

Holocene climate, fire and vegetation dynamics at the treeline in the Northwestern Swiss Alps

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Abstract Treelines are expected to rise to higher elevations with climate warming; the rate and extent however are still largely unknown. Here we present the first multi-proxy palaeoecological study from the treeline in the Northwestern Swiss Alps that covers the entire Holocene. We reconstructed climate, fire and vegetation dynamics at Iffigsee, an alpine lake at 2,065 m a.s.l., by using seismic sedimentary surveys, loss on ignition, visible spectrum reflectance spectroscopy, pollen, spore, macrofossil and charcoal analyses. Afforestation with *Larix decidua* and tree *Betula* (probably *B. pendula*) started at ~9,800 cal. B.P., more than 1,000 years later than at similar elevations in the Central and Southern Alps, indicating cooler temperatures and/or a high seasonality. Highest biomass production and forest position of ~2,100–2,300 m a.s.l. are inferred during the Holocene Thermal Maximum from 7,000 to 5,000 cal. B.P. With the onset of pastoralism and transhumance at 6,800–6,500 cal. B.P., human impact became an important factor in the vegetation dynamics at Iffigsee. This early evidence of pastoralism is documented by the presence of grazing indicators (pollen, spores), as well as a wealth of

archaeological finds at the nearby mountain pass of Schnidejoch. Human and fire impact during the Neolithic and Bronze Ages led to the establishment of pastures and facilitated the expansion of *Picea abies* and *Alnus viridis*. We expect that in mountain areas with land abandonment, the treeline will react quickly to future climate warming by shifting to higher elevations, causing drastic changes in species distribution and composition as well as severe biodiversity losses.

Keywords Palaeoecology · Treeline · Human impact · Vegetation history · Alps · Afforestation

Introduction

The treeline ecotone is the most conspicuous ecosystem boundary in mountain landscapes. It separates two ecosystems with different species pools, microclimates and ecosystem services: open alpine meadows and closed mountain forests (e.g. Körner 2003, 2012; Holtmeier 2009). The

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treeline ecotone is generally defined as the transition between closed forests (timberline or forest limit) and open alpine meadows (tree species limit). The treeline itself is the limit of single trees higher than 2 m (Arno and Hammerly 1984; Körner 2003; Tinner and Theurillat 2003). Palaeobotanical approaches such as pollen or macrofossil analyses are best suited to reconstruct timberline oscillations, while treeline oscillations are difficult to capture due to the weak signal released by single trees (Tinner 2007). The altitudinal difference between the two limits is ca. 100–200 m under natural conditions (Arno and Hammerly 1984). With the term “treeline vegetation” we refer to the ecotone between closed forests and the uppermost single trees.

Mountain ecosystems are thought to react very sensitively to environmental change and should be among the first to detect the impact of climate change (IPCC 2007). The upper limit of tree growth on a regional scale (e.g. the Alps) is determined mainly by temperature (Tranquillini 1979; Körner 2003, 2012; Ellenberg and Leuschner 2010). In the European Alps this is a mean temperature of ~ 6.5 °C during the growing season or a mean July temperature of 8–10 °C (Lang 1994; Landolt 2003; Holtmeier 2009; Körner 2012). Since the alpine treeline is mainly temperature limited, projected global warming should lead to a shift in the position and composition of mountain vegetation. This process is already observable in alpine herb (Theurillat and Guisan 2001; Walther et al. 2005; Pauli et al. 2012; Gottfried et al. 2012) and tree (Gehrig-Fasel et al. 2007; Harsch et al. 2009; Leonelli et al. 2011) communities, although with substantial regional differences.

In mountain regions with a long history of human settlement like the European Alps, the treeline has been also affected by human land use for millennia (e.g. Schmidt et al. 2002; Wick et al. 2003; Gobet et al. 2003; Blarquez et al. 2009; Ellenberg and Leuschner 2010; Valsecchi et al. 2010). Palaeoecology provides an important tool for estimating future changes by analyzing the reaction of the treeline vegetation to climatic changes and human impact in the past (Tinner 2007; Gosling and Bunting 2008). As a consequence, there is a growing number of studies that have reconstructed past vegetation dynamics at the treeline in the European Alps (e.g. Wick and Tinner 1997; Wick et al. 2003; Gobet et al. 2003; Tinner and Kaltenrieder 2005; Nicolussi et al. 2005; Lotter et al. 2006; Blarquez et al. 2009; Berthel et al. 2012) and other important mountain ranges around the world (e.g. Whitlock 1993; Fall 1997; Horrocks and Ogden 2000; Seppä et al. 2002; Di Pasquale et al. 2008; Tinner et al. 2008a).

Alpine lakes are natural archives that can be used to reconstruct the local and regional vegetation by analyzing pollen, spores and plant macrofossils deposited in the sediment. Since pollen grains are easily transported by wind over large distances, macrofossils or stomata from needles are more suited to reconstruct the local presence of trees (Lang 1994; Tinner 2007; Birks and Bjune 2010).

However, to gain a better understanding about the drivers of vegetation changes in the catchment of the lake, it is important to consider several independent proxies (Birks and Birks 2006). Hence multi-proxy studies are at the moment the state-of-the-art for reconstructing fluctuations of treeline vegetation in the past.

In this study we present a new multi-proxy reconstruction of treeline vegetation dynamics from Iffigsee (2,065 m a.s.l.) in the Bernese Alps, Switzerland (Fig. 1). The lake is located at today's potential treeline and therefore ideally suited for reconstructing past fluctuations of treeline vegetation. We are particularly interested in the afforestation connected to the rapid warming at the beginning of the Holocene, because the temperature increase of 2–4 °C (Lotter et al. 2000; Heiri et al. 2003a; Heiri and Millet 2005) is in its magnitude and rapidity comparable to the predicted warming of 3–5 °C by the end of this century (IPCC 2007; CH2011 2011). This is to date the only multi-proxy treeline vegetation study in the Northern Swiss Alps, as the other comparable record from Sägistalsee (1,935 m a.s.l.) lacks this specific time period (Fig. 1; Wick et al. 2003). The second reason for choosing this study site is the long history of human presence in the area. Iffigsee lies on the way to an important mountain pass in prehistoric times (Schnidejoch, Fig. 1), documented by numerous archaeological finds spanning from the Neolithic to the Middle Ages. A Roman tavern on its western shore underscores the importance of the pass in ancient times (Grosjean et al. 2007; Hafner 2008, 2009).

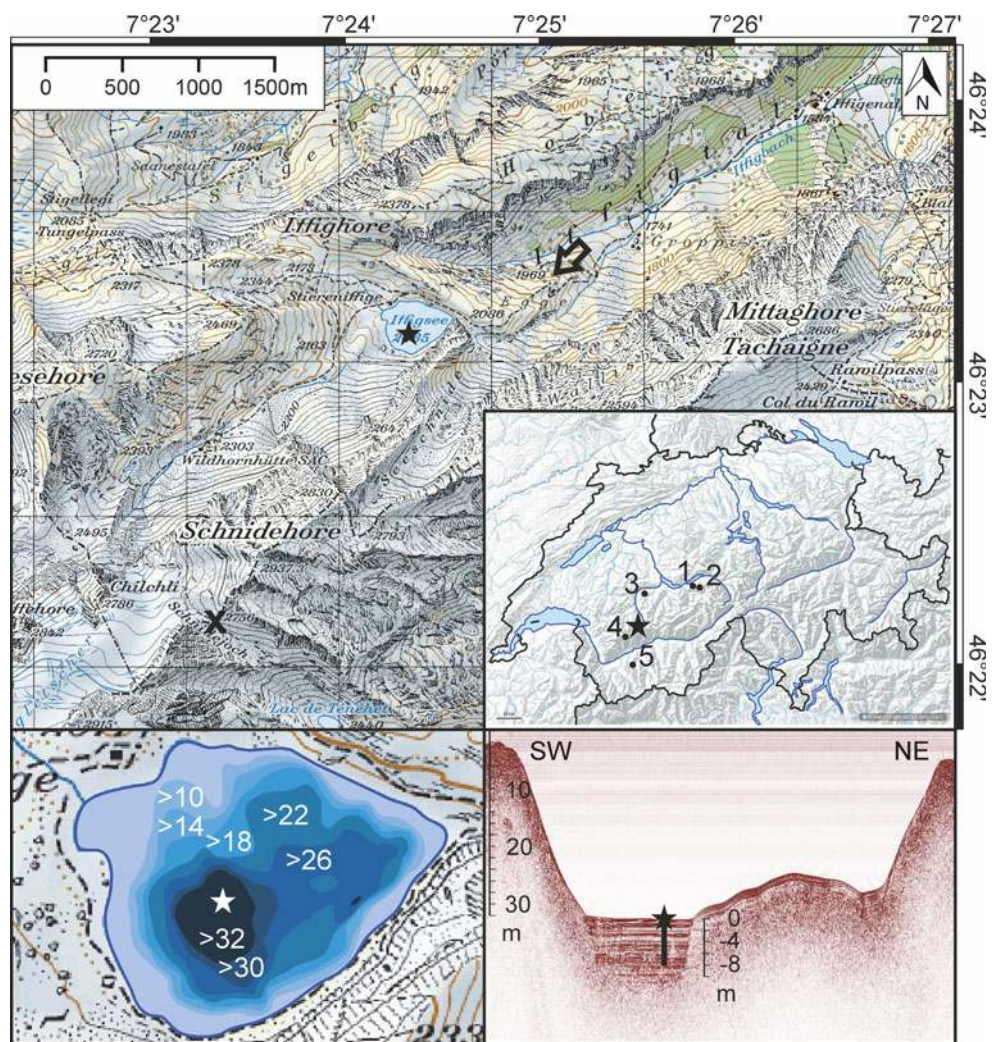
The aims of this study are (1) to determine the timing of afforestation at the beginning of the Holocene, (2) to reconstruct the vegetation history and natural species composition during the Holocene and (3) to assess the impact of human land use on the vegetation at the treeline.

Study site

Iffigsee is a mesotrophic, alpine lake in the Bernese Alps (Switzerland; 46°23'N, 7°24'E) at 2,065 m a.s.l. (Fig. 1). The lake has a maximum water depth of 33 m, a surface area of 10 ha and drains a catchment area of 461 ha (Guthruf et al. 1999). It is geologically located within the Helvetic nappes (Wildhorn nappe). The lake has only a minor surface inflow on the northwestern shore and no surface outflow. Instead 90–95 % of the total water inflow originates from subaquatic springs and the lake is drained by several subaquatic outflows. During spring snowmelt, the water table can rise up to 6 m (Guthruf et al. 1999).

The present climate at Iffigsee is characterized by 1,800 mm annual rainfall and a mean annual temperature of 1.0 °C. The warmest month is July with a mean temperature of 8.9 °C, the coldest is January with a mean temperature of –6.0 °C (Interpolated between the meteorological stations Adelboden and Jungfrauoch, MeteoSchweiz 2005).

Fig. 1 Map of the study area with Iffigsee (2,065 m a.s.l.), showing the coring location (star 46°23' 12"N, 7°24'22"E), the mountain pass and archaeological site Schnidejoch (cross) at 2,756 m a.s.l. and the present location of the timberline (arrow) at 1,900 m a.s.l. Upper right inset shows a map of Switzerland with the study site (star) and other important palaeorecords: 1 Sägistalsee (1,935 m a.s.l.), 2 Bachalpsee (2,265 m a.s.l.), 3 Schwarzmoos (1,770 m a.s.l.), 4 Emines (2,288 m a.s.l.), 5 Gouillé Rion (2,343 m a.s.l.). Left inset shows a bathymetric map of Iffigsee with the coring location (star) and the lake depths in metres. Lower right inset shows a seismic profile of Iffigsee with the coring location (star), water depth (left scale), sediment depth (right scale) and the core depth.



The present vegetation around Iffigsee consists of alpine meadows that are used as pastures on the north and west shore and a steep rock cliff and scree slope on the south and southeast side of the lake (Fig. 1). The timberline in the area is located 150 m below the lake at ~1,900 m a.s.l. and is formed by *Larix decidua* (larch), *Pinus cembra* (stone pine) and *Picea abies* (spruce; Fig. 1). Single trees of *L. decidua* >2 m grow at the lake and nearby slopes, placing the treeline at ~2,100 m a.s.l., indicating that tree growth in the absence of pastoralism is possible at these high altitudes, despite the very open alpine vegetation. The lake is part of the nature reserve Gelten-Iffigen and is listed as a landscape of national importance in Switzerland.

Materials and methods

Seismic survey and sediment coring

In May 2010 a high-resolution (3.5 kHz) reflection seismic survey was performed providing information on the

seismic stratigraphy and lake-basin morphology. Based on these data, the coring location was located in the deepest part of the lake (Gilli et al. 2013; Fig. 1). Four parallel sediment cores (IFF A–IFF D) were retrieved in June 2010 with the help of an UWITEC piston corer. The composite sediment core has a length of 786 cm. In the laboratory the sediment cores were cut and then photographed in both the fresh and oxidized states of the sediment surface.

Chronology

The age-depth model used for the analyses is based on 15 radiocarbon dates from terrestrial plant macrofossils (Table 1) and Pb/Cs-dating for the top 20 cm of the sediment. The age-analysis of the terrestrial macrofossils was carried out by the Poznan University Radiocarbon laboratory and the Radiocarbon laboratory of the Institute of Ion Beam Physics at the ETH Zurich using accelerator-mass-spectrometry (AMS). The Pb/Cs-dating was performed at the Eawag in Dübendorf. The radiocarbon-dates were calibrated to years before present (cal. B.P.) with the

Table 1 Radiocarbon dates from the Iffigsee sediment record

Depth (cm)	Lab. code	Material	¹⁴ C-Age (yrs B.P.)	Calibrated age (yrs B.P., 2σ-range)
93–95	Poz-45473	<i>Dryas octopetala</i> L, <i>Larix decidua</i> N, periderm	310 ± 30	302–462
140–142	ETH-41795	<i>Picea abies</i> twig	755 ± 40	653–756
215–217	Poz-45472	<i>Dryas octopetala</i> L, <i>Larix decidua</i> N, coniferous BS	1,870 ± 35	1,719–1,880
249.3	Poz-39380	Root indet.	2,460 ± 30	2,363–2,704
298.2	ETH-42602	<i>Dryas octopetala</i> L, <i>Larix decidua</i> N, deciduous twig	3,545 ± 40	3,705–3,959
311–313	Poz-45470	<i>Dryas octopetala</i> L, <i>Pinus cembra</i> N	3,965 ± 35	4,297–4,523
351–353	Poz-45474	<i>Dryas octopetala</i> L, <i>Larix decidua</i> N, coniferous BS	4,500 ± 40	4,982–5,304
367–369	Poz-45469	<i>Pinus cembra</i> A, <i>Dryas octopetala</i> L	4,845 ± 35	5,481–5,650
385.2	ETH-41796	Wood indet.	5,350 ± 50	5,997–6,275
424.2	Poz-39382	Coniferous periderm	6,225 ± 35	7,014–7,251
455–457	Poz-45468	<i>Dryas octopetala</i> L, deciduous twig	7,140 ± 50	7,850–8,040
487–489	ETH-42601	<i>Dryas octopetala</i> L, <i>Larix decidua</i> N+M	7,985 ± 40	8,659–8,999
527–529	ETH-42104	<i>Dryas octopetala</i> L, Caryophyllaceae S	8,725 ± 45	9,553–9,887
571.1	ETH-42600	<i>Dryas octopetala</i> L	9,035 ± 55	9,932–10,288
782–786	Poz-45467	<i>Dryas octopetala</i> L, dicot. L	9,810 ± 90	10,821–11,607

B.P. Before Present (A.D. 1950), cal. calibrated (clam, IntCal09 Reimer et al. 2009), L leaves, N needles, BS bud scales, A anthers, M mesoblasts, S seeds

program clam (Blaauw 2010) using the IntCal09 calibration curve (Reimer et al. 2009). The same program was also used to construct an age-depth model based on Monte-Carlo sampling with 1,000 iterations and linear interpolation between the weighted means of all iterations at a specific depth (Blaauw 2010; Fig. 2).

Pollen, macrofossil and charcoal analyses

For the analysis of pollen and microscopic charcoal one sample of 1 cm³ every 8 cm was analyzed with the exception of the sequences 8–88 and 680–776 cm, where we took one sample every 16 cm and the sequence 375–402 cm where the sampling was continuous (i.e. every cm). A total of 112 pollen samples were treated with KOH, HCl, HF and acetolysis, following standard preparation procedures (Moore et al. 1991). To estimate charcoal and pollen concentrations (grains cm⁻³) and calculate pollen influx (grains cm⁻² yr⁻¹), *Lycopodium* tablets were added to the samples prior to the chemical and physical treatments (Stockmarr 1971). The samples were mounted in glycerine and analyzed under a light microscope. Pollen grains, spores and other non-pollen palynomorphs (NPP) were identified using palynological keys and photo atlases (Moore et al. 1991; Reille 1999; Beug 2004; Cugny et al. 2010) as well as the reference collection of the University of Bern. The minimum number of pollen grains counted was 400 per sample, excluding the pollen of aquatic plants and spores. In total 143 different pollen types were identified. Plant stomata found in the pollen slides were identified with the key of Trautmann (1953). Microscopic

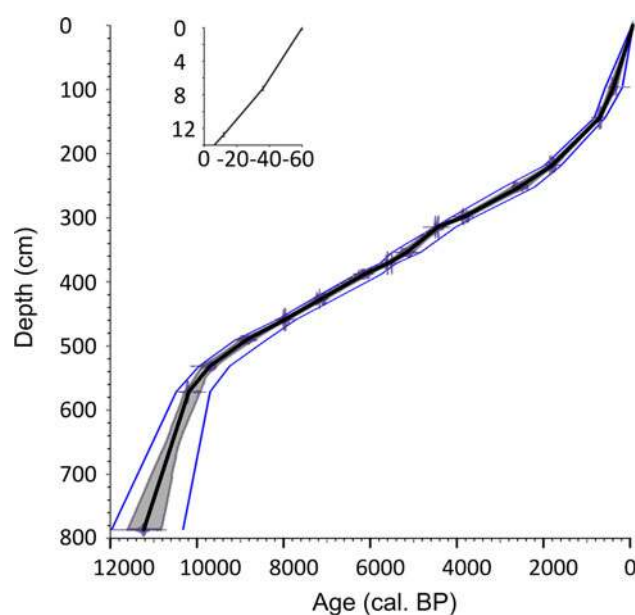


Fig. 2 Age-depth model of the sediment from Iffigsee based on Monte-Carlo sampling and linear interpolation (black line; Blaauw 2010). Blue curves show the probability distribution of the 15 radiocarbon dates, the grey area the 95 % confidence interval of the clam model and the dashed blue lines the 95 % confidence interval of the mixed effect model (GAM; Heegaard et al. 2005). Inset shows the topmost 14 cm based on Pb/Cs-Dating

charcoal >10 μm was counted on the pollen slides following Tinner and Hu (2003) and Finsinger and Tinner (2005) and concentrations (particles cm⁻³) and influx (particles cm⁻³ yr⁻¹) were estimated.

The pollen diagrams were subdivided into local pollen assemblage zones (LPAZ) with the program ZONE 1.2

written by Steve Juggins, following the zonation method of optimal sum of squares partitioning (Birks and Gordon 1985). The statistically significant zones were identified with the program BSTICK following the broken-stick method (Bennett 1996).

For the macrofossil analysis, samples of 2 cm thickness and a volume of 10–15 cm³ were taken at the same depths as for the pollen analysis (every 8 cm), with the exception of the sections 248–336 and 424–494 cm where the sampling resolution was 4 cm. The sections 200–248, 336–424, 494–572 and 770–784 cm, were sub-sampled continuously, yielding a sample every 2 cm. The samples were then sieved with a mesh size of 200 µm and identified under a binocular microscope using the reference collection of the University of Bern and macrofossil keys (e.g. Lévesque et al. 1988; Schoch 1988). The macrofossil concentrations are calculated for a standard volume of 12 cm³.

Pollen and plant macrofossils were used to reconstruct the regional to local vegetation history, while micro- and macroscopic charcoal (from pollen slides and macrofossil samples respectively) were used to reconstruct the regional to local fire history (Conedera et al. 2009). Further approaches such as background analysis for macroscopic charcoal, identification of fire events and fire intervals (e.g. Whitlock and Larsen 2002; Colombaroli et al. 2010) were not applied, given the non-continuous nature of our charcoal record.

VIS-RS and LOI analyses

The split cores were scanned with non-destructive reflectance-spectroscopy in the visible range (VIS-RS) using a GretagMacbeth Spectrolino with 2 mm sampling resolution (Rein and Sirocko 2002; Trachsel et al. 2010). The scanner measures the reflectance of visible light (380–730 nm) from the sediment in 10 nm spectral bands. We used the spectral index relative absorption band depth between 660 and 670 nm (RABD_{660;670}) which is a proxy for the I-band absorption of sedimentary chlorin (diagenetic products of chlorophyll-a) and thus lake productivity (Das et al. 2005; Wolfe et al. 2006; von Gunten et al. 2009, 2012; Saunders et al. 2013).

To determine the organic matter and carbonate content of the sediment, 83 samples from the same depths as the pollen record were treated by the Loss-On-Ignition method after Heiri et al. (2001).

Numerical methods

We analyzed the pollen percentage data with a detrended correspondence analysis (DCA), to identify gradients in the vegetation composition over time (Birks and Gordon 1985;

Ter Braak and Prentice 1988), using Canoco 4.5 (Ter Braak and Šmilauer 2002). Since the gradient length of the first axis of the DCA was 2.5 standard deviations and the sample plot of a principal component analysis (PCA) showed a strong horseshoe effect, we decided to use an unimodal response model, i.e. DCA (Ter Braak and Prentice 1988; Legendre and Birks 2012).

Results and interpretation

Lithology and chronology

The top of the sediment core consists of silty gyttja with distinct laminations (0–700 cm, 10,800 cal. B.P., Fig. 3). Silt to clay-sized detrital minerals form non-annual laminations, whereat single laminae represent individual rain-fall and/or snowmelt events in the catchment area (Fig. 3; Gilli et al. 2013). These clastic laminations are especially well pronounced in the topmost 120 cm of the sediment sequence. The lowermost sediments between 786 and 700 cm (11,200–10,800 cal. B.P.) are generally coarser grained (silt to sand) and characterized by a lower organic content of <4 % in respect to the overlying sediments where organic content reaches 4–10 %.

The age-depth model (Fig. 2) is characterized by a high sedimentation rate for the oldest part of the core (786–571 cm, 11,200–10,000 cal. B.P.), suggesting unstable soils with increased erosion. Between 10,000 and 1,800 cal. B.P. (571–216 cm) the sedimentation rate is fairly constant. In the uppermost part of the core, from ~1,800 cal. B.P. (216–0 cm) the sedimentation rate increases again to values as high as 0.2 cm yr⁻¹.

Vegetation and fire history

The pollen and macrofossil diagrams (Figs. 3 and 4) are subdivided into five statistically significant LPAZ, which are discussed separately.

The oldest pollen assemblage zone LPAZ IFFP-1 (11,240–10,350 cal. B.P.) is dominated by *Pinus cembra* and *sylvestris*-type pollen as well as herbs, mainly Poaceae (grasses) and *Artemisia* (wormwood). The high pollen proportion of *Pinus sylvestris* (scots pine) and *P. cembra* (stone pine) can be attributed to long distance transport of the pollen grains and little local pollen production by the sparse alpine vegetation. This phenomenon is well known in high-alpine lakes (e.g. Lang 1994; Lotter et al. 2006; Berthel et al. 2012) and can be identified by consulting stomata or plant macrofossils (Lang and Tobolski 1985; Tinner et al. 1996; Birks and Birks 2006). The number of macrofossils in this zone is very low (Fig. 4). The only identifiable plant remains are leaves of *Salix serpyllifolia*

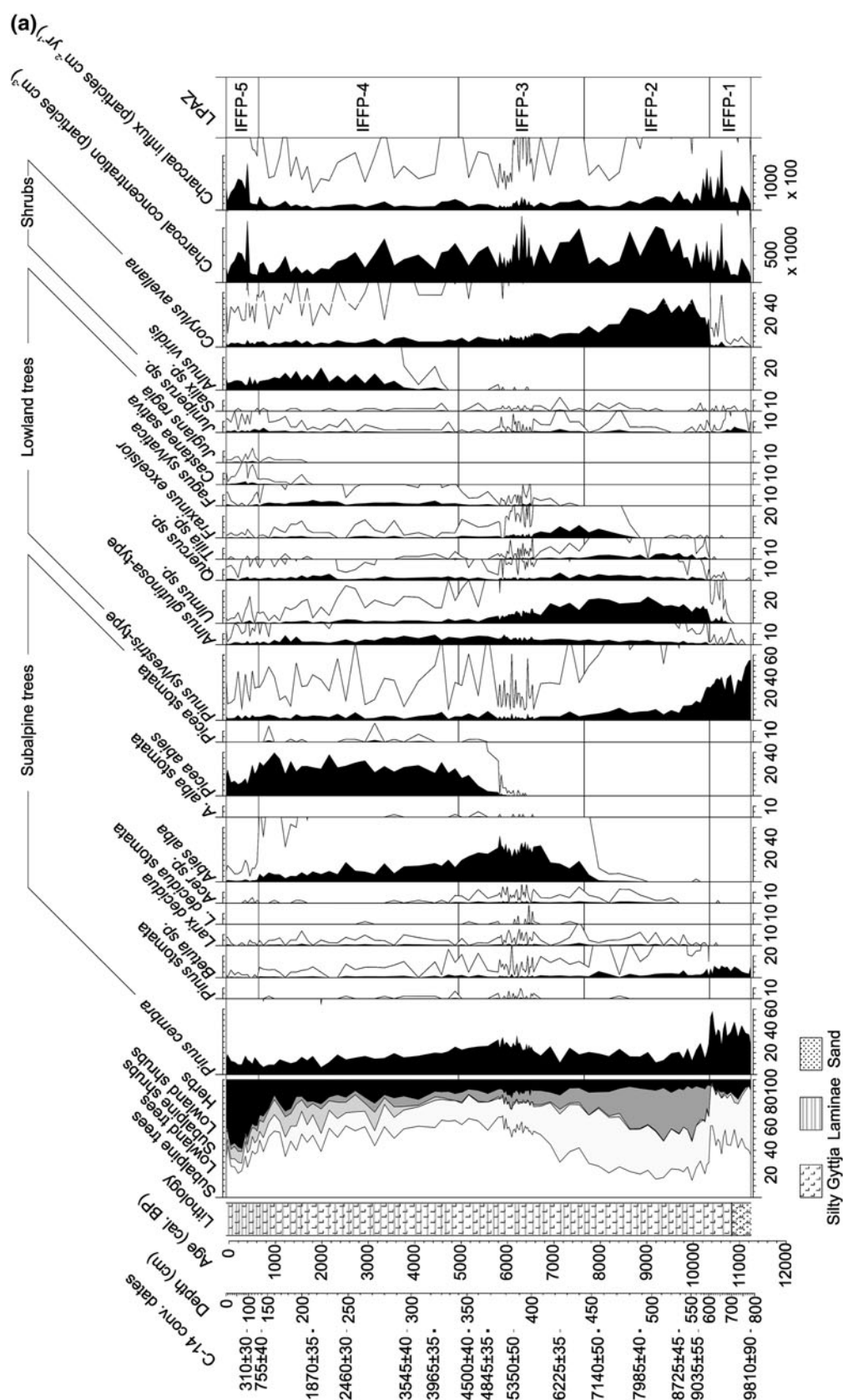


Fig. 3 Selected pollen, spore and stomata percentages of the Iffigsee record based on the terrestrial pollen sum as well as lithology, charcoal concentration and influx values. Empty curves show 10× exaggerations. LPAZ local pollen assemblage zones. Analysis: Christoph Schwörer

(thyme-leaved willow), and *Dryas octopetala* (mountain avens) as well as a seed of *Sedum* sp. (stonecrop). Together, the pollen and macrofossil records suggest that vegetation around Iffigsee consisted of sparse alpine tundra. Charcoal concentrations and influx values have a marked peak at the end of this zone at 10,600 cal. B.P., suggesting a high regional fire activity (Conedera et al. 2009). The first macroscopic charcoal particle appears towards the end of this zone at 10,450 cal. B.P., suggesting that local fires occurred around Iffigsee.

Temperate lowland trees and shrubs such as *Ulmus* sp. (elm), *Quercus* sp. (oak), *Tilia* sp. (linden) and *Corylus avellana* (hazel) expanded at lower elevations in LPAZ IFFP-2 (10,350–7,650 cal. B.P.), while the first trees became established in the catchment of Iffigsee. The diversity of the macrofossil assemblage strongly increases with seeds of different herbs and leaves of different *Salix* (willow) species, suggesting the establishment of more diverse local environments. The first arboreal remains, a fruit of *Betula* sp. (tree birch) and a needle of *Larix decidua* (larch) are found at 10,020 and 9,950 cal. B.P. respectively, indicating local growth of single trees around Iffigsee (Fig. 4). However, the interpretation of single *L. decidua* needles is difficult. Since larch sheds its needles every year they accumulate in high numbers in lake or mire sediment, if trees are locally present (Tinner and Theurillat 2003). Furthermore, both *L. decidua* needles and *Betula* sp. fruits are easily transported by wind and could have been blown into the lake from lower elevations (Tinner et al. 1996). On the other hand, since the sediment core comes from the centre of a deep lake and only 12 cm³ of sediment was analyzed, we expect low numbers of macrofossils and therefore interpret single findings as local presence (Heggen Presthus et al. 2012). The timberline reached the lake after ~9,800 cal. B.P., when *L. decidua* needles appear regularly in the sediment. Open timberline conditions lasted until ~9,200 cal. B.P., when an increase in *L. decidua* needles points to the establishment of forests dominated by larch and birch around the lake. Microscopic charcoal influx values are exceptionally high at the beginning of this zone, before dropping to lower but still high values. Charcoal concentrations, however, show a different pattern with lower values at the beginning of the zone and two distinct peaks at 9,140 and 8,630 cal. B.P. (Fig. 3). This disparity between influx and concentration values points to an overestimation of the influx due to an artefact in the age-depth model. Both influx and concentrations decrease towards the end of this zone after 8,500 cal. B.P. Macroscopic charcoal particles occur only in the first half of this zone from 9,950–9,150 cal. B.P., suggesting that the relevance of local fires decreased.

Pinus cembra expanded in the catchment of Iffigsee at ~7,200 cal. B.P. (LPAZ IFFP-3; 7,650–4,940 cal. B.P.), shifting its range upwards from lower elevations and

forming mixed stands with *L. decidua*. *Abies alba* (silver fir) expanded at the same time in the region and single trees even reached the catchment of Iffigsee around 6,500 cal. B.P., as indicated by stomata (Fig. 3), even though no needles were found in the macrofossil record (Fig. 4). *L. decidua* needles reach the highest numbers throughout the sediment record at 6,560 cal. B.P. After this peak, larch declined rapidly, probably due to competition with *P. cembra*. Notable is the synchronous appearance of *Urtica dioica* (stinging nettle), *Rumex acetosa*-type (common sorrel) and the fungal spore *Sporormiella* at ~6,500 cal. B.P. (Fig. 3). Around 5,600 cal. B.P. spruce (*Picea abies*) expanded at Iffigsee as indicated by stomata and needles and quickly became the dominant tree species at lower elevations. Microscopic charcoal concentration and influx rise to a distinctive peak at the beginning of this zone at 7,550 cal. B.P. with several more peaks of similar or slightly lower magnitude throughout this zone. The impacts of these fire events on the mountain vegetation are evident in the decline of subalpine tree species shortly afterwards. The presence of charcoal in the macrofossil record suggests that fires occurred in the catchment of Iffigsee.

Pollen data suggest that during LPAZ IFFP-4 (4,940–640 cal. B.P.), *Picea abies* became the dominant tree species in the region while *P. cembra* and *A. alba* continued to decline. The large fluctuations of the subalpine tree pollen sum are conspicuous (Fig. 3). *Alnus viridis* (green alder) expanded at 4,000 cal. B.P. and quickly became the dominant shrub species in the pollen record. The low number of tree macrofossils in the sediment record after ~4,800 cal. B.P. suggests treeline conditions with scattered trees of *L. decidua*, *P. cembra* and *Picea abies* in the catchment of Iffigsee (Fig. 4). At the end of this zone, the diversity and the number of macrofossils, especially shrubs and herbs, strongly increase while pollen percentages of subalpine trees dramatically decline, pointing to a collapse of high-altitudinal forests in the region. Several peaks in the microscopic charcoal concentration and influx values occur in this zone, though regional fire activity decreased slightly after ~4,000 cal. B.P., possibly due to lower fuel availability (deforestation). Macroscopic charcoal particles were only found at the end of this zone from 2,430–1,210 cal. B.P., suggesting moderate local fire activity.

Herbs, mainly Poaceae and Cichorioidae, dominate LPAZ IFFP-5 (640 cal. B.P.—present), pointing to the expansion of open meadows. The pollen values of subalpine trees drop drastically, most notably *Picea abies* and *A. alba*, suggesting widespread deforestation (Fig. 3). Macrofossils are generally very scarce in this zone. Notable are the synchronous peaks of micro- and macrospores of *Selaginella selaginoides* (spikemoss), a plant typical of open alpine or subalpine meadows (Lauber et al. 2012). About 300 years ago, the last trees disappeared from the

catchment of Iffigsee and the present alpine vegetation established. A recovery of subalpine trees is only evident in the two most recent pollen samples. Microscopic charcoal influx and concentration rise to a short but massive peak at 400 cal. B.P., suggesting a last regional pulse in fire activity. After a second peak at 200 cal. B.P., the microscopic charcoal influx and concentration values steadily decline. No macroscopic charcoal particles were found in this zone, suggesting that local fires were rare or irrelevant.

Numerical analyses

The results of the ordination analysis are shown in a sample- and species-scatterplot (Fig. 5a, b) as well as in the sample scores of the first and second DCA axis over time (Fig. 6c, d). In the sample plot, samples are nicely grouped following the five statistically significant pollen assemblage zones LPAZ IFFP-1 to 5. Axis 1 of the species scores shows a gradient connected to human impact, from Cerealia-types (cereals), *Plantago lanceolata* (ribwort plantain) and *Alnus viridis* to *Pinus sylvestris*, *Tilia* and *Pinus cembra*. DCA axis 2 probably follows a climatic gradient from thermophilous taxa such as *Corylus avellana*, *Ulmus* and *Quercus* to more cold-adapted *Juniperus* (juniper), *Betula* and *Artemisia*.

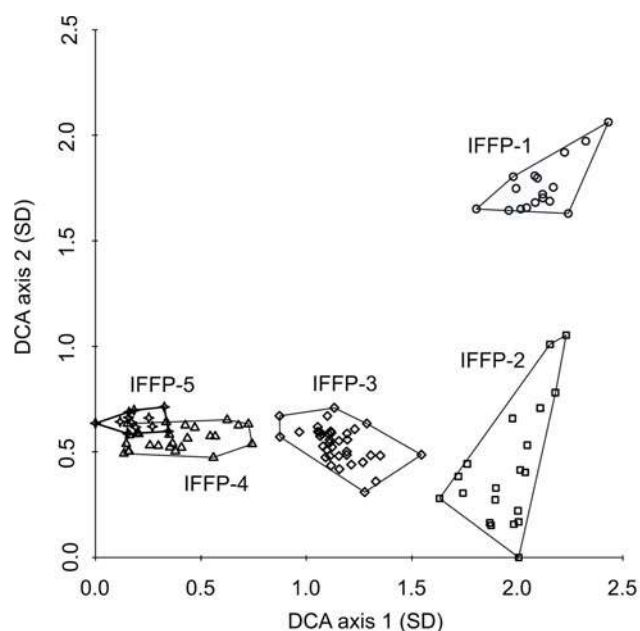
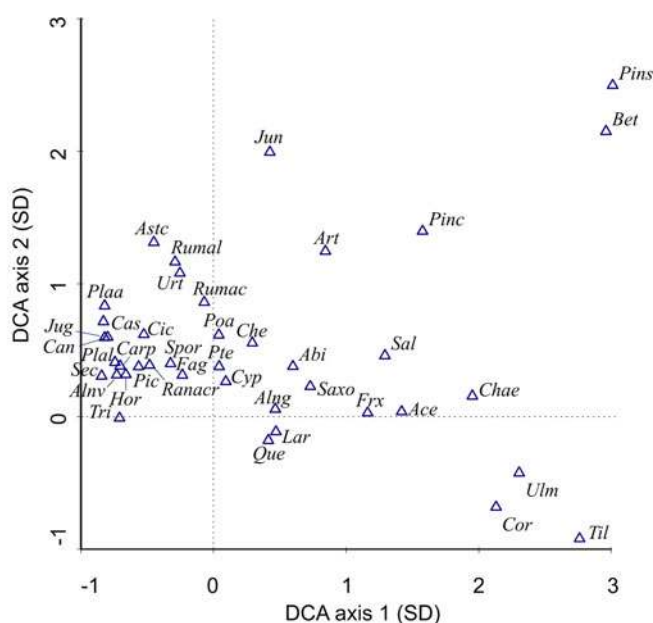


Fig. 5 DCA scatterplots of (left) sample and (right) species scores. The samples are grouped according to the local pollen assemblage zones (LPAZ). Abi: *Abies alba*, Ace: *Acer* sp., Alng: *Alnus glutinosa*-type, Alnv: *Alnus viridis*, Art: *Artemisia* sp., Astc: Asteraceae, Bet: *Betula* sp., Cas: *Castanea sativa*, Can: *Cannabis sativa*, Carp: *Carpinus betulus*, Chae: *Chaerophyllum*-type, Che: Chenopodiaceae, Cic: Cichorioideae, Cor: *Corylus avellana*, Cyp: Cyperaceae, Fag: *Fagus sylvatica*, Frx: *Fraxinus excelsior*, Hor: *Hordeum*-type Jug: *Juglans regia*, Jun: Juncaceae, Lar: *Larix decidua*, Pic: *Picea abies*, Pinc: *Pinus*

Abiotic parameters

The amount of organic matter in the sediment of Iffigsee is generally low, i.e. <10 %, as indicated by loss on ignition at 550 °C (LOI 550, Fig. 6e). The organic content is very low at the bottom of the core but quickly rises to around 5 % by ~10,300 cal. B.P., suggesting increasing lake productivity and/or soil stabilization. A second and third rise to values around 6 and 8 % is evident at ~8,000 and 4,000 cal. B.P. respectively, before the values drop again after ~2,000 cal. B.P., when forests were disrupted and erosion increased. The carbonate content of the sediment as indicated by LOI 950 (Fig. 6f) starts with high values of ~25 % at the beginning of the record, pointing to enhanced influx of lithogenic sediment from the catchment, but quickly drops to low values of around 10 % by ~10,300 cal. B.P. when soils stabilized. Towards the end of the core, the carbonate content increases again after ~2,000 cal. B.P., suggesting higher erosion either directly due to inwash of allocthonous carbonates or indirectly due to the dilution of organic matter by a higher sedimentation rate.

The proxy for lake productivity inferred from scanning visible reflectance spectroscopy VIS-RS, RABD_{660;670} (Fig. 6g) follows the main trend of LOI 550, with very low values in the early Holocene, higher values in the mid to late



cembra, Pins: *Pinus sylvestris*-type, Plaa: *Plantago alpina*, Plal: *Plantago lanceolata*, Poa: Poaceae, Pte: *Pteridium aquilinum*, Que: *Quercus* sp., Ranacr: *Ranunculus acris*-type, Rumac: *Rumex acetosa*-type, Rumal: *Rumex alpinus*-type, Sal: *Salix* sp., Saxo: *Saxifraga oppositifolia*-type, Sec: *Secale*-type, Spor: *Sporormiella* sp., Til: *Tilia* sp., Tri: *Trisetum*-type, Ulm: *Ulmus* sp., Urt: *Urtica dioica*. DCA axis 1 shows a gradient from pristine to anthropogenic samples and species scores, axis 2 a bipartition between cold, unforested (LPAZ IFFP-1) and warm, forested environments (LPAZ IFFP-2 to 5)

Fig. 6 Comparison of the main biotic and abiotic proxies of Iffigsee with different climate records. **a** Percentage of subalpine tree pollen based on the total (red) and subalpine (blue) pollen sum. By calculating the pollen percentages based on the subalpine pollen sum (blue curve), the influence of lowland taxa is excluded. **b** Stacked macrofossil record of subalpine tree macrofossils. Red: *Betula* sp., gold: *Larix decidua*, blue: *Pinus cembra*, green: *Picea abies*, grey: coniferous tree remains indet. **c** DCA axis 1 and **d** axis 2 of the Iffigsee pollen record. **e** Percentage of Loss-On-Ignition (LOI) at 550 °C as a proxy for organic content of the sediment. **f** Percentage of LOI at 950 °C as a proxy for carbonate content of the sediment. **g** Relative absorbance band depth centred on the wavelengths 660/670 nm from visible light reflectance spectroscopy as a proxy for primary production in the lake. The red line is the LOESS smoothed data. **h** July temperature reconstruction based on a chironomid transfer function from Hinterburgsee. The light blue line is the unsmoothed temperature reconstruction, the red line the LOESS smoothed data, the dashed horizontal line the current mean July T (Heiri et al. 2003a). **i** July and **j** January solar insolation (Laskar et al. 2004). **k** Glacier recessions in the Swiss Alps indicating warm time periods (Joerin et al. 2006). **l** Cold and wet phases identified from Central European pollen and macrofossil records (Haas et al. 1998)

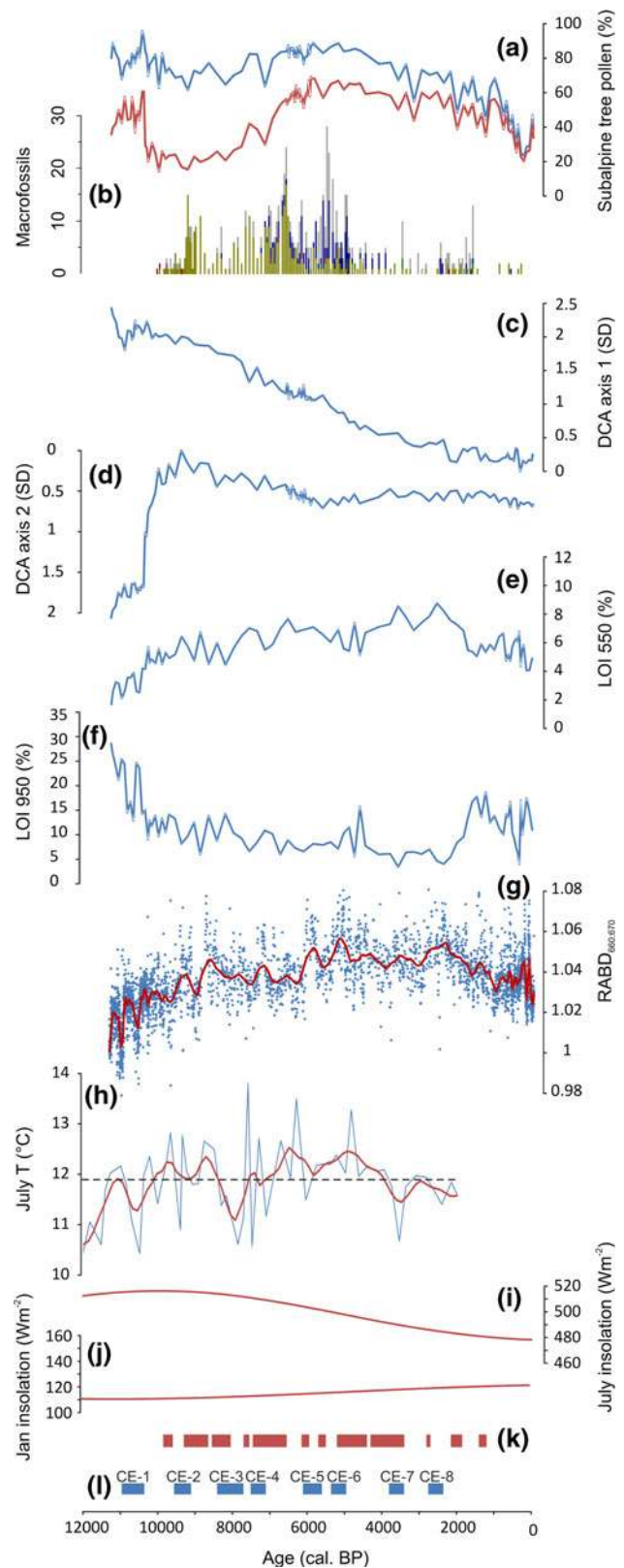
Holocene, and highest values between 5,000 and 2,000 cal. B.P., before dropping again at the end of the record. The two proxies for organic content or lake productivity LOI 550 and RABD_{660;670}, measured by two independent methods, have an R^2 value of 0.73 (data not shown). These data support our interpretation of maximum lake productivity and/or minimum erosion at ~8,000–2,000 cal. B.P. on the basis of LOI. Due to the increased sedimentation rate after ca. 2,000 cal. B.P., the estimation of lake productivity is no longer possible.

Discussion

Afforestation lag and high fire activity

Our data indicate that the Holocene afforestation at Iffigsee was delayed compared to other sites at lower elevations in the Northern Alps (Tobolski and Ammann 2000; Heiri et al. 2003b; Rey et al. 2013) or to similar study sites at the treeline in the Central and Southern Alps (Lang and Tobolski 1985; Tinner et al. 1996; Wick and Tinner 1997; Tinner and Kaltenrieder 2005; Gobet et al. 2005; Valsecchi and Tinner 2010). At Gouillé Rion (2,343 m a.s.l.), the first arboreal macrofossils were found only decades after the end of the Younger Dryas, suggesting rapid upslope movement of forest in response to Holocene climatic warming. Other high-elevation sites in the Northern Alps such as Bachalpsee (2,265 m a.s.l.) suggest that the Iffigsee afforestation lag of ~1,500 years was probably a regional treeline depression pattern and not just a local occurrence (Welten 1982; Wick et al. 2003; Lotter et al. 2006).

The expansion of the dominant tree species, such as *Abies alba* and *Picea abies* for instance, is in good agreement with the poorly resolved nearby site of Schwarzmoos (1,700 m a.s.l.; Wegmüller and Lotter



1990). Lags of ~500–1,000 years are evident if compared with Sägstalsee (1,935 m a.s.l.) and Bachalpsee (2,265 m a.s.l.), two sites further north (Fig. 1; Wick et al. 2003;

Lotter et al. 2006). In contrast to these studies, larch played an important role in the Holocene mountain vegetation in the Iffigsee area, possibly due to slightly more continental conditions.

The high charcoal-inferred natural fire activity at the beginning of the Holocene could have contributed to keeping the vegetation open around Iffigsee. However, this explanation seems unlikely since no pioneer species were advantaged by fire. The repeated occurrence of fire events throughout the Holocene differs from other records in the Northern Alps, where fire was recorded only after the onset of the Bronze Age, i.e. after $\sim 4,200$ cal. B.P., and was mainly of anthropogenic origin (Wick et al. 2003; Heiri et al. 2003b; Lotter et al. 2006). Instead, regional fire activity at Iffigsee decreased after $\sim 4,000$ cal. B.P. Thus, the fire history of Iffigsee resembles more that of sites in the Southern and Central Alps, where fires were common and occurred under natural conditions (Wick and Tinner 1997; Gobet et al. 2003; Tinner and Kaltenrieder 2005; Valsecchi and Tinner 2010; Blarquez and Carcaillet 2010). A reason for this could be the location of the study site at the southern edge of the Northern Alps.

The impact of climate on the vegetation at the treeline

During the Late Glacial, the site was still covered by glaciers. Only after the Younger Dryas cold period did the glaciers recede from the site and the lake begin to collect sediment. Temperature reconstructions from chironomids, cladocera and oxygen isotope series show a rapid warming after the Younger Dryas in the Northern Alps of $2\text{--}3$ °C, with summer temperatures during the early Holocene possibly even higher than today (Lotter et al. 2000; Heiri et al. 2003a; Heiri and Millet 2005; Larocque-Tobler et al. 2010). Highest temperatures were reached at $\sim 9,800$ cal. B.P. (Fig. 6h). This is exactly when the first larch stands appeared around Iffigsee, pointing to an expansion in response to warmer summer conditions (Fig. 6b). In the Central and Southern Alps, the treeline reached similar or even higher elevations shortly after the end of the Younger Dryas at 11,300 cal. B.P., rising ~ 800 m in altitude in ca. two centuries (Lang and Tobolski 1985; Wick and Tinner 1997; Gobet et al. 2005; Tinner and Kaltenrieder 2005; Blarquez et al. 2009; Valsecchi and Tinner 2010). Migrational lags of tree species can be ruled out as a reason for the late afforestation at Iffigsee, since several tree taxa such as *Betula*, *Pinus* and *L. decidua* were already growing at lower elevations within a distance of 30 km (Wegmüller and Lotter 1990; Welten 1982; Tobolski and Ammann 2000; Rey et al. 2013). The upper limit of forest growth during the Younger Dryas was between 925 and 1,230 m a.s.l. in the Northern Alps (Welten 1982; Tobolski and Ammann

2000), that is ~ 400 and 600 m lower than in the Central and Southern Alps, respectively (Tinner and Kaltenrieder 2005; Gobet et al. 2005; Vescovi et al. 2007). This gradient of the upper limit of forest growth during the Younger Dryas as well as the Late glacial, indicates lower temperatures in the Northern compared to the Central and Southern Alps, which has been confirmed by chironomid-inferred temperature reconstructions (Samartin et al. 2012). Furthermore, Samartin et al. (2012) show that the warming at the end of the Younger Dryas was of lower amplitude in the Northern Alps than in the Central and Southern Alps. Both factors, colder temperatures during the Younger Dryas and a smaller warming at the beginning of the Holocene, might sufficiently explain the delayed afforestation in the Northern Alps.

The treeline vegetation in the early Holocene consisted mainly of larch and birch trees. Similar forest types today occur in the Northern Ural and Eastern Siberia, both areas with a dry continental climate (Breckle et al. 2002; Burga et al. 2004). A high seasonality in the early Holocene due to higher summer and lower winter solar insolation compared to today (Laskar et al. 2004; Fig. 6i, j) probably resulted in comparable climatic conditions with very cold winters and short, warm summers. The shorter growing season due to orbital forcing may have caused or at least contributed to the afforestation lag in the Northern Alps as well. However, very continental conditions $\sim 11,600\text{--}10,000$ cal. B.P. are also reported from other areas of the Alps (e.g. Tinner and Kaltenrieder 2005).

The treeline quickly moved to higher elevations and closed forest became established around Iffigsee at $\sim 9,200$ cal. B.P. in response to the onset of the Holocene Thermal Maximum (HTM, Fig. 6h, k). Superimposed on this multi-millennial trend, pronounced centennial scale reversals such as the 8.2 ka event clearly had an impact on the mountain vegetation around Iffigsee as evidenced by the decline of *L. decidua* stands and the expansion of *Juniperus* shrublands at that time.

Vegetation composition of the mountain forest in the Iffigsee area changed only after a climatic shift towards more oceanic conditions with higher precipitation and milder winters around 7,500 cal. B.P. that has been documented by rising lake levels in the Jura Mountains and eastern France (Magny 2004; Magny et al. 2011). *P. cembra* was now finally able to grow in the catchment of Iffigsee and mesophilous *A. alba* expanded at lower elevations.

The highest timberline position (macrofossils) was reconstructed for the period between 7,000 and 5,000 cal. B.P., during the HTM. According to the chironomid-inferred temperature reconstructions, the HTM was ~ 1.5 °C warmer than today, which is in good agreement with Global Circulation Models (Fig. 6h, k; Heiri et al. 2003a;

Renssen et al. 2012). Since the nearby site of Emines at 2,288 m a.s.l. was never forested, we can constrain the location of the timberline to between 2,065 and 2,288 m a.s.l., most probably at \sim 2,250 m a.s.l. (Berthel et al. 2012). This highest timberline position in the study area is in good agreement with Wick et al. (2003) and Lotter et al. (2006) who, on the basis of incomplete Holocene records, suggested that the timberline in the Northwestern Alps reached 2,265 m a.s.l. between 6,000 and 3,000 cal. B.P.

The impact of human land use on the vegetation at treeline

Archaeological finds from Schnidejoch (2,765 m a.s.l.), the mountain pass located only 3 km from the study site (Fig. 1), prove that people were at least travelling through the area as early as 6,800 cal. B.P. (Grosjean et al. 2007; Hafner 2009, 2012). On the other side of the Schnidejoch Pass, in the Valais, people were living in settlements from at latest the Late Mesolithic (8,000 cal. B.P.) and were practicing agriculture from at least 7,500 cal. B.P. (Curdy 2007; Tinner et al. 2008b; Colombaroli et al. 2013).

The first continuous presence of the coprophilous fungus *Sporormiella* and plants associated with high nutrient conditions, such as *Urtica dioica* or *Rumex acetosa*-type at 6,500 cal. B.P., suggests that Neolithic people did not only cross the Schnidejoch Pass but were already modifying the vegetation by grazing livestock. This is to our knowledge some of the earliest evidence of pastoralism above the timberline and possibly transhumance in the Alps, and is supported by the archaeological finds at Schnidejoch, for example a bowl made of elm wood used to collect liquids such as water or milk (Fig. 7). A series of fire events between 6,400 and 6,100 cal. B.P. and a corresponding decline of subalpine trees (mainly *A. alba*) even suggest that Neolithic people used fire to clear the mountain forest at high elevations to expand the pastures. In other parts of the Alps, the earliest clearly distinguishable human impact in pollen records has been detected mostly during the Late Neolithic or early Bronze Age (\sim 4,500 cal. B.P. e.g. Tinner et al. 1996; Wick and Tinner 1997; Schmidt et al. 2002; Wick et al. 2003; Gobet et al. 2003; Blarquez et al. 2009; Röpke et al. 2011). In the forelands north and south of the Alps however, fire had already been used by humans to open the vegetation since the onset of the Neolithic at \sim 7,500 cal. B.P. (Tinner et al. 2005).

The mass expansion of *Picea abies* and *Alnus viridis* at \sim 5,300 and 4,500 cal. B.P. respectively can probably be attributed to human impact as well. Spruce survived the last ice age in refugia in the Southeastern Alps and spread rapidly in the Southern and Eastern Alps after the warming in the early Holocene (Lang 1994; Latałowa and van der Knaap 2006). Establishment in the Northwestern Alps occurred only between

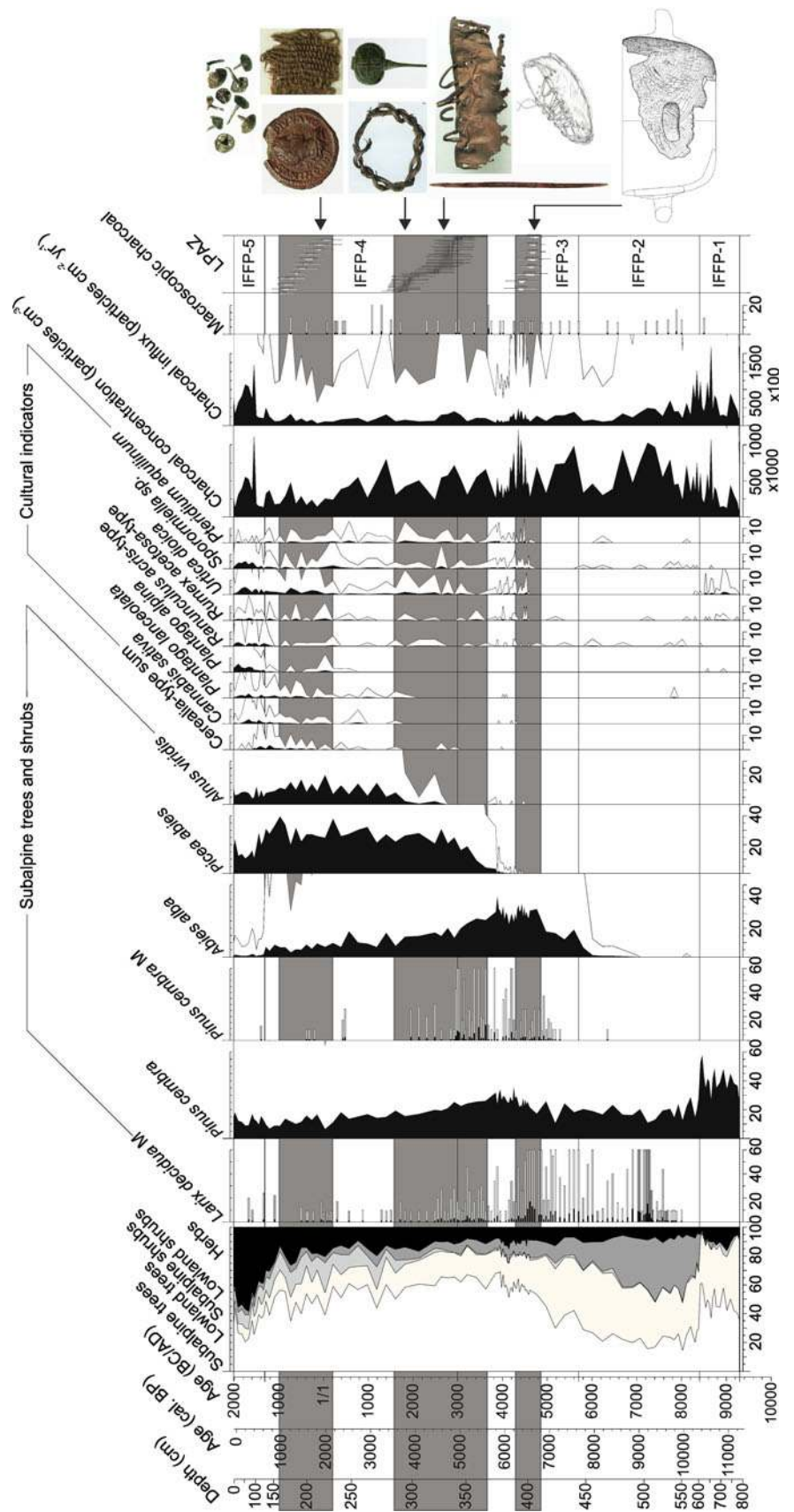
6,000 and 5,000 cal. B.P., even though summer temperatures were warmer in the early Holocene than today. Different reasons have been put forward to explain the late establishment of *Picea abies*, such as migrational lag (Lang 1994), limited moisture availability (Henne et al. 2011) and/or anthropogenic impact (Markgraf 1970; Rey et al. 2013). Our data indicate that the expansion of spruce occurred immediately after several distinct fire events that were most probably caused by humans (Fig. 7). Spruce was probably prevented from expanding into the Northwestern Alps because of limited moisture availability in the early Holocene and competition with already established forest trees such as *P. cembra*, *L. decidua*, *A. alba* and *Fagus sylvatica* (beech) after \sim 7,500 cal. B.P. Spruce expanded only with the opening of the mountain forest by humans when it could become established in the forest clearings and outcompete the other tree species. In contrast disturbance-tolerant *Alnus viridis* directly benefited from repeated fires and expanded in the Bronze Age throughout the alpine region (Welten 1982; Tinner et al. 1996; Gobet et al. 2003; David 2010; Rey et al. 2013). The low number of tree macrofossils during the Bronze Age (4,200–2,800 cal. B.P.) point to a lowering of the timberline, caused by humans in combination with a shift to cooler temperatures after the end of the HTM (Fig. 6b, l; Haas et al. 1998; Heiri et al. 2003a).

Our data suggest that during the first half of the Holocene, lake productivity (LOI 550 °C, VIS-RS RABD_{660;670} indicative of sedimentary chlorin) was mainly driven by temperature and/or reduced erosion in response to maximum forest cover. However the highest values of lake productivity are reached in the second half of the Holocene when temperatures were colder, possibly due to nutrient input from erosion or livestock grazing around the lake.

During the Bronze Age (ca. 3,100 cal. B.P.) the timberline was locally pushed below Iffigsee for the first time, following a big fire event (Fig. 7). The mountain forest could recover only partially, and open parkland typical of the treeline ecotone persisted. Intensification of forest clearings occurred during Roman Times (cal. A.D. 100) and the Migration period (cal. A.D. 500–800) and coincided with a cluster of archaeological finds from the same time at Schnidejoch (Fig. 7). During the Roman Empire, a building on the shore of Iffigsee provided shelter for travelers, highlighting the importance of the nearby mountain pass (Hafner 2008). This is reflected in our palaeorecord by the expansion of coprophilous fungi (*Sporormiella*) and a marked decrease in DCA axis 1 (Fig. 6c). The high sedimentation rate due to erosion and inwash of allochthonous carbonates (LOI 950 °C, Fig. 6f) caused by extended cattle grazing probably masks a clear nutrient signal in the lake productivity.

The mountain forest in the area could recover for a short period (cal. A.D. 900–1,150), but after cal. A.D. 1150 heavy erosion caused by the clearing of the remaining forest and probably by intensive grazing points to over-exploitation of

Fig. 7 Combined pollen, spore macrofossil and charcoal diagram from Iffigsee compared to the age of archaeological finds from Schnidejoch (grey shaded area). Among the material culture remains are a wooden bowl (ca. 6,800 cal. B.P.), a leather legging and shoe (ca. 4,800 cal. B.P.), a wooden bow (ca. 4,800 cal. B.P.), a bronze needle and braided wooden rings (ca. 3,800 cal. B.P.), and a Roman coin, shoe nails and tunic (ca. 1,900 cal. B.P.). Empty curves and bars are 10× exaggerations



the fragile alpine landscape by man. This is supported by the lowest values of DCA axis 1 in the record (Fig. 6c). In the late Middle Ages the historically documented shift from subsistence agriculture with livestock and crop production to cattle grazing for meat and dairy production (Aerni 1990) is well documented by the increase of coprophilous fungi and grazing indicators such as *Plantago alpina* or *Rumex acetosa* (Fig. 7).

Finally, the increase in forest area of the last fifty years can be attributed to the decreasing importance of pastoralism in the Swiss Mountains and the concentration of summer farming in the best areas (Gehrig-Fasel et al. 2007).

Conclusions

We provide the first multi-proxy study from treeline vegetation in the Northern Alps, which covers the entire Holocene. During the first half of the Holocene, treeline vegetation was primarily controlled by temperature and other climatic factors such as the moisture regime and seasonality. This study provides further evidence of a pronounced climatic gradient across the Alps in the early Holocene, with colder temperatures in the Northern as opposed to the Central and Southern Alps, resulting in a lagged afforestation of ~1500 years. Our study shows that under natural conditions, as in the early Holocene, mountain vegetation was in equilibrium with climate and reacted very quickly to millennial to decadal scale climatic changes, such as the Holocene Thermal Maximum or the 8.2 ka cold event. When humans started to use the alpine meadows as pastures, land use became the primary factor for local vegetation distribution and composition. Our study provides strong evidence of pastoralism above the timberline in the Alps during the Neolithic (ca. 6,800 cal. B.P.), more than a millennium before the Tyrolean Iceman (Müller et al. 2003). This supports the paradigm shift in Alpine Archaeology that the agricultural revolution in the Neolithic was not confined to the alpine forelands or the valley floors, but extended all the way to alpine meadows above the timberline (Bortenschlager 2000; Spindler 2005; Reitmaier 2012). The distance between our study site and the nearest known settlements in the Valais suggests that Neolithic herdsman were already practicing transhumance.

With the projected temperature rise of 1.2–4.8 °C (compared to the reference period 1980–2009) in Switzerland by the end of this century (CH2011 2011), mountain ecosystems will probably experience temperatures that exceed those of the warmest periods of the Holocene (Heiri et al. 2003a; Renssen et al. 2012). Our results imply that under low land use forests will respond rapidly by shifting to higher altitudes, even surpassing the highest positions of ~2,250 m a.s.l. reached during the Holocene. Traditional pastoralism above the current treeline, however, has the potential to impede or at least slow down the expansion of mountain forest to higher

altitudes. This is supported by grazing experiments, which show that low numbers of herbivores can efficiently prevent trees from establishing above the treeline (Speed et al. 2010, 2011). In places where pastures are abandoned, we expect treeline vegetation to rise several hundred metres by the end of this century, a process already observable in the Alps (Gehrig-Fasel et al. 2007). This will severely impact the biodiversity of the alpine landscape, since alpine plants will in turn be forced to migrate to higher altitudes. Upslope migration implies a reduction of possible habitats due to topographic and/or edaphic constraints (Theurillat and Guisan 2001). Regardless of migration capacity, extinctions of alpine plants may occur where mountain peaks or ranges will be low enough to support future forest growth.

With warmer mean temperatures during all seasons, less mean summer precipitation and declining land use, species composition of mountain forests in the Northwestern Alps will drastically change. Taking the HTM as closest analogue to moderate future warming and low human impact, we can anticipate that treeline forests dominated by larch (*Larix decidua*) and stone pine (*Pinus cembra*) and mixed subalpine forests with silver fir (*Abies alba*), will replace the nearly pure, anthropogenic stands of spruce (*Picea abies*) which are dominant today.

These conclusions emphasize the importance of palaeoecology for assessing the resilience and reaction of mountain vegetation to disturbances and climate change. Projected climate warming is likely to lead to dramatic changes in mountain ecosystems with severe loss in biodiversity, underscoring the paramount importance of greenhouse gas mitigation.

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