Early human impact (5000–3000 BC) affects mountain forest dynamics in the Alps

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Summary

1. The resilience, diversity and stability of mountain ecosystems are threatened by climatic as well as land-use changes, but the combined effects of these drivers are only poorly understood.

2. We combine two high-resolution sediment records from Iffigsee (2065 m a.s.l.) and Lauenensee (1382 m a.s.l.) at different elevations in the Northern Swiss Alps to provide a detailed history of vegetational changes during the period of first pastoralism (ca. 7000–5000 cal. BP, 5000–3000 BC) in order to understand ongoing and future changes in mountain ecosystems.

3. We use palaeoecological methods (fossil pollen, spore, microscopic charcoal and macrofossil analysis) as well as ecological ordination techniques and time-series analysis to quantify the impact of fire and grazing on natural mountain vegetation at Iffigsee.

4. Fire was used by Neolithic people to create pastures at timberline and clear forests for arable farming in the valley. This had a significant, long-term effect on the mountain vegetation and a negative impact on keystone forest species such as *Abies alba*, *Larix decidua* and *Pinus cembra*.

5. The mass expansion of *Picea abies* at ca. 5500 cal. BP (ca. 3500 BC) was facilitated by anthropogenic disturbance (fire, grazing and logging) causing an irreversible decline in *Abies alba*. Temperate *Abies alba* forests, which existed under warmer-than-today conditions, might be better adapted to projected climate change than today's drought-sensitive *Picea abies* forests, especially under low anthropogenic disturbance following land abandonment.

6. *Synthesis.* Human impact for millennia has shaped mountain vegetation in the Alps and still continues to have a large effect on today's species composition and distribution. Fire and traditional pastoralism have the potential to mitigate the effects of climate change, maintain species-rich high-alpine meadows and prevent biodiversity losses.

Key-words: biodiversity, climate change, conservation ecology, cross-correlations, fire, grazing, macrofossils, Neolithic, palaeoecology and land-use history, pollen

Introduction

Mountain ecosystems such as the European Alps are particularly vulnerable to global change due to steep climatic and ecological gradients (Theurillat & Guisan 2001; IPCC 2007; Körner 2012). Climate change is expected to lead to an upward shift of plant species, which can already be observed in some cases (e.g. Walther, Beißner & Burga 2005; Harsch *et al.* 2009; Pauli *et al.* 2012) and will inevitably lead to a substantial reduction of the species' ranges or even extinction due to topographic or edaphic constraints (Theurillat & Guisan 2001). Projected changes in temperature and precipitation might also lead to a range contraction of forest species with

great economic value in Europe such as *Picea abies* L. (Norway spruce) or *Pinus sylvestris* L. (Scots pine) at the expense of more drought-adapted but economically less valuable Mediterranean oaks, potentially causing economic losses of several hundred billion Euros for the European timber industry (Hanewinkel *et al.* 2013). Besides climate, human activities are undergoing rapid shifts as well. In the European Alps, for example, land use has been an important driver of vegetation dynamics and species distribution for millennia (e.g. Tinner, Ammann & Germann 1996; Tasser & Tappeiner 2002; Gobet *et al.* 2003; Blarquez *et al.* 2009; Valsecchi *et al.* 2010; Schwörer *et al.* 2014b). With the abandonment of agricultural land due to concentration of summer farming in favourable areas (MacDonald *et al.* 2000), the response of mountain vegetation to climate change might be accelerated (Theurillat &

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Guisan 2001; Gehrig-Fasel, Guisan & Zimmermann 2007). Traditional land use (grazing, small-scale agriculture) on the other hand has the potential to mitigate the effects of climate change on the alpine vegetation by preventing the establishment of trees (Colombaroli *et al.* 2010; Speed *et al.* 2010; Hoiss *et al.* 2013; Schwörer *et al.* 2014b). However, the combined effects of climatic and land-use changes are only poorly understood, due to the complexity of the system and the long time-scales involved (decades to centuries; Hoiss *et al.* 2013).

Palaeoecology provides a holistic approach of quantifying the long-term effects of climate and/or human land use on vegetation dynamics in the past and can therefore give important insights into possible future changes. The rapid upward shift of timberline in the Alps in response to the climate warming at the beginning of the Holocene, for example, indicates that mountain forests can react to the projected rise in temperatures within decades to centuries (e.g. Tinner & Kaltenrieder 2005). However, some past changes in species distributions are still a matter of controversy. The spread of *P. abies* in Central Europe, for example, has puzzled palaeoecologists for decades. The present distribution of *Picea abies* in Europe is divided in two distinct areas, a north-eastern boreal distribution and a south-central distribution in mountain regions of temperate Europe. Both palaeoecological data as well as genetic analyses indicate separate glacial refugia (Lang 1994; Vendramin *et al.* 2000; Giesecke & Bennett 2004). The expansion of *P. abies* in Scandinavia from a refugium in Russia is an example of the recolonization of a major tree species after the last ice age that has been discussed extensively (e.g. Giesecke & Bennett 2004; Bradshaw & Lindbladh 2005; Seppä *et al.* 2009). The south-central populations survived the last ice age in refugia close to the Alps: in the Apennines, the south-eastern Prealps, the Carpathians and probably in the Balkans (Lang 1994; Ravazzi 2002). With the climate warming at the onset of the Holocene, *P. abies* rapidly spread in the Eastern Alps but lagged the expansion into the Western Alps by ca. 3000–6000 years (van der Knaap *et al.* 2005; Latałowa & van der Knaap 2006). This delay in *P. abies* establishment has been interpreted as migrational lag (Lang 1994), limited moisture availability (Henne *et al.* 2011), climatic changes (Wick & Tinner 1997), competition with other tree species (mainly *Abies alba* Mill. (silver fir); Ravazzi 2002), anthropogenic disturbance (Markgraf 1970; Rey *et al.* 2013) or a combination of these factors. Given this plethora of partly contrasting hypotheses, a better understanding of the drivers of the past expansion of *P. abies* is needed in order to make projections about the future distribution of this paramount forest species.

In a recent study, we presented the first contiguous high-resolution pollen record from the Northern European Alps to assess the Holocene *P. abies* expansion dynamics in the montane vegetation belt at the site Lauenensee (1382 m a.s.l.; Rey *et al.* 2013; Fig. 1). Here, we expand this study in both time and space using a well-dated, contiguous, high-quality sediment record from the nearby site Iffigsee (2065 m a.s.l.; Fig. 1), located almost 700 m above Lauenensee, at the present treeline. This approach, with two similarly investigated
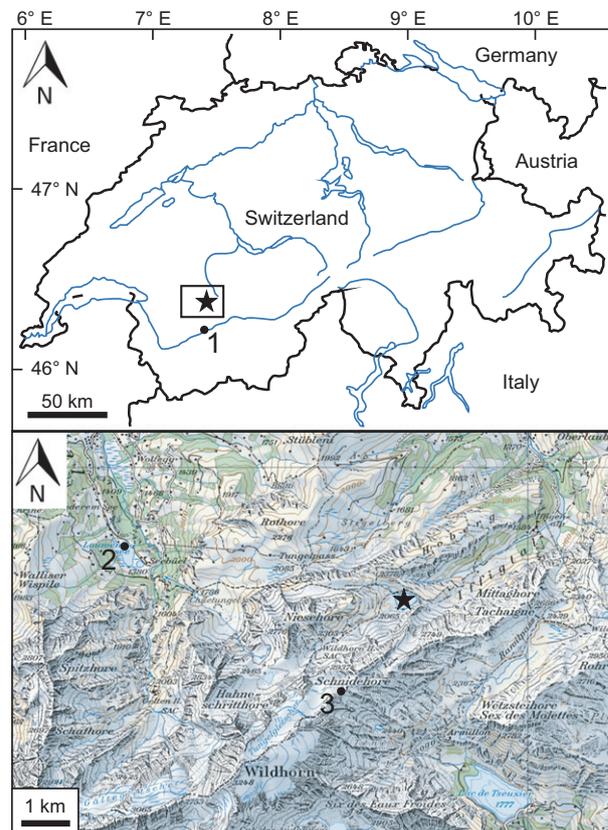

Fig. 1. Map of Switzerland (top) and the study area (bottom) showing the study site Iffigsee at 2065 m a.s.l. (star) and other important sites in the region: 1. Neolithic settlements at Sion (Curdy 2007), 2. Lauenensee (1382 m a.s.l.), 3. the archaeological site and mountain pass Schnidejoch (2765 m a.s.l.). Map reproduced by permission of Swisstopo.

neighbouring sites (ca. 6 km) at different elevations, allows us to investigate the spatial and temporal reproducibility of our high-resolution sequences. A signal that is recorded in both sites likely stems from extra-local to regional processes and therefore allows us to draw conclusions that go beyond a single case study. In addition, differences among the sites point to ecologically relevant dissimilarities between the two diverse vegetation types (montane vs. subalpine/alpine). Even though multisite approaches have been carried out at other regions in the Alps (e.g. Welten 1982; Heiri *et al.* 2003b; Wick *et al.* 2003; Lotter *et al.* 2006), this is to our knowledge the first time that vegetation dynamics on a regional scale are analysed quantitatively using contiguous high-resolution sediment records in the European Alps. This study therefore helps to address some of the most pressing questions in ecology, for example the response trajectories of plant communities under changing climatic and land-use conditions or the environments required to maintain biodiversity under global change.

Our aim is to investigate the impact of fire and grazing on mountain vegetation and biodiversity during the period of first pastoralism in the Alps (ca. 7000–5000 cal. BP, ca. 5000–3000 cal. BC). We are particularly interested in the effect on

important forest species such as *Picea abies*, *Abies alba*, *Pinus cembra* L. (Swiss stone pine) and *Larix decidua* Mill. (European larch). We use contiguous, high-resolution pollen, spore, macrofossil and charcoal analyses and apply direct and indirect gradient analysis (Ter Braak & Prentice 1988; Lepš & Šmilauer 2003; Legendre & Birks 2012) as well as time-series analyses (Tinner *et al.* 1999) to quantify long-term changes in the mountain vegetation in response to fire and grazing. This allows us to better assess the causes and consequences of the late expansion of *P. abies* in the Western Alps. Finally, we compare our results with available climate reconstructions and discuss the implications for global change and climate warming biology.

Materials and methods

STUDY SITE

Iffigsee (2065 m a.s.l.) is an alpine lake in the north-western Swiss Alps (46°23′N, 7°24′E; Fig. 1), with a maximum water depth of 33 m, a surface area of 10 ha and a catchment area of 461 ha (Guthruf, Zeh & Guthruf-Seiler 1999; Schwörer *et al.* 2014b). The present climate of the study area is characterized by high annual precipitation (mean 1800 mm year^{-1}) and cool annual temperatures (mean 1.0 °C). The mean temperatures of the warmest and coldest month are 8.9 (July) and −6.0 °C (January), respectively (climate data linearly interpolated to the elevation of Iffigsee from the two nearby meteorological stations Adelboden (1320 m a.s.l.) and Jungfraujoch (3580 m a.s.l.); MeteoSchweiz 2005). The present vegetation around Iffigsee consists of alpine meadows with isolated larch trees > 2 m at or slightly above the elevation of the lake, placing treeline at ca. 2100 m a.s.l. Timberline is located at ca. 1900 m a.s.l. in the study area and consists of *L. decidua*, *P. cembra* and *P. abies*. Iffigsee lies on the way to an important mountain pass (Schnidejoch, 2765 m a.s.l.; Fig. 1) that has been used as a travel route since prehistoric times (Grosjean *et al.* 2007; Hafner 2012).

CHRONOLOGY

Full methodological descriptions of the sediment coring as well as chronology, pollen, macrofossil and charcoal analyses of the entire Holocene sequence are provided in Schwörer *et al.* (2014b). The chronology

of the high-resolution sequence is based on the ages of 7 terrestrial plant macroremains (Table 1), which were AMS-radiocarbon-dated and calibrated with the program clam (Blaauw 2010), using the IntCal13 calibration curve (Reimer *et al.* 2013). Clam was also used to calculate an age-depth model (Fig. 2) based on Monte Carlo sampling with 10 000 iterations using a smoothing spline (with a smoothing level of 0.3). The sedimentation rate fluctuates between 22 and 37 years cm^{-1} with a mean depositional time of 28 years cm^{-1} (Fig. 2).

HOLOCENE VEGETATION HISTORY

The study site became deglaciated at the onset of the Holocene, after the Younger Dryas cold phase (ca. 11 650 cal. BP) and the lake basin started to collect fine-grain sediment at ca. 11 200 cal. BP. Sparse alpine meadows were replaced by larch forest at ca. 9800 cal. BP (Fig. S1 in Supporting Information). After ca. 7200 cal. BP, *P. cembra* formed a mixed forest with *L. decidua* at Iffigsee until *A. alba* and *P. abies* reached the area at ca. 6500 and 5500 cal. BP, respectively. Anthropogenic disturbance caused timberline to drop below the elevation of Iffigsee several times after ca. 4800 cal. BP. Present alpine meadows were established during the Middle Ages (ca. 1400 cal. AD; Fig. S1.). Today, the area around Iffigsee is used as a pasture for cattle during the summer months (July–September). A full account of the vegetation history of Iffigsee can be found in Schwörer *et al.* (2014b).

POLLEN, MACROFOSSIL AND CHARCOAL ANALYSES OF THE HIGH-RESOLUTION SEQUENCE

We analysed a total of 65 contiguous samples of 1 cm^3 between 416 and 352 cm (ca. 6960–5160 cal. BP) for pollen, spores and microscopic charcoal. The minimum number of pollen grains counted per sample was 400. In total, 98 different pollen types were identified. For the macrofossil and macroscopic charcoal analysis, 32 contiguous samples (with a sample thickness of 2 cm and a volume of ca. 12 cm^3) were sieved with a mesh size of 200 μm and identified under the stereo microscope.

We used microscopic charcoal influx (particles cm^{-2} year^{-1}) as a proxy for regional fire activity and regarded the occurrence of macroscopic charcoal particles as evidence of local fire activity (Whitlock & Larsen 2002; Conedera *et al.* 2009). We counted charcoal particles > 10 and < 500 μm on the pollen slides following Tinner & Hu (2003) and Finsinger & Tinner (2005) and calculated concentrations and influx values. To quantify the impact of grazing on the vegetation,

Table 1. Radiocarbon dates of the high-resolution Iffigsee sediment record (416–352 cm, 6960–5160 cal. BP)

Depth (cm)	Laboratory code	Material	^{14}C-Age (years BP)	Calibrated Age (years BP, 2σ-range)	Calibrated Age (years BP, weighted average)
351–353	Poz-45474	*Dryas octopetala* L, *Larix decidua* N, Coniferous BS	4500 ± 40	4985–5304	5158
367–369	Poz-45469	*Pinus cembra* A, *Dryas octopetala* L	4845 ± 35	5482–5650	5579
385.2	ETH-41796	Wood indet.	5350 ± 50	5998–6275	6081
391–393	BE-1819	*Larix decidua* M, *Salix* sp. B	5407 ± 22	6189–6279	6293
398.2	BE-1494	Wood indet.	5782 ± 23	6504–6650	6515
407–409	BE-1495	*Dryas octopetala* T	5944 ± 23	6680–6847	6781
424.2	Poz-39382	Coniferous periderm	6225 ± 35	7014–7251	7134

BP, Before Present (AD 1950), calibrated with clam (IntCal13; Reimer *et al.* 2013); L, leaves; N, needles; B, bud; BS, budscales; A, antheres; M, mesoblasts; T, twig.
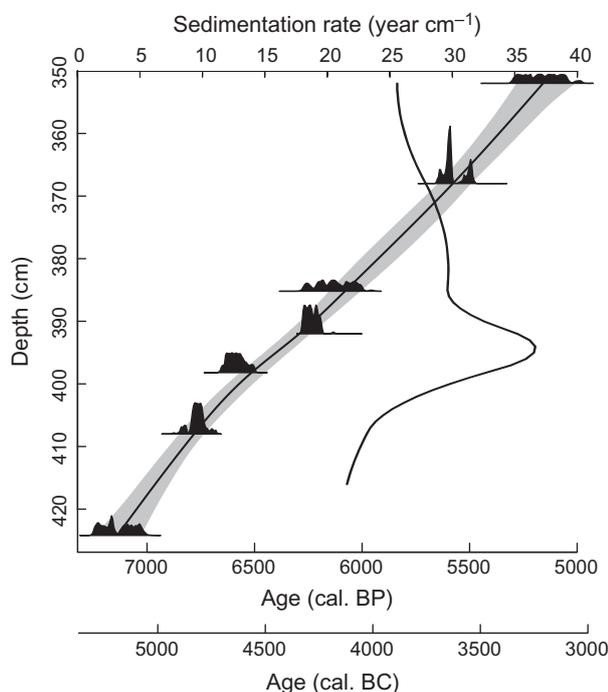
Fig. 2. Age-depth model and inferred sedimentation rate of the Iffigsee high-resolution sediment sequence (352–416 cm). The seven radiocarbon dates used to calculate the age-depth model are shown as probability distributions (small histograms). The 95% confidence interval of the age-depth model (grey area) was calculated with the program clam (Blaauw 2010) by fitting 10 000 smoothing splines to randomly selected dates from the radiocarbon probability distributions. The black line inside the grey area represents the best fit. The vertical solid black curve represents the inferred sedimentation rate.

we used spores of the coprophilous fungi *Sporormiella sp.* as a proxy for herbivore density (Cugny, Mazier & Galop 2010; Baker, Bhagwat & Willis 2013; Etienne *et al.* 2013). Even though the fungi also grow on the dung of wild herbivores, it is commonly used as a proxy for past pastoralism and anthropogenic impact in mountain environments (Cugny, Mazier & Galop 2010; Schwörer *et al.* 2014b).

BIODIVERSITY ESTIMATIONS

To estimate species richness of the surrounding vegetation at Iffigsee, we used a metric of palynological evenness, that is probability of inter-specific encounter (PIE), palynological richness (PRI) and evenness-detrended palynological richness (DE-PRI; Colombaroli & Tinner 2013). To identify changes in the species pool, we use breaking points in the log-transformed taxa accumulation curve (Giesecke, Ammann & Brande 2014). Palynological richness (i.e. number of pollen types per sample) has been used in many palaeoecological studies to infer past species richness (e.g. Birks & Line 1992; Odgaard 1999; Colombaroli *et al.* 2013) but is often biased by palynological evenness (Odgaard 2007). We first applied rarefaction analysis to estimate the number of pollen types in every sample, based on a constant sum of 400 pollen grains (=minimum pollen sum in all samples). We then estimated the probability of interspecific encounter (i.e. the probability that two pollen drawn randomly from the sample belong to the same species; Hurlbert 1971) and calculated the evenness-detrended palynological richness to account for a possible bias caused by a few dominant taxa in the pollen sample according to Colombaroli *et al.* (2013). This procedure removes the evenness trend from the palynological richness by using an ordinary

least square regression (OLS) between PRI (dependent) and palynological evenness (independent variable) and calculating residuals of pollen richness (PRI–palynological evenness). In our interpretation, only if both the palynological richness and the evenness-detrended palynological richness agree (i.e. show similar changes), we assume that our species richness estimates are unaffected by evenness effects. The complete procedure to calculate the evenness-detrended palynological richness is presented in Colombaroli & Tinner (2013). Changes in the accumulation of taxa in the record indicate changes in the species richness and evenness. To identify such breaking points, we divided the log-transformed taxa accumulation curve (i.e. the accumulation of number of pollen types as well as the pollen sum over consecutive samples) into linear segments using a threshold of $R^2 = 0.95$ after Giesecke, Ammann & Brande (2014). For all the analyses, we used the program R statistics (R Development Core Team 2011).

ORDINATION ANALYSIS

Principle component analysis (PCA; Ter Braak & Prentice 1988; Lepš & Šmilauer 2003; Legendre & Birks 2012) is a statistical procedure used here to identify gradients in vegetation composition over time. We first analysed the pollen percentage data of the high-resolution sequence with a detrended component analysis (DCA; Ter Braak & Prentice 1988; Lepš & Šmilauer 2003; Legendre & Birks 2012) using Canoco 4.5 (Ter Braak & Šmilauer 2002), to determine the appropriate response model (i.e. unimodal vs. linear). Since there is only little turnover in the species composition in the high-resolution sequence as identified by the gradient length of the first DCA axis (1.074 SD), we used linear response models, that is PCA and RDA.

TIME-SERIES ANALYSES (CROSS-CORRELATIONS)

To identify leads and lags in the relationship of fire and grazing with the vegetation, we used linearly detrended pollen percentage data, macrofossil concentrations and charcoal and *Sporormiella* influx values to calculate cross-correlations (Tinner *et al.* 1999) using the software MYSTAT 12 (Systat 2007). We compared charcoal and *Sporormiella* influx values with pollen percentages, since trends in the sedimentation rate or internal changes in the percentage data could lead to spurious correlations if the same units are compared with each other (i.e. influx vs. influx or percentages vs. percentages). We calculated cross-correlation coefficients for the pollen percentage data at ±10 lags, corresponding to ±290 years, with one lag corresponding to 29 ± 7.5 years. The significance of the correlations was tested by computing ±2 standard errors of the Pearson correlation coefficients, corresponding to a two-sided significance level (α) of 5% (Tinner *et al.* 1999). To minimize the effect of autocorrelation and 'false positives' due to multiple correlations, we calculated correlation coefficients only for ±10 lags. The total number of reasonably interpretable lags is generally considered to be a third of the sample size (Legendre & Legendre 2012).

Results

POLLEN, MACROFOSSIL AND CHARCOAL INFERRED VEGETATION AND FIRE DYNAMICS

The proxies we used to reconstruct the local to regional vegetation and fire dynamics have different spatial scales. Plant macrofossils may primarily represent local vegetation composition, due to low dispersal of ca. 1–100 m around the site

(Birks 2003; Tinner 2007). Macroscopic charcoal may come from several hundred metres around the site and represents local fire activity (Conedera *et al.* 2009). Pollen and microscopic charcoal can be dispersed by wind over large distances (up to 20–50 km) and may represent extra-local to regional vegetation and fire dynamics (Conedera *et al.* 2006, 2009). The source area of pollen deposited in a lake mostly depends on pollen dispersal, lake-size and vegetation openness (Bunting *et al.* 2004), with most of the pollen coming from ca. < 1 km in the case of smaller lakes, such as Iffigsee (Conedera *et al.* 2006), while microscopic charcoal may come from larger distances (20–50 km, Tinner *et al.* 1998).

The macrofossil analysis indicates that mixed larch – stone pine forests, which had established during the Early Holocene, dominated the vegetation at Iffigsee at the beginning of the high-resolution sequence (ca. 7000 cal. BP; Fig. 3). Just below the site (ca. 1000–2000 m a.s.l.), the forests were probably dominated by *A. alba* since ca. 7500 cal. BP. Mainly, as a consequence of warmer summer temperatures (Heiri *et al.* 2003a), *A. alba* expanded its range up to the elevation of Iffigsee at ca. 6600 cal. BP, as evidenced by few stomata in the sediment record (Fig. 4). Nevertheless, timberline forests were rather open and dominated by *L. decidua*, as documented by the highest numbers of larch needles in the macrofossil record. After ca. 6600 cal. BP, *L. decidua* declined (needles, pollen; Figs 3 and 4), while *P. cembra* expanded after ca. 6200 cal. BP (pollen, macrofossils; Figs 3 and 4). These stone pine – larch forests persisted until ca. 5600 cal. BP at Iffigsee. *Picea abies* established at the lake at ca. 5650 cal. BP (single needle found; Fig. 3). The expansion of *P. abies* coincided with a steady decline of *A. alba* in the pollen record, whereas other important tree species such as *P. cembra* or *L. decidua* were not affected (Fig. 4). Towards the end of the contiguous high-resolution analyses, *P. abies* dominated forests below ca. 2000 m a.s.l. together with *A. alba*, whereas at the elevation of Iffigsee, *P. cembra* and *L. decidua* were also present (Figs 3 and 4).

Microscopic charcoal concentrations and influx values indicate three periods with increased fire activity in the study region at ca. 7000–6700, 6500–6000 and 5600–5100 cal. BP. Low numbers of macroscopic charcoal particles in the macrofossil record suggest that at least some fires occurred sporadically in the catchment of the lake (Fig. 3).

BIODIVERSITY RECONSTRUCTION

Both palynological richness (PRI) and evenness-detrended palynological richness (DE-PRI) suggest an initial decrease of species diversity from 7000 to 6600 cal. BP, a marked peak at ca. 6400 cal. BP and an increasing trend after ca. 6300 cal. BP (Fig. 5g). The good agreement between PRI and DE-PRI indicates that the general trends in palynological richness are not affected by the evenness of the pollen assemblage. The palynological evenness as inferred by the probability of interspecific encounter (PIE) shows a decreasing trend between 7000 and 5900 cal. BP and a strong increase afterwards (Fig 5e). The lowest values of palynological evenness during ca. 6000–5800 cal. BP correspond to the highest percentages

of subalpine tree pollen (especially *A. alba*) in the record (Fig. 4), indicating that PIE is related to vegetation openness. The log-transformed taxa accumulation curve could be broken into two linear segments centred on ca. 6800 cal. BP suggesting a shift in diversity dynamics at this time (Fig. S2).

ORDINATION ANALYSIS

The first and second axis of the PCA explain 47.7% and 26.8% of the variance in the pollen data in the studied time period. The species and sample scatterplot (Fig. 6) as well as the sample scores of PCA axis 1 over time (Fig. 5h) reveal that the first axis relates to the establishment of *P. abies* after ca. 5600 cal. BP in the area. Interestingly, *P. abies* is strongly correlated with plant species indicative of disturbance or open conditions such as *Alnus viridis* (Chaix) DC. (green alder) and *Helianthemum* sp. (rockrose). The high amount of variance explained by PCA axis 1 (47.7%) clearly shows the drastic impact of the establishment of *P. abies* on mountain vegetation. PCA axis 2 probably represents a gradient in forest openness, showing a positive correlation with lowland species such as *Ulmus sp.* (elm), *Corylus avellana* L. (hazel) or *Tilia sp.* (linden) as well as herbs (Poaceae, *Chaerophyllum*-type) and a negative correlation with subalpine forest species such as *A. alba* and *P. cembra*. Indeed, sample scores of PCA axis 2 over time show the same pattern as the index of palynological evenness through time (Fig. 5f,h).

TIME-SERIES ANALYSIS

Cross-correlation analysis of microscopic charcoal influx vs. selected plant taxa can identify leads and lags in the relationship of key species with fire. Pollen percentages of *P. abies* have a significant positive correlation with microscopic charcoal influx from lag −1 to lag +10 (ca. 30 years before until ca. 290 years after the time of a fire; Fig. 7). *Abies alba* on the other hand shows a pronounced negative correlation with fire, which is significant at lags −3 to +4 as well as lag +6 (i.e. ca. 90 years before and up to 180 years after a fire). *Pinus cembra* also shows a significant negative correlation with microscopic charcoal influx, but only after the time of fire at the lags +3, +5 and +8 (ca. 90, 150 and 240 years after a fire). Pollen percentages of *L. decidua* are significant negatively correlated with microscopic charcoal at lag +1 (ca. 30 years after a fire). Pollen percentages of Poaceae are significantly positively correlated with microscopic charcoal at lag +1 and +3 (ca. 30 and 90 years after a fire). Spores of *Sporormiella*, a coprophilous fungi that is indicative of high numbers of herbivores (i.e. grazing), have a very strong, significant positive correlation with microscopic charcoal influx at lag 0 ($r = 0.35$; Figs 7 and 8). Correlograms of the correlation coefficients at lag 0 between microscopic charcoal influx and selected pollen types from Iffigsee and Lauenensee also show a significant positive correlation of cultural indicators and herbs at both sites (Fig. 8), whereas trees such as *A. alba* at Iffigsee and *Fagus sylvatica* at Lauenensee show a significant negative correlation.
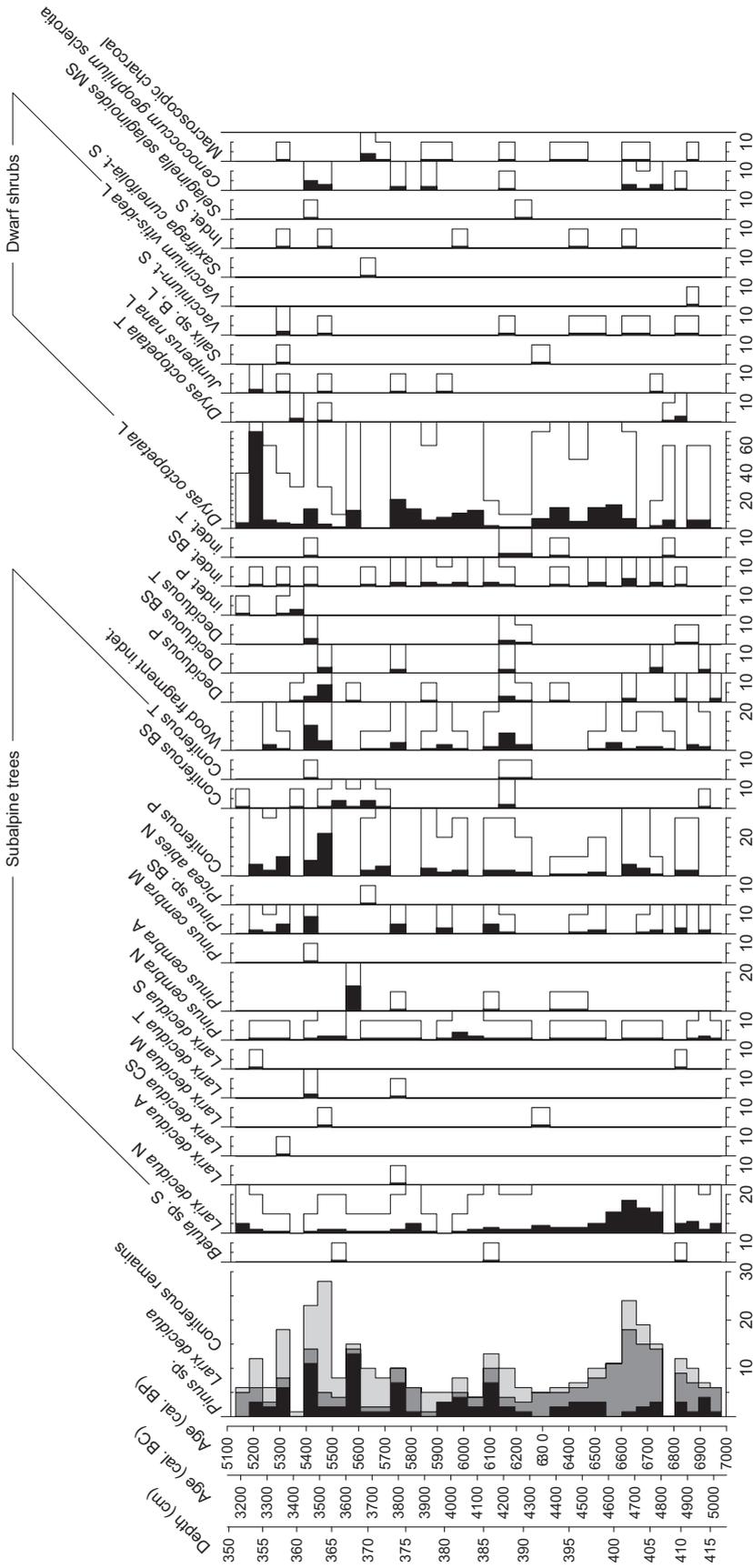
Fig. 3. Macrofossil diagram of the contiguous Iffigsee high-resolution sequence showing selected taxa only. S = seeds, N = needles, A = anthers, CS = conescales, M = mesoblasts, T = twigs, BS = budscales, P = periderm, L = leaves, B = buds, MS = macrospores. Empty bars show 10× exaggerations. Analysts: Petra Kaltenrieder and Stephanie Frei.
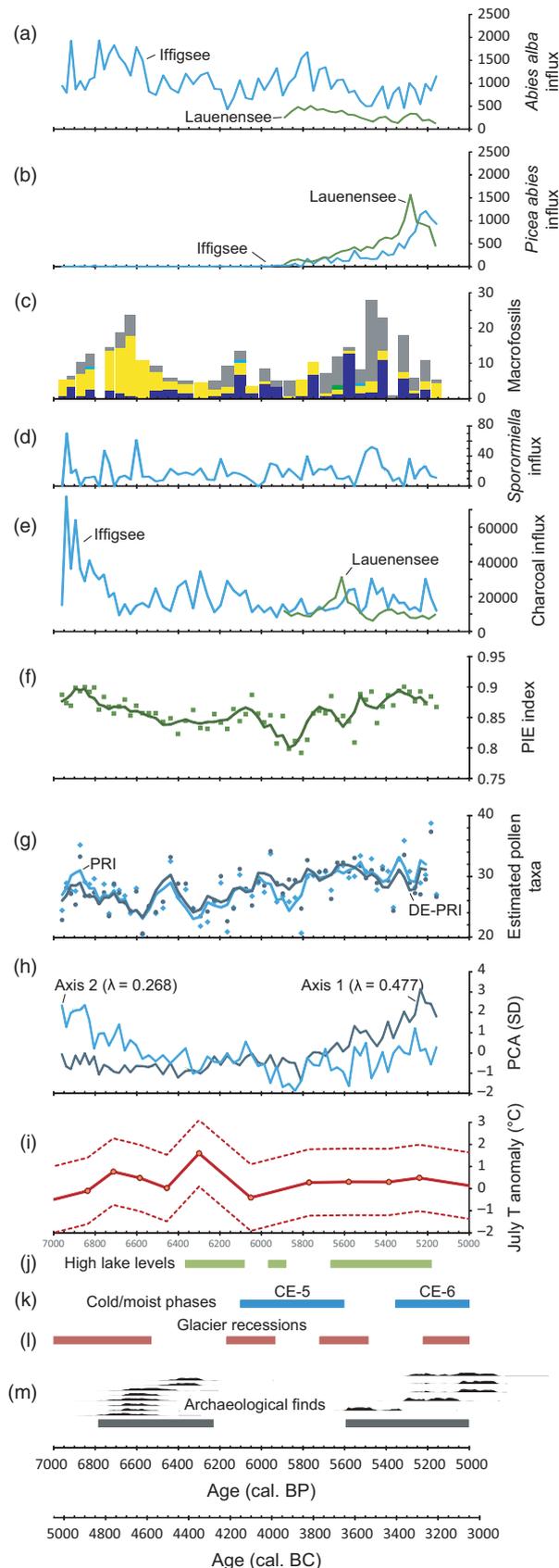
Fig. 4. Selected pollen, spore and stomata percentages as well as charcoal concentration and influx values of the contiguous Iffigsee high-resolution sequence. Empty curves show 10× exaggerations. Analyst: Christoph Schwörer.

Fig. 5. (a, b) Pollen influx values (# cm^{-2} year^{-1}) of Abies alba and Picea abies at Iffigsee and Lauenensee, respectively. (c) Stacked macrofossil record of subalpine tree remains at Iffigsee. Blue = Pinus cembra, yellow = Larix decidua, green = Picea abies, light blue = Betula sp., grey = indet. coniferous. (d) Sporormiella influx values at Iffigsee, (e) microscopic charcoal influx at Iffigsee and Lauenensee. Note that the influx curve of Lauenensee is exaggerated by 10× for comparison. (f) Palynological evenness (PIE) and (g) palynological richness (PRI, light blue) as well as evenness-detrended palynological richness (DE-PRI, dark blue) as proxies for biodiversity. The smoothed lines are a three samples running mean. (h) PCA axis 1 and 2. (i) July-temperature anomalies (solid line) from the chironomid-inferred Hinterburgsee temperature reconstruction including root mean square error of prediction (RMSEP; dotted lines) of 1.51 °C (Heiri et al. 2003a). (j) Periods of high lake levels in Central Europe after Magny (2004). (k) Cold and wet phases identified from Central European pollen and macrofossil records after Haas et al. (1998). (l) Glacier recessions in the Swiss Alps indicating warm time periods after Joerin, Stocker & Schlüchter (2006). (m) ^{14}C-Dates of archaeological finds from the Schnidejoch indicating human presence in the area (Hafner 2012).

Pollen percentages of *A. alba*, *P. cembra* and *L. decidua* show no significant correlation with influx values of the fungal spore *Sporormiella*, which we use as a proxy for pastoralism in the area (Fig. 7). However, *Urtica dioica* L. (stinging nettle), a plant species indicative of very high nitrogen conditions in the Alps usually caused by emiction, is positively correlated with *Sporormiella* influx at lag +2 (ca. 60 years after grazing), supporting the close link between *Sporormiella* occurrence and grazing activities. *Picea abies* pollen percentages are significantly positively correlated with *Sporormiella* at lags +8 to +10 (ca. 240–290 years after grazing), possibly pointing to long-term beneficial effects of grazing on spruce.

Discussion

FIRE VARIABILITY AS A DETERMINANT OF VEGETATION DYNAMICS BETWEEN 5000 AND 3000 BC

Fire activity had a significant and long-lasting impact on the vegetation around Iffigsee, as shown by both time-series and ordination analysis (Figs 6–8, Table S1). Fire affected both vegetation structure and composition by, for example, disfavouring fire-sensitive species (*P. cembra*, *A. alba*) as well as promoting open habitat and facilitating the expansion of *P. abies* (Figs 4, 6 and S3). The lack of an immediate response in most other species suggests that fires around Iffigsee were small and isolated (< 10 ha) and did not result in large contiguous areas of tree mortality. Today's moist climate with high precipitation values in the Northern Alps limits fire spread (Zumbrunnen *et al.* 2009). In Switzerland, for example, the mean fire size during the period 2001–2010 was 3.3. ha (Wastl *et al.* 2013). Even in the drier Central Alps, joint palaeoecological and simulation studies indicate that fires became rarely bigger than 10 ha throughout the Holocene (Colombaroli *et al.* 2010). Fires on small spatial scales may also explain the minor role of fire in the
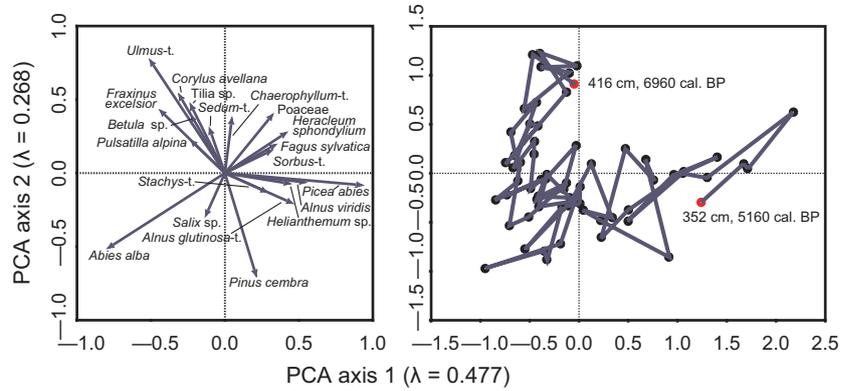
Fig. 6. PCA scatterplots of (left) species and (right) sample scores. The first axis explains 47.7% of the variance in the data set and the second axis 26.8%. Subalpine tree species are printed in bold.

vegetational change at Iffigsee as suggested by hRDA (Table S1, Fig. S3). While microscopic charcoal influx at Iffigsee explains only up to 8.1% of the variance in the vegetation data (at lag +2), charcoal influx explains up to 30% of the variance in more fire-prone Mediterranean ecosystems (at lag 0, Colombaroli *et al.* 2009), where fires occur on larger spatial scales (Wastl *et al.* 2013). A comparison of the fire histories of Iffigsee and nearby Lauenensee (1382 m a.s.l., ca. 700 m lower and 6 km away from Iffigsee) indicates that regional fires that affected both high- and low-altitude sites were indeed rather infrequent. Given the chronological uncertainties, a prominent peak in fire activity at Lauenensee at ca. 5600 cal. BP most probably corresponds to increased fire activity at ca. 5550 cal. BP in the Iffigsee record (Fig. 5e).

Even though most of the fires in our record occurred probably on small spatial scales (< 10 ha), we would expect initially high severity fires that resulted in a drastically reduced biomass of the burned area. However, fire severity and extent is difficult to infer from microscopic charcoal data alone. Pollen analysis (e.g. an increase in herbaceous pollen taxa) can be used as indirect evidence for high severity (i.e. crown) fires (Minckley & Shriver 2011).

DRIVERS OF FIRE VARIABILITY: CLIMATE OR HUMAN IMPACT?

In the Alpine region, climate (e.g. by controlling fuel moisture) and anthropogenic disturbance (i.e. slash-and-burn
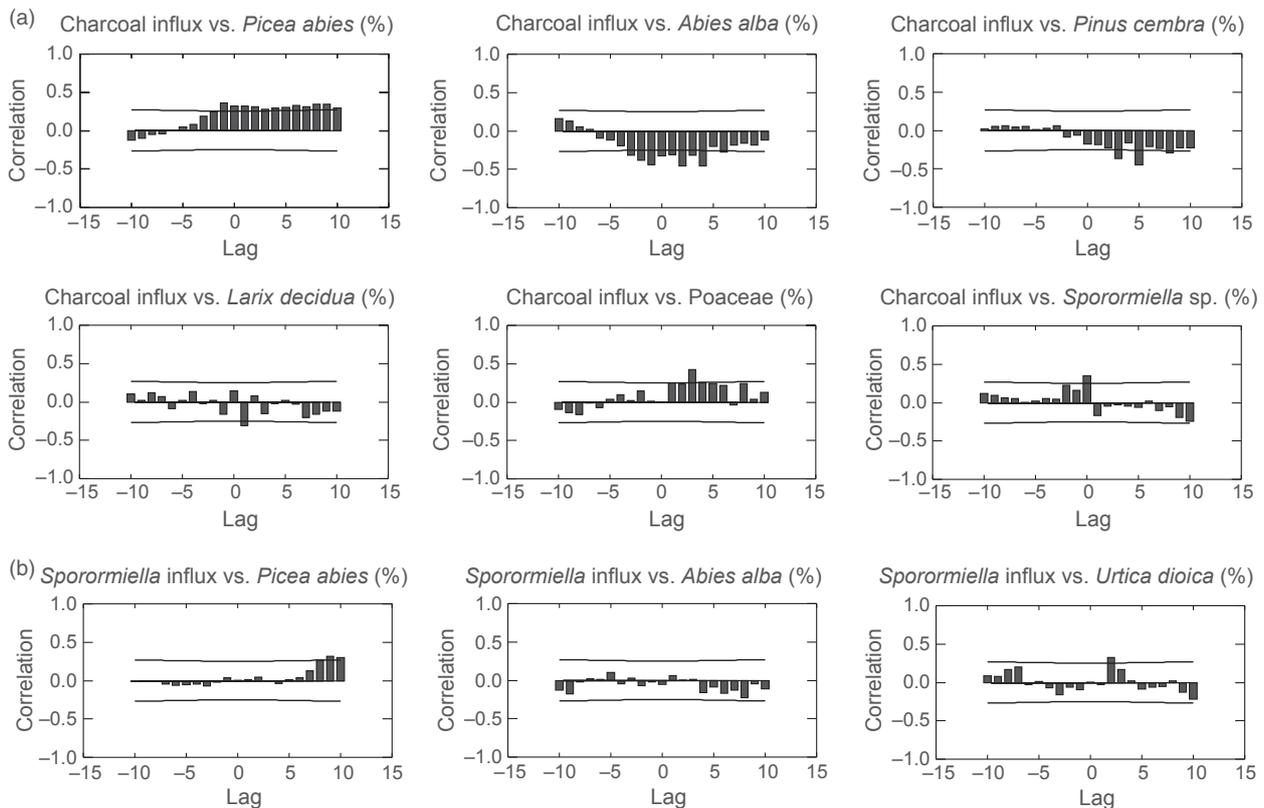

Fig. 7. Cross-correlation analysis of (a) microscopic charcoal influx and (b) *Sporormiella* influx vs. selected taxa from the high-resolution sequence (6960–5160 cal. BP). 1 lag = 29 ± 7.5 years. The solid black lines mark the significance level ($P < 0.05$). [Correction added on 12th February 2015, after first online publication: missing labels added to Figs 7 and 8]
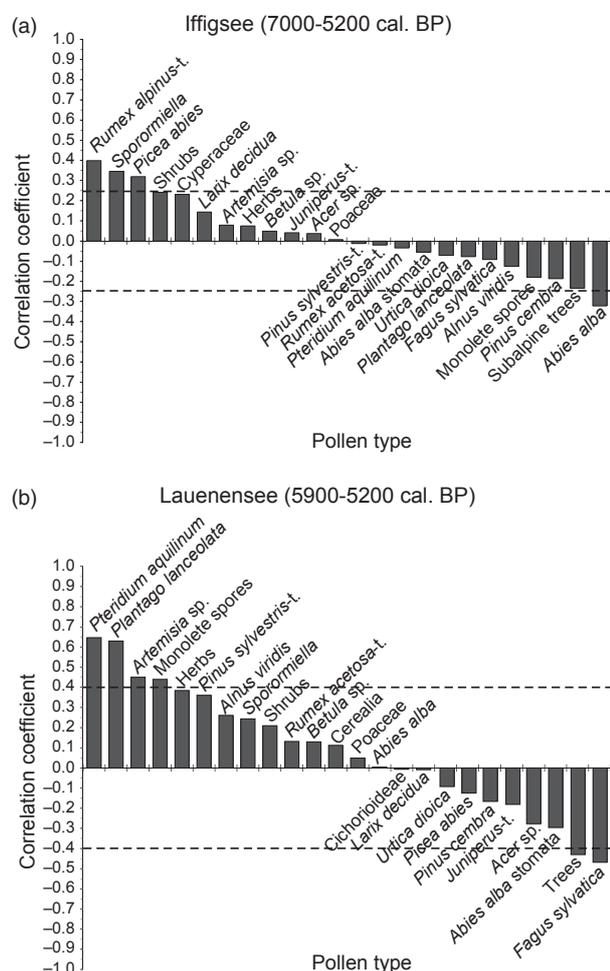
Fig. 8. Correlograms showing correlation coefficients between microscopic charcoal influx and selected pollen and spore types for (a) Iffigsee and (b) Lauenensee. The dashed lines mark the significance level ($P < 0.05$).

agriculture) are both important drivers of fire variability at centennial to millennial scales. For instance, warmer and drier conditions normally increase fire frequency due to reduced fuel moisture (Zumbrunnen *et al.* 2009). In the long term, a decoupling of fire and climatic control has been attributed to human impact, overriding the effect of natural ignition in alpine ecosystems (Colombaroli *et al.* 2010). In our record, phases of higher fire activity (ca. 7000–6700, 6500–6000 and 5600–5100 cal. BP) seem not to be related to warmer temperatures as recorded by chironomid-inferred July-T reconstructions (Fig. 5e,i). The strong significant positive correlation of the fungal dung spore *Sporormiella* and the grazing indicator *Rumex alpinus* with microscopic charcoal influx instead suggests that the fires around Iffigsee were of anthropogenic origin (Figs 7 and 8). Archaeological finds dating back to 6500–6800 cal. BP at Schnidejoch (2765 m a.s.l.), a nearby mountain pass connecting the Central with the Northern Alps (Fig. 1), prove that Neolithic people were at least passing through the area (Hafner 2012). High numbers of dung spores (*Sporormiella*) and pollen types indicative of

high nutrient conditions such as *Urtica dioica* and *Rumex acetosa*-t. (sorrel) from the Iffigsee record provide evidence for grazing activities since ca. 7000 cal. BP (5000 cal. BC, Fig. 4). The presence of permanent settlements on the other side of the Schnidejoch pass (in the Valais, Fig. 1; Curdy 2007; Colombaroli *et al.* 2013) suggests that people already practiced transhumance (i.e. movement of livestock to higher elevations in summer) since the Neolithic (Schwörer *et al.* 2014b). Our new high-resolution record shows that the Neolithic herdsmen probably burned the forests at timberline to expand the pastures for grazing already as early as 7000 cal. BP.

Long periods of low fire activity at Iffigsee can be linked to lower anthropogenic disturbance. Indeed, the period of ca. 6000–5600 cal. BP is synchronous with a prominent gap in the age of the artefacts at Schnidejoch (ca. 6250–5600 cal. BP, Fig. 5m) and a period with colder/moister climate (CE-5, Fig. 5k, Haas *et al.* 1998) leading to a recovery of subalpine tree species at Iffigsee (Figs 3 and 4). Separations between age cohorts of archaeological finds at Schnidejoch have been linked to glacial advances due to climatic cooling, effectively blocking the pass for travel (Grosjean *et al.* 2007). Towards the end of the cold phase, alpine glaciers receded (ca. 5700 cal. BP; Fig. 5l, Joerin, Stocker & Schlüchter 2006), people could cross the mountain pass again, and fire activity increased. Taken together, the qualitative comparison of fire history with palaeoclimatic reconstructions and archaeological evidence strongly suggests a humanization of the fire regime already 7000 years ago (5000 cal. BC). However, fire occurrence was never completely decoupled from climatic conditions.

The use of fire by Neolithic people is also evident in Lauenensee (1382 m a.s.l.), at lower elevation. The first unambiguous signs of agricultural activities (pollen of cereals and *Plantago lanceolata* L.) have been found after ca. 5800 cal. BP (Rey *et al.* 2013). Cross-correlation analysis in the time period 5900–5200 cal. BP revealed that fire was significantly positively correlated with cereals and *Plantago lanceolata* (ribwort plantain), whereas *Sporormiella* showed no significant correlation (Fig. 8; Rey *et al.* 2013), suggesting that at lower elevations, fire was used to clear forests for the cultivation of crops. In combination with our data from Iffigsee, we interpret this as unambiguous evidence for transhumance, with a clear compartmentalization of agricultural activities with arable farming at lower elevation and pastoralism at the alpine meadows since at least 6000 years. To our knowledge, this is the oldest high-resolution and high-precision evidence for mid-Neolithic transhumance in the Alps. The onset of pastoralism and the anthropogenic use of fire in alpine areas have commonly been attributed to the Late Neolithic/Early Bronze Age (ca. 4500 cal. BP; e.g. Tinner, Ammann & Germann 1996; Gobet *et al.* 2003; Blarquez *et al.* 2009), although it has been proposed that the Tyrolean Iceman (dated to ca. 5200 cal. BP) was a shepherd and that transhumance in the Eastern Alps started as early as ca. 6200 cal. BP (Bortenschlager 2000; but see Oeggl, Schmidl & Kofler 2009).

IMPACT OF ANTHROPOGENIC FIRE AND LAND USE ON MOUNTAIN FORESTS AND BIODIVERSITY

The most significant change in the subalpine vegetation at Iffigsee, as identified by PCA axis 1 (Fig. 6), is the local establishment of *P. abies* and the concurrent decline of *A. alba* between ca. 5650 and 5400 cal. BP (Fig. 5a,b). Cross-correlation analysis reveals that anthropogenic fire had a significant long-term effect on important species of mountain forests for up to 200 years (Fig. 7). Key species such as *A. alba*, *P. cembra* or *L. decidua* show a strong negative response to fire, indicating direct as well as indirect negative effects of high severity fires. Interestingly, *A. alba* (but not *P. cembra*) already shows a significant negative correlation up to 90 years prior to the fire. Tinner *et al.* (1999) suggested that a similar Neolithic pattern in the Southern Alps was caused by anthropogenic disturbance (e.g. forest pasture) before maximum fire activity. At lower altitudes at Lauenensee, *A. alba* is also negatively correlated with charcoal influx during the period 5900–5200 cal. BP, indicating a high sensitivity of *A. alba* to fire disturbance throughout its altitudinal range (Rey *et al.* 2013). The negative response of both *A. alba* and *P. cembra* to high anthropogenic fire activity is in agreement with other studies throughout the Alps (e.g. Tinner *et al.* 1999; Ali *et al.* 2005; Wick & Möhl 2006; Blarquez & Carcaillet 2010; Colombaroli *et al.* 2010).

The almost synchronous local expansion of *P. abies* at Iffigsee and nearby Lauenensee around 5500 cal. BP (Fig. 5b) suggests a common driver. *Picea abies* is the only subalpine tree species in our record that shows a significant positive correlation with fire (Fig. 7). However, fire disturbance was probably not the only cause for the expansion of *P. abies*, since the Iffigsee sediment record shows earlier periods of high fire activity (Fig. S1). The high-resolution sequences of Iffigsee and Lauenensee rather suggest that the expansion of *P. abies* was facilitated by the negative effects of recurring anthropogenic fires and possibly disturbance by human land use (e.g. grazing or logging) on competitors of spruce such as *A. alba* and *P. cembra*. Silver fir forests established ca. 2000 years earlier in the region (8200–7500 cal. BP; Heiri *et al.* 2003b; Wick *et al.* 2003; Lotter *et al.* 2006; Tinner & Lotter 2006; Rey *et al.* 2013; Schwörer *et al.* 2014b) and may have prevented the westward expansion of *P. abies* by occupying its ecological niche (Ravazzi 2002; Latałowa & van der Knaap 2006). *Abies alba* is extremely shade tolerant, less drought-sensitive than *P. abies* (which could be a reason for the earlier expansion, see Henne *et al.* 2011), has a broad temperature range (Ellenberg & Leuschner 2010; Tinner *et al.* 2013) and could therefore outcompete *P. abies* in the mid-Holocene. However, *A. alba* is highly sensitive to disturbance such as fire, browsing or logging (Tinner *et al.* 1999; Tinner & Lotter 2006). When the dense forest was opened by anthropogenic disturbance and *A. alba* populations declined, *P. abies* could expand in the subalpine vegetation belt. Our disturbance hypothesis is supported by a decline in pollen influx values of *A. alba* during the local establishment of *P. abies* at both Iffigsee and Lauenensee, which indicates a real decrease in *A. alba* density (vs. being just an artefact of the pollen percentage calculation; Fig. 5a, b). The strong competition between the two tree species is also evident in direct (RDA) and indirect (PCA) gradient analyses (Figs 6 and S3).

Recent studies indicate that the mass expansion of *P. abies* in Scandinavia could have been facilitated by anthropogenic fire disturbance as well (Bjune *et al.* 2009; Hörnberg *et al.* 2012). Other studies that document a slow but steady front-like expansion of *P. abies* in Scandinavia suggest that *P. abies* was able to invade the boreal forest naturally by outcompeting previously established tree taxa (Giesecke & Bennett 2004; Seppä *et al.* 2009). This seems in contrast to our data that show an expansion of *P. abies* in south-central Europe only after the decline of dominant tree taxa such as *A. alba* due to anthropogenic disturbance (i.e. fire, grazing or logging). The two different expansion histories may be linked to the different forest ecosystems present prior to the invasion of *P. abies*. Whereas in Scandinavia, mixed boreal forests were dominated by *Pinus*, *Betula* and *Alnus* with widespread *Tilia* and *Corylus* (Seppä *et al.* 2009), the mountain forests in the Northern Alps were dominated by *Pinus cembra*, *A. alba*, *L. decidua* as well as deciduous trees such as *Betula*, *Ulmus* or *Acer* (Fig. S1; Schwörer *et al.* 2014b). In particular, *A. alba* that is not present in Scandinavia and can occupy similar habitats as *P. abies* was probably a superior competitor under natural or quasi-natural conditions (i.e. absent to low anthropogenic disturbance). A delay of the *P. abies* expansion by its strong competitor *A. alba* has already been suggested by other studies (Ravazzi 2002). In Scandinavia, the expansion of cool and moist spruce forests changed the natural fire regime and led to a reduction of fire activity (Ohlson *et al.* 2011). In contrast, our time-series analysis suggests that *P. abies* possibly increased natural fire activity in the Alps (significant positive correlation at lag −1, i.e. ca. 30 years before a fire, Fig. 7). On the other hand, increased anthropogenic disturbance could be responsible for both an increase in fire activity through intentional burning of the forests and an increase of *P. abies* in the landscape through disfavouring competitors (Tinner *et al.* 1999).

Pastoralism around Iffigsee in the Neolithic had probably only a small-scale direct effect on important forest species (e.g. *Abies alba*) and on vegetation structure (e.g. treeline ecotone). Either the number of animals was too small to have an impact on the vegetation at a larger scale or grazing was concentrated on the alpine meadows and had no immediate effect on forest species. The low number of *Sporormiella* percentages compared to the Iron Age or the Middle Ages; periods with marked forest clearings suggests the former (Fig. S1). However, a study from the French Alps that compared influx values of *Sporormiella* with historically documented numbers of livestock (Etienne *et al.* 2013), may suggest that several hundred animals have been grazing around Iffigsee during certain periods of the high-resolution sequence. Indeed, the positive correlation of *Sporormiella* influx with *Urtica*

dioica indicates that, already in the Neolithic, pastoralism caused an accumulation of nutrients around the lake. The low taxonomic resolution of pollen analysis in some herbaceous plant families (such as Poaceae, Cyperaceae, Chenopodiaceae; Beug 2004) might also mask a change in grassland vegetation due to grazing.

The increasing trend in species richness after ca. 6300 cal. BP as well as its close association with plant species indicative of disturbance or open environments suggests that low-impact agriculture led to an increase in biodiversity. However, a breaking point in the taxa accumulation curve suggests a shift in species richness already at ca. 6800 cal. BP (Fig. S3). This coincides with the onset of grazing of alpine pastures and intentional burning of timberline forests at Iffigsee. At lower elevations, cross-correlation analysis of charcoal influx and palynological richness at Lauenensee shows a significant positive correlation 30 years after a fire (Rey *et al.* 2013), confirming the link between higher biodiversity and anthropogenic fire disturbance at the onset of arable farming. The overall increase in biodiversity in response to opening of the forest by anthropogenic disturbance agrees with previous studies in the Alps (e.g. Valsecchi *et al.* 2010; Colombaroli *et al.* 2013) as well as theoretical principles such as the intermediate disturbance hypothesis (Grime 1973). The increase in spatial heterogeneity of the landscape caused by humans (fire, grazing, and logging) also contributed to a higher biodiversity by raising the beta diversity (Whittaker 1960; Tuomisto 2010).

CLIMATIC IMPACTS ON MOUNTAIN FORESTS IN THE PAST AND IMPLICATIONS FOR THE FUTURE

Besides anthropogenic fire activity, climate was still an important driver of ecosystem dynamics at Iffigsee. The good agreement between peaks in the macrofossil records and independent temperature reconstructions (Fig. 5c,i) as well as model output of a dynamic vegetation model (Schwörer, Henne & Tinner 2014a) indicates that forests close to timberline reacted sensitively to small changes in temperature. Recent model-data comparisons at Iffigsee suggest that low moisture availability prevented *P. cembra* from establishing at Iffigsee in the Early Holocene (Schwörer, Henne & Tinner 2014a). The expansion of *P. cembra* and the decreasing importance of *L. decidua* at Iffigsee may therefore be attributed to a combination of progressive soil development and a period of a colder and wetter climate after ca. 6350 cal. BP (Fig. 5j,k; Haas *et al.* 1998; Magny 2004). However, *P. cembra* as a late-successional species (Ellenberg & Leuschner 2010) could also have profited from a phase of low fire activity after ca. 6100 cal. BP. A similar vegetation progression at Gouillé Rion (2343 m a.s.l.) in the Central Alps with initially pure stands of *L. decidua* from 11 350 to 9600 cal. BP and a collapse after ca. 8400 cal. BP was probably related to climatic cooling and a shift to a moister climate (Tinner & Kaltenrieder 2005). The striking similarity of the vegetation progression over centuries and millennia at both sites suggests climate as a common driver, since human

impact on the vegetation during the Mesolithic (ca. 11 300–7500 cal. BP / 9300–5500 BC) can be considered negligible (Colombaroli *et al.* 2013). It has been suggested that the mass expansion of *P. abies* in the Alps was caused by phases of cold and wet climate as well (Wick & Tinner 1997). However, our study shows that climate alone was not the only determinant of vegetational change. The mass expansion of *P. abies* was rather facilitated by a decline of *A. alba* due to anthropogenic disturbance supporting an early hypothesis of Markgraf (1970).

The human-induced shift from silver fir forests to spruce forests in the mid-Holocene has important implications for the stability, resilience and diversity of future forests in the Alps and in Europe. Under natural conditions (i.e. no anthropogenic disturbance), *A. alba* has a much broader climatic range and can form forests under colder (at timberline) as well as warmer conditions (at the Mediterranean coast) than observed today (Tinner *et al.* 2013). *Abies alba* stomata in the Iffigsee sediment record and the negative correlation with fire support this hypothesis. With temperatures projected to rise up to 4.8 °C and precipitation to drop by 30% in summer by the end of this century (IPCC 2007; CH2011 2011), temperate *A. alba* might be better adapted to the climatic changes than the boreal, drought-sensitive *P. abies*, especially under lower anthropogenic disturbance as observed today and projected for the future (land-use abandonment). Mixed forests with silver fir can therefore be expected to show a higher resilience to climate change and thus provide more provisional (e.g. timber) and other ecosystem services than monoculture spruce forests (Gamfeldt *et al.* 2013) and maintain the natural diversity of mountain forests in the Alps.

Conclusions

Even though climate was still an important driver of vegetation dynamics in the Neolithic, humans already had a significant impact on mountain vegetation by burning forests to expand pastures at timberline and create open areas for arable farming in the valley floors. We can link the expansion of *P. abies* in the Northern Alps to anthropogenic fire events that disadvantaged *A. alba*, which occupies the habitats of *P. abies* under slightly warmer and drier natural conditions (i.e. no anthropogenic disturbance). This suggests that *A. alba* might be more competitive than *P. abies* in the future, under warmer temperatures, drier summers and abandonment of marginal agricultural areas. It also shows that in the Alps and other mountain areas with a long history of human presence, the distribution of species and vegetation dynamics have been shaped by millennia of land use. Our study suggests that fire and traditional pastoralism have the potential to maintain the high biodiversity of mountain ecosystems by preventing the upward shift of mountain forest into alpine meadows. Policy programmes such as ecological compensation areas (ECA) that give a financial incentive to carry on pasturing in remote areas, can therefore preserve species-rich high-alpine meadows for the future.

Acknowledgements

Data accessibility

All data are deposited in the Alpine Palynological Database (ALPADABA) and the European Pollen Database (http://www.europeanpollendatabase.net).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Direct gradient analysis.

Figure S1. Pollen diagram of the entire Iffigsee record (11 200 cal. BP–present).

Figure S2. Taxa accumulation curve.

Figure S3. hRDA-biplot.

Table S1. Redundancy analysis (RDA).