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Palaeoecological multiproxy reconstruction captures long-term climatic and anthropogenic impacts on vegetation dynamics in the Rhaetian Alps

Laura Dziomber[a,b,*], Erika Gobet[a,b], Maria Leunda[a,b,c,e], Lisa Gurtner[a], Hendrik Vogel[b,d], Nicolas Tournier[b,d], Adrianus Damanik[b,d], Sönke Szidat[b,f], Willy Tinner[a,b], Christoph Schwörer[a,b]

[a] Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland
[b] Oeschger Centre for Climate Change Research, University of Bern, Hochschulstrasse 4, CH-3012 Bern, Switzerland
[c] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
[d] Institute of Geological Sciences, University of Bern, Baltzerstrasse 1+3, CH-3012 Bern, Switzerland
[e] Department of Plant Biology and Ecology, University of the Basque Country, Barrio Sarriena, s/n, 48940 Leioa, Spain
[f] Department of Chemistry, Biochemistry and Pharmaceutical Sciences, University of Bern, Freiestrasse 3, CH-3012 Bern, Switzerland

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ABSTRACT

Alpine ecosystems are particularly affected by climate change due to their high sensitivity to temperature variations. Understanding the response of vegetation to rapid temperature increase and human impact is necessary to produce accurate and reliable predictions of future mountain vegetation and mitigate climate change impacts. Our multiproxy study reconstructs climate, fire, and vegetation dynamics over the last 14,200 cal. BP at Lai da Vons (1991 m a.s.l.), a subalpine lake situated in the treeline ecotone in Eastern Switzerland. Our results based on geochemical analysis (XRF), pollen and charcoal analysis, and high-resolution macrofossil analysis reveal that early afforestation started already at the onset of the Holocene, dominated by *Pinus cembra* and *Larix decidua*. Larch and stone pine formed closed forests at the site at 10,300 cal. BP. From 9500 cal. BP onwards, when summer temperatures were warmer than today, *Picea abies* expanded simultaneously with *Abies alba*. In the past 6500 years, increasing human impact, culminating during two main phases of landscape opening and intensification of fire regime, led to a progressive increase of species richness. Considering future climate change, an upward shift of treeline and timberline is expected in the absence of domesticated herbivores. We advocate that low-intensity pastoralism in such a cultural landscape is essential to preserve the plant diversity of species-rich mountain meadows.

1. Introduction

Climate change is drastically affecting ecosystems worldwide (IPCC, 2022). A global increase in temperature from 1.5 to 4 °C is expected by the end of this century due to anthropogenic greenhouse gas emissions. The impact of anthropogenic climate change is already evident in numerous weather and climate extremes worldwide, such as heat waves and droughts (Fischer and Knutti, 2015; Otto et al., 2016; Philip et al., 2020; Seneviratne et al., 2021; Clarke et al., 2022) together with a global decline in biodiversity across all major groups of organisms (Noss, 2001; Malcolm et al., 2006; Bestion et al., 2020). Biodiversity is also threatened by the direct anthropogenic destruction of habitats and homogenization of the landscape, primarily due to the intensification of agriculture and prioritization of economic interests before intrinsic value (Vitousek et al., 1997; Rosales, 2008; IPBES, 2018; Ortiz et al., 2021). Facing significant changes in environmental settings, organisms could potentially adapt to the new conditions (Birks, 2019; Schwörer et al., 2022), move to stay in their appropriate climatic niche, or suffer from population decline and possibly local to total extinction. Such processes currently represent an important challenge for species due to rapid changes in climatic conditions. In the alpine context, the impact of humans on ecosystems is significantly amplified, particularly given the fragility of biodiversity (Tinner and Ammann, 2005; Huber et al., 2006; Jacobsen et al., 2012; Schwörer et al., 2015). Mountains are characterized by steep climatic and ecological gradients resulting from the topography that amplifies the effects of climatic changes. On the other

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* Corresponding author.
E-mail address: laura.dziomber@unibe.ch (L. Dziomber).

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hand, plant species can track their optimal climatic niche relatively easily by moving a few hundred meters upslope. However, these range shifts pose a problem when species cannot relocate to higher elevations, as the absence of suitable niches, the reduction of available area or soil becomes a limiting factor (Guisan and Theurillat, 2000; Theurillat and Guisan, 2001).

As global temperatures continue to rise, a shift in the distribution of plant species is to be expected (Chen et al., 2011; Rumpf et al., 2018), as well as changes in the timing of seasonal events, such as seed germination (Mondoni et al., 2012), the flowering of plants (Keller et al., 2005) or plant-pollinator relationships (Vitasse et al., 2021). Besides climate change, the primary way human activities affect vegetation is through land use changes, such as deforestation and forest management, agriculture, and urbanization, which alter the landscape and can reduce the suitable habitat and diversity of plant populations (Niedrist et al., 2009). In addition, the introduction of non-native species also poses new challenges. Alien species can outcompete native species for resources, leading to declines in biodiversity and changes in the structure of ecosystems (Davis et al., 2000; Becker et al., 2005; Pauchard et al., 2009). In this context, there is an interest in understanding how vegetation changes over longer time scales. Long-term vegetation responses to climatic and anthropogenic disturbances are of significant interest in producing reliable predictions (Birks, 2019). Recent studies show the necessity of such records to understand implications for conservation biology, decision-makers, and modeling the future impact of climate on ecosystems (Willis and Birks, 2006; Pardi and Smith, 2012; Davies et al., 2014; Schwörer et al., 2014a; Garcés-Pastor et al., 2022; Schwörer et al., 2022). Even though this climate crisis is unprecedented, studying the reaction of organisms to past changes might help assess future vegetation trajectories (Nieto-Lugilde et al., 2021).

One of the most recent changes in temperature of a homologous range is the transition between the Younger Dryas and the Holocene, approximately 11,700 years ago, when temperatures increased by 3–4 °C in decades to a few centuries (Heiri et al., 2014b). Therefore, this period represents an analogue to current and future anthropogenic temperature change regarding rate and amplitude. Lake sediments are of great interest in palaeoecological research as they provide optimal conditions for the conservation of biotic proxies, such as pollen, charcoal, and other plant remains (Lang et al., 2023). Such archives capture local, extra-local, and regional information. Small lakes in mountain systems such as the Alps have the potential to contain sedimentary records that span the entire Holocene and, in some instances, also go back to the Late Glacial. Reconstruction of vegetation dynamics should ideally be conducted in a multi-proxy perspective, combining several datasets such as pollen, plant macrofossils, and other proxies from the same record to reconstruct past vegetation communities (Birks and Birks, 2006; Birks, 2019).

The Rhaetian Alps lie partly in Eastern Switzerland and are home to a high diversity of plant species. Since the 1930s, knowledge about regional vegetation history has been developed (Firbas and Preuss, 1934; Firbas, 1950; Welten, 1958; Burga, 1982; Birks and Berglund, 2018). Recent studies from other areas of the Alps have found that human activity has altered the vegetation composition and distribution over thousands of years (e.g., Gobet et al., 2003; Schwörer et al., 2015; Garcés-Pastor et al., 2022; van Vugt et al., 2022) and is one of the main drivers of vegetation changes in the Alps. Humans transform their environment to support their livelihood, by practicing agriculture or constructing settlements. For example, the introduction of livestock grazing in the Neolithic period, the expansion of agriculture during the Bronze Age, and the development of infrastructure in recent times have all impacted the natural vegetation. Several archaeological findings provide evidence of human activity during the Neolithic in the Central and Rhaetian Alps (e.g., Rageth, 1991; Stöckli et al., 1995; Crotti, 2008; Cornelissen and Reitmaier, 2016). Mountain passes were likely used by groups of humans as migration pathways already before the Neolithic period, such as the Splügen Pass (Wick, 1994; Fedele, 2016) or the Maloja Pass (Ilyashuk et al., 2009). In the Engadine, studies show an expansion of human populations and an intensification of land use in the area during the Neolithic period, resulting in a landscape transformation that is still evident today (Gobet et al., 2003). Burga (1980) investigated the vegetation history of the area north of the Splügenpass through several palaeo-records (including Lai da Vons, 1991 m a.s.l.; Palé digl Urs,1834 m a.s.l.; Crapteig, 1020 m a.s.l.) and reconstructed the vegetation dynamics regionally per taxon. Burga suggested that the forest at Lai da Vons was established during the Preboreal i.e., 11,700 to 10,100 cal. BP (calibrated years before present). He also documented the onset of agricultural activities at 4770 years BP (5610–5315 cal. BP) that significantly impacted the vegetation in this region. However, the pioneering study of Burga (1980) at Lai da Vons is based on pollen data only, and the age-depth model is based on just three radiocarbon dates. The chronology of the vegetation history is therefore not well constrained, leaving some uncertainties in attributing vegetation changes to climatic events and human activity, locally and regionally. Furthermore, there was a significant expansion of palaeoecological knowledge due to a growing number of studies conducted in the Central and Rhaetian Alps. Consequently, it is crucial to consider this expanded body of research when re-examining the vegetation history of the area. Additionally, comparing these findings with other biotic and abiotic proxies is essential to better understand the various factors influencing vegetation dynamics.

This new study based on lake sediments of Lai da Vons delivers a new site chronology, higher resolution pollen analysis, and additional proxies. The lake's location at the treeline ecotone is ideal for investigating treeline and timberline fluctuations in time. The reanalysis of Lai da Vons allows a comparison to the previous analysis from the mire (Burga, 1982) and regional studies. We reconstructed vegetation dynamics using multiproxy analyses, such as pollen, non-pollen microfossils, charcoal, macroscopic plant remains, and geochemical results of the last 14,200 years. This study explores three primary research foci 1) Treeline and timberline dynamics at the study site and in the region. 2) The expansion of the main conifer species since the Bølling-Allerød in the Rhaetian Alps. 3) The anthropogenic footprint of human activity in the area since the last 6500 years. Overall, studying long-term vegetation changes in mountain ecosystems is critical to understanding the impact of human activity on the natural environment and disentangling the different drivers of ecosystem dynamics to develop strategies for sustainable land use and conservation of biodiversity in the future. Thus, there is an urgent need for high-resolution, multiproxy studies and longer records to track the evolution of the landscape through time.

2. Material and methods

2.1. Study site

Lai da Vons (46.585875°N, 9.385697°E) is situated in the Rhaetian Alps (Eastern Switzerland, Fig. 1A), in the Canton of Grisons, within the Natural Parc *Beverin*. The lake is located at 1991 m a.s.l. and has a maximum water depth of 5 m (Fig. 1B). The lake's surface is 2.8 ha, and the catchment area is approximately 55 ha. Lai da Vons lies within the treeline ecotone in the upper subalpine zone (Fig. 1C). The lake is located on a Late Pleistocene moraine; the glacier probably retreated during the Oldest Dryas or, at the latest, at the onset of the Bølling interstadial (ca. 14,700 cal. BP). The terminal moraine is a few dozen meters away, south of the lake. Geologically, the study area comprises the Suretta nappe (gneiss formation) in the east and Jurassic sediments in the west, with the lake situated on a fracture, contributing to lake formation (Supplementary figure 1). The lake possesses a small inlet in the north and an outlet in the south. The present climate at the study site is characterized by a mean July temperature of around 9.6 °C, while the mean January temperature is about −7 °C. The annual precipitation is about 1400 mm (Meteoswiss, extrapolated from the closest meteorological station Hinterrhein, 1611 m a.s.l., for the reference period

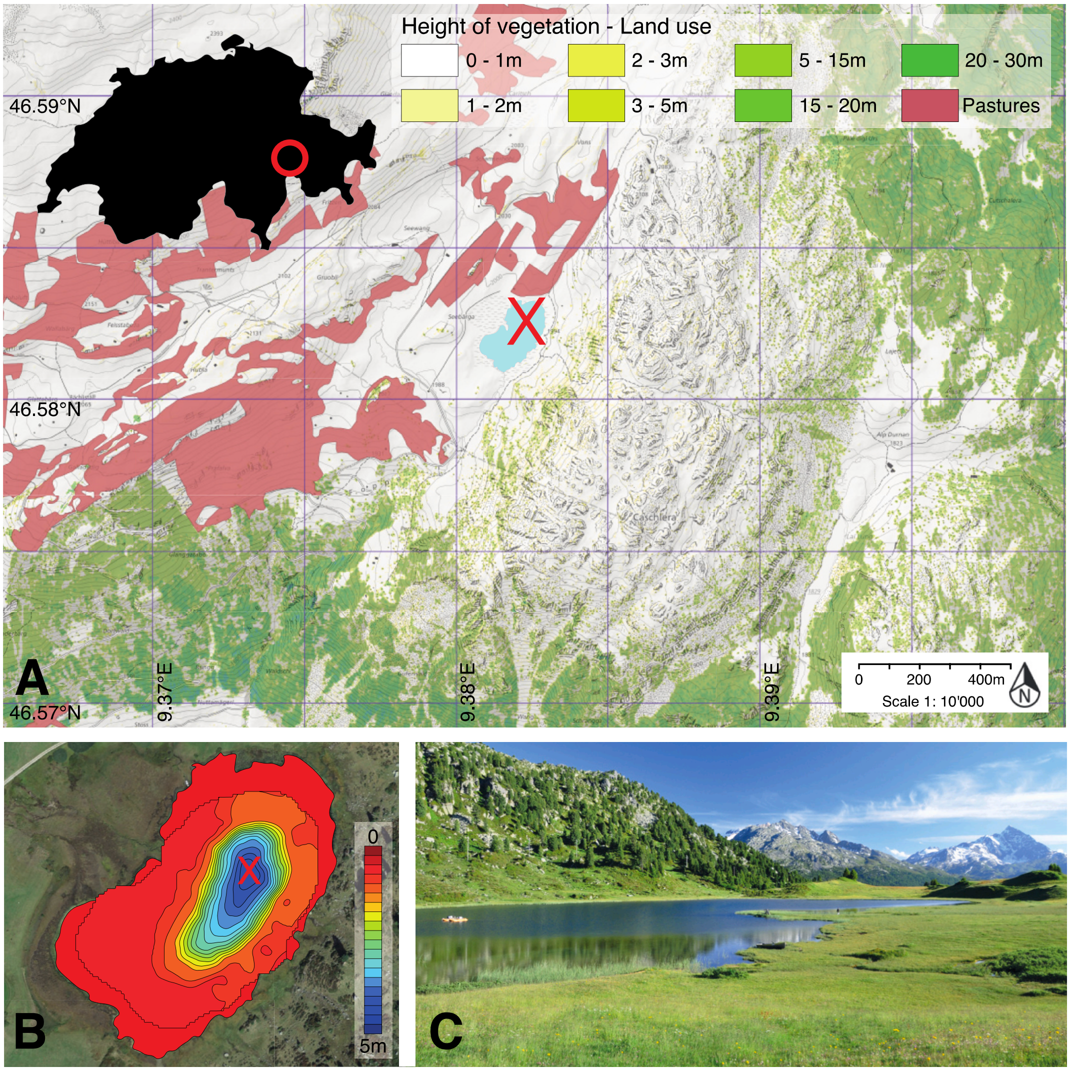


Fig. 1. Overview of the study area. The location of Lai da Vons (1991 m a.s.l.) within Switzerland is marked by a red circle. (A) Regional map showing vegetation height and land use around the lake; a red cross marks the study site (coordinates: 46.585967 °N, 9.385691 °E). (B) Bathymetric map and coring site (red cross), scale is showing the depth of the lake. (C) Picture from the study site (July 2020) showing the view from the northeast to the southwest with a coring platform at the coring location visible on the left side of the picture. Note the open forest dominated by *Pinus cembra* on the eastern side of the lake in the background. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1960–1990). The geological and hydrological nature of Lai da Vons makes it an ideal candidate for preserving sedimentary sequences.

Today, the vegetation in the study area is primarily composed of species-diverse subalpine and alpine meadows used for haymaking and as pastures in summer, as well as open forest stands (Fig. 1A). At direct proximity to the lake shore, fen vegetation dominates, including *Carex* sp. On the steeper eastern slope, open stands of *Pinus cembra* and *Larix decidua* occur with many dwarf shrubs in the undergrowth, such as *Rhododendron ferrugineum* and *Vaccinium myrtillus* (Fig. 1C). A detailed extant vegetation survey adapted from Burga (1979) is available in Supplementary Figure 2. The timberline at the study site is situated below the lake (around 1850 m a.s.l., Fig. 1), but can regionally reach up to 2000 m a.s.l. The treeline in the area lies at ca. 2100–2200 m a.s.l. Subalpine forests mainly consist of *Picea abies* with *Larix decidua* and *Pinus cembra* at higher elevations, but also deciduous species (e.g., *Betula pendula, Sorbus aucuparia*).

We performed a bathymetric study of the site using a *Humminbird Helix7 Fishfinder* in June 2020 (Fig. 1B) to map the morphology of the lake and identify the optimal coring location. We cored the lake at its deepest point (5 m of water depth) in July 2020 using a modified *Streif–Livingston* piston corer with a core diameter of 50 and 80 mm. We recovered three parallel cores, LDV-A, LDV-B, and LDV-C. We also sampled the water–sediment interface using a UWITEC gravity corer. We visually parallelized the different sediment cores using lithological markers, resulting in a master core of 756 cm. For this study we analyzed only the uppermost 350 cm.

2.2. *X-ray fluorescence (XRF) analysis*

We acquired high-resolution element geochemistry data at the Institute of Geological Sciences of the University of Bern using an ITRAX-XRF core scanner (Cox Ltd.). We used a chromium anode X-ray tube set to 30 kV and 50 mA. All individual core sections were scanned with a longitudinal resolution of 0.5 cm and an integration time of 30 s. The Late Glacial-Holocene transition was in addition scanned at 200 μm (from 265 to 360 cm) also using an integration time of 30 s. We plotted the data with R v.4.1.3, aligned the data with the master core, and plotted the results in Tilia v.2.6.1 (Fig. 3).

2.3. Macrofossil analysis

Plant macrofossils indicate the local presence of specific taxa (Tinner and Theurillat, 2003). Conifer needles can therefore be interpreted as an indication of treeline or timberline conditions (Schwörer et al., 2014b; Lang et al., 2023). The presence and abundance of macroscopic charcoal can be used to estimate local fire activity.

We collected 293 sediment subsamples from 4 to 80 cm^3, representing 1 to 10 cm slices, and analyzed the macrofossil composition to study the local vegetation dynamics around the coring site. We identified macrofossils using identification keys (e.g., Birks, 2013; Cappers and Bekker, 2022) and the reference collection at the Institute of Plant Sciences of the University of Bern (IPS). Macrocharcoal was identified together with the uncharred macrofossils to reconstruct local fire activity. We counted needle fragments and converted them to needle equivalents, based on the maximum number of either needle tips or bases. To highlight the primary succession of coniferous species (*Larix decidua, P. cembra, P. sylvestris/mugo, Picea abies,* and *Abies alba*), we conducted a macrofossil analysis with a specific focus on identifying conifer needles. All samples were sieved using a 200 μm mesh and distilled water. We generated a nearly contiguous record of conifer needles (see details of samples counted in Fig. 4). The macrofossil diagram was plotted using a custom R Script (available on GitHub and in the supplementary material) and Tilia v.2.6.1. All samples were normalized to a constant sediment volume of 20 cm^3.

2.4. Chronology

During macrofossil analysis, we collected terrestrial material for ^{14}C dating. Twenty samples were analyzed at the Laboratory for the Analysis of Radiocarbon with AMS (LARA) of the University of Bern (description of samples and results are provided in Table 1). We calibrated the raw data to years before present (cal. BP) using the calibration model IntCal20 (Reimer et al., 2020) recommended for northern hemisphere terrestrial ^{14}C dates. Our age–depth model for Lai da Vons is based on 20 AMS dates calculated using the "*Bacon*" function of the package *Rbacon* version 2.5.8 (Blaauw and Christen, 2011), implemented in R (version 4.1.3, R Core Team, 2023). Additionally, we also plotted a mixed effect model with a 95% confidence interval considering between-object variance following Heegaard et al. (2005).

2.5. Palynology and microfossil analyses

We subsampled sediments for pollen, non-pollen palynomorphs (NPP, e.g., spores from ferns and fungi), stomata, and microscopic charcoal. We collected 82 subsamples of 1 cm^3 throughout the upper part of the core (from 0 to 342 cm) based on regular sampling intervals of 8, 4, 2, and 1 cm. Our primary emphasis is on treeline and timberline dynamics in the Early and Mid Holocene and the expansion of *Picea abies* and *Abies alba.* We, therefore, took subsamples every 2 cm from the first occurrence of the taxa of interest at 288 cm to 242 cm (30 samples). The sharp transition between clay and gyttja was sampled continuously (296–298 cm, three subsamples). We treated sediments in the pollen laboratory at the IPS, following the standard procedure with HCl, HF, KOH, sieving with a 500 μm-mesh, decanting, and acetolysis (Moore et al., 1991). We added *Lycopodium* spores beforehand to estimate pollen and microcharcoal concentration and influx values (Stockmarr, 1971). The samples were mounted in glycerin and analyzed under a light microscope at 400 × or 1000 × magnification. We counted microscopic charcoal and calculated concentration and influx following Tinner and Hu (2003) and Finsinger and Tinner (2005) to reconstruct regional fire activity. We identified pollen, spores, stomata, and other NPPs using reference keys (Trautmann, 1953; Beug, 1961; Moore et al., 1991) and the reference collection at the IPS. Generally, the samples were counted to sums of approximately 500 pollen grains of terrestrial plants, excluding aquatic plants and spores. We calculated pollen percentages using the sum of terrestrial pollen types only. Pollen taxa are categorized into arboreal pollen (AP), composed of trees and shrubs, and non-arboreal pollen (NAP), corresponding to herbs (Fig. 5).

Table 1

Radiocarbon dates from the Lai da Vons sedimentary record. Cal: calibrated, indet.: indeterminate.

Laboratory code	Depth (cm)	Material dated	^{14}C-Age (BP)	Calibrated age (cal. BP)	Modeled age (cal. BP)
BE-19635.1.1	64–66	*Larix decidua* needles, *Picea abies* needles	1440 ± 40	1290–1385	1345
BE-15800.1.1	112–115	Conifer periderm, terrestrial remains indet.	2720 ± 95	2700–3075	2600
BE-19634.1.1	122–124	*Larix decidua* needles, *Picea abies* needles, conifer periderm	2625 ± 40	2710–2790	2770
BE-19633.1.1	130–132	Wood indet., *Larix decidua* needle, *Picea abies* needle, conifer periderm	2985 ± 95	3025–3090	3030
BE-19632.1.1	176–178	Conifer budscales, seed indet., terrestrial remains indet.	3995 ± 50	4345–4580	4550
BE-19631.1.1	178–180	*Larix decidua* seeds, *Larix decidua* needles, leaf fragments indet., conifer budscales	4155 ± 25	4610–4735	4640
BE-19630.1.1	182–184	*Picea abies* needles, conifer seeds, conifer budscales, bark indet.	4245 ± 25	4815–4855	4800
BE-19629.1.1	202–203	*Larix decidua* needles, *Picea abies* needles, conifer periderm, leaf fragments indet.	4996 ± 55	5605–5765	5700
BE-15799.1.1	205–207	*Larix decidua* needles, conifer seed, conifer budscales, conifer periderm	5110 ± 45	5745–5930	5870
BE-19628.1.1	211–212	*Picea abies* needles, conifer seeds, conifer budscales, leaf fragments indet.	5440 ± 25	6200–6250	6240
BE-19627.1.1	216–217	*Picea abies* needle, *Larix decidua* seed, conifer periderm	5610 ± 45	6305–6455	6400
BE-19626.1.1	230–232	*Larix decidua* seed, seed indet., conifer budscales	6330 ± 25	7240–7310	7215
BE-19625.1.1	248–250	*Carex* seed, *Larix decidua* seeds, *Pinus cembra* needles	7330 ± 50	8020–8205	8130
BE-15798.1.1	264–265	*Salix herbacea* twig	8320 ± 35	9260–9455	9310
BE-15797.1.1	270–272	*Larix decidua* needles, *Betula* fruits, conifer periderm, conifer budscales	8790 ± 80	9555–9960	9765
BE-15796.1.1	279–281	*Betula* fruits, conifer periderm, conifer budscales, leaf fragments indet.	9165 ± 75	10,205–10,505	10,340
BE-19624.1.1	293–295	*Larix decidua* needles, conifer anther, conifer budscale, leaf fragments indet.	9885 ± 65	11,195–11,405	11,350
BE-19623.1.1	300–302	Leaf fragments indet., *Larix decidua* needle	10,035 ± 165	11,710–11,930	12,050
BE-19622.1.1	314–316	*Salix herbacea* leaf, leaf fragments indet.	11,785 ± 70	13,575–13,785	13,530
BE-15794.1.1	318–320	*Salix herbacea* leaf	12,040 ± 135	13,600–14,295	13,650

2.6. *Statistical methods*

We identified statistically significant local pollen assemblage zone (LPAZ) in the pollen percentage data, using optimal partitioning by sum-of-squares (Birks and Gordon, 1985) and the broken-stick model (Bennett, 1996) in R v. 4.1.3 (R Core Team, 2023). We performed an ordination analysis to identify major gradients in vegetation composition through time. We first used a detrended correspondence analysis (DCA) to select the optimal response model; the length of DCA axis 1 is 1.8, suggesting that linear methods are more suitable. Therefore, we performed a principal component analysis (PCA) on square-root transformed pollen percentage data. We calculated and plotted results using Canoco v.5.1 (ter Braak and Šmilauer, 2017) and R v.4.1.3. We kept only the 20 most representative taxa in the dataset for the final figure (Fig. 6).

To study changes in biodiversity over time, we calculated the palynological richness index (PRI) and evenness-detrended palynological richness index (DE-PRI, Colombaroli et al., 2013). We also calculated the probability of interspecific encounter (PIE, Hurlbert, 1971) used as a proxy for evenness to explain divergent biodiversity trends in PRI and DE-PRI.

To summarize the land use activity, we calculated the land-use probability index (LUP, Deza-Araujo et al., 2022). The LUP is calculated using targeted species representative of human activities, such as Cerealia type, *Cannabis* type, *Castanea sativa, Juglans regia, Plantago lanceolata* type, and *Urtica dioica* considering their diagnostic value for different vegetation types. We selected the anthropogenic indicator values (AIV) recommended for the subalpine domain in the northern Alps.

3. Results

3.1. *Lithology and chronology*

The recovered sediment sequence mainly consists of clay from 756 to 296 cm, with a sharp transition to calcareous gyttja at 296 cm (Fig. 2). We recovered and dated 20 terrestrial macrofossil samples using ^{14}C dating techniques (Table 1). The oldest recovered organic material at a depth of 318–320 cm dates to 14,295–13,600 cal. BP, indicating that the Lai da Vons sediment record covers the time from the Bølling-Allerød interstadial until the present.

3.2. *Element geochemistry*

The transition between clay and gyttja in the sediment at a depth of 296 cm is dated to ca. 11,500 cal. BP (Fig. 3) and is accompanied by an abrupt change in element composition. Before 11,500 cal. BP, lithogenic elements such as Ti show high values, indicating deposition of sediments dominated by detrital clastics during the Late Glacial. On the other

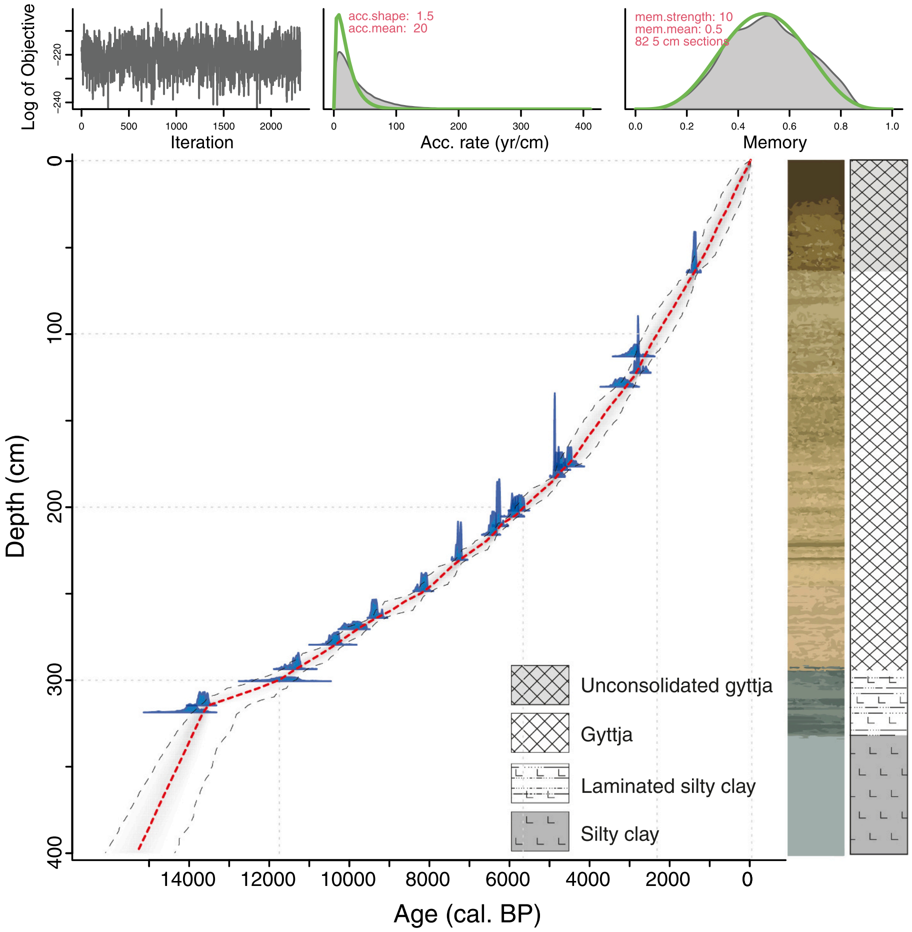


Fig. 2. Age–depth model of the Lai da Vons sedimentary sequence calculated using a Bayesian approach with the *rbacon* package (Blaauw and Christen, 2011) and the IntCal20 calibration curve (Reimer et al., 2020). Blue probability density plots: 20 calibrated radiocarbon dates used to fit the model; red line: best estimate of the age–depth model; gray shading: 95% confidence intervals of the model; gray dashed lines = 95% confidence interval of a mixed effect model considering between-object variance (Heegaard et al., 2005). On the right side, sediment description of the core as well as aspect and color. Top left: Number of Markov Chain Monte Carlo (MCMC) iterations used to generate the probability distribution of the model. Top middle: Prior (green) and posterior (gray) distributions of the sediment accumulation rates. Top right: Prior (green) and posterior (gray) distributions of memory (dependence of the sediment accumulation rate between neighboring depths). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

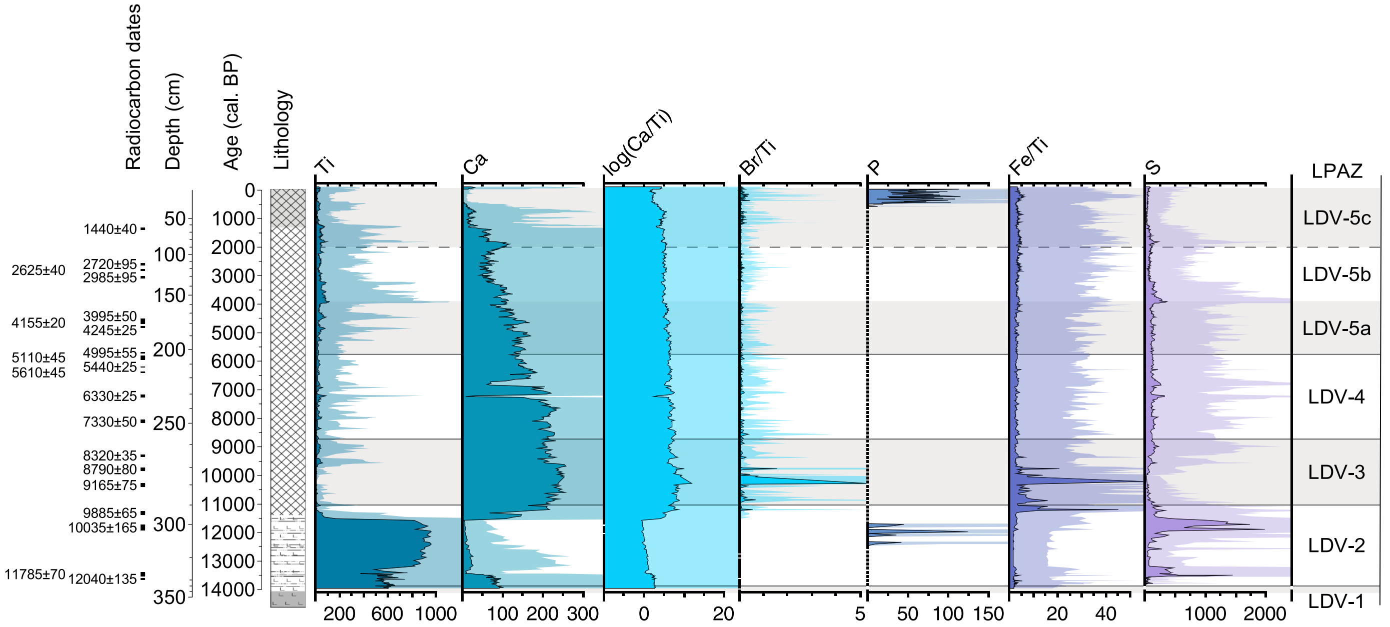


Fig. 3. XRF results of Lai da Vons (in counts s^{-1}, cps). Ti: Titanium (lithogenic input); Ca: Calcium (endogenous carbonate, lake water temperature, and productivity); log-transformed Ca/Ti ratio (endogenous carbonate, lake water temperature, and productivity); Br/Ti ratio: Bromine (organic material, productivity); P: Phosphorous (sedimentary P-retention);. Fe/Ti ratio (authigenic iron); S: Sulfur (reducing conditions, authigenic sulfide formation). Lighter shades show a 10x exaggeration. LPAZ correspond to statistically significant local pollen assemblage zones 1–5.

hand, Ca values, indicating endogenic carbonate deposition, increased sharply after the lithological transition, with the highest values between 11,000 and 8500 cal. BP. Br, an indicator for organic matter content, increased linearly from the transition at 11,500 cal. BP until the present, suggesting a steady increase in productivity in the lake. At 4000 cal. BP and 2000 cal. BP, lithogenic elements show two increases, followed closely by sharp decreases in these erosion indicators. Phosphorus (P) counts show two main increases, one before 11,500 cal. BP and one in the last 500 years. These may suggest P remobilization from developed topsoils where it is bound to Fe-oxyhydroxides, or increased nutrient input from animal dung and subsequent P burial under reducing conditions.

3.3. *Vegetation and fire history*

The pollen diagram (Fig. 5) is divided into five statistically significant local pollen assemblage zones (LPAZ). We further divided the uppermost LPAZ (LDV-5) into three statistically non-significant sub-zones (LDV-5a–LDV-5c, see Fig. 5).

Shrubs and herbs dominate LPAZ LDV-1 (14,150–13,900 cal. BP). *Juniperus* type represents 30% of the overall pollen assemblage. Herbaceous pollen, such as Poaceae, *Artemisia*, and Chenopodiaceae, represents up to 50% of the pollen sum. Pollen of trees such as *Pinus sylvestris* type (25%) probably reflect long-distance transport. This assemblage documents the establishment of pioneer vegetation consisting of herbs and shrubs on undeveloped soils after the glacier retreat. This is also confirmed by the local presence of the dwarf shrub *Salix*

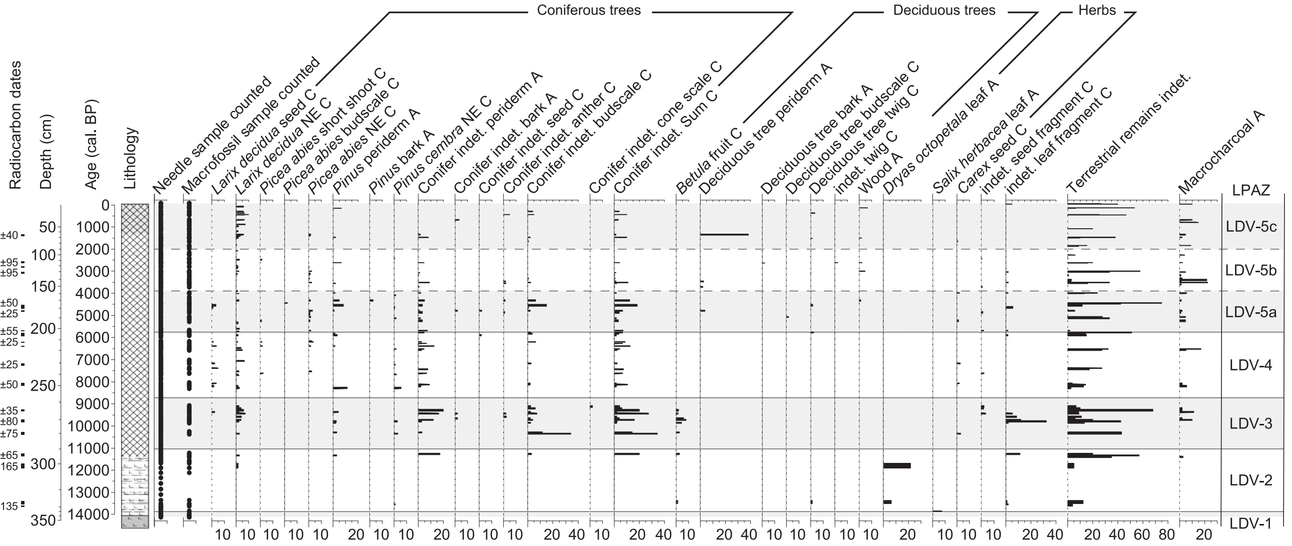


Fig. 4. Summary macrofossil diagram. Plant and macrocharcoal concentration per 20 cm^3. Indet. = indeterminate, C = counts, A = area in mm^2, NE = needle equivalent. LPAZ correspond to statistically significant local pollen assemblage zones 1–5.

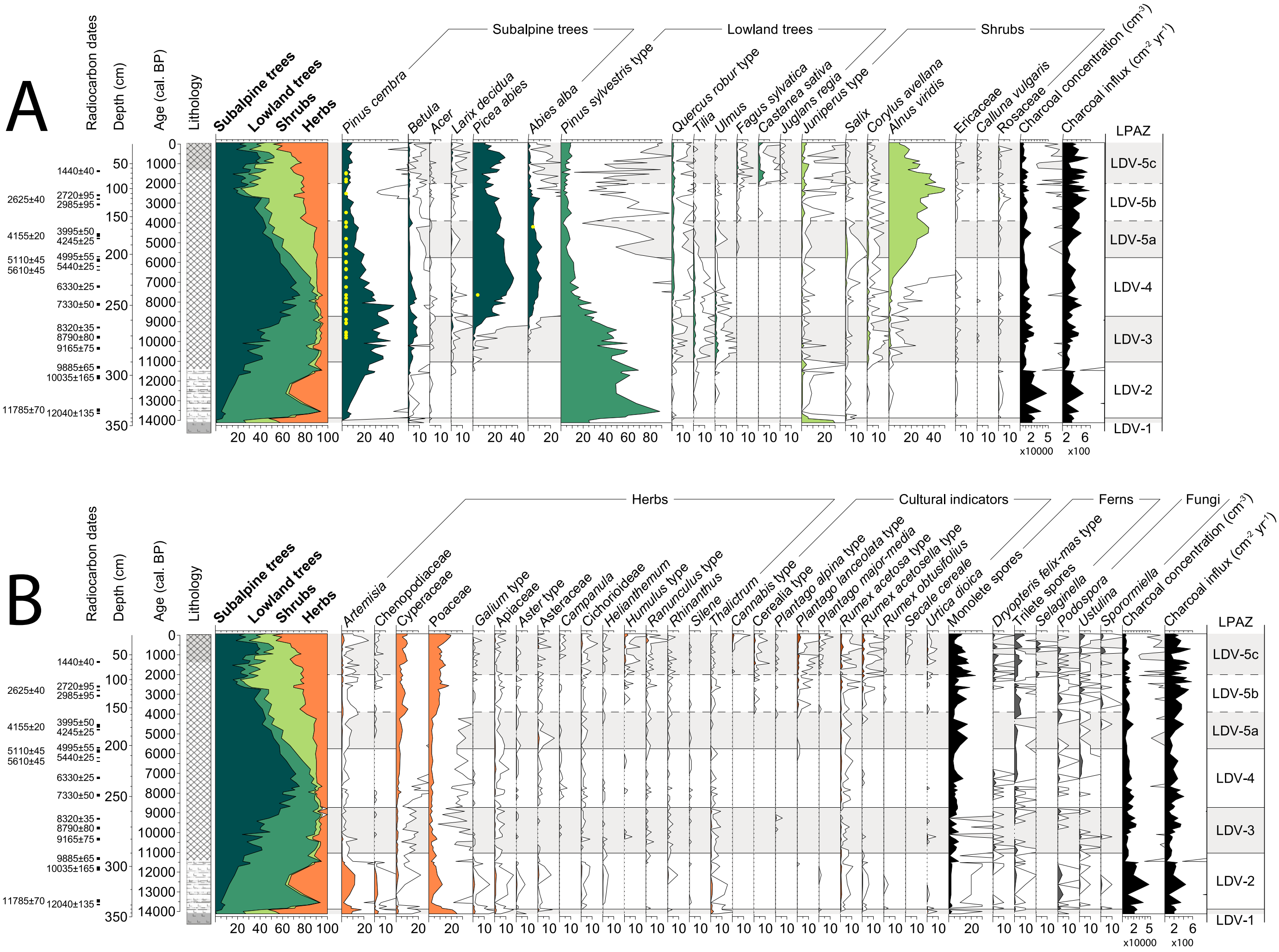


Fig. 5. Summary pollen diagram of selected taxa. A) Selected pollen percentages and stomata presence (yellow dots) of the arboreal vegetation (subalpine and lowland trees, shrubs) at Lai da Vons based on the total terrestrial pollen sum, together with ^{14}C dates, lithology, microscopic charcoal concentrations and influx values. Data are plotted on an age scale. Empty curves show 10x exaggeration. LPAZ correspond to statistically significant local pollen assemblage zones 1–5. B) Selected pollen percentages of the non-arboreal vegetation, including cultural indicators, as well as fern and fungal spores (e.g *Sporormiella, Ustulina, Podospora*). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

herbacea (leaf of *S. herbacea,* see macrofossil diagram Fig. 4). Microcharcoal influx is rather low (up to 300 particles per cm^{-2} yr^{-1}) suggesting low-frequency fire regime at the regional scale. The absence of macroscopic charcoal points toward an absence of local fire activity.

At the beginning of the next LPAZ (LDV-2, 13,900–11,050 cal. BP), a drastic increase of *P. sylvestris* type (pollen up to 90%) occurred together with a significant drop in herbs such as Poaceae (from 25 to 5%), *Galium* type, Chenopodiaceae and *Artemisia*. The macrofossil record attests to the local presence of *Betula* (fruit), *Dryas octopetala* (leaf), and possibly also *P. cembra* (burnt needle) at 13,500 cal. BP. The pollen assemblage and the macrofossil record suggest a succession from tundra vegetation to open treeline conditions. In the second stage, according to our depth age model, NAP increases again (from 5 to 30 %) from ca. 13,000 to 12,000 cal. BP, driven by Poaceae and *Artemisia*, and AP decreases, with *P. sylvestris* type declining to 50%, suggesting that tundra vegetation was recovering. In the third stage, from ca. 12,000 cal. BP to the end of this LPAZ, AP such as *P. cembra*, *P. sylvestris* type, and *Betula* increases, reaching up to 90% at ca. 11,500 cal. BP. In agreement, the first occurrence of macrofossils of *Larix decidua* at 11,900–11,700 cal. BP coincides with the first occurrence of *L. decidua* pollen, indicating the local establishment of single larch trees and treeline conditions around the site at the onset of the Holocene. Microcharcoal concentration fluctuates between 200 and 800 particles per cm^{-2} yr^{-1} indicating rather high regional fire activity. However, a low abundance of macroscopic charcoal (Fig. 4, 0–2.5 mm^2 cm^{-3} at 11,450 cal. BP), suggests few local fires in the catchment.

LDV-3 (11,050–8900 cal. BP) is characterized by the dominance of *P. cembra* in the pollen record (30–40%), as well as the onset of the empirical limit or a marked increase in deciduous trees and shrubs such as *Tilia, Ulmus, Betula, Quercus, Acer*, *Corylus avellana* and *A. viridis* at the beginning of this zone. *Picea abies* and *Abies alba* reach the empirical limit at 10,200 and 9500 cal. BP, respectively, and markedly increase toward the end of this zone. *P. sylvestris* type pollen percentages decline from 60 to 20%. Macrofossils of conifers increase drastically (Fig. 4), with *P. cembra* and *L. decidua* needles as well as *P. cembra* stomata documenting the local presence of these trees around the lake. The local presence of *Betula* trees is also confirmed by several fruits in the macrofossil record (at 9900–9800 cal. BP). From 10,000 cal. BP onwards, our results suggest that closed forests dominated by conifers expanded in the area around the site, and the location of the timberline moved above the lake. Microcharcoal increases from 200 up to 400 particles per cm^{-2} yr^{-1} and coincides with two peaks of macrocharcoal remains (from 1 to 10 mm^2 cm^{-3}) at 9420 and 9750 cal. BP. The charcoal record suggests the low local and regional fire activity at Lai da Vons.

Subalpine pollen percentages (Fig. 5) with values up to 70 % suggest that during the next LPAZ LDV-4 (8900–5800 cal. BP), closed subalpine forests prevailed around the lake. *Picea abies* reaches the highest pollen percentages of the record with 35%. *Pinus cembra* declines from 45% to 20% but is still locally abundant, as the stomata and macrofossil record suggest. The uppermost part of the zone is characterized by a substantial increase of *A. viridis* (5 to 20%) and a decrease in the deciduous trees *Ulmus, Betula,* and *Tilia.* The pollen and macrofossil data suggest closed subalpine forest conditions with increasing disturbance from ca. 6500 cal. BP onwards. With only one main peak of local fire activity at 6500 cal. BP (17 mm^2 cm^{-3}), the fire regime stays similar to the previous LPAZ.

LDV-5a (5800–3900 cal. BP) is characterized by the continuing increase of *A. viridis*, reaching a first peak of ca. 35%, and the general decrease of conifers (*Picea abies*, *P. cembra, P. sylvestris* type, and *A. alba*). Nevertheless, the occurrence of a single *A. alba* stoma, as well as needles of *P. cembra, Picea abies,* and *L. decidua,* still suggest rather closed forest conditions. Microscopic charcoal concentration and influx show a marked peak at ca. 4500 cal. BP, coinciding with the peak in *A. viridis*. This suggests that the pollen-inferred increase in green alder thickets was driven by fire disturbance.

At the beginning of the next subzone (LDV-5b, 3900–2000 cal. BP), AP values decrease sharply (from ca. 90% to 70%) when *Fagus sylvatica* pollen, and several cultural indicators such as Cerealia type, *Rumex acetosella* type, and *Plantago lanceolata* type reach first continuous presences. *Alnus viridis* pollen percentages show some fluctuations but reach a marked peak with highest values in the record (from ca. 30% to 50%) at 2500 cal. BP. This peak coincides with a drastic drop in *Picea abies, P. cembra,* and *A. alba,* as well as with an increase in microcharcoal influx (400 to 600 particles cm^{-2} yr^{-1}). Macrocharcoal concentration peaks at 3500 cal. BP (from 1 to 20 mm^2 cm^{-3}). The data suggests regional forest openings and a possible intensification of fire activity, although the abundant conifer needles in the macrofossil record indicate still forested environments around the study site.

The last subzone of the diagram (LDV-5c 2000 cal. BP–present) is characterized by the marked increase in herbs (up to 45%) and the expansion of human-indicator taxa such as Cerealia type and *Secale cereale,* as well as fruit-trees such as *Castanea sativa* and *Juglans regia*, resulting from long-distance transport of lowland cultivation. On the other hand, *A. viridis* pollen percentages decrease from 60 to 25%. *Larix decidua, Picea abies,* and to some extent, *A. alba* show an increase after ca. 1000 cal. BP for a few centuries before sharply declining again. *Larix decidua* needles are present in the macrofossil record until the present, whereas no *Picea abies* or *P. cembra* needles occur in the uppermost part of the core. At 780 cal. BP, macrocharcoal concentration values peaked again (from 0 to 13 mm^2 cm^{-3}). The combined pollen and macrofossil evidence suggests the establishment of treeline conditions with a mosaic of tree stands, together with subalpine and alpine meadows in the last centuries.

3.4. Numerical analyses

The Principal Component Analysis (PCA) results of the pollen dataset indicate that the first and second PC-axis represent 73.6% of the total variance (Fig. 6). PCA axis 1 explains a large part of the total variance, accounting for 53.7%. PC1 scores over time (Fig. 6) show a close correlation with the percentages of *P. sylvestris* type pollen in the dataset. In the PCA biplot, PCA axis 1 shows a gradient from natural, Late Glacial, and Early Holocene environments characterized by *P. sylvestris* type, *Artemisia* and Chenopodiaceae, but also *P. cembra, Tilia,* and *Ulmus* (all having high PC1 scores), to a landscape increasingly dominated by anthropogenic activities, aligned with cultural indicators (e.g., Cerealia type, *Plantago lanceolata* type, or *Rumex acetosella* type with negative PC1 scores).

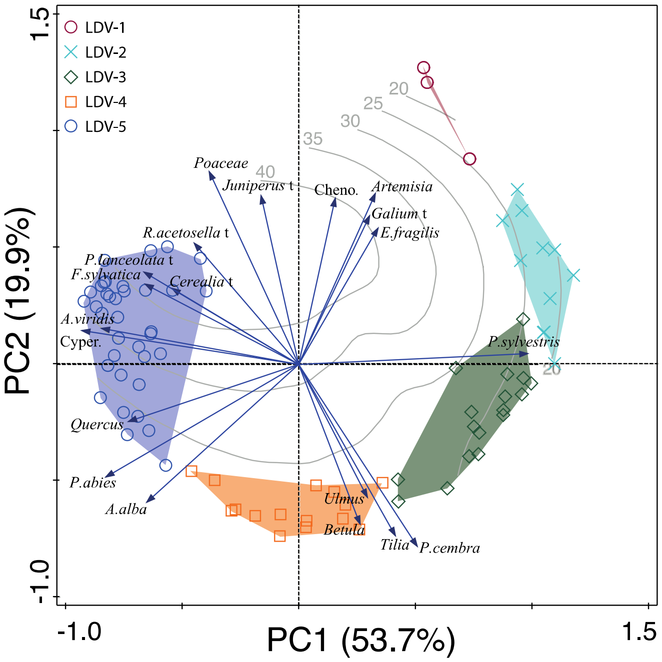
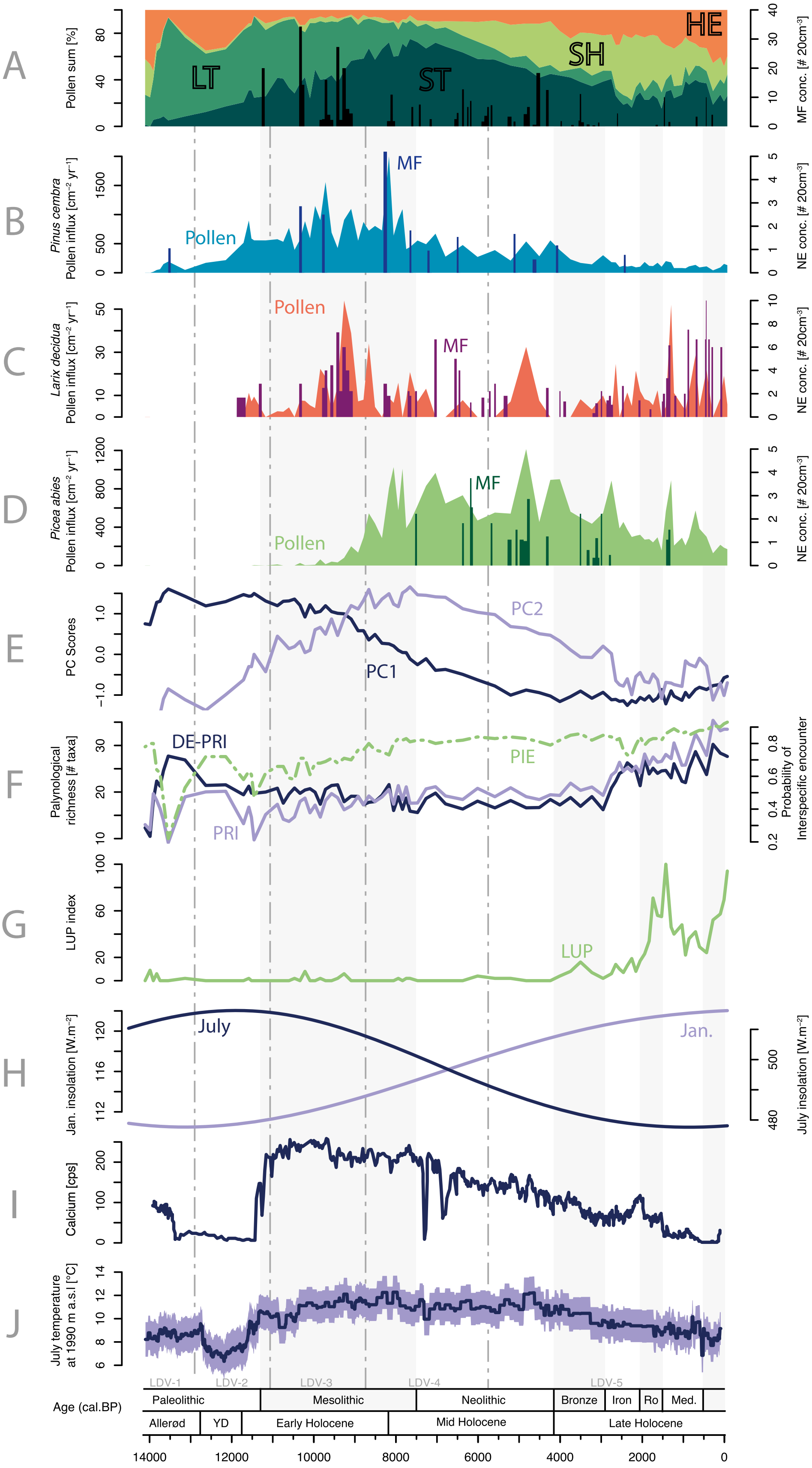


Fig. 6. Principal component analysis (PCA) biplot showing both species (blue arrows) and sample scores (symbols). The first axis explains 53.7% of the variance, and the second axis 19.9%. The isolines represent the rarefied number of different pollen types in the samples. Cyper. = Cyperaceae, Cheno. = Chenopodiaceae, t = type. Colored shapes correspond to samples originating from the same LPAZ. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

PCA axis 2 explains 19.9% of the total variance, showing a clear separation between tree and herb taxa, with negative values representing tree taxa (e.g. *P. cembra, Tilia, Ulmus, Betula*) and positive scores indicating herbs (Poaceae, Chenopodiaceae*, Artemisia*) and disturbance-adapted shrubs (*Juniperus* type, *A. viridis*). Agreeing with our interpretation of summarizing forest conditions and landscape openness, PC2 scores correlate well with the subalpine tree pollen percentage curve (see Fig. 7A and E). From the beginning of the record until the onset of the Holocene, PC2 scores are negative. There is a rapid increase at the transition between the Late Glacial and the Holocene (ca. 11,700 cal. BP). The scores remain stable until 7500 cal. BP, to only decrease until today, except for a short recovery during Medieval times (1000–500 cal. BP). Overall, our PCA biplot nicely summarizes vegetation trajectories since the Late Glacial. From open, natural environments during LDV-1 and 2, the landscape changed to closed forests without human activities in LDV-3. LDV-4 shows increasing disturbance but still forested conditions, whereas LDV-5 marks the transition to an open landscape with a clear signal of human activities.

Palynological richness (PRI) and detrended palynological richness (DE-PRI) are similar throughout the record, except between 14,200 and 13,000 cal. BP when *P. sylvestris* is highly dominant in the pollen record and PIE low, pointing to distortions of palynological richness by uneven conditions. PRI and DE-PRI are stable around 20–30 taxa until 4000 cal. BP, when there is a first slight increase, followed by a marked increase in PRI and DE-PRI at 2800 cal. BP. The land-use probability index (LUP, Deza-Araujo et al., 2022) shows similar trends as the PRI and DE-PRI,



(caption on next page)

Fig. 7. Summary results of Lai da Vons. A) pollen percentage diagram of subalpine trees (ST), lowland trees (LT) shrubs (SH), and herbs (HE) as well as conifer indet. macrofossil sum (contains indet. coniferous seeds, periderm, bud scales, cone scales). B) Pollen influx (light blue) and macrofossil concentration (dark blue) of *Pinus cembra.* C) Pollen influx (light orange) and macrofossil concentration (dark pink) of *Larix decidua.* D) Pollen influx (light green) and macrofossil concentration (dark green) of *Picea abies*. E) Sample scores of PCA axis 1 (dark purple) and PCA axis 2 (light purple). F) proxies for richness and palaeodiversity: Palynological richness (PRI, light purple), detrended palynological richness (DE-PRI, dark purple), and pollen evenness (PIE, light green). G) Agricultural land use probability (LUP, light green, Deza-Araujo et al., 2022) indicating human impact. H) January (light purple) and July (dark purple) insolation (Laskar et al., 2004). I) Calcium counts s^{-1} (cps; endogenous carbonate, lake water temperature, and productivity). J) Reconstructed July air temperatures at the elevation of the lake (1991 m a.s.l.) calculated using a stacked chironomid-based temperature reconstruction (Heiri et al., 2015). Mean reconstruction (dark purple line) and lower and upper limit (light purple range). The vertical gray dashed lines represent the pollen zone boundaries. Alternating white and gray shading indicates cultural periods. Ro: Roman time, Med: Medieval time, YD: Younger Dryas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

with a first increase of LUP values at 4000 cal. BP (during the Bronze Age, Fig. 7G). LUP increases drastically during the transition between the Iron Age and the Roman time (around 2000 cal. BP), only to peak at the end of the Roman time (1500 cal. BP). A significant drop in LUP values occurs during the migration period and early medieval period (1500–1000 cal. BP). From 1000 cal. BP onwards, LUP increases constantly until the present suggesting intensified land use.

4. Discussion

4.1. Early treeline dynamics at Lai da Vons

Based on the oldest radiocarbon date from our record (320–318 cm, 14,300–13,600 cal. BP) the lake was formed by deglaciation processes during the Bølling-Allerød interstadial at the latest. Reconstructed steppe-tundra vegetation with high amounts of *Juniperus* type and *Artemisia* from pollen samples below the lowermost radiocarbon date suggest that glaciers could have receded even earlier in the area. Our results agree well with the earlier study by Burga (1982) from Lai da Vons, which also shows steppe-tundra vegetation in the oldest samples. Burga (1982) attributed the beginning of lake formation and sediment accumulation to the Oldest Dryas, so before 14,600 cal. BP, although purely based on biostratigraphy without physical dating. Other lakes in the region at similar elevations, such as Maloja Riegel (1865 m a.s.l.; Ilyashuk et al., 2009), also became ice-free before the start of the Last Interstadial (ca. 14,600 cal. BP). The first warming pulse after the Last Glacial Maximum (LGM; 23,000–19,000 cal. BP) with a temperature increase of ca. 1–2 °C around the European Alps occurred during Heinrich event 1 ca. 16,500–16,100 years ago (Samartin et al., 2012b; Bolland et al., 2020; Rey et al., 2020). This warming may have triggered glacier retreats in the Alps that could have led to the formation of Lai da Vons (Maisch, 2000; Ivy-Ochs et al., 2008).

A sharp increase in arboreal pollen indicates that forests expanded below our study site during the Bølling-Allerød interstadial i.e., from 14,600 cal. BP onwards. In response to a rapid temperature increase of ca. 3–4 °C within a few decades at the start of the interstadial (Samartin et al., 2012a, 2012b; Heiri et al., 2014b; Bolland et al., 2020), forests were able to spread in the lowlands north of the Alps (Ammann, 1989; Lotter, 1999; Rey et al., 2020), and timberline positions rose to at least 1500 m a.s.l. in the southern Alps (Vescovi et al., 2007, 2018). The treeline in the Central Alps might have even reached up to 2000 m a.s.l. during this period (Lang and Tobolski, 1985; Rey et al., 2022). The presence of a single, charred needle of *P. cembra* and a single fruit of *Betula* during the Bølling-Allerød in the sediment record of Lai da Vons suggests that timberline was close to the lake during this period, and few trees might have reached the elevation of our site, indicating open treeline conditions. This is further corroborated by high AP percentages (>80%) and influx values of *P. cembra* reaching 750 grains cm^{-2} yr^{-1} at ca. 13,500 cal. BP, which is similar to the documented forested period in the Holocene and above the pollen influx threshold for treeline based on Tinner and Theurillat (2003).

In the forelands of the Northern Alps, boreal forests dominated by *Betula* established at ca. 14,500 cal. BP after a pronounced expansion of *Juniperus* (the so-called "juniper-peak"; Ammann et al., 2013; Rey et al., 2020). At higher elevation, the occurrence of the *Juniperus* expansion is not very well documented as most subalpine lakes were still covered by glaciers during the Bølling-Allerød. At intermediate elevations in the Northern and Central Alps (Lauenensee, 1300 m a.s.l.; Lac de Champex, 1470 m a.s.l.; Rey et al., 2013, 2022), the peak in *Juniperus* pollen is followed by the expansion of birch forests as well. However, although we observe a pronounced juniper peak in the Lai da Vons sediment record, it seems that in contrast to sites in the Northern Alps or the Swiss Plateau, *Betula* did not play a significant role in subsequent forest expansion in the Rhaetian Alps at the beginning of the Bølling-Allerød. Instead, forests in the lower valleys were mostly dominated by pine. Similar low values of *Betula* during the Late Glacial are also described at Lago di Origlio in Southern Switzerland (Tinner et al., 2005), and at Maloja Riegel (Ilyashuk et al., 2009) and Hopschensee (Welten, 1982) in the Central Alps. The absence of pine in the forelands of the Northern Alps during the Bølling has been mainly attributed to migrational lag (Ammann et al., 2013; Lischke et al., 2013). However, the relatively short distance between our site and the Swiss Plateau (ca. 70 km) and estimated spreading rates of ca. 100–500 m yr^{-1} for *P. sylvestris* type (Feurdean et al., 2013; Giesecke and Brewer, 2018; Tinner et al., 2023), make this explanation seem less likely.

The opening of forests and re-expansion of steppe tundra that is dated in our record to ca. 13,000 cal. BP can most likely be attributed to the Younger Dryas cooling (ca. 13,000–12,000 cal. BP). Since there are no ^{14}C-dates available at this depth, the beginning of this period is chronologically not well constrained. However, many other sites in the Alps show a similar opening of forests and a timberline depression of 200 to 300 m (Burga, 1988) linked to a decrease in temperature of ca 3.5 °C (Ilyashuk et al., 2009).

The afforestation at Lai da Vons started with the Younger Dryas–Holocene transition at 11,700 cal. BP. The first *L. decidua* needles in the macrofossil record confirm the local presence of single trees. The rapid upward shift of the treeline at 11,700–11,500 cal. BP was most likely in response to the Holocene warming of 3–4 °C during this period (Fig. 6; Heiri et al., 2014a). Farther to the south but at higher elevation, at Lago Basso (2250 m a.s.l.), first *L. decidua* macrofossils are documented at 11,300–11,000 cal. BP (Wick and Tinner, 1997) and in the Engadine at Lej da San Murezzan (1768 m a.s.l.) at 11,400–11,300 cal. BP (Gobet et al., 2005). Similarly, in the Western Central Alps at Gouillé Rion (2343 m a.s.l.), the first larch trees reached the site at 11,350 cal. BP (Tinner and Kaltenrieder, 2005). Compared to higher elevation sites in the Central Alps, the immediate establishment of single trees in response to the rapid warming at the beginning of the Holocene at Lai da Vons, can likely be explained by its lower elevation and therefore slightly warmer temperatures and closer proximity to the treeline during the Younger Dryas. This, however, brings the question of why sites at lower elevations in the Engadine show a pronounced lag in afforestation of 300–400 years (Gobet et al., 2005). The authors hypothesized that forests could have established earlier at higher elevations because of reduced competition with alpine plants and propose a delayed downhill expansion of *L. decidua* and *P. cembra* into the preexisting Younger Dryas alpine meadows. Another possibility could be lower temperatures on the valley floor of the Engadine due to pronounced cold air pooling. Early deglaciation, higher regional temperatures, and favorable environmental conditions at Lai da Vons could explain the very early establishment of trees at such an elevation, even a bit earlier than most at sites in the Engadine. In contrast, at sites at similar elevations in the Northern Alps (e.g., Iffigsee at 2065 m a.s.l.; Bachalpsee at 2265 m a.s.l.; Schwörer et al., 2014a; Lotter et al., 2006) establishment of treeline conditions is documented only after 9800 cal. BP. This significant delay in afforestation has been attributed to higher summer temperatures in the Central than Northern Alps (Schwörer et al., 2014b) as confirmed by a dynamic vegetation model (Schwörer et al., 2014a). Our record clearly suggests that climatic conditions around Lai da Vons must have been similar to the Central Alps, with higher seasonality and potentially higher solar insolation due to reduced cloud cover resulting in higher treeline elevation compared to the Northern Alps. Indeed, highest values of calcite precipitation according to our XRF results (Figs. 3 and 7I), suggest relatively warm summer temperatures during the Early Holocene. Warmer water temperatures reduce the solubility of CO_2, favoring the formation of solid carbonates (Davies et al., 2015). Moreover, higher temperatures promote ecosystem productivity. In the case of Lai da Vons, temperature and productivity are key drivers of endogenic carbonate precipitation.

Our macrofossil and pollen records at Lai da Vons indicate that timberline in the form of closed larch-stone pine forests reached the site at ca. 10,300 cal. BP, when summer temperatures further increased after the Preboreal Oscillation i.e., a centennial-scale cold excursion (Haas et al., 1998; Heiri et al., 2014b). In the Engadine, at a lower elevation (1768 m a.s.l.), the timberline reached the valley floor at ca. 10,700 cal. BP, as documented by a continuous record of *L. decidua* from this time onwards and the presence of *P. cembra* macrofossil at 10,400 cal. BP (Gobet et al., 2005).

4.2. Shift in subalpine forest composition during the Holocene

The onset of the Holocene is marked by an abrupt change in sedimentation rates and sediment composition (from clay to gyttja) at 11,500 cal. BP. This transition is also evident in the XRF data, as a marked shift from elevated to low levels of Al, K, Si, and Ti within decades. This change in sediment composition serves as a distinctive marker for the onset of the Holocene at Lai da Vons. The transition from the local pollen zone (LPAZ) LDV-2 to LDV-3, denoting regional vegetation change, occurred slightly later, around 11,050 cal. BP. This time lag of approximately 450 years between the climate change inferred from geochemical data and the corresponding vegetation response, highlights the complex dynamics between climate change and the ecological responses of plants, illustrating that it may take several centuries for ecosystems to reach a new equilibrium in response to shifts in environmental conditions such as temperature (Tinner et al., 2023). This inertia can be explained by both population dynamic and competition processes and has been documented in other palaeoecological studies (Höhn et al., 2022), as well as modeling output (Schwörer et al., 2014a).

Early Holocene forests around the study site mostly comprised subalpine taxa such as *Betula*, *L. decidua, P. sylvestris,* or possibly *P. mugo,* and *P. cembra*, whereas temperate tree species such as *Tilia* and *Ulmus* expanded at lower elevations (Crapteig; Burga, 1979). This vegetation composition is maintained until ca. 9500 cal. BP like at other sites in the region, where *Betula,* and *P. cembra* are documented together with temperate taxa (e.g., *Tilia, Ulmus*) in the pollen record (Wick and Tinner, 1997). However, it is not likely that temperate species reached our site at almost 2000 m a.s.l., given that the pollen abundances are low, and macrofossils are missing. From 9500 cal. BP onwards, the high summer temperatures during the Holocene Thermal Maximum (HTM; Renssen et al., 2012; Fischer et al., 2018; Lang et al., 2023) probably triggered a further upward shift of the treeline above the study site. During this time, *P. abies* and *A. alba* expanded within a few centuries in the region, coinciding with a noticeable decline in the abundance of *P. cembra*, *Betula*, and temperate trees in the lowlands. The expansion of *P. cembra* and *Betula* during the Early Holocene agrees well with other records from the Eastern Alps (e.g., Pini, 2002; Gobet et al., 2003), while the expansion of *Picea abies* in the Western Alps is delayed by several thousand years. Only ca. 150 km to the west, in the Bernese Alps, *Picea abies* expanded only after ca. 7000–5000 cal. BP (Wick et al., 2003; Rey et al., 2013; Schwörer et al., 2014a; Garcés-Pastor et al., 2022). This pattern suggests a postglacial recolonization of *Picea abies* from East to West, with a marked slowdown of the westward expansion at ca. 8–9° longitude in Central Switzerland (Burga, 1988; Ravazzi, 2002; Latałowa and van der Knaap, 2006; Lang et al., 2023) or diverging environmental controls (Henne et al., 2011). Many hypotheses have been put forward to explain the delayed expansion of spruce in the Western Alps, among them climate and/or soil conditions (Henne et al., 2011), migrational lag (Lang, 1994), human impact (Markgraf, 1970; Schwörer et al., 2014b) and competition with other tree species, mainly *A. alba* (Ravazzi, 2002). Since *P. abies* populations were established a few centuries earlier in our study region (empirical limit: 10,200 cal. BP) than *A. alba* (empirical limit: 9500 cal. BP), they had a competitional advantage and could already form closed stands. The very shade-tolerant and temperate *A. alba* apparently did not have a problem invading these high-elevation stands, creating a mixed subalpine forest. However, since *P. abies* is less shade tolerant than *A. alba*, dense silver fir forests might effectively prevent population expansion of spruce under natural conditions, as observed in the Western Alps even at treeline elevations. At Lai da Vons, *P. abies* is present locally at least since 7600 cal. BP, as documented by the finding of one stoma and several needles. *A. alba* was most likely abundant in forests of the montane or lower subalpine vegetation belt. The presence of a single stoma of *A. alba* dated to 4200 cal. BP indicates that silver fir was even able to grow at timberline, together with *Picea abies, P. cembra* and *L. decidua.* Similar non-analogue forest types with temperate *A. alba* growing together with cold-adapted tree species such as *P. cembra* have been documented by macrofossils in the Northern Alps even at sites higher than Lai da Vons (Wick et al., 2003; Lotter et al., 2006). Considering that *A. alba* was also forming stands at the shores of the Mediterranean Sea and can thrive under warm mesomediterranean climates (Colombaroli et al., 2007; Walder et al., 2021) this demonstrates its capacity to tolerate a wide range of environmental conditions throughout the Holocene period and other Interglacials (Zagwijn, 1996; Lang et al., 2023). Indeed, palaeoecological evidence suggests that the environmental niche of silver fir was considerably larger prior to human induced disturbance (Tinner et al., 2013). Under future conditions of global warming, *A. alba* could therefore provide essential ecosystem services, particularly in maintaining stand and slope stability (Ruosch et al., 2016).

4.3. Anthropogenic disturbance in the region

The pollen data show the mass expansion of *A. viridis* thickets from 6500 cal. BP onwards, rapidly becoming one of the dominant taxa in the record. *Alnus viridis* is a disturbance-adapted shrub that expands due to natural disturbances such as rockslides, landslides, avalanches, and anthropogenic disturbances. This characteristic expansion during the Mid to Late Holocene is observed in many other subalpine sites in the Engadine (Gobet et al., 2003), south of the Splügenpass (Wick and Tinner, 1997) and other areas of the Alps (e.g., Furlanetto et al., 2018; van Vugt et al., 2022). At Lai da Vons, the occurrence of *Plantago lanceolata* type at 5800 cal. BP, suggests the presence of pastoral activity in the vicinity of the lake. Simultaneously, the disturbance-sensitive species *A. alba* experienced a decline, whereas *A. viridis* thickets thrived substantially. Additionally, archaeological findings confirm the presence of Neolithic settlements in the wider area, such as the Domleschg, the Upper Engadine and the Misox (Gobet et al., 2003; Cornelissen and Reitmaier, 2016; Altorfer et al., 2021). These nearby settlements suggest that humans used the study area in the subalpine belt to pursue a pastoral lifestyle. The proximity of the site to several mountain passes (e.g., Splügenpass; Wick and Tinner, 1997), which could have been used as pathways from the southern Alps, also suggests that agricultural activities in the region around the study area is likely. The presence of humans in the Alps at major passes during the Neolithic period is underscored by the finding of the body of Ötzi at the Tisenjoch pass in the Tyrolean Alps (Oeggl et al., 2007; Pilø et al., 2023) or a collection of artifacts discovered at the Schnidejoch pass in the Swiss Alps (Hafner, 2012; Hafner and Schwörer, 2018), suggesting that humans actively used alpine areas since millennia.

At the onset of the Bronze Age, from 4000 cal. BP onwards, the presence of several cultural indicator taxa, such as cereal pollen grains, and an associated peak in macrocharcoal, indicate an increase in human agricultural activities. This translates to a decrease in *A. viridis* thickets, which had previously probably benefited from forest clearance by humans using fire but finally declined with the intensification of land use during the Bronze Age. Reduced woodland cover likely reflects a lowering of the tree line as well. In the Upper Engadine, regional population growth during the Bronze Age resulted in changes and intensification in both arable and pastoral farming (Lang et al., 2023) and the establishment of larch meadows, along with the exploitation of copper (Gobet et al., 2003).

We observe a second opening of the landscape from 2800 cal. BP onwards, during the Iron Age, as suggested by a drastic drop in arboreal pollen (AP) percentages and the establishment of many herbaceous species. The increase and diversification of anthropogenic indicator taxa and a slight increase in the land use probability index (LUP) indicate a moderate augmentation of human activities. The increase in charcoal influx most likely shows the anthropogenic forest clearances by fire. Unlike forests, meadows tend to support more diverse plant communities due to increased light availability, nutrient cycling, and reduced competition from shade-tolerant species. The introduction of livestock into these subalpine meadows, therefore, plays a crucial role as grazing animals help maintain the openness of the landscape, prevent the encroachment of shrubs and trees, and create a mosaic of different vegetation types that further contribute to species diversity. Consequently, our palaeodiversity analysis shows a strong increase in plant species richness at the beginning of the Iron Age.

With the beginning of the Roman rule after the subjugation of Rhaetian tribes by Drusus and Tiberius in 15 BCE (Hirt, 2011), a drastic increase in the LUP index occurred, suggesting a strong intensification of agricultural activities (including sweet chestnut cultivation at lower elevation). Remarkably, this led to a decline in the abundance of green alder thickets, probably due to an increasing volume of livestock in the area. A recent study from the southern Alps has shown quantitatively that green alder negatively responds to high numbers of livestock (van Vugt et al., 2022), particularly sheep and goats (Pauler et al., 2022). Although the landscape around the lake was rather open, the continuous presence of larch needles in our record still points to local forest stands, most likely at the rocky hill to the east of the lake. However, open stands of *L. decidua* and herbaceous plants are also characteristic of larch meadows (Zoller et al., 1996, 1998; Gobet et al., 2003). In this region, the expansion of larch meadows was primarily driven by human activities aiming at livestock grazing and timber production (Garbarino et al., 2013) The preference for larch meadows and disturbances resulted in the decline of *P. cembra* and *A. alba*, which is observed in the Lai da Vons area. This decline could be attributed to the sensitivity of *P. cembra* and *A. alba* to disturbances like fire and browsing, while *L. decidua* exhibits a greater resistance. In addition, human intervention favored *L. decidua* over less desirable tree species like *P. cembra*, as evidenced by the removal of *P. cembra* seedlings by farmers leasing pastures in certain regions of the western Italian Alps to maintain economically important meadows (Motta et al., 2006). A similar dynamic is observed in other regions, such as the Upper Engadine (Gobet et al., 2003), the Lower Engadine (Zoller et al., 1996) and the Lepontine Alps (van Vugt et al., 2022), where larch meadows established earlier than at Lai da Vons, during the Bronze Age.

Right at the end of the Roman period, our pollen record shows an increase of tree and shrub taxa (e.g., *Picea abies*, *A. alba*, and *A. viridis*) together with an increase of arboreal macrofossils, a significant drop in cultural indicators (mostly *Plantago lanceolata* type), and, therefore, a decrease of the LUP index. These patterns suggest a decline in land use and the abandonment of cultivated land. With the limitations in data resolution and chronological control in the upper part of the record, this phase of land abandonment likely coincides with the great migration period that occurred between ca. 400–600 AD (ca. 1550–1350 cal. BP) after the collapse of the Western Roman Empire. This pattern of vegetational change is also observed at other subalpine sites of similar elevation (Müller et al., 1999; Tinner et al., 2003; Schwörer et al., 2014b; van Vugt et al., 2022). The recovery of subalpine forests and the following decline in plant richness at Lai da Vons could be an illustrative example of the potential impacts of future globalization when local land use may collapse.

During the past 500 years, geochemical data show a potential switch in land use activity, with a strong increase in phosphorus (P) content of the sediment. This peak is consistent with an increase in herbs (e.g. Poaceae, *Artemisia*, cultural indicators), the LUP index, and *Sporormiella*. It also coincides with major forest clearances and inventions during the Middle Ages and continues until modern times with the Industrial Revolution as a turning point for agricultural systems in Western Europe. However, our record of the last 500 years does not have sufficient sampling and chronological precision to adequately address the impact of recent land use changes on the vegetation. It is notable however, that the uppermost samples show a slight decline in plant richness, possibly linked to forest expansion following land abandonment of marginal areas during the last century (Gehrig-Fasel et al., 2007) as also observed in high-resolution palynological records (e.g., Tinner et al., 1998; Van Vugt et al., 2022; Brugger et al., 2021).

4.4. *Implications of past land use activities for future vegetation dynamics*

We could show that agricultural activities, particularly pastoralism in the subalpine belt, led to the creation of species-diverse meadows and an overall increase in plant richness at Lai da Vons (Figs. 6 and 7), which is in line with many other recent palaeoecological studies from the Alps (e.g., Giesecke et al., 2019; Garcés-Pastor et al., 2022; van Vugt et al., 2022). Because of centralized and industrial farming that leads to the abandonment of cultivated land in marginal areas, the presence of livestock in the subalpine belt is slowly reducing (Gehrig-Fasel et al., 2007; Niedrist et al., 2009). The abandonment of subalpine pastures is triggering a recolonization and expansion of *A. viridis*. Even at a low shrub cover, *A. viridis* significantly reduces both plant species richness and beta diversity, whereas in dense stands, the negative impact on diversity is even more pronounced (Zehnder et al., 2020). Zehnder et al. (2020) advocate limiting the growth of *A. viridis* to maintain plant species diversity in the subalpine zone of the Swiss Alps. One possible approach to controlling the spread of *A. viridis* is introducing or increasing the number of livestock (van Vugt et al., 2022). Ruminants such as domesticated goats and sheep are suggested as the best candidates to reduce the cover of green alder thickets (Zehnder et al., 2020; Pauler et al., 2022). Today at our study site, haymaking, as well as grazing by goats and sheep, still limits the propagation of *A. viridis*. However, to prevent future biodiversity losses, management strategies are necessary, particularly, since climate change also puts alpine meadows at risk. A potential increase of up to 5.4 °C in annual temperatures, as projected for the end of the century (CH2018, 2018), could lead to an upward shift of treeline by 700 m (Theurillat and Guisan, 2001; Schwörer et al., 2014b), threatening the existence of alpine meadows. Several authors conclude that maintaining meadows is possible through low-intensity agropastoralism (Colombaroli et al., 2013; Schwörer et al., 2014a; Garcés-Pastor et al., 2022). On the other hand, our record also documents a reduction in subalpine forest diversity with increasing human land use. Particularly *A. alba,* which realized its potential niche in the Lai da Vons area between 8000 and 5000 cal. BP during the HTM, declined with increasing land use in the Late Holocene. As a disturbance-sensitive taxon, *A. alba* tends to disappear in areas with excessive pastoralism and high fire activity

(Tinner et al., 2013). Nevertheless, traditional agricultural practices in the Alps have the potential to limit the expansion of tree species into the alpine belt. Implementing low-intensity land use practices is suggested as a viable approach to conserving alpine meadows' biodiversity and promoting more diverse forests.

5. Conclusions

The sedimentary sequence of Lai da Vons represents a unique long-term record of high-elevation vegetation changes in the Rhaetian Alps. It documents more than 14,000 years of vegetation dynamics, particularly tree- and timberline changes, and the transition from natural ecosystems to managed landscapes on local to regional scales. This reanalysis of the sedimentary archive of Lai da Vons is based on a well-constrained chronology. Macrofossils are a powerful tool for local environmental reconstruction and agree well with pollen influx values. The vegetation at the study site and in the region is driven by climatic changes from the Late Glacial until ca. 6500 cal. BP. Particularly remarkable is the very fast upward shift of treeline in response to climate warming at the beginning of the Holocene. Our results show that individual trees can respond rapidly to rising temperatures by establishing in alpine meadows within decades. In light of ongoing and future climate change, we therefore expect an immediate upward shift of treeline in the absence of high grazing pressure by herbivores. Below the timberline, in subalpine and montane forests, our data suggests that competition and legacy effects result in a slower reorganization of forest ecosystems, with transitional stages characterized by non-analogue species composition. From ca. 6500 cal. BP onwards, vegetation is mostly controlled by the impact of humans on the landscape, mainly for pastoral use.

Today, farming practices within alpine regions face a critical threat due to the centralized and industrialized nature of food production in the lowlands, where machines can be used most efficiently, leading to the abandonment of remote areas (Gehrig-Fasel et al., 2007). To address this challenge, palaeoecological reconstructions can provide a robust foundation for developing ecosystem management strategies that can effectively maintain future ecosystem services. It is imperative to prioritize conservation, restoration and mitigation strategies that adopt long-term perspectives, as they redefine the conventional definition of a natural landscape. Additionally, such efforts should encompass a comprehensive understanding of species interactions and tolerances, as mitigating the effects of climate change on species diversity necessitates understanding both population dynamics and adaptation mechanisms (Hu et al., 2009). In this context, the integration of ancient DNA (aDNA) studies emerges as a novel tool for understanding the implications of climate change at the population level (Parducci and Petit, 2004; Parducci et al., 2017; Schwörer et al., 2022). Addressing the challenges of alpine plant populations requires a multiproxy approach that considers the complex interactions between climate change, land use patterns, and ecological dynamics. Incorporating conservation, restoration and mitigation strategies informed by palaeoecological studies will enhance our chance of combatting the dual challenges of the climate and biodiversity crises and aid in preserving diverse alpine landscapes for future generations.

Authors contributions

Conceptualization: Laura Dziomber, Christoph Schwörer. Data acquisition: All authors. Writing - original draft preparation: Laura Dziomber, Christoph Schwörer. Writing - review and editing: all authors; Funding acquisition: Christoph Schwörer.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Pollen and macrofossil records are available on the Neotoma database and in the supplementary material. Code for macrofossil resampling is available at https://github.com/SilberdistL/tilia_macros.git

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2023.105020.

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