent terrestrial pollen sum
0
1,000
2,000
3,000
4,000
5,000
6,000
7,000
8,000
9,000
10,000
11,000
11,540
12,000
-2,000
-1,000
1/1
1,000
2,000
3,000
4,000
5,000
6,000
7,000
8,000
9,000
10,000
0
50
100
150
200
250
300
350
400
450
500
550
600
650
985 ± 70
1,300 ± 25
1,530 ± 25
1,980 ± 20
2,275 ± 15
2,465 ± 15
3,580 ± 25
3,740 ± 15
3,825 ± 20
4,530 ± 20
4,860 ± 20
5,660 ± 20
5,975 ± 20
6,885 ± 20
7,890 ± 20
8,620 ± 60
10,035 ± 40
Organic-rich gyttja
Diatom-rich gyttja
Clay

Fig. 3 Partial pollen record for Grosssee. Selected pollen types are presented as % of the terrestrial pollen sum; monolete spores, fungal spores and charcoal as influxes (spores or particles cm^{-2} yr^{-1}). *Empty curves* indicate 10 x exaggerations. The *dashed purple line* indicates the median age (11,540 cal BP) of the bottommost ^{14}C sample. Dates below this line, indicated by the *light grey field*, are loosely estimated according to a linear interpolation corresponding to an increase in *P. sylvestris* values at around 11,900 cal BP as observed at other Swiss alpine sites of similar elevation (e.g. Lac de Champex; Rey et al. 2021). *LPAZ* local pollen assemblage zone, *NPP* non-pollen palynomorph, *PRI* palynological richness estimated using rarefaction (as number of taxa; unavailable for the four bottommost samples due to low pollen counts)

of the landscape with a return to an abundant presence of herbs (30–65%) including the highest evidence yet of pollen types indicative of human impact. Percentages of most lowland and subalpine trees showed an initial decline and then stable low abundances. Declines, though slight, were particular recorded for woody species including *Quercus*, *A. glutinosa*-type, *F. sylvatica*, *A. viridis*, and *C. avellana.* Increases in herbaceous openland taxa including Poaceae, Cichorioideae, *P. lanceolata*, *P. major*, *P. alpina*, *R. acetosa*, *R. acris*, *Potentilla*, *Gnaphalium* and other Asteraceae, Apiaceae, Chenopodiaceae, and *Thalictrum* attest to the increasingly more open landscape. The common presence of other herbaceous taxa including *Bartsia*, *Filipendula*, *Galium*, and *Phyteuma* provides evidence of the diversity of this most recent zone.

This zone also had the highest overall percentage of cultural indicators: *Castanea sativa*, *J. regia*, *Cannabis sativa*, Cerealia-type, *Secale*, and previously mentioned pasture indicators such as *Plantago* spp. NPP influxes remained high. Although influx of monolete spores had slightly declined (ca. 1,380 cal BP to maximum 8,150 spores cm^{-2} yr^{-1}), total influx of spores from coprophilous fungi had reached its highest value (ca. 345 spores cm^{-2} yr^{-1}). Likewise, microscopic charcoal had reached its highest overall influx (ca. 13,280 particles cm^{-2} yr^{-1}) in this zone.

Numerical analyses

Pollen analyses resulted in the identification of 147 terrestrial and three aquatic pollen types, and NPPs belonging to nine fern spore types and spores from six coprophilous- and two wood-destroying fungi. Considering terrestrial pollen alone, PRI (Fig. 3) revealed lowest diversity with 19–24 taxa at the beginning of the Holocene period from 11,390 to 10,750 cal BP. PRI then rose to 29–42 taxa over the course of the Holocene with a general increase in the number of taxa during the Mid- to Late Holocene. Diversity was highest with 50–61 taxa from the Late Middle Ages to the mid-20th century AD (AD 1210–1943) and declined again to 37 taxa in the topmost samples.

Results of the DCA are shown in scatterplots for samples and for pollen taxa (Fig. 4). Axis 1 explains 26.4% of the variation and shows a strong separation of Late Glacial samples (GS-1 and GS-2) from those of the Holocene (GS-3 through GS-5). Of note, the latest grouping of sites (GS-5) shows a tendential return to conditions similar to the Late Glacial along axis 1. Axis 2 explains 9.8% of the variation and shows a clear Holocene succession over the course of 10,600 years, spreading samples from the different pollen zones more-or-less in chronological order (GS-3 through GS-5). Taxa scores support this interpretation. Early Holocene thermophilous taxa including *Ulmus*, *Tilia*, *C. avellana*, *F. excelsior*, and *Acer* as well as *P. cembra* have high axis-2 scores. Middle Holocene taxa including *Quercus* and *F. sylvatica* are characterized by intermediate scores on axis 2. They are accompanied by the strong and continued presence of *A. viridis*, monolete fern spores, and spores from coprophilous fungi. Further transitions to Late Holocene pasture indicators (*P. major*, *P. lanceolata*, and *Rumex alpina*) and cultivated taxa (*Cannabis sativa*, *Castanea sativa*, *J. regia*, Cerealia-type, and *Secale*) that have low axis-2 scores are also clearly visible.

Discussion

Vegetation patterns during the Late Glacial period and transition into the Holocene

The earliest recovered sediments at Grosssee accumulated during the Younger Dryas cooling (~12,700–11,600 cal BP), a marked cold period at the end of the Late Glacial period (Ilyashuk et al. 2009; Ivy-Ochs et al. 2009; Heiri et al. 2015). The large proportions of Poaceae with *Artemisia*, Cyperaceae and lower amounts of *Galium*, *Thalictrum*, Chenopodiaceae, and other Asteraceae types such as *Achillea*-type and *Gnaphalium*-type pollen are characteristic of alpine tundra vegetation (Burga and Perret 1998), and their dominance in Late Glacial sediments at Grosssee (Fig. 3) indicates that the landscape was generally open.

Juniperus, a pioneer of poor undeveloped soils (Enescu et al. 2016), had reached its maximum abundance in the sediment record of Grosssee during the Late Glacial, with highest percentages of 15–20% from 12,335 to 11,970 cal BP. Tree *Betula* and occasionally *Salix* were also present, as well as very low amounts of tundra-type shrubs including *Ephedra fragilis*, *E. distachya*, and *Hippophaë rhamnoides.*

Pollen of *P. sylvestris*, another pioneer of poor soils (Houston Durrant et al. 2016b), was also present in large percentages (5–30%) in the Late Glacial sediments of Grosssee. At that time, it had been a dominant tree species on the Swiss Plateau (Welten 1982; Rey et al. 2017,

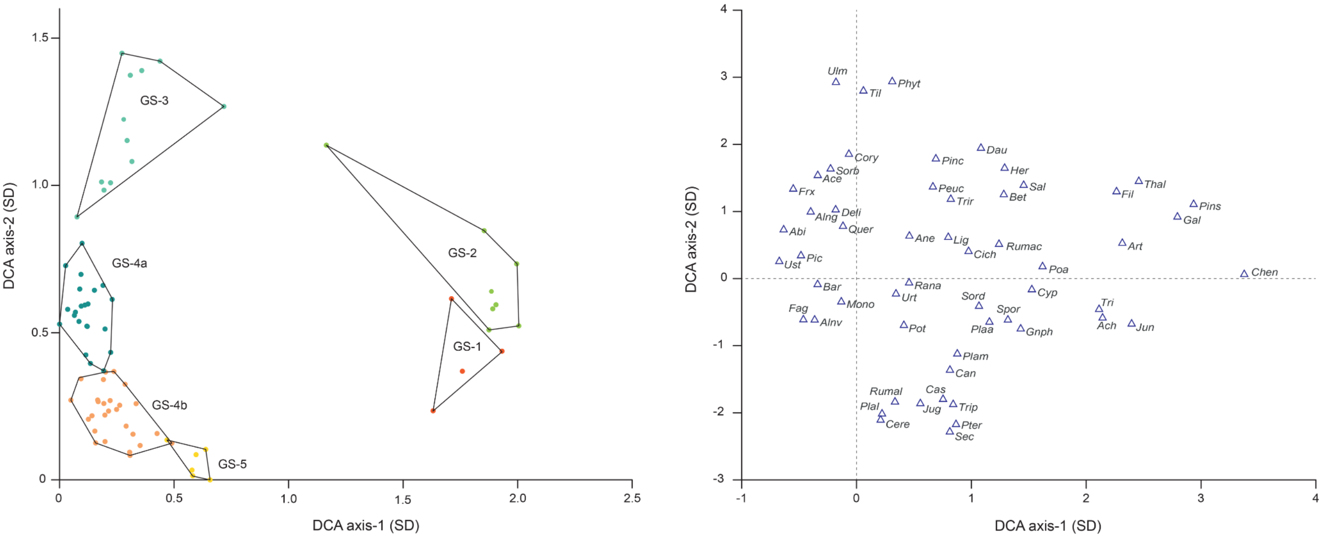


Fig. 4 DCA scatterplots of (left) sample scores grouped according to local pollen assemblage zones (LPAZ) and (right) species scores. Abi: *Abies alba*, Ace: *Acer*, Alng: *Alnus glutinosa*-type, Alnv: *A. viridis*, Ane: *Anemone/Clematis*-type, Art: *Artemisia*, Bar: *Bartsia*-type, Bet: *Betula* (tree), Can: *Cannabis sativa*, Cas: *Castanea sativa*, Cere: Cerealia-type, Chen: Chenopodiaceae, Cich: Cichorioideae, Cory: *Corylus avellana*, Cyp: Cyperaceae, Dau: *Daucus carota*, Deli: *Delitschia*-type, Fag: *Fagus sylvatica*, Fil: *Filipendula*, Frx: *Fraxinus excelsior*-type, Gal: *Galium*, Gnph: *Gnaphalium*-type, Her: *Heracleum*, Jug: *Juglans regia*, Jun: *Juniperus*, Lig: *Ligusticum mutellina*, Mono: Monolete, Peuc: *Peucedanum*-type, Phyt: *Phyteuma*, Pic: *Picea abies*, Pinc: *Pinus cembra*-type, Pins: *P. sylvestris*-type, Plaa: *Plantago alpina*, Plal: *P. lanceolata*, Plam: *P. major*, Poa: Poaceae, Pot: *Potentilla*-type, Pter: *Pteridium aquilinum*, Quer: *Quercus*, Rana: *Ranunculus acris*-type, Rumac: *Rumex acetosa*-type, Rumal: *R. alpinus*-type, Sal: *Salix*, Sec: *Secale*, Sorb: *Sorbus*, Sord: *Sordaria*-type, Spor: *Sporormiella*-type, Thal: *Thalictrum*, Til: *Tilia*, Tri: Trilete, Trip: *Trifolium pratense*, Trir: *T. repens*, Ulm: *Ulmus*, Urt: *Urtica*, Ust: *Ustulina deusta*

2020), and its pollen was present in very high percentages in sediment records of several other upland sites (Gobet et al. 2003; Rey et al. 2022). Missing macrofossils and stomata from this period at Grosssee do not allow conclusions about its actual presence at the site. Yet, given its aspect as a super producer of wind-dispersed pollen (Traverse 2008) together with its occurrence at a range of elevations and its abundance on the Swiss Plateau (Welten 1982; Rey et al. 2017, 2020), the very high percentages in early Grosssee sediments were likely due to long-distance transport from lower elevations (Berthel et al. 2012; Ammann et al. 2014; Lang et al. 2023).

At the transition from the Late Glacial period to the Holocene, later successional vegetation was expanding in the landscape, and the previously mentioned tundra herbs and Poaceae were now in clear decline. *P. sylvestris* had increased and became the dominant taxon in the record. The transition to the much warmer (i.e. by up to 4 °C in summer temperature (Ilyashuk et al. 2009; Renssen et al. 2012; Heiri et al. 2015)) Early Holocene potentially triggered the clearly visible changes in vegetation. These pronounced changes in vegetation also correspond to the change in lithology from clays to diatom-rich gyttja (Fig. 3).

Afforestation at Grosssee

The timing of afforestation at Grosssee is difficult to estimate from the present study alone given the lack of a continuous macrofossil analysis and the first appearance of stomata (of *A. alba*, *P. abies*, and *Pinus*) only at 7,870 cal BP (Fig. 3). The study at the adjacent Seebenalp, however, identified stomata in consecutive samples beginning after the empirical limit of *Ulmus* had been reached in the pollen record but before its expansion (Perret 1993). Comparing the pollen diagrams from Grosssee and Seebenalp allows a rough estimation of afforestation at Grosssee at ca. 10,800 cal BP, about 400 years after the lithological change in the sediments. This also fits well with reported dates of afforestation or reforestation at other sites of similar altitude in Switzerland. Pollen of tree species including *Betula*, *P. cembra*, and *P. sylvestris* were present in Grosssee sediments from that time and these were likely among the first tree species to settle in the catchment. Afforestation began between ca. 11,600 and 9,800 cal BP at other studied Swiss mountain lakes, e.g. at ca. 11,600 cal BP at Lauenensee (Rey et al. 2013), ca. 11,500 cal BP at Lac de Champex (Rey et al. 2022), ca. 11,000 cal BP at Hinterburgsee (Heiri et al. 2003), Lej da San Murezzan, and Lej da Champfer (Gobet et al. 2003), ca. 10,300 cal BP at Lac de Bretaye (Thöle et al. 2016), and ca. 9,800 cal BP at Iffigsee (Schwörer et al.

2014) (see ESM 2 Fig. S1 for an overview of the location of these sites relative to Grosssee). Afforestation generally occurred considerably earlier at low vs. high altitude sites and earlier in the central and southern vs. northern Swiss Alps (Schwörer et al. 2014). The delay of up to 500–1,000 years in the northern Swiss Alps might be due to cooler temperatures and/or greater seasonality (Schwörer et al. 2014) or due to a combined effect of Late Glacial/Early Holocene cooling events (Haas et al. 1998; von Grafenstein et al. 1999; Tinner and Kaltenrieder 2005).

At most sites in the northern and central Alps, afforestation was generally with tree *Betula* and *P. sylvestris* (Gobet et al. 2003; Rey et al. 2013, 2022) and to some extent with *P. cembra* (Thöle et al. 2016) and *P. mugo* (Heiri et al. 2003). *Larix decidua* was generally more important at southern sites across the European Alps and never established large natural populations in the central or northern Swiss Alps (Da Ronch et al. 2016). At Grosssee, *L. decidua* pollen was present in a single sample at ca. 4,370 cal BP. Locally occurring *L. decidua* seems to have been limited due to unfavourable conditions such as higher humidity as well as its difficulty to root well in Verrucano and in Verrucano schists (Roth 1912).

Early Holocene rise and fall of thermophilous taxa

By the start of the Early Holocene, previously extensive grasslands around Grosssee were strongly reduced. Consistently low influxes of monolete fern spores as well as microscopic charcoal indicate low levels of environmental disturbance. From ca. 11,000 cal BP onwards, percentages of *P. sylvestris* pollen declined sharply (Fig. 3). This was potentially due to competition with thermophilous deciduous lowland shrubs and trees such as *C. avellana*, *Ulmus*, *Tilia*, *Quercus*, *A. glutinosa* and/or *A. incana* (both in *A. glutinosa*-type), and *F. excelsior*, which appear in the record in close sequence followed by a low maximum peak of nearly 20% of *P. cembra* (ca. 8,800–8,200 cal BP). The first increases in pollen of thermophilous taxa reflect the establishment of mixed-oak forests at lower elevations (Welten 1982; Rey et al. 2017, 2020).

From the beginning of GS-3 at around 10,550 cal BP, there was a prominent rise in the percentages of both *Ulmus* and *C. avellana. Ulmus* reached a stable Holocene maximum of 20% from 10,350 to 7,870 cal BP and *Corylus* a unimodal maximum of 55% at 9,960 cal BP followed by a steady decline over ca. 3,000 years. At comparable sites in the Swiss Alps (Heiri et al. 2003; Thöle et al. 2016), C. *avellana* likewise show a unimodal maximum and apparent decline due to competition with other tree taxa. Compared to *Ulmus* at Grosssee, only *A. glutinosa*-type, which both arrived and expanded later, was present in relatively high abundances during the Early Holocene (from ca. 9,500 cal BP). Several comparative sites (e.g. Heiri et al. 2003; Wick et al. 2003; Rey et al. 2013; Schwörer et al. 2014; Thöle et al. 2016) show both the same lower abundances of *A. glutinosa*-type pollen and then its persistence to the present day compared to *Ulmus*, which became very rare.

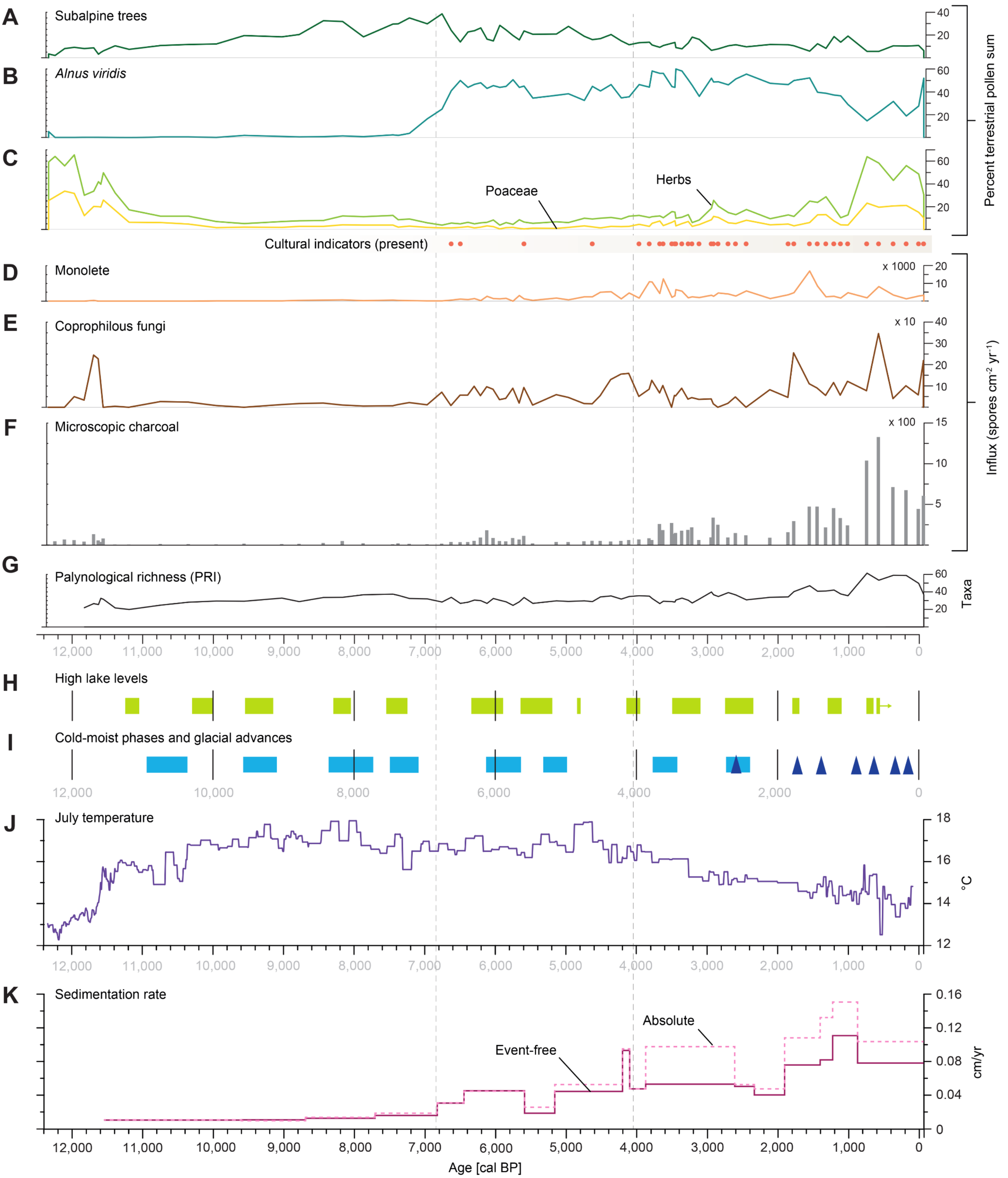
Compared to other thermophilous taxa, *F. excelsior*, a lowland species in the northern parts of its range (Beck et al. 2016), appeared about 1,000 years later at Grosssee. *Fraxinus excelsior* and other thermophilous taxa are generally limited to lower altitudes (San-Miguel-Ayanz et al. 2016), and their low abundances might imply that they had not reached the lake catchment.

The rise in these taxa can be attributed to rapid warming after ca. 11,600 cal BP (Heiri et al. 2015). In particular, summer temperatures in central Europe were up to 3 °C warmer compared to preindustrial levels (Renssen et al. 2012) during the Holocene Thermal Maximum (ca. 11,000–5,000 cal BP) (Renssen et al. 2012; Heiri et al. 2015). This potentially led to the expansion and temporary dominance of these taxa at lowland to montane and possibly also subalpine sites in the Swiss Alps (Litt et al. 2009; Rey et al. 2013, 2017; Lang et al. 2023) and in the pollen record at Grosssee often at the expense of *P. sylvestris*. Thöle et al. (2016) have attributed the decline of *P. sylvestris* to the expansion of these lowland taxa, but at Grosssee, *P. sylvestris* was already in decline (Fig. 3). It is possible that the expansion of these species prevented the resurgence of *P. sylvestris* in the catchment at Grosssee.

Early- to Mid-Holocene arrival of *Abies alba*, *Picea abies*, and *Fagus sylvatica*

Based on pollen data (empirical limits), *A. alba* and *P. abies* both became established at around 8,800 cal BP. The first stomata of *A. alba* and *P. abies* appeared at 7,870 cal BP. Macrofossil evidence from Sägistalsee (Wick et al. 2003) and Hinterburgsee (Heiri et al. 2003) documents *A. alba* (8,500 to 8,200 cal BP) expanding earlier than *P. abies* (6,150 and 6,000 cal BP) at both sites. The earlier expansion of *P. abies* at Grosssee might be expected given its slow spatial expansion from east to west (Burga and Perret 1998; van der Knaap et al. 2005).

Rey et al. (2013) have attributed the expansion of *A. alba* around 7,500 cal BP at Lauenensee to a shift to moister climate conditions (Fig. 5I) (Haas et al. 1998; Heiri et al. 2003), which is also reflected by regionally higher lake levels (Fig. 5H) (Magny 2004). At Grosssee, while *P. abies* expanded in the catchment around 7,500 cal BP, *A. alba* seemed to have been restricted. It was slow to establish, reached percentages at most up to 8%, and failed to expand further. At other sites (e.g. Heiri et al. 2003; Wick et al.



2003; Rey et al. 2013; Schwörer et al. 2014; Thöle et al. 2016; Rey et al. 2022), A. *alba* had established larger populations but then declined with the arrival of *P. abies* and *A. viridis* and likely also due to changing climatic conditions as well as environmental disturbances (Wick and Tinner 1997; Gobet et al. 2003; Heiri et al. 2003; Wick et al. 2003; Rey et al. 2013).

Mesophyllic *F. sylvatica* is drought sensitive and typical of moist oceanic climates (Roth 1912; Houston Durrant et al. 2016a). It migrated into central Europe from south to

Fig. 5 Comparison of biotic and abiotic proxies from Grosssee with selected regional climate records. Percentages of **A** subalpine tree pollen, **B** *Alnus viridis*, and **C** herbs and Poaceae; presence/absence of cultural indicators (*Plantago lanceolata* and Cerealia-type pollen only, following Tinner et al. 2003). Influx of **D** spores of monolete ferns, **E** coprophilous fungi, **F** microscopic charcoal particles. **G** Rarefaction indicating the palynological richness (PRI), displayed as number of taxa. **H** Lake-level fluctuations in the western Swiss Plateau based on sediment analyses (Magny 2004), **I** Central European cold and wet phases (blue rectangles) based on pollen and macrofossil data (Haas et al. 1998). Published dates were calibrated in CALIB 8.2 (Reimer et al. 2020) with SD set to 50 years to match the interval in the original publication. Advances of the Greater Aletsch Glacier (dark blue triangles) (Holzhauser et al. 2005) based on dendrochronological dating (prior to 650 cal BP) and on archaeological or historical evidence afterwards. **J** Chironomid-derived average July temperatures (Heiri et al. 2015) estimated for an elevation of 1,000 m a.s.l. **K** Sedimentation rates calculated based on absolute (dashed line) and event-free (solid line) sediment depth and ages presented in Table 1, representing overall and background sedimentation at Grosssee, respectively. Dashed vertical lines correspond to the transition between local pollen assemblage zones GS-3 and GS-4a and GS-4a and b at 6,840 and 4,045 cal BP, respectively

north (Brewer et al. 2017). Its appearance coincided with a shift towards a moister, more oceanic climate following the 8.2 ka event (Tinner and Lotter 2001, 2006), and it became the dominant tree species in lowland Switzerland (Rey et al. 2019). The establishment of stable populations of *F. sylvatica* (and *A. alba)* may have contributed further to the decline of *C. avellana*, as suggested by Heiri et al. (2003). At Grosssee, *F. sylvatica* reached its empirical limit at ca. 8,400 cal BP and expanded from 5,800 cal BP to levels between 5 and 15% that persisted up until ca. 1,000 cal BP. Afterwards, it declined.

Mid-Holocene expansion and dominance of *Alnus viridis*

Early occurrences of *A. viridis*-pollen suggest that populations of *A. viridis* became established very early (9,600 cal BP) at Grosssee and at other sites in Eastern Switzerland, such as Lej da Murezzan and Lej da Champfer (Gobet et al. 2003) compared to other Swiss sites of similar elevation on the north side of the Alps (ESM 2 Fig. S1, Table S1). On the south side of the Alps, *A. viridis* became established even earlier, between 12,000 and 11,100 cal BP at reported sites (Wick and Tinner 1997; Vescovi et al. 2018). Major increases in this pollen type later in the record indicate that, unlike all other Swiss sites including Lej da Murezzan and Lej da Champfer (Gobet et al. 2003), A. *viridis* reached its rational limit and expanded much earlier and to a greater extent at Grosssee (ca. 7,200 cal BP) (ESM 2 Table S1). This is more than 2,000 years earlier than at Hinterburgsee in the Bernese Alps (Heiri et al. 2003), the next earliest comparable site, and up to 3,000 years earlier than at comparable sites in the central and southwestern Swiss Alps. The increase of *A. viridis* pollen at Grosssee is distinct from very low percentages prior to ca. 7,400 cal BP to values around 50% at ca. 6,800 cal BP. At the same time, percentages of *A. glutinosa*-type, the second *Alnus* pollen type in the record, decrease from moderate abundances of ca. 10–15% around 7,400 cal BP to lower values of around 5% by ca. 6,900 cal BP. A few sporadic, possibly misidentified *A. glutinosa*-type pollen can, therefore, not be expected to explain or to have contributed to this major rise in *A. viridis*.

Published studies (e.g. Welten 1982; Gobet et al. 2003; Rey et al. 2022) addressing the expansion of *A. viridis* have looked at links to climate and human impact, with Welten (1982) substantiating strong links between intensified land use and the profound expansion of *A. viridis* in the Valais. In particular, he suggested that subalpine forests were destroyed by upland inhabitants in efforts to acquire land for cattle pastures (Welten 1982). Wick and Tinner (1997) have also suggested human habitat modification supporting its expansion. For example, during the late Neolithic and Early Bronze Age *A. viridis* was likely used as winter fodder and to promote favourable habitats for tall herbs and edible forbs. Several other studies (e.g. Tinner et al. 1996; Gobet et al. 2003; Berthel et al. 2012; Rey et al. 2013, 2022) have suggested that disturbance caused by fire activities may have favoured this species.

Shortly before the expansion of *A. viridis* at Grosssee, there was a decline in pollen amounts from subalpine trees (Fig. 5A), such as tree *Betula* and *P. cembra*, which could have been an effect of the 8.2 ka cold event (Tinner and Lotter 2001; Kofler et al. 2005). At that time, temperatures had shortly declined, lake levels in the west Swiss Midlands were high, and the region experienced a cold- and moist phase (Fig. 5J, H and I; Haas et al. 1998; Tinner and Lotter 2001; Magny 2004). Despite a gradual recovery of subalpine trees over the next ca. 1,200 years, it is possible that this and other factors contributed to conditions supporting the expansion of *A. viridis* at Grosssee. Huber and Frehner (2012) have noted that *A. viridis* thrives in cool and moist conditions and particularly favours steep north facing slopes (often > 40%) of the subalpine zone. It grows exceptionally well on schists, lime-poor soils, bare ground, unstable surfaces, and locations prone to avalanches where less tolerant trees and shrubs are excluded (Huber and Frehner 2012).

At around 6,800 cal BP, thermophilous lowland taxa including *Ulmus*, *Tilia*, *A. glutinosa*, and *C. avellana* were all in clear decline. Likewise, subalpine tree *Betula*, *P. cembra*, *Sorbus*, *A. alba*, and *P. abies* were declining. While pollen percentages of herbs show only a very slight increase, pollen of cultural indicators (Cerealia-type and *P. lanceolata*, Tinner et al. 2003) were entirely new to the catchment (Fig. 5C). By 6,600 cal BP, *A. viridis* had established very extensive populations as evidenced by a presence of

30–50% in the pollen record. The above-described vegetation changes since 6,800 cal BP were accompanied by the first increases in fern spores (i.e. monolete), increases in coprophilous fungi (e.g. *Sporormiella*), and an increase in microscopic charcoal (Fig. 5D, E and F), indicative of disturbance, the presence of grazers, and fire activities, respectively. A trend toward a cooler and moister climate during the Mid- to Late Holocene (Heiri et al. 2015) together with these factors would have promoted the dominance of *A. viridis* in the landscape. *A. viridis* is especially well suited at settling disturbed and unstable habitats (Huber and Frehner 2012), which are indicated by the rise in erosion at Grosssee (Fig. 5K; Glaus 2018) and increased influx of fern spores. Grazing activities including cattle trampling of pastures would have further promoted its expansion (Huber and Frehner 2012). In its growth habit, *A. viridis* can establish dense thickets, which halt further succession of a site by preventing the settlement of trees (Anthelme et al. 2002).

After dominating the landscape at Grosssee for over 5,500 years, *A. viridis* declined between ca. 2,000–1,000 cal BP as it did at other subalpine sites on the north side of the Alps (ESM 2 Table S1) in agreement with the findings of Welten (1982). Tinner et al. (1996) have suggested that the effects of human habitat modification had a role in this trend, due to intensified land use favouring the expansion of meadows and pastures (Tinner et al. 1996). In recent times, *A. viridis* has rebounded at Grosssee and some other sites in the northern Swiss Alps (Rey et al. 2013; Thöle et al. 2016).

Role of vegetation on erosion

At Grosssee, flooding and erosion increased from around 6,800 cal BP onwards, with even higher frequencies and magnitudes after ca. 4,000 cal BP (Glaus 2018). This is also reflected in distinct increases in sedimentation rates in the record starting around 6,800 cal BP and and again at 4,000 cal BP, with highest values in overall sedimentation rates reached in the past ca. 2,000 years (Figs. 2 and 5K). This pattern was likely associated with a coupling of natural conditions such as slope and soil erodibility (Cerdan et al. 2010; Arnaud et al. 2016) together with changes in vegetation, patterns of land use, and climatic effects. Interestingly, there was a pronounced change in pollen assemblages (GS-3 to GS-4a transition, at around 6,800 cal BP (Fig. 5, dashed line)) when erosion and sedimentation rates began to increase (Glaus 2018; Fig. 5K). Both subalpine and lowland trees were in clear decline, possibly indicating deforestation. This trend was accompanied by persistently high percentages of disturbance-associated *A. viridis*. At the same time, simultaneous increases in influxes of monolete fern spores and spores from coprophilous fungi as well as spores of the wood-rot fungus *U. deusta*, are likewise apparent. Ferns, a component of pioneer vegetation and particularly associated with secondary succession (Gobet et al. 2003; Walker and Sharpe 2010), provide further evidence of disturbance in the landscape. Spores from coprophilous fungi, such as *Sporormiella*, together with the very first *P. lanceolata* pollen indicate the presence of grazers (Behre 1988) and evidence of pastures (Tinner et al. 2003). Likewise, microscopic charcoal, a classic fire indicator (e.g. Gobet et al. 2003; Tinner et al. 2005) followed a similar pattern and suggests open land expansion through deforestation by burning. The increased presence of *U. deusta* may indicate a further weakening of woody species in forests (Terho and Hallaksela 2008).

The regular presence of Cerealia-type pollen and *P. lanceolata* together with the marked and rather synchronous increase of NPPs and microscopic charcoal influxes at Grosssee after 4,000 cal BP (Fig. 5) match the increases in both flooding and erosion (Glaus 2018; Fig. 5K), thus providing very strong evidence for human impact as the main trigger. As indicated by the increase in grass and herb pollen, land use seems to have been intensifying with the expansion of open lands. Human impacts appear to have been particularly pronounced at several sites in Switzerland during the Early Bronze Age (Tinner et al. 1996; Gobet et al. 2003; Wick et al. 2003; Schwörer et al. 2015). This pattern toward open landscapes would have incurred the loss of penetrating root systems, further destabilizing soils and increasing erodibility. High proportions of herbs (e.g. Poaceae) together with high abundances of charcoal are also observed in the Grosssee record when sedimentation rates increased further during the past 2,000 years. This again supports the interpretation that high levels of human activity may have contributed to elevated levels of erosive input into the lake.

As indicated above, *A. viridis* may have been favoured by disturbances that may also have led to enhanced erosion. Opinions are conflicting as to whether *A. viridis* itself helps to prevent or contributes to erosion. Several aspects about *A. viridis* counteract erosion. It forms well-developed penetrating root systems, thereby limiting the scouring of the substrate during avalanches (Huber and Frehner 2012). Its root structure additionally roughens the soil surface, slowing flow speeds of surface waters, while opening the ground to allow for quick infiltration during rainfalls. Further, its dense growth dampens the erosive impact of heavy rain (Huber and Frehner 2012). On the other hand, its elastic stems bend downward during heavy snows, forming extensive slides for multiple successive avalanches (Mürner 1999; Richard 1995; as cited in Huber and Frehner 2012).

Pastoral and agricultural indicators during the Late Holocene

The presence of pollen of cultivated plants such as Cerealia-type, *Secale*, *Cannabis sativa*, *Castanea sativa*, and *J. regia* in sediment records from Europe are good indicators of agri- and arboriculture (Behre 1981; Tinner et al. 2003; Conedera et al. 2004; Deza-Araujo et al. 2022). Pollen of certain forb taxa such as general pasture indicators: *P. lanceolata*, *P. major*, *R. acris;* wet meadow indicators: Asteraceae, Poaceae, Ranunculaceae, *Rumex acetosa*, *P. lanceolata*, *P. majo*r, Cyperaceae, Apiaceae; dry pasture indicators: *Jasione* and *Campanula*, *Juniperus*, *Calluna;* and ruderal indicators: *Artemisia*, Chenopodiaceae, *Urtica* can allow for conclusions to be made based on past vegetation assemblages (Behre 1981). All these groups were present or had increased in abundance at Grosssee during the Late Holocene, potentially indicating an increase in the diversity of habitat types. This is supported by the increase in PRI (Figs. 3 and 5G) that coincides with the opening of landscapes and increase in indicators signalling human impact.

Over the past 4,000 years at Grosssee, pastoral and agricultural indicators regularly appeared in the pollen record, grasses and more so herbs increased in abundance, and influxes of monolete fern spores and spores from coprophilous fungi as well as microscopic charcoal were all high and increasing (Fig. 5). Taken together, these indicate intensified land use. From ca. 1,800–1,200 cal BP and especially from ca. 1,100 cal BP until the past 100 to 200 years, the landscape at Grosssee was particularly wide open. This alludes to a further intensification of land use and potentially to changes in agricultural patterns. At Grosssee, while Cerealia-type pollen appeared for the first time at 5,600 cal BP, *Secale* only appeared in the record at around 1,550 cal BP (AD 400).

Increasing percentages of *Castanea* pollen from the 1st century AD in northern Switzerland, and southern France and Germany have been attributed to the Romans (Conedera et al. 2004). *Castanea sativa* prefers an oceanic climate and has been able to become established in the Walensee region in mixed beech-oak forests (Roth 1912). The climate moderating effects of the lake Walensee and the foehn winds allow for suitable conditions in the region, and this species is particularly competitive on the large areas of silicate-rich sediments closer to the lake where moisture is higher (Roth 1912). Declines in *F. sylvatica* can be observed in the pollen assemblages at Grosssee after 1,000 cal BP as percentages of *Castanea* increase. During the 13th–15th centuries, *Castanea sativa* was more widely distributed and of higher importance (i.e. as a staple food) in the region compared to today (Roth 1912). Today in upland beech-oak forests, stunted *Castanea sativa* only occur on the margins and never inside where it is outcompeted by *F. sylvatica*. With around 1,850 trees, one of the largest sweet chestnut forests north of the Alps still belongs to the town of Murg, ca. 4 km from Grosssee (Ehrensperger 2020).

The first historical reference to Grosssee (Seebenalp) is from a 13th century document referring to its value as a pasture (Rigendinger 2007). Further activities such as the 13th century clearing of the slopes west of Flums and the 14th century cattle tax (Rigendinger 2007) may hint at the expansion and intensified use of upland pastures. Interestingly, these events coincide with the period of maximum openness at Grosssee when the percentage of herbs ranged from 60 to 65%. Moreover, they correspond to the period of highest pollen diversity. Over the last 100 to 200 years, land use patterns have changed further because of industrialization and several other socioeconomic and demographic considerations. At Grosssee, particularly the renewed increase in subalpine shrubs, primarily *A. viridis*, is apparent, suggesting less intensified pasturing and catchment clear-cutting in recent decades. This agrees with increases in tree and shrub pollen recorded in many other pollen records from the subalpine vegetation zone (e.g. Hausmann et al. 2002; Wick et al. 2003; Rey et al. 2013; Garcés-Pastor et al. 2022).

Conclusions

The overall sequence of succession in vegetation assemblages around Grosssee from the Late Glacial period to the modern day generally match those of other Swiss sites of similar elevation. Early changes began with the gradual closing of the landscape and afforestation most likely with tree *Betula*, *P. sylvestris*, and *P. cembra*. This led to the rise of thermophilous trees and then their replacement by extensive *A. viridis* thickets and the establishment of *P. abies* and mixed beech-oak forests. At Grosssee during the Mid-Holocene, *A. viridis* underwent a profound expansion at ca. 7,000 cal BP, which is about 2,000 years earlier than at the next comparable site in the northern Alps (Hinterburgsee). A combination of site-specific attributes including optimal substrate and exposition, a climatic shift to a cooler and moister environment, and human impacts through increased grazing and possibly regional fires likely worked together to promote its early and extensive expansion. Locally increased erosion that followed soon after from 6,800 cal BP onwards and intensified from ca. 4,000 cal BP onwards and again around ca. 2,000 cal BP are well explained by changes in the vegetation and inferred human activities at Grosssee. In particular, the landscape opened and land uses (e.g. grazing) intensified from the Mid- to Late-Holocene and have apparently promoted the erodibility of the catchment soils and led to the very strong and unusual increase in flood layers and erosive input into the lake recorded from ca. 6,000 cal BP onwards. Land use and grazing activities also seem to have played a major role in promoting diversity in the vegetation over the last 1,000 years.

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