



14,500 years of vegetation and land use history in the upper continental montane zone at Lac de Champex (Valais, Switzerland)

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Abstract

Forests in the upper continental montane zone are important ecotones between lowland and subalpine forest ecosystems. A thorough understanding of the past vegetation dynamics at mid elevation is crucial to assess past and future altitudinal range shifts of tree species in response to climate change. Lake sediments from Lac de Champex (1,467 m a.s.l.), a small lake in the Canton Valais in the Central Swiss Alps were analysed to reconstruct the vegetation, land use and fire history for the last 14,500 years, using pollen, macrofossils, non-pollen palynomorphs and charcoal. The record indicates that the tree line had already reached the Champex area during the Allerød (14,000 cal BP) but dropped below the lake's catchment during the Younger Dryas cooling (12,750–11,550 cal BP). Reforestation started again with *Betula* and *Pinus sylvestris* in the Early Holocene at 11,500 cal BP in response to rapid climate warming. Temperate tree species (*Ulmus*, *Tilia*, *Quercus*, *Acer*) may have reached the altitude of the lake during the Holocene Thermal Maximum (ca. 10,000–5,000 cal BP). Mixed forests with mesophilous *Abies alba* were dominant between 7,500 and 5,000 cal BP. The mass expansions of *Picea abies* after 5,000 cal BP and *Alnus viridis* thickets after 4,500 cal BP were directly linked to increasing human disturbance. High values of coprophilous *Sporormiella* fungal spores and cereal pollen suggest pastoral and arable farming at the site from the Late Neolithic/Early Bronze Age onwards (5,000 cal BP). Our data imply that vegetation at intermediate elevation was less affected by human activities than at higher or lower elevations but that these areas served as important stations between the permanent settlements in the valleys and the seasonally occupied alpine huts at higher elevations. We argue that future climate warming will lead to drastic reorganizations of mountain ecosystems.

Keywords Afforestation · Alpine farming · Central Alps · Human impact · Palaeoecology · Tree line

Introduction

Mountain ecosystems are considered to be particularly prone to environmental changes since distances for vertical migration are short and ecological gradients are generally steep (IPCC 2014). The projected temperature increase by the end of the 21st century will likely lead to drastic shifts in the vegetation ranges and might result in a loss of biodiversity (CH2011 2011; IPCC 2014; Trisos et al. 2020). Specifically, temperate tree species (such as *Ulmus*, *Tilia*, *Acer*) may invade the boreal forests at mid altitudes (Thöle et al. 2016) and an upward movement of the tree line is very likely, replacing species-rich alpine meadows (Gehrig-Fasel et al. 2007; Harsch et al. 2009). However, to predict future changes in mountain ecosystems, it is essential to understand species responses to climate and human impacts over long

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(decadal to millennial scale) time periods. Here, palaeoecological approaches (e.g. sedimentary pollen and plant macrofossil analyses) are best suited to study long-term changes in terrestrial ecosystems and to constrain responses of key tree species to climatic and land use change.

Reconstructions of past vegetation dynamics have a long tradition in the Alps (e.g. Welten 1950a, b, 1944, 1952, 1982a; Zoller 1960; Burga 1980). Yet, only a limited number cover the mid altitudes (Welten 1982a, b; Rey et al. 2013) and some of the older studies do not have a reliable radiocarbon chronology (Welten 1982a, b), which is crucial for site-to-site comparisons at centennial time scales (Rey et al. 2019b). The consideration of plant macrofossil assemblages is particularly important for tree line reconstructions to unambiguously confirm the local presence of tree species (Birks 2001). Unfortunately, only a few well-dated, multiproxy reconstructions in the Alps are available (Gobet et al. 2003; Tinner and Theurillat 2003; Wick et al. 2003; Genries et al. 2009; Blarquez et al. 2010; Berthel et al. 2012; Rey et al. 2013; Schwörer et al. 2014; Thöle et al. 2016; Finsinger et al. 2021) and modern studies from the upper continental montane zone in the Central Alps (ca. 1,300–1,850 m a.s.l., Landolt et al. 2015) are currently lacking.

Mountain regions have been affected by land use for millennia (e.g. Gobet et al. 2003; Wick et al. 2003; Lotter et al. 2006; Rey et al. 2013). On the one hand, the impacts of human activities at the tree line in the upper subalpine zone are well-documented (Finsinger and Tinner 2007; Schwörer et al. 2014; Dietre et al. 2020) and it is known that many high elevation sites were used for pastoral farming since at least the Neolithic (ca. 7,500 cal BP, Schwörer et al. 2015). On the other hand, human activities and their impacts at mid altitudinal locations between the permanent settlements in the valleys and the seasonally occupied mayens and alpages (montane, subalpine and alpine huts) or camps at higher elevations remain ambiguous. Only few settlements above 1,000 m a.s.l. are documented for the Late Iron Age and beyond (> 2,050 cal BP, David-Elbiali 1994; Curdy 2007), even though crop cultivation in the upper continental montane zone would have been possible and is documented until the recent past (Landolt et al. 2015). However, an in-depth assessment of the land use history (arable vs. pastoral farming) at mid altitudes is missing so far.

In the current study, we present the results of a new, well-dated multiproxy reconstruction from Lac de Champex, Valais, Switzerland (1,467 m a.s.l.), covering the last 14,500 years. The lake is located in the upper continental montane zone and is well-suited for reconstructing the vegetation and land use history at mid altitudes. Our novel site may help to determine changes in tree line elevation since the Last Glacial Maximum (LGM) with the help of pollen and plant macrofossil analyses. Special attention is paid to tree line fluctuations between the Bølling (ca. 14,500 cal BP) and the onset of the Holocene (ca.

11,500 cal BP) as well as to the early human impact from ca. 7,000 cal BP onward. The aims of this study are to (1) improve our understanding of changes in tree line position in response to climatic changes before the Holocene and (2) to assess the farming history of the upper continental montane zone.

Study site

Lac de Champex is a small mountain lake in the Pennine Alps ca. 15 km south of Martigny (Valais, Switzerland; Fig. 1). The lake (46°1'39.025"N, 7°07'07.943"E) is situated at 1,467 m a.s.l. on siliceous bedrock (Schmid et al. 2004). The lake surface area is 0.11 km² and the maximum water depth is 5.2 m. There are two small open inlets in the West and one covered outlet in the East. One of the inlets is an artificial water channel (French 'bisse') probably built in the Middle Ages, bringing fresh water from the neighbouring Arpette Valley (Lugon 1927).

The mean annual temperature is ca. 5.6 °C based on the closest weather station in Montana at similar altitude (1,427 m a.s.l.) ca. 40 km from Lac de Champex (MeteoSwiss 2021). The highest average temperatures are reached in July with ca. 14.4 °C and the lowest mean temperatures are measured in January with ca. – 2.1 °C. The annual precipitation is 786 mm down in the valley in Orsières (929 m a.s.l.) ca. 2 km from the lake (MeteoSwiss 2021). The precipitation is evenly distributed throughout the year.

The lake is located in the upper continental montane zone (Landolt et al. 2015). Typical for this ecotone is the transition from pine-dominated (continental montane zone) to spruce-dominated forests (subalpine zone). Most of the surrounding area is covered by more or less closed forests dominated by coniferous tree species (*Picea abies*, *Pinus sylvestris* and *Larix decidua*) and few deciduous *Betula pendula*. The present tree line is at ca. 2,400 m a.s.l. on the slopes of the Catogne mountain north of the lake. Peatlands exist in the western part of the lake, close to the inlets. The modern village Champex-Lac is situated along the northern and eastern lake shores and developed from a mayen with local fields ('champ' = field in French). There is a high density of archaeological sites in the region covering the Mesolithic to Modern times (Fig. 1). Most of the sites are located along the main valleys (Val d'Entremont, Val de Bagnes, Rhône Valley). Those valleys were important pathways for crossing the Alps via mountain passes such as Col du Gd-St-Bernard.

Materials and methods

Coring and chronology

In October 2015, two parallel sediment cores (CHX-A and CHX-B) were taken in the eastern part of the lake at a water

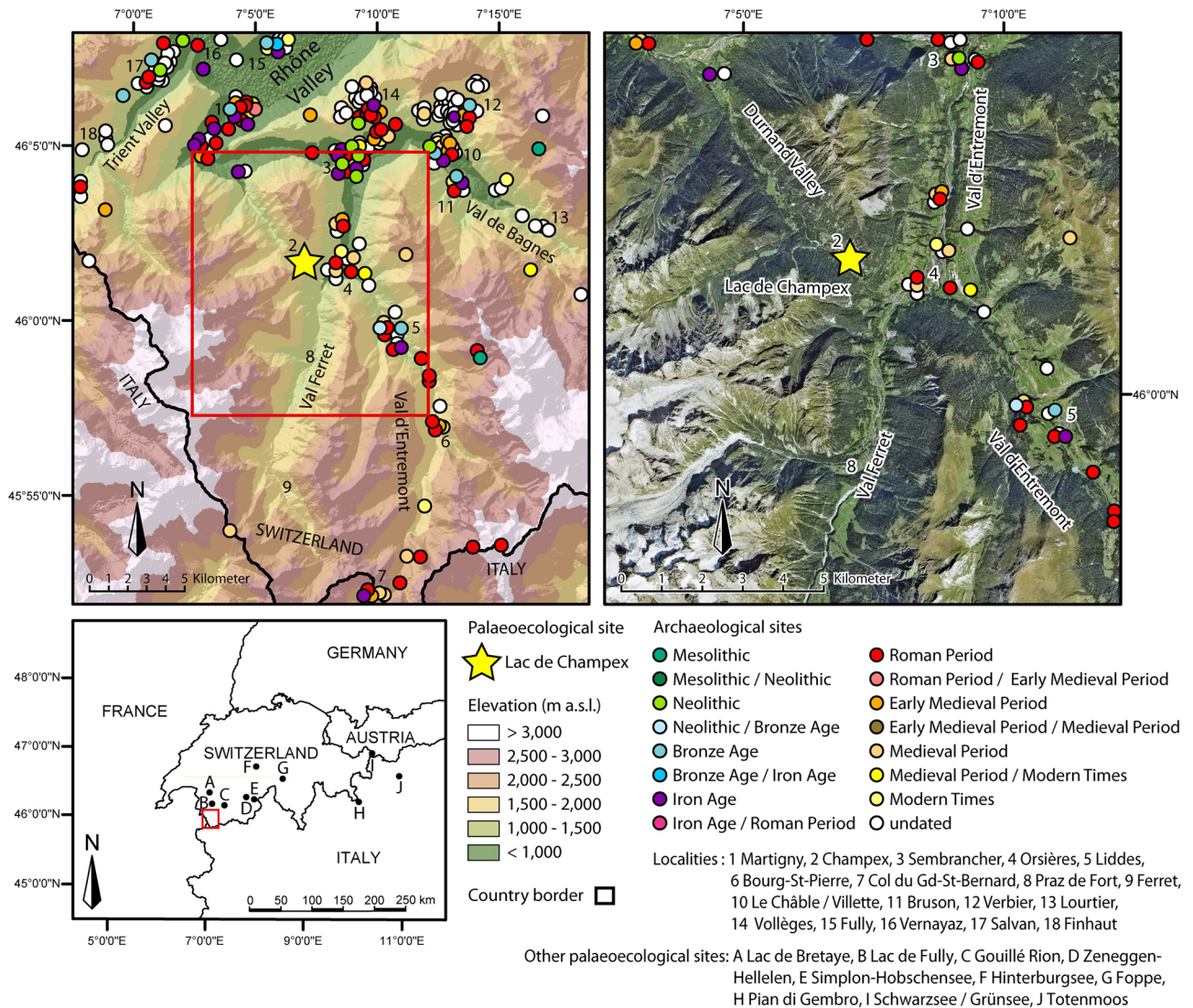


Fig. 1 Overview map of Lac de Champex (1,467 m a.s.l., yellow star) and the study region (Canton of Valais, Switzerland) including a selection of other discussed palaeoecological sites (black circles,

letters), archaeological sites (Mesolithic to Modern Times, coloured circles) and other localities (settlements/mountain pass, numbers). Source of the maps: NASADEM 2020, swisstopo

depth of 5.2 m using an UWITEC-piston corer (core diameter: 66 mm, coring chamber: 3 m). A total coring depth of 6.5 m was reached. One additional surface core (CHX-S1) was retrieved to recover the surface sediments. Core segments were cut into 1 m intervals in the field and then integrated to one master sequence of 612.5 cm in the laboratory based on visually identified, lithological marker layers.

The age-depth model is based on 13 radiocarbon dates from terrestrial plant macrofossils, the Laacher See Tephra (LST) and one pollen stratigraphical marker (Table 1). The radiocarbon contents of the plant macrofossils were measured at the LARA laboratory at the University of Bern (Szidat et al. 2014). Two additional radiocarbon dates were rejected prior to the age-depth modelling. The program

CALIB 8.2 was used to calibrate the radiocarbon dates using the IntCal20 calibration curve (Reimer et al. 2020). The age-depth model was calculated with the program Clam 2.2 using linear interpolation between dates (Blaauw 2010). The final model output runs within the 2σ confidence envelope of a generalized mixed-effect regression (GAM, Heegaard et al. 2005) and the 95% (2σ) probabilities of the calibrated radiocarbon ages (Fig. 2).

Pollen, spores, non-pollen palynomorphs, microscopic charcoal, and macrofossil analysis

A total number of 109 subsamples for pollen, spores, non-pollen palynomorphs (NPPs), and microscopic charcoal

Table 1 Radiocarbon dates, calibrated ages, and pollen-inferred age from the Lac de Champex record. Uncertainties of ^{14}C ages refer to 68% probabilities (1σ) whereas ranges of calibrated and modelled ages represent 95% probabilities (2σ)

Code	Depth [cm]	Material/ Comments	^{14}C age (BP) ^a	Median age (cal BP) ^b	Age 2σ range (cal BP) ^b	Modelled age (cal BP) ^c
BE-10044.1.1	105–106	Anther indet, bud scale indet, needles indet	$1,915 \pm 30$	1,830	1,740–1,925	- (rejected)
BE-10045.1.1	124.5–125.5	Needles indet, seed indet	$1,920 \pm 20$	1,840	1,745–1,915	- (rejected)
BE-10046.1.1	166–167	Needles indet	995 ± 40	880	790–960	845
BE-5979.1.1	193–195	<i>Larix decidua</i> needles	$1,045 \pm 20$	945	920–970	945
BE-5980.1.1	217–219	<i>Picea abies</i> seed	$1,925 \pm 20$	1,845	1,745–1,920	1,850
BE-5981.1.1	237–239	<i>P. abies</i> twig	$2,915 \pm 30$	3,055	2,965–3,160	3,050
BE-5982.1.1	267–269	<i>Abies alba</i> needles, <i>Pinus sylvestris</i> needles	$3,715 \pm 20$	4,040	3,985–4,145	4,035
BE-5983.1.1	293–295	<i>A. alba</i> seed, <i>A. alba</i> seed wing	$4,515 \pm 20$	5,150	5,050–5,305	5,145
BE-6997.1.1	315–317	<i>A. alba</i> cone scale	$5,285 \pm 20$	6,085	5,950–6,180	6,085
BE-6998.1.1	335–337	<i>A. alba</i> needles, <i>L. decidua</i> remains	$6,010 \pm 20$	6,850	6,785–6,935	6,845
BE-6999.1.1	347–349	<i>A. alba</i> needle, <i>P. sylvestris</i> cone scale	$6,280 \pm 20$	7,215	7,165–7,255	7,215
BE-7000.1.1	363–365	<i>P. sylvestris</i> cone scale, leaf fragments	$6,975 \pm 20$	7,810	7,725–7,920	7,805
BE-7001.1.1	389–391	Leaf fragments, terrestrial plant remains	$7,705 \pm 50$	8,485	8,405–8,590	8,490
BE-7002.1.1	411–413	<i>Betula</i> fruit, bud scale indet, periderm indet	$8,815 \pm 25$	9,840	9,695–10,120	9,830
BE-5984.1.1	430.5–431.5	<i>Betula</i> fruits, deciduous bud	$9,640 \pm 25$	11,030	10,800–11,180	11,035
LST	449.5	Laacher See Tephra	–	13,035 ^d	12,885–13,185 ^d	13,025
Mid Bølling	472	Pollen-inferred age (<i>Juniperus</i> and <i>Betula</i> trend)	–	14,440 ^d	–	14,435

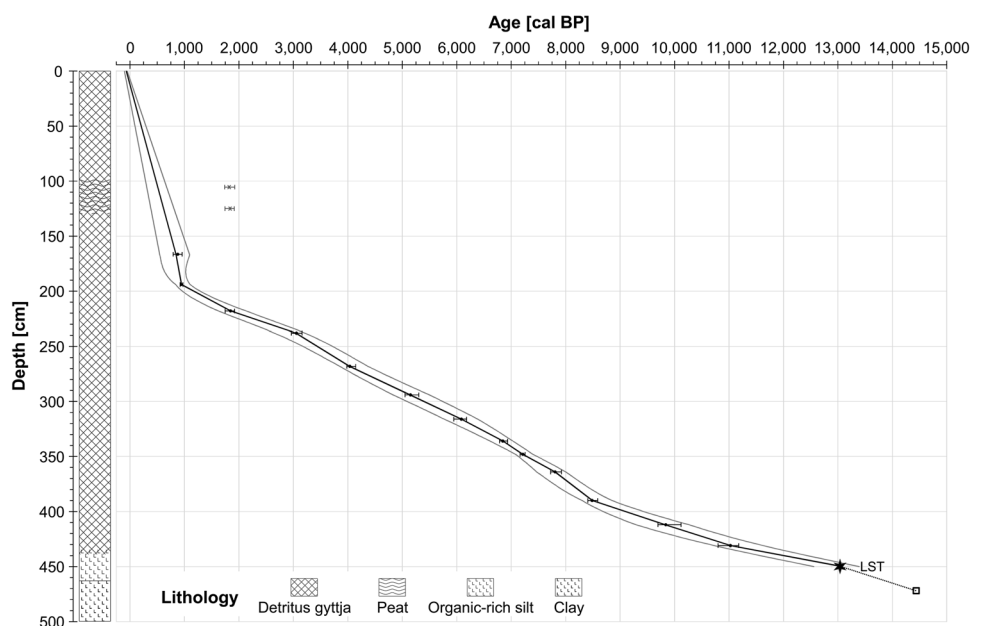
^aStuiver and Polach (1977)^bReimer et al. (2020)^cBlaauw (2010)^dvan Raden et al. (2013)

LST Laacher See Tephra, indet indeterminate

analysis were retrieved from the sediment core. The sampling volume was 1 cm^3 for each subsample. 81 subsamples were evenly taken along the core (i.e. every 2, 4 or

16 cm depending on the sedimentation rate). The remaining 28 subsamples were taken continuously from 222 to 194 cm (Late Iron Age to Early Medieval period high

Fig. 2 Age-depth model and lithology of Lac de Champex. Black dots show the calibrated ages with 95% (2σ) probabilities (IntCal20, Reimer et al. 2020). The two topmost ages (dark grey crosses) are outliers. The empty black square in the bottom marks one additional pollen-inferred age (mid-Bølling). The black line is the modelled chronology (linear interpolation with the program clam 2.3, Blaauw 2010). The grey lines represent the 95% (2σ) probabilities of a generalized mixed-effect regression model applied to the record (GAM, Heegaard et al. 2005). LST Laacher See Tephra (black star)



resolution interval). All palynological subsamples were chemically treated with 10% HCl, 10% KOH, 40% HF and acetolysis, sieved through a mesh size of 0.5 mm and mounted in glycerine following standard preparation protocols (Moore et al. 1991). *Lycopodium* tablets (University of Lund batch no. 3862 with 9,666 spores per tablet) were added prior to the chemical treatment to estimate pollen, spore, NPP and microscopic charcoal concentrations (Stockmarr 1971). Pollen and spores were identified under a light microscope (Leica, Germany) at 400× magnification using photo atlases (Reille 1992) and palynological keys (Moore et al. 1991; Beug 2004). 129 different pollen types were found and generally pollen sums of > 500 were reached (> 350 for three samples from the bottom of the sediment core below 462 cm). No subsamples were analysed below 472 cm due to very low pollen concentrations. The pollen record (Fig. 3) was separated into local pollen assemblage zones (LPAZ) inferred by optimal sum-of-squares partitioning (Birks and Gordon 1985). Four statistically significant zones were identified using the broken stick model following Bennett (1996). For discussion/presentation of the results, LPAZ CHX-2 was split into three additional subzones, and CHX-3 and CHX-4 were split into two subzones. All these subzones were not statistically significant. The pollen results are presented in percentages calculated based on the terrestrial pollen sum (Figs. 3 and 4). *Cannabis sativa* was excluded from the terrestrial pollen sum to avoid possible artificial pollen input from hemp retting influencing the percentage abundances. The various coniferous stomata were identified following Trautmann 1953 and Finsinger and Tinner 2020. Stomata are presented as presence / absence (Fig. 3). Microscopic charcoal particles > 10 µm were counted following Tinner and Hu (2003) and Finsinger and Tinner (2005). The results of microscopic charcoal and spores as well as the NPP counts are presented as influx (particles/spores cm⁻² yr⁻¹, Fig. 3).

121 subsamples for macrofossil analysis were taken along the sediment core. The uppermost 191 cm and the bottom part (below 472 cm) of the sediment sequence were not systematically analysed. A sieve with 200 µm mesh width was used to separate the macrofossils from the fine-grained sediment. The macrofossils were identified under a stereomicroscope with the help of keys (e.g. Schoch et al. 1988) and the reference collection at the Institute of Plant Sciences of University of Bern. The calculated macrofossil concentrations are based on a standard volume of 9 cm³. For better comparison, the same zonation as for the pollen results (LPAZ) was used for the macrofossil record (Fig. 5). All pollen and macrofossil figures were plotted in Tilia 2.0.60 and finalized in CorelDraw.

Quantitative analyses

Rarefaction analysis (Birks and Line 1992) was applied to assess the palynological richness (PRI). The calculations are based on the lowest terrestrial pollen count, which was 360 pollen grains at 462 cm sediment depth. Subsequently, the probability of interspecific encounter (PIE, Hurlbert 1971) as measure of palynological evenness and evenness-detrended palynological richness (DE-PRI) were calculated following Colombaroli and Tinner (2013). PRI and DE-PRI are given as number of different pollen types per counted 360 pollen grains and PIE as probability index (0–1, Fig. 3).

Ordination analysis was implemented to identify trajectories in vegetation composition over time (Birks and Gordon 1985; ter Braak and Prentice 1988). We chose a detrended correspondence analysis (DCA, Birks and Gordon 1985) with detrending by segments and without down-weighting of rare species for our model calculations (length of first axis 2.01 SD units; Fig. 3 and ESM). Finally, we calculated correlation coefficients to test for significant relationships between microscopic charcoal and selected pollen types. A *t*-test was applied to investigate whether the correlation coefficients differ significantly from 0 ($r \neq 0$, $\alpha = 5\%$, two-sided, Bahrenberg et al. 2008). The selected time window for the analysis was the Late Iron Age to the Early Medieval (ca. 2,100–950 cal BP, Figs. 4 and 6). The vegetation composition for this time period was relatively stable indicating no major trends that could have affected the correlation calculations. All statistical analyses were conducted in R (R Development Core Team 2020), Canoco 5 (Šmilauer and Lepš 2014) and MYSTAT 12 (student version of SYSTAT 12).

Results and interpretation

Lithology and chronology

The bottom of the sediment core (below 463 cm) consists of silty clay. The sediment then changes to organic-rich silt until 439 cm. According to the age-depth model (Fig. 2), the sedimentation rate was low (ca. 50 yrs cm⁻¹) in this bottom part of the sediment sequence. After a short transition of 4 cm, the sediment consists of gyttja. The sedimentation rate remains very low and stable. Only for the uppermost ca. 190 cm, there is a steep increase of the sedimentation rate (ca. 5 yrs cm⁻¹) probably due to higher erosional input from the Middle Ages onward. Between 130 and 99 cm depth, the sediment is moderately enriched by peat material. The two rejected radiocarbon dates fall exactly into this peaty layer. Most likely, the peat and old plant material preserved therein was washed into the lake during the construction of the water channel and possibly peat cutting during the Middle Ages. Hence, the too old ages of the two outlying

Fig. 3 Lac de Champex sediment sequence and pollen record. Presented are the radiocarbon dates, the lithology, percentages of selected pollen types and *Pteridium aquilinum* (fern spores), presence of stomata (black dots), microscopic charcoal and *Sporormiella* (coprophilous fungal spores) influx values (particles/spores $\text{cm}^{-2} \text{yr}^{-1}$), the palynological richness (PRI; black line), the evenness-detrended palynological richness (DE-PRI; dark grey line), the palynological evenness (PIE) as well as the detrended correspondence analysis (DCA) axis 1 scores. Empty curves represent the 10× exaggerations. *LST* Laacher See Tephra, *LPAZ* local pollen assemblage zones. The light grey bar marks the position of the high-resolution section of the record shown in Fig. 4

radiocarbon dates are probably a result of reworking processes and need to be rejected.

Vegetation and fire history

The pollen and macrofossil diagrams (Figs. 3 and 5) are subdivided into four statistically significant LPAZ. Four statistically not significant zone boundaries delimit additional subzones (CHX-2a, 2b, 2c, 3a, 3b, 4a and 4b).

CHX-1 (14,500–13,620 cal BP), *Juniperus-Betula-Poaceae* LPAZ

Pollen of herbs (*Poaceae*, *Artemisia*, *Helianthemum*, *Rubiaceae* and *Thalictrum*) and shrubs (*Juniperus*, *Hippophaë rhamnoides*, *Ephedra distachya*-type and *Salix*) dominates with values up to 90%. The pollen assemblage suggests the establishment of pioneer vegetation shortly after the site had become ice-free. The most frequent tree pollen is *Betula*, which is increasing from 10 to 30% throughout the zone. This trend is supported by regular finds of *Betula* fruits (from ca. 14,000 cal BP onwards), indicating local occurrence of birch trees close to the lake at the onset of the Allerød (13,900 cal BP, van Raden et al. 2013). Microscopic charcoal influx values are very low ($< 40 \text{ particles cm}^{-2} \text{yr}^{-1}$) and macroscopic charcoal pieces are absent, suggesting scarce regional and local fire activity.

CHX-2a (13,620–12,770 cal BP), *Pinus-Betula* sub-LPAZ

The onset of this subzone is marked by a sharp increase of tree pollen percentages (up to 90%) mainly resulting from *P. sylvestris*-type. The dominance of *P. sylvestris*-type pollen is underlined by a single pine bud scale find, which may indicate the occurrence of pine trees not far from the site. Meanwhile, pollen percentages of shrubs and herbs are first decreasing and then markedly increase again (up to 55%) towards the end of the subzone. At the same time, no more plant macrofossils occur in the record, which is likely related to a drop of the tree line below the site as a result of the Younger Dryas cooling after 12,700 cal BP, as inferred from the strong arboreal pollen (AP) decline

(from $> 80\%$ to $> 60\%$). The charcoal values are slightly increasing (microscopic charcoal influx up to $220 \text{ particles cm}^{-2} \text{yr}^{-1}$), which could point to a higher fire activity due to increased fuel availability.

CHX-2b (12,770–11,690 cal BP), *Pinus-Poaceae-Artemisia* sub-LPAZ

Open vegetation dominated in the area around the lake in this subzone as indicated by fairly high herb pollen percentages (35–55%). The most common herbaceous taxa are *Poaceae* (around 15%) and *Artemisia* (around 10%). *Juniperus* pollen percentages are at 5% whereas *P. sylvestris*-type values decrease to 40–50%. A first stoma of *Juniperus* in the upper part of the subzone may indicate the re-colonization of the area around the lake by the first shrubs at the end of the Younger Dryas at ca. 11,800 cal BP. Microscopic charcoal influx drops again ($< 80 \text{ particles cm}^{-2} \text{yr}^{-1}$), suggesting lower fire activity as a consequence of lower fuel availability.

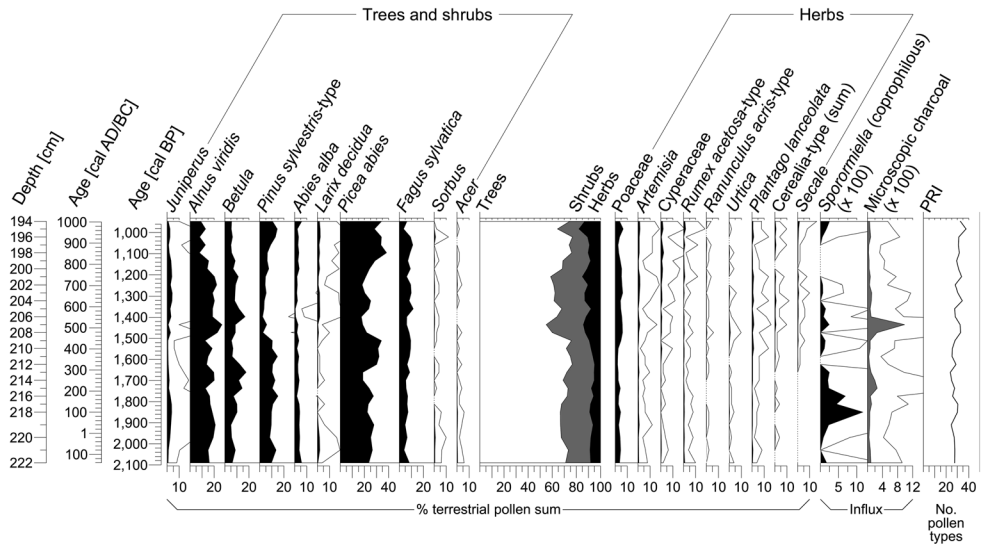
CHX-2c (11,690–9,960 cal BP), *Pinus-Betula* sub-LPAZ

The presence of plant macrofossils from *Betula* and *P. sylvestris*, *Pinus* stomata as well as increased pollen percentages of *Betula* (up to 20%) and *P. sylvestris*-type (up to 70%) indicate that forests recovered shortly after 11,500 cal BP in response to climate warming at the beginning of the Holocene (e.g. Heiri et al. 2014, 2015). Pollen of temperate trees and shrubs (*Alnus glutinosa*-type, *Corylus avellana*, *Quercus*, *Tilia*, *Ulmus*) either occur for the first time or increase, indicating the establishment of temperate deciduous forest in the lowlands, while macrofossil evidence for a local presence at the site (e.g. bud scales) is lacking. Microscopic charcoal shows an increase (up to $275 \text{ particles cm}^{-2} \text{yr}^{-1}$) and this trend is underlined by regular finds of macroscopic charcoal, together suggesting higher regional and local fire activity, which was probably related to the continental climate in the Early Holocene, with warm and dry summers as well as increased fuel biomass (Tinner and Lotter 2001; Heiri et al. 2014).

CHX-3a (9,960–7,470 cal BP), *Pinus-Betula-Larix decidua* sub-LPAZ

Pollen percentages of *Betula* and *P. sylvestris*-type show similar values (around 30%). Together with regular finds of *Betula* and *Pinus sylvestris* macrofossils, they indicate that mixed pine-birch forests prevailed around Lac de Champex. At the same time, pollen percentages from temperate deciduous species are highest (e.g. 20% for *C. avellana*), and *L. decidua* pollen as well as *Fraxinus excelsior* pollen occurs for the first time. Regular finds of *L. decidua* macrofossils and stomata are indicative of the spread of larch trees into

Fig. 4 Lac de Champex high resolution section. Presented are the percentages of selected pollen types, microscopic charcoal and *Sporormiella* (coprophilous fungal spores) influx values (particles/ spores $\text{cm}^{-2} \text{yr}^{-1}$) and the palynological richness (PRI). Empty curves represent the 10 \times exaggerations



the mixed pine-birch forests. In the upper part of the subzone, *A. alba* pollen and macrofossils appear for the first time, suggesting that silver fir trees established regionally at around 8,200 cal BP (empirical pollen limit) and locally at ca. 7,500 cal BP (first macrofossils). Charcoal influx values fluctuate around 300 particles $\text{cm}^{-2} \text{yr}^{-1}$ and macroscopic charcoal pieces occur only sporadically. Hence, local fires became less frequent, whereas the regional fire activity remained at a high level. Moisture availability increases could be the reason for this shift in the fire regime, with lower flammability of the forests around the lake resulting from increased orographic precipitation.

CHX-3b (7,470–4,630 cal BP), *Abies alba*-*Pinus*-*Larix decidua* sub-LPAZ

Abies alba became the dominant tree in the forests as indicated by pollen percentages reaching almost 40%, numerous stomata as well as macrofossil finds. Plant remains of *L. decidua* are more frequent as well, suggesting a co-dominance of larch trees in the forests. An *Acer* bud scale and some *Betula* fruits indicate that deciduous trees were present too. *P. abies* and *A. viridis* pollen reach their empirical limits at 6,000 and 5,500 cal BP respectively, suggesting first establishment of stands in the Champex area. At ca. 7,000 cal BP (5050 cal BC), *Plantago lanceolata* pollen appears in the pollen sequence, documenting the onset of agricultural activities close to the site. Pastoral farming was intensified after 5,500 cal BP (3550 cal BC) as indicated by higher local fire activity (continuous macroscopic charcoal curve) and frequent finds of *Sporormiella* (coprophilous fungal spore), a proxy for livestock farming (Rey et al. 2013; Schwörer et al. 2015). *P. abies* pollen percentages start to rise contemporaneously while *A. alba* percentages

are decreasing, announcing the next pronounced change in forest composition.

CHX-4a (4,630–1,120 cal BP), *Picea abies*-*Alnus viridis*-*Larix decidua* sub-LPAZ

Picea abies pollen becomes dominant (values up to 30%) while *A. alba* pollen percentages are massively decreasing (<5%). In contrast, disturbance-adapted *A. viridis* is spreading in the area, as indicated by rising pollen percentages (up to 20%). Numerous finds of *L. decidua* stomata and macrofossils suggest that larch could cope with the generally increased disturbance and remained an important element in the forests. Continuous curves of *P. lanceolata* and *Cerealia*-type pollen as well as peaks of *Sporormiella* fungal spores suggest pastoral and arable farming activities close to the lake (also see Fig. 4). This general trend towards intensified land use is supported by maximum charcoal values (microscopic charcoal up to 2,300 particles $\text{cm}^{-2} \text{yr}^{-1}$ and continuous macroscopic charcoal curve) indicating higher fire activity likely originating from repeated regional to local slash-and-burn activities.

CHX-4b (1,120 cal BP-modern times), *Picea abies*-*Poaceae*-*Larix decidua* sub-LPAZ

This subzone delimits the last millennium with the most intense land use. The pollen and stomata records suggest that the surrounding forest was still composed of mainly *P. abies* and *L. decidua*, with a few *P. sylvestris*. *Alnus viridis* shrublands were replaced by open grasslands as indicated by the pollen percentages (herbaceous pollen up to 20%). Human indicator pollen (*P. lanceolata*, *Cerealia*-type, *Secale*, *Cannabis sativa*) occurs frequently and shows mostly closed curves, underlining the ongoing agricultural activities close

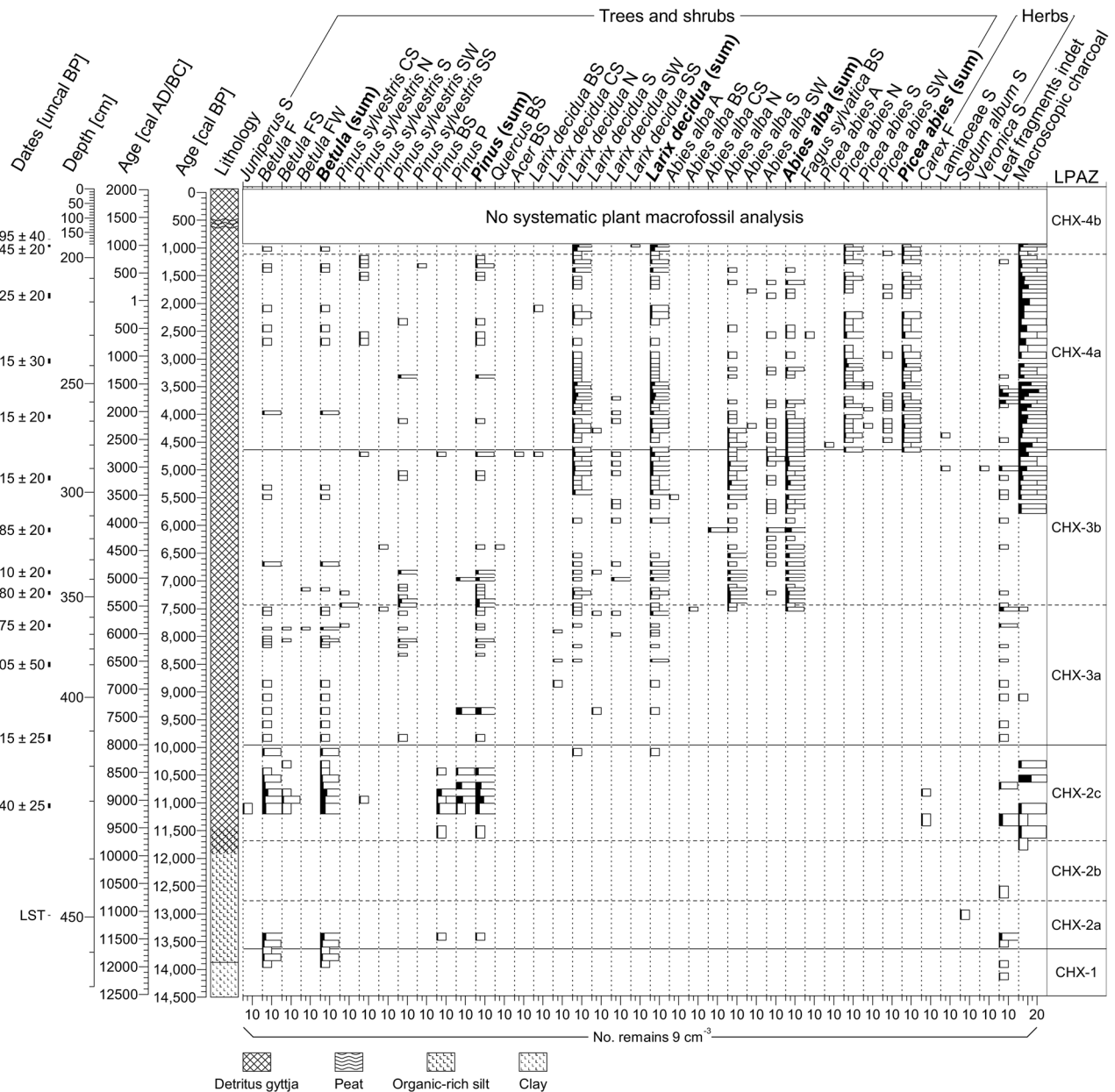


Fig. 5 Lac de Champex sediment sequence and macrofossil record. Presented are the radiocarbon dates, the lithology, concentrations (number of remains per 9 cm³) of selected plant macrofossils and macroscopic charcoal (particles ≥ 200 μm). Empty curves represent the 10× exaggerations. The uppermost ca. 190 cm of the sediment

core have not been analyzed. *LST* Laacher See Tephra, *LPAZ* local pollen assemblage zones, *indet* indeterminate, *A* anther, *BS* bud scale, *CS* cone scale, *F* fruit, *FS* fruit scale, *FW* fruit wing, *N* needle, *P* periderm, *S* seed, *SS* short shoot, *SW* seed wing

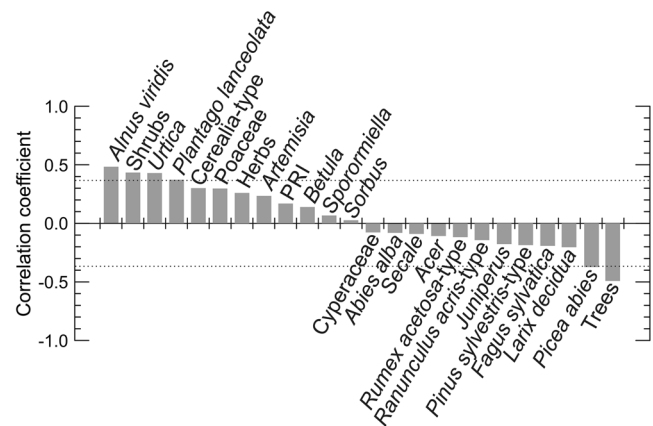
to the lake. A last pronounced microscopic charcoal peak at 880 cal BP (cal AD 1070) corresponds to a phase with the highest herb pollen percentages, suggesting that fires were used to remove shrubs and trees to keep the landscape open.

Quantitative analyses

The diversity estimates are very stable at around 20–30 taxa per sample throughout the record (Fig. 3). The numbers are

slightly higher (at 30 taxa per sample) after 2,000 cal BP, which is related to the intensified land-use and the introduction of new crops in the region (e.g. *Juglans regia*, *Secale*). The difference between PRI and DE-PRI is generally small, indicating that PRI is not much affected by evenness effects. PIE < 0.6 is recorded from 13,500 to 13,000 cal BP and from 11,500 to 11,000 cal BP, when *P. sylvestris* pollen grains are dominant (≥ 70% of the terrestrial pollen sum). Here, DE-PRI is notably higher than PRI which points to evenness

Fig. 6 Correlogram showing the correlation coefficients between microscopic charcoal influx and selected pollen types, *Sporormiella* and palynological richness (PRI) for the period 2,100–950 cal BP (150 BC–AD 1000, Fig. 4). The dotted lines mark the significance level ($P=0.05$)



distortions, likely leading to species richness being underestimated by PRI during both time intervals with strong *Pinus* dominance. The DCA results are explained by the increasing openness trend through time since DCA axis 1 goes very much in line with herbaceous pollen, Poaceae and *Artemisia* percentages (DCA axis 1 = 26.8%, DCA axis 2 = 19.2%, Figs. 3 and ESM).

The correlation coefficients (Fig. 6) point to significantly positive relationships between microscopic charcoal influx and percentages of shrubs (*A. viridis*), *Urtica* and *P. lanceolata* for the period 2,100–950 cal BP. On the other hand, percentages of trees (*P. abies*) show significant negative correlations with microscopic charcoal influx, suggesting that trees were most affected by fires whereas the expansion of *A. viridis* shrublands were favoured by fire disturbance.

Discussion

Tree line and forest dynamics during the last 14,500 years

Lac de Champex became ice-free shortly after the onset of the Bølling warming (14,600 cal BP, van Raden et al. 2013), which is confirmed by high *Juniperus* values (> 40%) in the pollen record. The massive expansion of juniper scrublands around 14,600–14,500 cal BP is typical for the Central European lowlands (Lotter 1999; Rey et al. 2017, 2020) and was caused by a rapid ca. 4–5 °C warming (Heiri et al. 2014, 2015; Bolland et al. 2020). The pollen and macrofossil records indicate that despite the major temperature increase, the area around the lake remained open, dominated by alpine tundra. The Valais site Zeneggen-Hellelen (Welten 1982b) at 1,510 m a.s.l. shows very similar results, suggesting that the tree line must have been at lower elevations during the Bølling interstadial. Subsequently, afforestation at mid altitudes (ca. 1,500 m a.s.l.) started around 14,000 cal BP approximately at the onset of the Allerød (ca.

13,900–12,700 cal BP, Ammann et al. 2013; Rach et al. 2014), which is confirmed by macrofossils from *P. sylvestris* and *Betula* at Lac de Champex and *Pinus stomata* at Zeneggen-Hellelen (Welten 1982b). The tree line may have even reached 2,000 m a.s.l. during the Allerød, as indicated by a few *Betula* fruits at Simplon-Hobschensee (2,018 m a.s.l., Lang and Tobolski 1985). However, these results must be interpreted with caution since strong and channelled wind close to the Simplon pass may have transported the rather light and winged *Betula* fruits from lower altitudes. Nevertheless, it could well be that birch stands could have grown just below 2,000 m a.s.l. setting the tree line a few hundred metres above Lac de Champex at 1,700–1,800 m a.s.l. This would agree well with the results from the Eastern Central Alps in the Lower Engadine, where Welten (1982a) found *Pinus stomata* at Schwarzsee (1,726 m a.s.l.) but none at Grünsee (1,836 m a.s.l.). Likewise, a tree line position as high as 1,700 m a.s.l. is documented in the Southern Alps during the Allerød as indicated by high concentrations of *Larix* needles and stomata at Totenmoos (1,718 m a.s.l., Heiss et al. 2005). Hence, a rise of the tree line from 800 to 1,000 m a.s.l. up to ca. 1,700 m a.s.l. in parts of the Southern and Central Alps during the Allerød warming is very likely (Vescovi et al. 2007, 2018). In contrast, the tree line in the Northern Alps, which are particularly prone to cold air intrusions from persisting ice caps in the North, must have been 300–400 m lower, not exceeding 1,400 m a.s.l. (Rey et al. 2013; Heiri et al. 2014).

During the Younger Dryas cooling (ca. 12,700–11,600 cal BP), Lac de Champex was not reached by re-advancing glaciers, comparable to many other sites in the Alps below 2,000 m a.s.l. (Welten 1982a, b; Lang and Tobolski 1985; Pini 2002; Heiss et al. 2005; Ilyashuk et al. 2009; Rey et al. 2013). The lack of tree macrofossil and stomata finds at our site as well as in the records from Zeneggen-Hellelen (Welten 1982b) and Simplon-Hobschensee (Lang and Tobolski 1985) and the expansion of alpine herbs indicate a drop of the tree line in the Central Alps below 1,400 m

a.s.l. However, the exact position of the tree line during the Younger Dryas is not clear, since suitable sites between the valley bottom and 1,400 m a.s.l. are lacking. The forests around many sites in the central alpine valleys and in the lowlands south and north of the Alps became rather open again (Welten 1982a, b; Vescovi et al. 2007; Colombaroli et al. 2013; Rey et al. 2017, 2020). In the Southern Alps, trees were present at Pian di Gembro (1,350 m a.s.l., Pini 2002) whereas treeless tundra vegetation was re-expanding at Foppe (1,470 m a.s.l., Vescovi et al. 2018), setting the tree line somewhere around 1,400 m a.s.l. North of the Alps, trees could grow at least up to 925 m a.s.l. as indicated by the record from Chutti (Welten 1982b). Thus, a central alpine tree line position around 1,000–1,400 m a.s.l. is very realistic, resulting in a lowering of the tree line by ca. 300–800 m during the Younger Dryas.

Reforestation at Lac de Champex started shortly after the end of the Younger Dryas between 11,500 and 11,200 cal BP with *P. sylvestris* and *Betula*, which agrees with the results from Zeneggen-Hellelen (1,510 m a.s.l., Welten 1982b). At Gouillé Rion (2,343 m a.s.l.), first macrofossils of trees were recorded already at 11,350 cal BP (Tinner and Kaltenrieder 2005). Hence, the rapid warming by about 4 °C (Schwander et al. 2000) at the onset of the Holocene was associated with a sudden upwards shift of the tree line by almost 1,000 m within a few centuries. This rapid afforestation of high elevations is recorded in many other sites in the Central and Southern Alps (Lang and Tobolski 1985; Wick and Tinner 1997; Gobet et al. 2005; Finsinger and Tinner 2007; Valsecchi and Tinner 2010). In contrast, the afforestation at higher elevations was delayed in the Northern Alps by almost 1,500 years, which is a regional phenomenon seen at many sites (e.g. Wick et al. 2003; Lotter et al. 2006) and is possibly caused by strong decreases in summer temperatures during the Preboreal Oscillation (11,350–11,100 cal BP), higher seasonality, and cold air spells from the North (Schwörer et al. 2014; Thöle et al. 2016).

After 10,000 cal BP, *L. decidua* expanded into the mixed pine-birch forests around Lac de Champex. The high summer temperatures during the Holocene Thermal Maximum (HTM, Heiri et al. 2015) may even have favoured the expansion of temperate trees such as *Quercus*, *Tilia*, *Ulmus* and *Acer* as documented by single macrofossil finds at Lac de Champex and even at higher elevation at Lac de Bretaye (1,780 m a.s.l., Thöle et al. 2016). Mixed pine-birch-larch forests prevailed until ca. 7,500 cal BP, when *A. alba* started to expand locally, while regionally it expanded earlier, around 8,200 cal BP. The spread of mesophilous *A. alba* and *F. sylvatica* at lower elevations was caused by a climatic shift towards more oceanic conditions with higher precipitation after the 8.2 ka event (Tinner and Lotter 2001, 2006), which is recorded as lake level rises on the western Swiss Plateau, in eastern France and in the Jura Mountains (Magny et al.

2011; Magny 2013). The expansion of *Abies alba* at higher altitudes after 7,500 cal BP is well-documented across the Western and Northern Alps (Heiri et al. 2003; Tinner and Kaltenrieder 2005; Rey et al. 2013; Schwörer et al. 2014; Thöle et al. 2016) and the lowlands north of the Alps (Lotter 1999; Becker et al. 2006; Wehrli et al. 2007; Gobet and Tinner 2012; Gobet et al. 2017; Rey et al. 2017, 2020). Based on macrofossil data, the highest regional tree line was located at ca. 2,530 m a.s.l. during the HTM between 7,000 and 5,000 cal BP (Tinner and Theurillat 2003). At the same time, the maximum tree line position was at about 2,250 m a.s.l. in the Northern Alps (Berthel et al. 2012; Heiri et al. 2014).

The onset of the massive *P. abies* expansion at 5,000 cal BP and the subsequent replacement of mixed *A. alba* forests after 4,500 cal BP is typical for the Valais and well-documented at many sites (Welten 1982b; Tinner and Theurillat 2003; Finsinger and Tinner 2007). The spread of *P. abies* around Lac de Champex coincides with high abundances of coprophilous *Sporormiella* fungal spores, which are a common proxy for grazing (e.g. Rey et al. 2013; Schwörer et al. 2014; Dietre et al. 2020). Therefore, increased pastoral activities might have facilitated the mass expansion of *P. abies* in the region, by negatively affecting disturbance-sensitive *A. alba*, which at these altitudes occupies similar ecological habitats. The establishment of *P. abies* in the Valais occurred at a similar time as at sites in the Northern Alps at ca. 6,000 cal BP (Tinner and Theurillat 2003; Rey et al. 2013; Schwörer et al. 2014, 2015; Thöle et al. 2016). However, the massive spread of the species in the Valais was somewhat delayed by 500 years compared to the Northern Alps, possibly due to limited moisture availability (Henne et al. 2011). Indeed, the Valais is characterized by a continental climate with rather dry summers (summer precipitation < 250 mm, Landolt et al. 2015), which might have favoured the deep-rooting but disturbance-intolerant *A. alba* compared to shallow-rooting and relatively drought-sensitive *P. abies* (Henne et al. 2011; Tinner et al. 2013), and allowed the species to persist longer than in the Northern Alps.

Our pollen record indicates the steady expansion of *A. viridis* thickets after 4,000 cal BP, which is in agreement with many sites in the Alps (Welten 1982a, b; Wick and Tinner 1997; Gobet et al. 2003; Tinner and Theurillat 2003; Wick et al. 2003; Lotter et al. 2006; Rey et al. 2013; Schwörer et al. 2014). Disturbance-adapted *A. viridis* seemed to have benefited from the intensified disturbance (i.e. fires and anthropogenic forest clearings) since the Bronze Age. Indeed, significant positive correlations between macroscopic charcoal influx and *A. viridis* percentages are recorded for the period 2,100–950 cal BP, whereas trees (including *P. abies*) suffered at the same time (Fig. 6). The most intense forest disruptions at Lac de Champex were recorded during the last 1,000 years. However, compared to sites at or just below the present-day tree line (e.g. Tinner and Theurillat 2003;

Lotter et al. 2006; Schwörer et al. 2014), the forest openings at Lac de Champex remained quite small, suggesting that some forests at mid altitudes were less affected by land use, a finding which is confirmed by the results from Hinterburgsee in the northern Swiss Alps (1,515 m a.s.l., Heiri et al. 2003).

Land use history since 7,000 cal BP

Numerous archaeological finds in the region (Figs. 1 and 7) indicate human presence since the Mesolithic (ca. 9,450 cal BP, 7500 cal BC). The Mesolithic site Pathiéfray close to the village Verbier is a good example of a seasonal camp or shelter probably used by hunters (Tamarcaz and Curdy 2013). However, those people hardly modified the vegetation

in a way that could be traced in palaeoecological records. The first signs of human land use around Lac de Champex are documented by cultural indicators such as *P. lanceolata* and *Sporormiella* around 7,000 cal BP (5050 cal BC). In agreement, regional archaeological finds indicate a first spread of permanent settlements of early farmers from the main Rhône Valley into Val d'Entremont during the Middle Neolithic (6,650–5,050 cal BP, 4700–3100 cal BC; Wermus 1981; Curdy 2007). The colonization of side valleys took place during a period of favourable warm and dry climate (Haas et al. 1998; Gobet et al. 2003; Rey et al. 2019a). The known settlements are all located in the valley bottoms, not exceeding 1,000 m a.s.l. (Curdy 2007). However, the higher altitudes were most likely occupied at least seasonally for

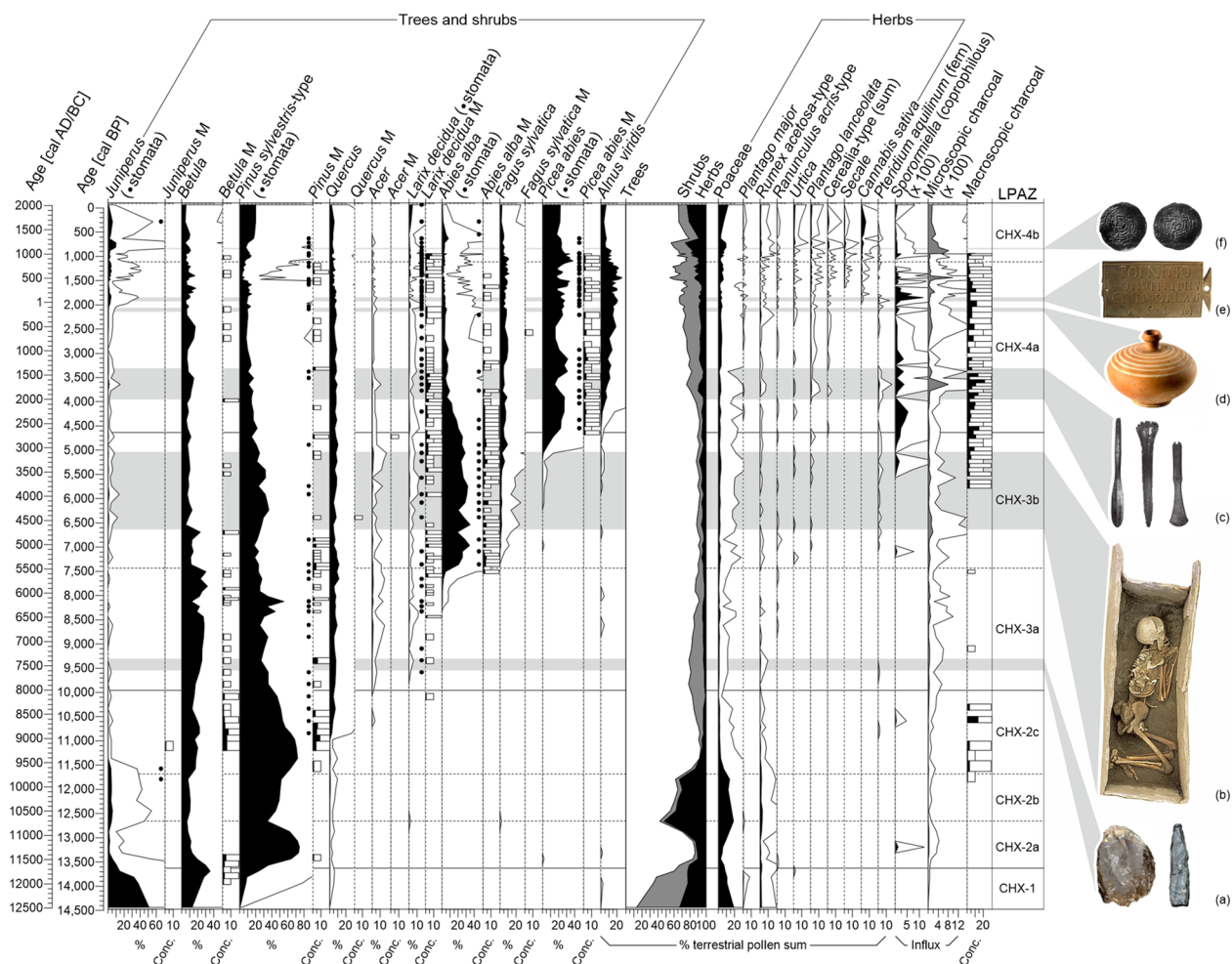


Fig. 7 Composite of the percentages of selected pollen types, microscopic charcoal and *Sporormiella* influx values (particles/spores $\text{cm}^{-2} \text{yr}^{-1}$), plant macrofossil and macroscopic charcoal concentrations (number of remains per 9 cm^3 , $\geq 200 \mu\text{m}$) and the regional archaeology (grey horizontal bars). Empty curves represent the $10\times$ exaggerations. LPAZ local pollen assemblage zones, M macrofossils (sum). (a) Formed crystal rocks from the Mesolithic (ca. 7600–7400 BP, Verbier La Chaux “Pathiéfray”, Tamarcaz and Curdy

2013), (b) Middle Neolithic grave (ca. 4700–3100 BC, Sembrancher “Cretaz-Polet”, Wermus 1981), (c) Short axe, sword and axe from the Early and Middle Bronze Age (ca. 2000–1350 BC, Liddes, Voutaz and Rouyer 2013), (d) Late Iron Age (La Tène) vase from a grave (ca. 200–100 BC, Sembrancher, Curdy 2013), (e) Roman votive tablet (ca. AD 1–100, Col du Gd-St-Bernard, Wiblé 2008), (f) Adalbert I denarius from a grave (AD 1111–1137, Bourg-St-Pierre “L’Hospitalet”, El Sherbini and Elsig 2001)

alpine pastoralism and transhumance as documented around the Schnidejoch Pass (Hafner and Schwörer 2018).

Land use increased notably in the region after 3,900 cal BP (1950 cal BC) during the Early Bronze Age as indicated by the massive expansion of *A. viridis*, high fire activity and the continuous occurrence of human indicator and other herbaceous pollen (*P. lanceolata*, Cerealia-type, *Rumex acetosa*-type) in our record. Maximum concentrations of *L. decidua* macrofossils point to the establishment of larch-meadows similar to the Upper Engadine (Gobet et al. 2003). Functional hilltop settlements at mid altitudes are documented at several sites in the Valais (e.g. Zeneggen-Kastelltschuggen at 1,600 m a.s.l., David-Elbiali 1994; Curdy 2007) and high percentages of Cerealia-type (up to 4%) at Zeneggen-Hellelen (Welten 1982b) unambiguously demonstrate that arable farming was practiced at 1,510 m a.s.l. Landolt et al. (2015) confirm that in general the upper continental montane zone is still well-suited for arable farming today but too dry for pastoral farming without irrigation. Former field terraces above Liddes (1,400–1,600 m a.s.l.) indicate that crop cultivation was important at mid altitudes until the recent past (Benkert et al. 2010). Similarly, in the Upper Engadine, ancient field terraces occur as high as 1,800 m a.s.l. in the subalpine zone (Gobet et al. 2003). Taken together, it is very likely that cereals were cultivated at or close to our site in the Val d'Entremont. However, the archaeological evidence of a permanent settlement during the Bronze Age at Lac de Champex is currently lacking.

For the Iron Age/Roman Period (ca. 2,750–1,500 cal BP, 800 BC–AD 450), there is a slight increase of human activities visible in our record. In addition, regional archaeology shows the highest density of finds (Fig. 1), indicating that the valleys were important pathways for crossing the Alps and rather densely populated, which is supported by palaeoecological evidence from the lowlands (Tinner et al. 2003; Rey et al. 2020). In agreement, the rather remote site Lac de Fully (2,135 m a.s.l., Finsinger and Tinner 2007) indicates the first substantial opening of the forests during this period and other subalpine sites point to an intensified land use (Tinner and Theurillat 2003). Pastoral farming was established with a widespread occurrence of seasonally occupied mayens and permanent villages at mid altitudes, as we know them today (Curdy 2007). This finding is supported by maximum influx values of *Sporormiella* spores in our record (Figs. 3, 4 and 7), suggesting that the area around Lac de Champex was probably used as an intermediate seasonal stop to reach the grazing grounds at higher elevation above the tree line.

The most intense land use activities are recorded for the last millennium at Lac de Champex. However, compared to other sites in the Alps at higher altitudes (Wick et al. 2003; Lotter et al. 2006; Schwörer et al. 2014; Thöle et al. 2016) and/or close to villages in the valley bottoms (Gobet et al.

2003; Curdy et al. 2009; Rey et al. 2013; Dietre et al. 2017), the forest openings remained less pronounced. The reason for such differences could be the less labour-intensive tree removal along the fairly open tree line ecotone at higher elevations and in the proximity of settlements compared to timber harvest in the rather closed forest at mid altitudes far away from villages. Alternatively, forests at intermediate altitudes were kept to protect the permanent settlements at lower altitudes from risks such as avalanches or debris flows, which are frequent in the Alps. Nevertheless, the construction of the artificial water channel from the neighbouring Arpette Valley (Lugon 1927) must have led to substantial changes in the lake ecosystems since a lot of fresh and oxygen-rich water was brought into the lake. From that time on, the lake was probably used as a natural freshwater reservoir to irrigate the meadows down in the valley around the village Orsières.

Conclusions

Our new palaeoecological record from Lac de Champex provides the first continuous and well-dated documentation of vegetation dynamics and land use from the upper continental montane zone of the Central Alps during the last 14,500 years. It suggests that first trees (*Betula* and *P. sylvestris*) were growing around the site at 1,500 m a.s.l. already during the Allerød (14,000 cal BP), which is in agreement with previous studies from the Central and Southern Alps. The tree line dropped below the site again during the Younger Dryas cooling (12,750–11,550 cal BP). Climate warming at the onset of the Holocene coincided with a rapid upward movement of the tree line between 11,500 and 11,200 cal BP, leading to the establishment of mixed birch-pine-larch forests at the lake. Favourable climatic conditions during the HTM probably even allowed for temperate tree species (i.e. *Ulmus*, *Tilia* and *Acer*) to grow at the elevation of our site. The expansion of mesophilous *A. alba* at 7,500 cal BP was likely caused by a climatic shift towards more oceanic conditions after the 8.2 ka event. The co-existence of shade-tolerant *A. alba* and heliophilous *L. decidua* over millennia is unique since similar forests do not occur anywhere in the Alps nowadays. The replacement of mixed silver fir forests by mixed spruce forests after 5,000 cal BP was likely triggered by increasing farming activities in the region but occurred ca. 500 years later than in the Northern Alps. This delay may be explained by limited moisture availability in the Central Alps. Frequent fires linked to land use promoted the mass expansion of *A. viridis* shrublands after 4,000 cal BP. Compared to sites at the tree line and in the lowlands, the area around Lac de Champex was less affected by human exploitation of the landscape. Nevertheless, for millennia the mid altitudinal sites may have served

as important linkages between the permanent settlements in the valleys and seasonally occupied mayens at higher elevations. Global warming will lead to unprecedented changes in the vegetation composition at mid altitudes in the Alps (Henne et al. 2011) thus temperate trees (*Acer*, *Ulmus*, *Tilia* and others) and deep-rooting, drought-tolerant *A. alba* may be able to re-establish, if browsing and fire do not become excessive, probably leading to more diverse forest ecosystems. However, warmer temperatures and drier summers may impede sustainable pastoral farming in the upper continental montane zone. More studies and a systematic reassessment of old palaeoecological records within the region (e.g. Zeneggen-Hellelen, Welten 1982b) are needed to better constrain the Holocene vegetational changes and the land use history at mid altitudes in this part of the Alps.

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Data availability All data is currently stored in the Alpine Pollen Database (ALPADABA) and will be made publicly available on Neotoma (<https://www.neotomadb.org>) upon publication of this article.

Declarations

Conflict of interest The authors have no conflict of interest to declare that are relevant to the content of this article.

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