

# Fire ecology of a tree glacial refugium on a nunatak with a view on Alpine glaciers

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## Summary

- In paleoecology, the function of biomass as a fire driver has become a focus of attention in cold ecosystems, and concerns have been raised about climate in this context. Little is known about the fire frequency and fire–plant relationships during glaciation when woodlands were limited and the climate was cold.
- Fire history and tree biomass were reconstructed from sedimentary charcoal and macroremains, respectively, archived in lake sediments from the western Alps. Two nunataks were investigated, both with lacustrine sediments covering the last 21 000 yr at least.
- During the Last Glacial Maximum (LGM) and the Lateglacial, fires occurred only on the nunatak sheltering woody plants. Cembra pine (*Pinus cembra*) and larch (*Larix decidua*) survived above glaciers during the LGM, thus evidencing a biological refugium and supporting the nunatak theory.
- We highlighted a long-term relationship between fires and dominant trees over the last 21 000 yr, where fire frequencies track the global climate and the local changes in tree biomass. Glacial climate (dry, cold) does not rule out fires. Fuel load and composition were significant fire drivers, with cembra pine dominating during colder periods with rare fires, and larch during the warmer Holocene with frequent fires. These findings increase knowledge of fire ecology in cold environments, and open perspectives in tree population genetics by considering new areas of tree glacial refugia in Europe.

## Introduction

In paleoecology, the function of biomass as a fire driver has recently become a focus of attention, and concerns have been raised about the impact of climate in this context (Bowman *et al.*, 2009). Surprisingly, little is known about the occurrences of fire during glaciation in middle and high latitudes when woody vegetation was limited, and the climate was colder and drier than the present interglacial, namely the Holocene. Fires are generally not expected in glacial and periglacial environments because of low temperatures and lack of woody fuel (Moritz *et al.*, 2012; Pausas & Ribeiro, 2013). When they do occur, fires affect shrubby tundras (Landhäusser & Wein, 1993; Higuera *et al.*, 2008). In such periglacial biomes during the 20<sup>th</sup> century, the assessed fire cycle is *c.* 9000 yr because fires are rare and affect small areas (Payette *et al.*, 1989), that is almost as long as the length of the Holocene (11 700 yr). The lack of fuel during glacial periods or in glaciated areas is the result of the limited number of growing degree-days irrespective of precipitation; the cool conditions also limit the initiation of fire seasons (Prentice *et al.*, 1993). Global warming, however, would stimulate fires in periglacial areas covered by tundra (Hu *et al.*, 2010; Abbott *et al.*, 2016), the composition of

which changes notably due to the invasion of shrubs or prostrate trees (Sturm *et al.*, 2001; Myers-Smith *et al.*, 2015) that provide fuel for fires. These fires would alter biogeochemical cycles by releasing large amounts of carbon sequestered in periglacial organic soils (Mack *et al.*, 2011). However, evidence for paleofires in glacial times remains rare (Bélanger *et al.*, 2014) because glacial archives are infrequent and, further, the idea of fires during a glacial period may be counterintuitive.

During the Last Glacial Maximum (LGM) large parts of lands north of 45°N were covered by periglacial biomes, such as tundra or shrubby tundra, where fires were certainly rare; however, the impact of fires on the global carbon cycle in these biomes could have been extremely important by analogy with the consequences of modern tundra fires (Mack *et al.*, 2011). During the LGM, valleys of mid-latitude mountains were partly filled by glaciers (Ehlers & Gibbard, 2004; Cossart *et al.*, 2010, 2012) and surrounding areas were covered by periglacial ecosystems, which are rarely described mainly due to a lack of archives. Their ecological dynamics are thus generally unknown, but evidence can come from proxies such as plant or animal macroremains in central Europe (e.g. Willis *et al.*, 2000; Juříčková *et al.*, 2014), Scandinavia (e.g. Kullman, 2006; Öberg & Kullman, 2011), central

Canada (Bélanger *et al.*, 2014) or Alaska (Brubaker *et al.*, 2005; Edwards *et al.*, 2014). Genetic studies also suggest that glacial refugia for plants and animals occurred in European areas that are classically considered as covered by steppes or tundras (e.g. Parducci *et al.*, 2012; Simonsen & Huemer, 2014; Daneck *et al.*, 2016). Modeling of ecological niches during the LGM completes this picture of cryptic glacial refugia, showing that boreal trees might have survived in central and east Europe (Svenning *et al.*, 2008) and that these woodlands could burn (Kaplan *et al.*, 2016). These empirical and model-based results contribute to change the view of a tree-less steppe or tundra during the LGM in large parts of middle Europe.

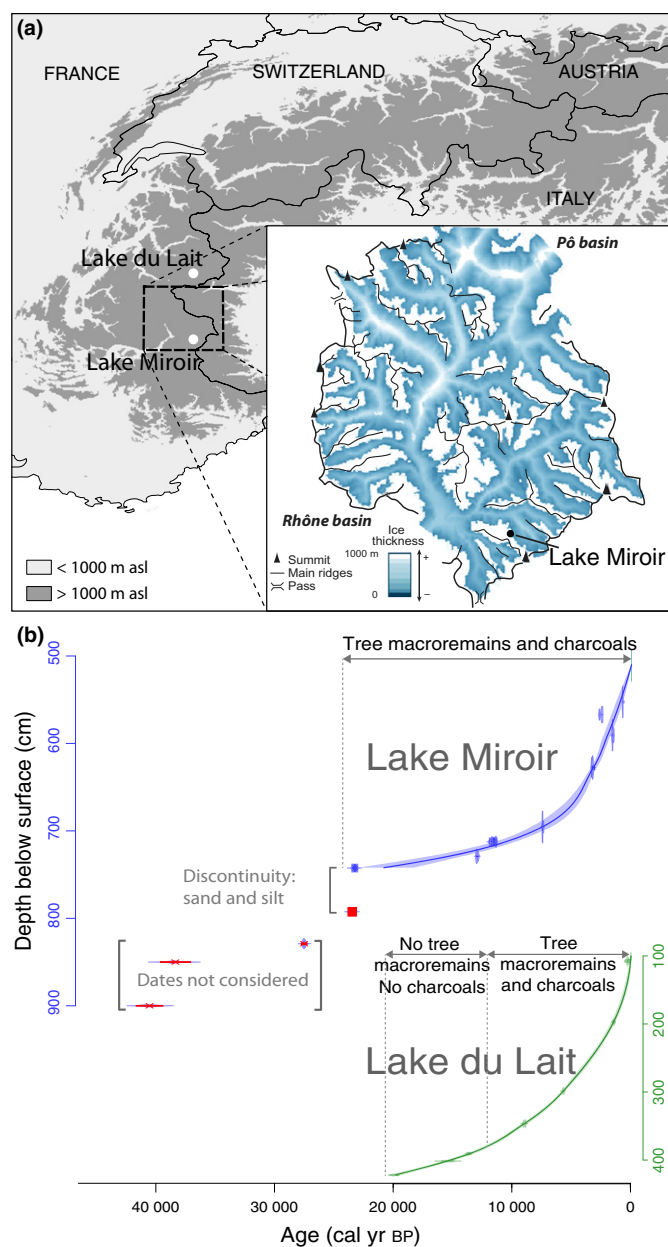
In the present study, we investigated lake sediments from two sites situated on potential nunataks in the western Alps (Fig. 1a). A nunatak is an isolated summit of a mountain ridge above glacier surface. One lake, Lake Miroir, has glacial sediments with plant macroremains and charcoal (Fig. 1b); the other lake, situated further north, Lake du Lait, shows similar age–depth patterns (Fig. 1b), but did not contain plant remains or charcoal during the LGM and the early Lateglacial. Sedimentary charcoal was used to reconstruct paleofires and plant macroremains were used for paleo-vegetation over the last 21 000 yr. The reconstruction of chronologies was based on radiocarbon dating and age–depth modeling (Blaauw, 2010). Mathematical algorithms allow the reconstruction of fire events, fire frequency and changes in fire regime (Blarquez *et al.*, 2013), whereas the biomass of main trees was estimated based on empirical models of basal area–macroremain relationships (Blarquez *et al.*, 2012), as basal area is the simplest proxy for accurately measuring tree biomass.

Here we question the ecological interplay between tree biomass and fires according to the site location on a nunatak surrounded by glaciers and the climatic changes since the LGM. The discussion further contributes to the debate on cryptic plant refugia (*sensu* Birks & Willis, 2008) and their genetic role on modern tree populations.

## Materials and Methods

### Study area

Lake Miroir is a subalpine lake, situated on a small plateau on a ridge of the Queyras massif in the dry, western Alps near the French–Italian border (Fig. 1a; 2214 m above sea level (asl); 44°38'03"N, 6°47'31"E, France; Supporting Information Fig. S1) and Lake du Lait is situated further north, on the southern slopes of the Vanoise massif (2180 m asl; 45°18'52"N, 6°48'55"E, France; Fig. S1). The present-day vegetation around Lake Miroir comprises a wooded subalpine grassland with *Larix decidua* Mill. (larch) and *Pinus cembra* L. (cembra pine) up to c. 2400 m asl; Lake du Lait is surrounded by a subalpine tree-less meadow. Meadows grazed in summer by sheep or cattle are dominated by Poaceae and Cyperaceae, with dwarf shrubs: *Vaccinium myrtillus* L., *V. vitis-idaea* L., *V. uliginosum* L., *Rhododendron ferrugineum* L., *Arctostaphylos uva-ursi* (L.) Spreng. and *Juniperus sibirica* Lodd. Ex Burgsd., with scattered mats of *Empetrum nigrum* subsp. *hermaphroditum* (Hagerup) Böcherserve.



**Fig. 1** (a) Location of Lake Miroir and Lake du Lait in the western Alps, France. The Lake Miroir site is mapped on the map of glaciers in the upper Durance valleys and adjacent valleys during the Last Glacial Maximum (adapted from Cossart, 2008, with permission). Both maps were generated with QGIS 2.6.1. asl, above sea level. (b) Age–depth distribution of  $^{14}\text{C}$  datings and associated model for Lake Miroir and Lake du Lait; periods with terrestrial plant macroremains and charcoal are indicated. The radiocarbon measurements of Lake Miroir are detailed in Table 1, and those of Lake de Lait are given in Carcaillet *et al.* (2009).

### Sampling and chronology setting

Sediments were collected using a Russian corer and a Kajak-Brinkurst sampler. Plant macroremains (needles, leaves, seeds, cones, pollen sacs, etc.) were retrieved from sediment cores at high resolution (0.5 cm at Lake Miroir; 1 cm at Lake du Lait) aiming to achieve a charcoal time resolution < 25 yr per sample, before radiocarbon dating was done. Extraction was carried out

**Table 1** Lake Miroir (western Alps, France) radiocarbon dates and associated information; radiocarbon measurements on bulk sediment were carried out on the extracted total organic carbon (TOC)

| Depth (cm)<br>below water<br>surface | Dated material   | <sup>14</sup> C dates (yr BP) | Lab. code |
|--------------------------------------|--|-------------------------------|-----------|
| 550–555                              | Needles ( <i>Pinus cembra</i> )  | 740 ± 30                      | Poz-18283 |
| 566–568                              | Bulk sediment, TOC   | 2420 ± 35                     | PoZ-27170 |
| 587–593                              | Needles ( <i>Pinus cembra</i> ,<br><i>Larix decidua</i> )                                    | 1640 ± 30                     | SacA-6886 |
| 625–630                              | Needles ( <i>Pinus cembra</i> ,<br><i>Larix decidua</i> )                                    | 3030 ± 35                     | Poz-18284 |
| 690–700                              | Needles ( <i>Pinus cembra</i> ,<br><i>Larix decidua</i> )                                    | 6520 ± 35                     | SacA-6887 |
| 710–715                              | Bulk sediment, TOC   | 10 100 ± 50                   | Poz-26075 |
| 710–716                              | Needles ( <i>Pinus cembra</i> ,<br><i>Larix decidua</i> ), seeds<br>( <i>Larix decidua</i> ) | 9980 ± 50                     | Poz-26221 |
| 728–730                              | Bulk sediment, TOC   | 11 090 ± 60                   | Poz-18340 |
| 740–745                              | Bulk sediment, TOC   | 19 320 ± 100                  | Poz-26074 |
| 790–795                              | Bulk sediment, TOC   | 19 520 ± 110                  | Poz-26077 |
| 828–830                              | Bulk sediment, TOC   | 23 300 ± 160                  | Poz-18341 |
| 849–851                              | Bulk sediment, TOC   | 34 030 ± 480                  | Poz-27171 |
| 899–901                              | Bulk sediment, TOC   | 35 940 ± 590                  | Poz-27172 |

using water sieving of soaked sediment, after which macroremains were taxonomically identified and counted. The abundance of macroremains was expressed in terms of accumulation rate (no. cm<sup>-2</sup> yr<sup>-1</sup>) using robust age–depth models from the LGM to the present (Fig. 1b) based on the topmost 10 <sup>14</sup>C measurements at Lake Miroir (Table 1; three glacial measurements older than 20 000 <sup>14</sup>C BP were ignored, Fig. 1b) and seven at Lake du Lait (Carcaillet *et al.*, 2009). Radiocarbon ages were calibrated in calendar years before present (hereafter cal BP) using CALIB v.7.0 (Stuiver & Reimer, 1993) with the Intcal13 dataset (Reimer *et al.*, 2013). The age–depth models were constructed by randomly picking an age within the entire distribution of each calibrated <sup>14</sup>C dating and then replicating 1000 times a locally weighted regression on these age–depth couples. The resulting age–depth models and their confidence intervals were evaluated based on the distribution of the regression replicates (Blaauw, 2010).

#### Terrestrial plant macroremains and biomass reconstruction

Needle accumulation rates cannot be directly used to assess the past abundance of larch and cembra pine. Differences in needle phenology between cembra pine, for which the life of needles is between 3 and 12 yr according to ecological conditions (Nebel & Matile, 1992; Li *et al.*, 2006), and larch, which is a deciduous conifer, result in an overrepresentation of larch needles in sediments (Blarquez *et al.*, 2012). We thus used transfer functions to estimate past larch and cembra pine basal areas. The transfer functions were based on the monitoring of needle fall over 3 yr using 30 traps situated in a subalpine mixed forest chiefly dominated by *P. cembra* and *L. decidua*, but with heterogeneous densities and age-structure of trees species. Some trees were > 600 yr old. We measured the basal area of all trees with a diameter > 5 cm at a height of 50 cm in forest stands around needle traps

using a 12-m-radius plot (450 m<sup>2</sup>). In total, the monitored forest covered 13 500 m<sup>2</sup>. The basal areas per species and per plot varied from 0 to 40.4 m<sup>2</sup> ha<sup>-1</sup> for *L. decidua*, and from 0 to 43.3 m<sup>2</sup> ha<sup>-1</sup> for *P. cembra*. We used calibration equations to convert needle accumulation rates (NAR<sub>f</sub>) into basal areas (BA<sub>f</sub>, m<sup>2</sup> ha<sup>-1</sup>):

$$BA_f = a_{\text{species}} \cdot \text{NAR}_f / (\text{NAR}_f + b_{\text{species}})$$

where  $a_{\text{Larix}} = 176.70$ ,  $b_{\text{Larix}} = 57.77$  and  $a_{\text{Pinus.cembra}} = 71.97$ ,  $b_{\text{Pinus.cembra}} = 0.6734$ . The adjusted  $R^2$  of the calibration equations was 0.64 (CV(root mean square error (RMSE)) = 0.036) for *Larix*, and 0.66 (CV(RMSE) = 0.065) for *P. cembra* (Blarquez *et al.*, 2012).

Absolute basal area values may be biased for a certain number of taphonomic reasons, notably the size of the lake surface (here 7170 m<sup>2</sup> for Lake Miroir, which is not directly comparable to plot sizes around the needle traps), and should be regarded as temporal indices of vegetation change. However, when transformed into percentages, reconstructed basal areas were useful to describe the contribution of larch and cembra pine to the total basal areas and thus their long-term changes in relative biomass.

#### Charcoal measurements and fire reconstruction

Contiguous subsamples of 1 cm<sup>3</sup> were taken for charcoal analysis along the cores. Sediments were bleached using a 10% NaOH solution and sieved through a 160 µm mesh. Charcoal surface areas were measured under a stereomicroscope coupled with a digital image analysis system. We used the age–depth model to calculate charcoal accumulation rates (CHAR; mm<sup>2</sup> cm<sup>-2</sup> yr<sup>-1</sup>). The assessment of fire events from the CHAR record is based on the CHARANALYSIS software (Higuera *et al.*, 2009) and the ensemble member procedure (Blarquez *et al.*, 2013). The CHAR is composed of two components: a high-frequency component, the CHAR peak, related to fire occurrence, and a slowly changing low-frequency component, the CHAR background, representing the long-term charcoal accumulation. To take into account the variability related to estimating the CHAR background, we ran 130 simulations: for each of the five smoothing methods available in the CHARANALYSIS software (Higuera *et al.*, 2009), we ran 26 CHAR background simulations with smoothing windows ranging from 250 to 1500 yr. For each simulation, the CHAR peak component was estimated by subtracting raw CHAR from the CHAR background component. The CHAR peak component is composed of two subpopulations: the CHAR noise represents normally distributed variation related to charcoal sampling, mixing and redistribution, while the CHAR fire exceeding this naturally occurring variation was related to the occurrence of one or more fires in the lake catchment area. We separated between CHAR fire and CHAR noise by fitting a Gaussian mixture model with two components on the CHAR peak. The 99<sup>th</sup> percentile of the fitted CHAR noise distribution was used to separate the two subpopulations. From those 130 simulations, we selected half of reconstructions (65) showing the higher signal to noise index (SNI > 3) and the lowest goodness of fit measure (i.e. high SNI

and low GOF, see Fig. S2 for reconstruction selection). Robust fire events (RFEs) were selected from those 65 simulations based on fire dates that were reconstructed by at least 75% of the simulations (Fig. S3).

RFEs were used to calculate fire return intervals (FRIs) and fire frequencies using a Kernel density estimation technique with a 700 yr bandwidth. We modeled the main change in FRI distribution using change point analysis (Killick & Eckley, 2014). To evaluate the sensitivity of the date of the main change in FRI distribution to varying fire event detection we replicated this analysis 999 times by bootstrap resampling the FRIs. Significant differences before and after the FRI main change were assessed using Mann–Whitney *U*-tests. Analyses were performed using the PALEOFIRE and CHANGEPOINT packages under R (Blarquez *et al.*, 2014).

### Climate data and reconstructions

The reconstruction of precipitation anomalies was inferred from four pollen sequences from the subalpine belt in the western Italian Alps (Ortu *et al.*, 2008), which are very close to our study area. The climate reconstructions are based on the principle of the modern analog method (Bartlein & Whitlock, 1993). We first averaged the reconstructed temperatures and precipitation data and then identified anomalies (Bartlein & Whitlock, 1993). The summer temperature anomalies from Davis *et al.* (2003, inferred from central western European pollen) and from Heiri *et al.* (2004, inferred from central Alpine chironomids) were also used for comparison with our local data. The  $\delta^{18}\text{O}$  anomalies were from a global series measured in Greenland (Grootes *et al.*, 1993; Andersen *et al.*, 2004) and from measurements taken in central Europe (von Grafenstein *et al.*, 1999). Finally, the solar irradiance reconstruction, reflecting the pattern of solar energy load released to the ground, was obtained from Berger & Loutre (1991).

## Results

### Sedimentology and chronology

At Lake Miroir, 494 cm of sediments (530–1024 cm below the water surface; Fig. S4) was sampled in the deepest part of the lake under 530 cm of water and ice (winter coring in 2006). Radiocarbon measurements were carried out on the whole core, although datings were rendered difficult below 720 cm depth (Figs 1b, S4). Indeed, sediments were extremely poor in organic matter including plant macroremains. From 720 to 1024 cm, accelerator mass spectrometry (AMS)  $^{14}\text{C}$  measurements on total organic matter isolated from sediment were performed. The oldest dates were  $35\,940 \pm 590$   $^{14}\text{C}$  BP at 900 cm below the water surface corresponding to an age between 39 790 and 41 670 cal BP ( $2\sigma$ ), with a more recent date of  $34\,030 \pm 480$   $^{14}\text{C}$  BP at 850 cm (Table 1), that is *c.* 39 500 cal BP. Both are older than the LGM. Below a depth of 775 cm, the sediment was mainly laminated blue–gray clay, more or less dark (Fig. S5). A sedimentological discontinuity appears from 765 to 750 cm, composed of sand

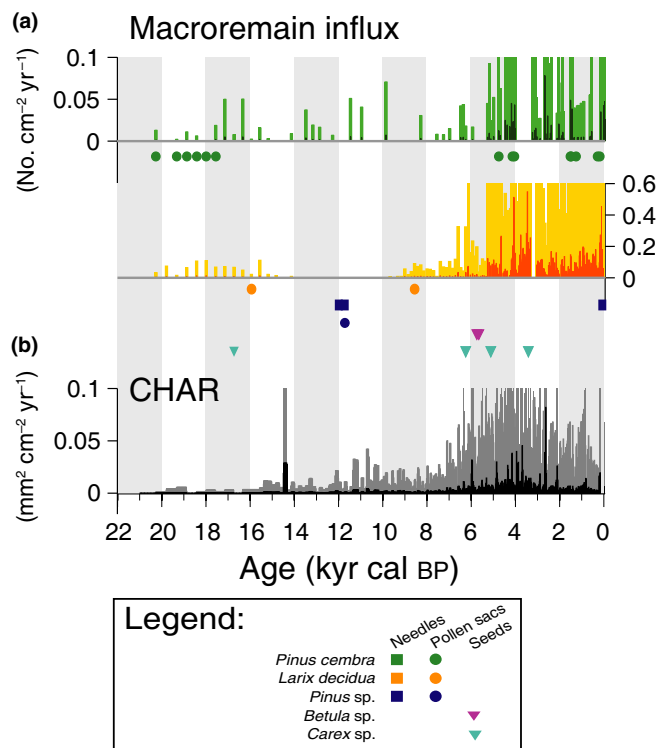
and silt (Fig. S4). Two identical  $^{14}\text{C}$  measurements ( $\chi^2$  test) were obtained below and above this discontinuity:  $19\,520 \pm 110$  and  $19\,320 \pm 110$   $^{14}\text{C}$  BP, respectively (*c.* 23 200 cal BP; Table 1). Above 750 cm depth, the pattern of sediment was continuous and organic rich above 702 cm. From 702 to 530 cm, the sediment was a laminated brown–reddish organic mud (gyttja), *a priori* corresponding to the Holocene (Fig. S5).

Only the top-most 220 cm (750–530 cm) was analysed for charcoal and plant macroremains. Height  $^{14}\text{C}$  measurements cover these 220 cm of postglacial sediments (Table 1). Finally, the age–depth model was calculated based the topmost  $^{14}\text{C}$  dates above this sandy discontinuity (blue model in Fig. 1b).

### Paleobotany and paleofires

Although geographically and topographically comparable, and showing a similar age–depth pattern, the sediments of Lake du Lait did not contain plant remains and charcoal during the LGM (Fig. 1a,b); the first woody occurrences were recorded during the Lateglacial (*i.e.* 14 600 cal BP) for birch and during the Holocene (*i.e.* 10 200 cal BP) for cembra pine, and 9000 cal BP for charcoal (Carcaillet *et al.*, 2009; Fig. 1b).

At Lake Miroir, among the different taxa recorded (Fig. 2), only data from the two dominant ones – cembra pine and larch – were



**Fig. 2** Lake Miroir (western Alps, France). (a) Accumulation rate (or influx) of needles (number  $\text{cm}^{-2} \text{yr}^{-1}$ ) of cembra pine (*Pinus cembra*) and larch (*Larix decidua*) plotted against time before present. Lighter colors represent 10× vertical exaggeration to illustrate low influx notably between 21 000 and 6000 cal BP. Dots correspond to occurrences of pollen bags. Other species occurrences are indicated in blue for other pine (*Pinus* sp.), in purple for birch (*Betula* sp.) and in turquoise blue for sedges (*Carex* sp.). (b) Charcoal series are exaggerated (5×) to illustrate occurrence rate of charcoal during the Last Glacial Maximum (LGM) and the Lateglacial.

converted into basal areas (Fig. 3). The other recorded taxa, namely *Pinus* sp. (probably *Pinus mugo-uncinata*), birch (*Betula* sp.) and sedges (*Carex* sp.), were recorded qualitatively over the last 21 000 yr (Fig. 2). The needle abundances of pine and larch were highly variable before 10 000 cal BP. Larch occurred at Lake Miroir before 15 000 cal BP, that is since the LGM, but cembra pine dominated the basal areas from 21 000 to 10 500 cal BP. Moreover, the finding of pine pollen sacs from 21 000 to 17 000 cal BP (Fig. 2a) indicates that, in some years, conditions were suitable for trees to flower and eventually to reproduce.

Sedimentary charcoal proved the occurrence of fires. The LGM and the Lateglacial samples were characterized by regular occurrences of fires whose frequencies increased after a tipping point identified at 10 700 cal BP (Fig. 4a). From 21 000 to 10 700 cal BP, the mean ( $\pm$  SD) FRI was long, specifically  $1120 \pm 460$  yr per fire (Fig. 4b). Glacial and Lateglacial fires were thus rare (Fig. 4b). The Holocene fire regime was characterized by a diminishing FRI (or increasing fire frequency) with a mean value of  $410 \pm 260$  yr per fire after the 10 700 cal BP tipping point (Fig. 4a), significantly different from FRI before 10 700 cal BP ( $P < 0.001$ ; Fig. 4a). From 12 000 to 4000 cal BP,

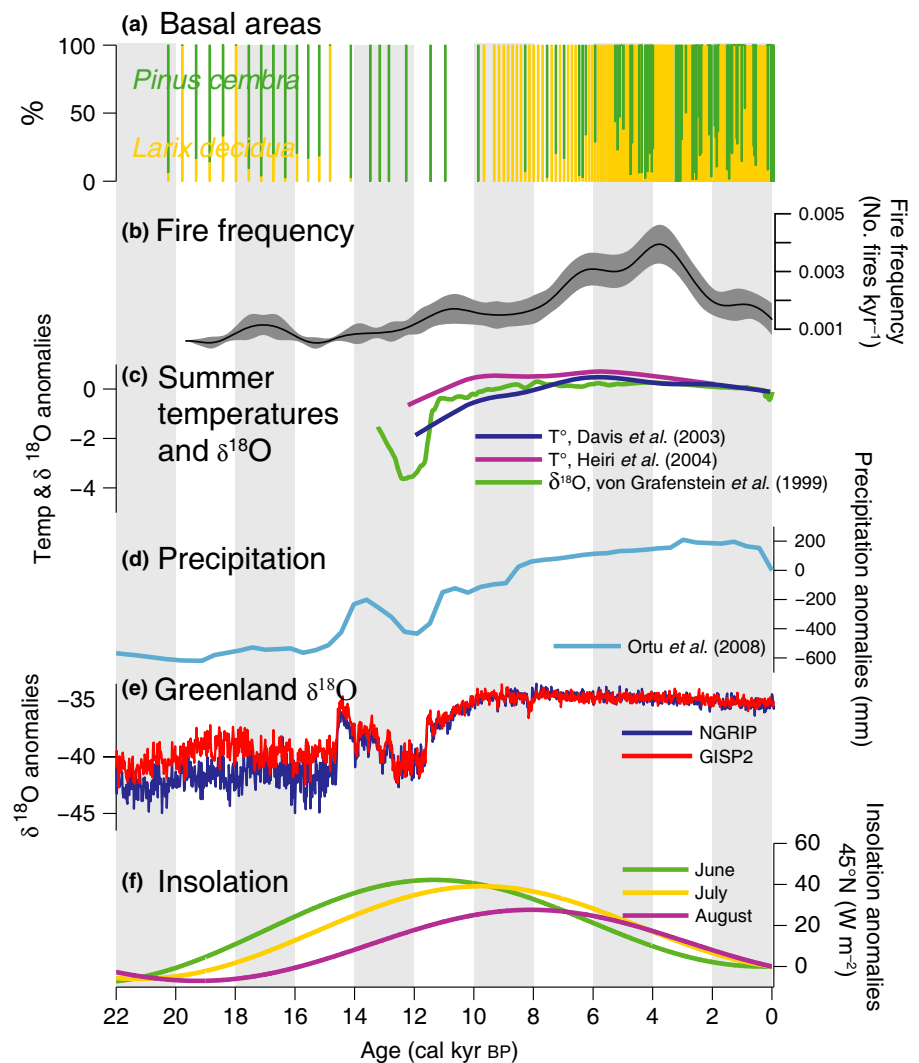
the increase in frequency was monotonic, but oscillated from 8000 to 4000 cal BP. Maximal fire frequency was at *c.* 4500–3500 cal BP. The last 4000 yr were characterized by a net reduction in frequency.

From 10 500 to 8 000 cal BP, larch dominated the biomass, and thereafter, pine and larch dominated alternately (Fig. 3a). However, the general pattern during the Holocene was a relative dominance of larch basal areas associated with shorter FRIs (higher fire frequency), compared to the Lateglacial period before the 10 700 cal BP tipping point, during which cembra pine dominated in association with long FRIs (Figs 3b, 4b,c).

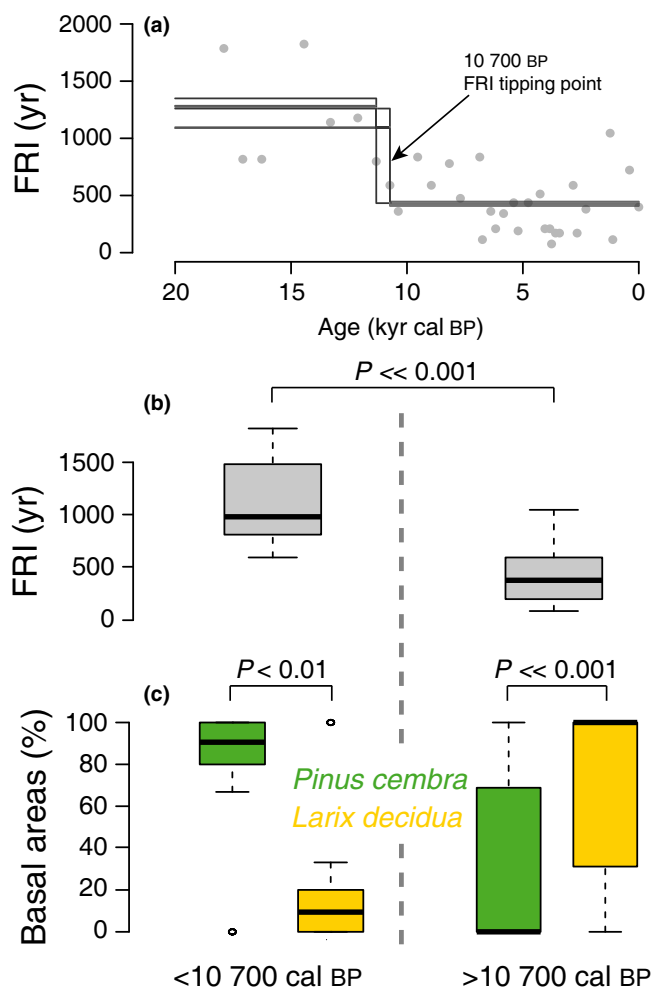
## Discussion

### The refugium and the nunatak theory

Here we provide new paleoecological findings highlighting the ecological functioning of isolated mountain woody ecosystems during glacial times and during the warming of the following millennia. Generally, these results deliver key data to understand how refugia could operate (Hampe *et al.*, 2013). The finding of



**Fig. 3** Reconstruction of fire and vegetation history at Lake Miroir (western Alps, France) vs regional climate synthesis. (a) Needle accumulation rates are transformed into relative basal areas (%) of *Pinus cembra* and *Larix decidua*; (b) median fire frequencies (fire number  $1000 \text{ yr}^{-1}$ ) and 90% confidence intervals based on an ensemble-member strategy; (c) summer temperatures and  $\delta^{18}\text{O}$  series in the northern Alps; (d) annual precipitation ( $\text{mm yr}^{-1}$ ); (e) global  $\delta^{18}\text{O}$  series from Greenland; (f) insolation curve showing actual growing months in the subalpine belt at  $45^\circ\text{N}$  (all references for the climate reconstruction and proxies are presented in the Material and Methods section).



**Fig. 4** Fire frequency and vegetation relationships at Lake Miroir (western Alps, France). (a) Fire return intervals (FRIs, years per fire) based on robust fire events (RFEs, gray dots) resulting from the ensemble-member strategy for all 65 simulations; the date of main FRI change, or tipping point, was calculated by change point analysis. (b) Box-plot of FRIs before and after the tipping point of 10 700 cal BP. (c) Box-plot of relative tree basal areas inferred from macroremains of *Pinus cembra* and *Larix decidua* before and after 10 700 cal yr BP. Significant differences before and after the FRI main shift were assessed using the Mann–Whitney *U*-test. The middle line of box-plots indicates the median value, the upper and the lower extents of the box represent the 75<sup>th</sup> and the 25<sup>th</sup> percentiles, the whiskers represent the upper and lower 1.5 $\times$  interquartile range, and the dots are the outlier values.

macroremains of larch and cembra pine during the LGM on the mountain sheltering Lake Miroir, which was above the glacier limit (Cossart *et al.*, 2012), supports the nunatak theory. The nunatak theory hypothesizes that unglaciated relief (mountain, ridges, cliff) existed in glacial areas where micro-organisms, plants and animals survived the last glacial times (Dahl, 1987). The evidence presented in this study has two implications: first, it provides insight on the LGM climate if we assume that the modern and LGM physiological limits of cembra pine and larch were equivalent, which would imply an LGM climate more favorable to tree growth than previously thought. Second, this finding could challenge the view in ecophysiology of wood productivity

and the upper treeline pattern that stress low temperature as the limiting factor for tree growth, and water loss during frozen months controlling the desiccation of the photosynthetic organs, needles in the case of larch and pine (Tranquillini, 1979; Körner, 2003). However, the very low and fluctuating abundances of woody macroremains from 21 000 to 9000 cal BP (Fig. 2a) indicate that the periglacial vegetation was certainly an alpine-tundra with scattered unproductive trees. Further, we cannot rule out that trees grew on glacier margins as observed in the Alaskan cordillera, resulting in superglacial woody vegetation (Stephens, 1969).

Several studies have demonstrated the presence of trees at sub-alpine altitudes within the inner Alpine area during the Lateglacial–Holocene transition (e.g. Lang & Tobolski, 1985; Tinner & Kaltenrieder, 2005; Blarquez *et al.*, 2010). However, our identification of this LGM refugium for cembra pine and larch is a new finding for this elevation, although it is well known that trees survived in the lowlands around the 45°N west of the Alps (syntheses in Carcaillet & Vernet, 2001 and Tzedakis *et al.*, 2013). A tree refugium on a nunatak within the glaciated Alps during the LGM has considerable consequences in terms of both population genetic and ecological conservation, as has been reported for spruce (*Picea abies*) in Scandinavia (Parducci *et al.*, 2012) where refugia have already been revealed, based on tree remains of spruce (e.g. Kullman, 1996; Öberg & Kullman, 2011) and also birch (Kullman, 1996). Other exceptional glacial refugia for trees were evidenced in Alaska (Brubaker *et al.*, 2005; Hu *et al.*, 2009; Edwards *et al.*, 2014) and in central Canada (Bélanger *et al.*, 2014). All these examples of glacial refugia challenge the classical view of post-glacial tree migrations (Feurdean *et al.*, 2013) and suggest that the survival capacities of trees in periglacial ecosystems are complex and clearly underestimated. Until now, cembra pine was thought to have survived the LGM somewhere between the eastern Alps and the eastern Carpathians (Zoller, 1981; Lang, 1994; Tzedakis *et al.*, 2013) although recent pollen-based observations suggest a refugium in the mountains of northern Italy (Ravazzi *et al.*, 2012). Regarding larch, its presence during the Lateglacial in the alpine hinterland is less controversial, but finding evidence of trees is exceptional at 2200 m asl in a mountain glaciated during the LGM. Larch can survive in harsh conditions due to its ability to reproduce by layering, thus avoiding the need for sexual reproduction, and because it is deciduous, allowing it to tolerate prolonged and severe frosts (Tranquillini, 1979). By contrast, cembra pine would not have such biological traits of multiplication. Both species can live up to 1000 yr (Serre, 1978; Carrer *et al.*, 2007). The survival of cembra pine in such glacial conditions implies periodic reproduction events, even if they were rare and exceptional, perhaps with similar patterns and processes to *Pinus longaeva* in the higher mountains of Nevada (LaMarche & Mooney, 1972).

#### A chronicle of woody biomass linked to climate

Subalpine sites did not generally support woody plants during periglacial periods. However, at Lake Miroir, trees were present during such times and their abundance followed known climatic

conditions (Fig. 3). Indeed, trees were not abundant before 9000 cal BP based on low needle influxes (Fig. 2a) when the climate was cold and dry (Fig. 3c,d) according to regional climatic reconstructions (Davis *et al.*, 2003; Heiri *et al.*, 2004; Ortu *et al.*, 2008), reflecting the global climate inferred from  $\delta^{18}\text{O}$  (Fig. 3e; von Grafenstein *et al.*, 1999; Andersen *et al.*, 2004). The abundance of needles increased from 9000 to 6000 cal BP, when the climate became warmer and wetter (Fig. 3c–e). However, the vegetation did not follow summer insolation anomalies, which reached a maximum between 14 000 and 8000 cal BP, depending on the growing season months considered (Fig. 3f; Berger & Loutre, 1991). We would expect that elevated solar irradiance could have promoted increased tree biomass growth, thus compensating for low temperatures before 12 000 cal BP. However, the biomass appears linked to air temperature and water availability, both rising after 11 700 cal BP, coinciding with the onset of the Holocene.

### Fire ecology of the refugium

The long FRI values during the LGM and the Lateglacial ( $1260 \pm 450$  yr per fire, mean  $\pm$  SD; Fig. 4a) are of a similar order of magnitude to those recorded during the 20<sup>th</sup> century in the shrub-tundra of eastern Canada or Alaska (Payette *et al.*, 1989; Higuera *et al.*, 2011; Rocha *et al.*, 2012), which demonstrates that our reconstructed Alpine pattern is plausible. During the cold LGM and Lateglacial (i.e. until 10 700 cal BP), cembra pine was dominant and associated with these long FRIs (Fig. 4b). However during the warmer Holocene, larch basal areas were linked to higher fire frequencies, that is short FRIs ( $430 \pm 260$  yr per fire; Fig. 4b), although we know that fires are generally stimulated by the accumulation of cembra pine biomass and also that a high frequency of fires can exclude cembra pine (Genries *et al.*, 2009a). Fires do not directly stimulate larch abundance (Genries *et al.*, 2009b), but these fires do reduce the abundance of cembra pine and other larch competitors, thus indirectly favoring larch (Blarquez & Carcaillet, 2010). Cembra pine is a highly flammable species susceptible to fire, especially at the regeneration stage when bark is very thin (Fréjaville *et al.*, 2013). Thereby, larch, which is much less flammable (Fréjaville *et al.*, 2013) and resistant to frequent fires such as those observed in northern Siberia (Kharuk *et al.*, 2011), is released from cembra pine competition under frequent fires. Ecologically, 10 700 cal BP clearly appears as a tipping point between two different ecosystem states, as revealed by the respective dominance of pine before and larch after.

While tree biomass was certainly limited by low summer temperatures and precipitation before 8000 cal BP, fire occurrences were probably favored by the low precipitation, which were 400–600 mm yr<sup>-1</sup> below modern values recorded in the western Alps (Fig. 3d; Ortu *et al.*, 2008). The glacial and postglacial temperatures did not prevent fires, but fire frequency was certainly controlled by the lack of woody fuel resulting from low temperatures and limited precipitation. After 10 000 cal BP, when temperatures and precipitation increased and provided better conditions for biomass build-up (Fig. 3c,d), fires became more frequent with

values oscillating between two and five events per 1000 yr (Fig. 3b). Although it is counterintuitive, this process of higher precipitation promoting fires is explained by the understorey fuel build-up, which is favored by precipitation during the years preceding the fire, whilst the fire-year itself must be characterized by a severe drought (Zumbrunnen *et al.*, 2009). Further, the seasonality of precipitation is crucial, not just the succession of wet and dry years. Indeed, rainy springs stimulate shrub biomass growth, and dry autumns favor the accumulation of fine fuel, which are both conditions crucial for the fire-prone status of high-altitude forest ecosystems (Fréjaville *et al.*, 2016). Within the Holocene, and mostly since 4000 cal BP, fire frequency depends on fluctuations of a non-natural factor, that is land use, which acts on the pattern and composition of vegetation and is interlinked to climate (Saulnier *et al.*, 2015; Leys & Carcaillet, 2016).

### Perspective on tree population genetics

If cembra pine and larch survived the LGM on nunataks in the southwestern Alps, these populations may have contributed to the recolonization of this area. They might be ancestors of modern populations of the southwestern Alps, but these lineages remain to be demonstrated by DNA. The genetic diversity of cembra pine decreases westwards in the Alps (Höhn *et al.*, 2009) and in Europe (Dzialuk *et al.*, 2014), and the western populations differ significantly from the eastern and the central populations (Mosca *et al.*, 2012), supporting the ‘abundant centre model’ (Dzialuk *et al.*, 2014). Classically (e.g. Zoller, 1981; Burga, 1988), ancestral populations of cembra pine during glacial times were confined to the Carpathians and east-central Europe. However, a refugium has been hypothesized in the southeastern Alps, which is supported by the different genetic pattern of western Alpine populations of cembra pine (Gugerli *et al.*, 2009), later supported by a pollen-based paleoenvironmental study that evokes refugia in the southern Italian Alps but without an accurate location of this refugium (Ravazzi *et al.*, 2012). With respect to larch, the western populations are genetically distinguished from the eastern ones (Mosca *et al.*, 2012). All these genetic studies match our evidence of western Alpine glacial refugia of cembra pine and larch, and support the hypothesis that, after the LGM, eastward colonizers would have encountered the westward expansion of populations that survived in the Carpathians or the southeastern Alps.

### Conclusion

Here we provide paleoecological evidence of a cryptic tree refugium and fires during glacial times at high altitude in the Alps. This refugium, situated on a mountain above a valley filled by glaciers (Fig. 1; Cossart *et al.*, 2012), corresponds with the ecological concept of a nunatak (Dahl, 1987), that is a mountain emerging from glaciers during glaciation. This nunatak sheltered a woody vegetation that burned episodically since 21 000 cal BP, including European larch and cembra pine (Fig. 2). Lake du Lait, situated at the same altitude in a nearby valley further north, was dated back to 21 000 cal BP, but its Lateglacial sediments contain neither plant macroremains nor charcoal before *c.* 9000 cal BP

(Carcaillet *et al.*, 2009). Because the site where charcoal fragments were recorded also presents plant remains originating during the LGM, we conclude that a glacial climate does not prevent the ignition of biomass and fire spread. Woody fuel is thus a key condition for wildfires, despite the glacial environment limiting primary productivity. A tree refugium on a nunatak has not been reported for trees in the Alps, in contrast to the Scandinavian Mountains. This finding contributes to our understanding of the effects of biomass and climate on fire occurrences. Finally, the exceptional occurrences of cembra pine and larch since the LGM indicate that the Lake Miroir site would have hosted genetic lineages of trees that could have colonized the western Alps during the deglaciation.

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## Author contributions

C.C. conceived and designed the study; C.C. and O.B. provided and conducted the data analyses; O.B. carried out the basal areas and fire frequency reconstructions; C.C. and O.B. conducted the interpretations. C.C. wrote the manuscript that was commented and improved by O.B.

## References

- Abbott BW, Jones JB, Schuur EAG, Chapin FS III, Bowden WB, Bret-Harte MS, Epstein OE, Flannigan MD, Harms TK, Hollingsworth TN *et al.* 2016. Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: an expert assessment. *Environmental Research Letters* 11: 034014.
- Andersen KK, Azuma N, Barnola JM, Bigler M, Biscaye P, Caillon N, Chappelaz J, Clausen HB, Dahl-Jensen D, Fischer H. 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* 431: 147–151.
- Bartlein PJ, Whitlock C. 1993. Paleoclimatic interpretation of the Elk Lake pollen record. In: Bradbury JP, Dean WE, eds. *Elk Lake, Minnesota: evidence for rapid climate change in the north-central United States*. New York, NY, USA: Geological Society of America, 275–293.
- Bélanger N, Carcaillet C, Padbury GA, Harvey-Schafer AN, Van Rees KJC. 2014. Periglacial fires and trees in a continental setting of Central Canada, Upper Pleistocene. *Geobiology* 12: 109–118.
- Berger A, Loutre MF. 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10: 297–317.
- Birks HJB, Willis KJ. 2008. Alpines, trees, and refugia in Europe. *Plant Ecology and Diversity* 1: 147–160.
- Blaauw M. 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology* 5: 512–518.
- Blarquez O, Carcaillet C. 2010. Fire, fuel composition and resilience threshold in subalpine ecosystem. *PLoS ONE* 5: e12480.
- Blarquez O, Carcaillet C, Elzein TM, Roiron P. 2012. Needle accumulation rate model-based reconstruction of palaeo-tree biomass in the western subalpine Alps. *The Holocene* 22: 579–587.
- Blarquez O, Carcaillet C, Mourier B, Bremond L, Radakovitch O. 2010. Trees in the subalpine belt since 11 700 cal. BP: origin, expansion and alteration of the modern forest. *The Holocene* 20: 139–146.
- Blarquez O, Girardin MP, Leys B, Ali AA, Aleman JC, Bergeron Y, Carcaillet C. 2013. Paleofire reconstruction based on an ensemble-member strategy applied to sedimentary charcoal. *Geophysical Research Letters* 40: 2667–2672.
- Blarquez O, Vannière B, Marlon JR, Daniou AL, Power MJ, Brewer S, Bartlein PJ. 2014. Paleofire: an R package to analyse sedimentary charcoal records from the Global Charcoal Database to reconstruct past biomass burning. *Computers and Geosciences* 72: 255–261.
- Bowman D, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP *et al.* 2009. Fire in the Earth system. *Science* 324: 481–484.
- Brubaker LD, Anderson PM, Edwards ME, Lozhkin AV. 2005. Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography* 32: 833–848.
- Burga CA. 1988. Swiss vegetation history during the last 18 000 years. *New Phytologist* 110: 581–602.
- Carcaillet C, Ali AA, Blarquez O, Genries A, Mourier B, Bremond L. 2009. Spatial variability of fire history in subalpine forests: from natural to cultural regimes. *Ecoscience* 16: 1–12.
- Carcaillet C, Vernet J-L. 2001. Comments on "The full-glacial forests of central and southeastern Europe" (Willis *et al.*, 2000). *Quaternary Research* 55: 385–387.
- Carrer M, Nola P, Eduard JL, Motta R, Urbinati C. 2007. Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps. *Journal of Ecology* 95: 1062–1083.
- Cossart E. 2008. Reconstitution de la géométrie 3D d'un glacier disparu et modélisation des conséquences de sa disparition – Le glacier durancien lors du Dernier Maximum Glaciaire. *Revue Internationale de Géomatique* 18: 95–111.
- Cossart E, Fort M, Bourles D, Braucher R, Siame L. 2012. Deglaciation pattern during the Lateglacial/Holocene transition in the southern French Alps. Chronological data and geographical reconstruction from the Clarée Valley (upper Durance catchment, southeastern France). *Palaeogeography Palaeoclimatology Palaeoecology* 315–316: 109–123.
- Cossart E, Fort M, Bourles D, Carcaillet J, Perrier R, Siame L, Braucher R. 2010. Climatic significance of glacier retreat and rockglaciers re-assessed in the light of cosmogenic dating and weathering rind thickness in Clarée valley (Briançonnais, French Alps). *Catena* 80: 204–219.
- Dahl E. 1987. The nunatak theory reconsidered. *Ecological Bulletin* 38: 77–94.
- Daneck H, Fer F, Marhold K. 2016. Glacial survival in northern refugia? Phylogeography of the temperate shrub *Rosa pendulina* L. (Rosaceae): AFLP versus chloroplast DNA variation. *Biological Journal of the Linnean Society* 119: 704–718.
- Davis BAS, Brewer S, Stevenson AC, Guiot J, Data contributors. 2003. The temperature of Europe during the Holocene reconstructed from pollen data. *Quaternary Science Reviews* 22: 1701–1716.
- Dzialuk A, Chybicki I, Gout R, Maczka T, Fleischer P, Konrad H, Curtu AL, Sofletea N, Valadon A. 2014. No reduction in genetic diversity of Swiss stone pine (*Pinus cembra* L.) in Tatra Mountains despite high fragmentation and small population size. *Conservation Genetics* 15: 1433–1445.
- Edwards ME, Armbruster WS, Elias SE. 2014. Constraints on post-glacial boreal tree expansion out of far-northern refugia. *Global Ecology and Biogeography* 23: 1198–1208.
- Ehlers J, Gibbard PL, eds. 2004. Quaternary glaciations – extent and chronology. In: *Development in quaternary science, Part 1: Europe, vol. 2*. Amsterdam, the Netherlands: Elsevier, 475.
- Feurdean A, Bhagwat SA, Willis KJ, Birks HJB, Lischke H, Mickler T. 2013. Tree migration-rates: narrowing the gap between inferred post-glacial rates and projected rates. *PLoS ONE* 8: e71797.



- Fréjaville T, Curt T, Carcaillet C. 2013. Bark flammability as a fire-response trait for subalpine trees. *Frontiers in Plant Science* 4: 466.
- Fréjaville T, Curt T, Carcaillet C. 2016. Tree cover and precipitation seasonality drive the understory flammability in mountain forests of the Alps. *Journal of Biogeography* 43: 1869–1880.
- Genies A, Mercier L, Lavoie M, Muller SD, Radakovitch O, Carcaillet C. 2009a. The effect of fire frequency on local cembra pine populations. *Ecology* 90: 476–486.
- Genies A, Morin X, Chauchard S, Carcaillet C. 2009b. The function of surface fires in the dynamics and structure of a formerly grazed old subalpine forest. *Journal of Ecology* 97: 728–741.
- von Grafenstein U, Erlenkeuser H, Brauer A, Jouzel J, Johnsen SJ. 1999. A mid-European decadal isotope-climate record from 15,500 to 5,000 years B.P. *Science* 284: 1654–1657.
- Groote P, Stuiver M, White J, Johnsen S, Jouzel J. 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. *Nature* 366: 552–554.
- Gugerli F, Rüegg M, Vendramin GG. 2009. Gradual decline in genetic diversity in Swiss stone pine populations (*Pinus cembra*) across Switzerland suggests postglacial re-colonization into the Alps from a common eastern glacial refugium. *Botanica Helvetica* 119: 13–22.
- Hampe A, Rodriguez-Sanchez F, Dobrowski S, Hu FS, Gavin DG. 2013. Climate refugia: from the Last Glacial Maximum to the twenty-first century. *New Phytologist* 197: 16–18.
- Heiri O, Tinner W, Lotter AF. 2004. Evidence for cooler European summers during periods of changing meltwater flux to the North Atlantic. *Proceedings of the National Academy of Sciences, USA* 101: 15285–15288.
- Higuera PE, Brubaker LB, Anderson PM, Brown TA, Kennedy AT, Hu FS. 2008. Frequent fires in ancient shrub tundra: implications of paleorecords for arctic environmental change. *PLoS ONE* 3: e0001744.
- Higuera PE, Brubaker LB, Anderson PM, Hu FS, Brown TA. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79: 201–219.
- Higuera PE, Chipman ML, Barnes JL, Urban MA, Hu FS. 2011. Variability of tundra fire regimes in Arctic Alaska: millennial scale patterns and ecological implications. *Ecological Applications* 21: 3211–3226.
- Höhn M, Gugerli F, Abran P, Bisztray G, Buonamici A, Cseke K, Hufnagel L, Quintela-Sabaris C, Sebastiani F, Vendramin GG. 2009. Variation in the chloroplast DNA of Swiss stone pine (*Pinus cembra* L.) reflects contrasting post-glacial history of populations from the Carpathians and the Alps. *Journal of Biogeography* 36: 1798–1806.
- Hu FS, Hampe R, Petit RJ. 2009. Paleoecology meets genetics: deciphering past vegetation dynamics. *Frontiers in Ecology and the Environment* 7: 371–379.
- Hu FS, Higuera PE, Walsh JE, Chapman WL, Duffy PA, Brubaker LB, Chipman ML. 2010. Tundra burning in Alaska: linkages to climatic change and sea ice retreat. *Journal of Geophysical Research—Biogeosciences* 115: G04002.
- Juríčkova L, Horáková J, Ložek V. 2014. Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils. *Quaternary Research* 82: 222–228.
- Kaplan JO, Pfeiffer M, Kolen JCA, Davis BAS. 2016. Large scale anthropogenic reduction of forest cover in Last Glacial Maximum Europe. *PLoS ONE* 11: e0166726.
- Kharuk VI, Ranson KJ, Dvinskaya ML, Im ST. 2011. Wildfires in northern Siberian larch dominated communities. *Environmental Research Letters* 6: 045208.
- Killick R, Eckley IA. 2014. changepoint: an R package for changepoint analysis. *Journal of Statistical Software* 58: 1–19.
- Körner C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Berlin, Germany: Springer-Verlag.
- Kullman L. 1996. Norway spruce present in the Scandes Mountains, Sweden at 8000 BP: new light on Holocene tree spread. *Global Ecology and Biogeography* 5: 94–101.
- Kullman L. 2006. Late-glacial trees from arctic coast to alpine tundra: response to Birks *et al.* 2005 and 2006. *Journal of Biogeography* 33: 376–378.
- LaMarche VC, Mooney HA. 1972. Recent climatic change and development of bristlecone pine (*P. longaeva* Bailey) krummholz zone, Mt. Washington, Nevada. *Arctic and Alpine Research* 4: 61–72.
- Landhäuser SM, Wein RW. 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: climate-change-vegetation-response hypotheses. *Journal of Ecology* 81: 665–672.
- Lang G. 1994. *Quartäre Vegetationsgeschichte Europas. Methoden und Ergebnisse, vol. 118*. Jena, Germany: Gustav Fisher.
- Lang G, Tobolski K. 1985. Hobschensee—Late-Glacial and Holocene environment of a lake near the timberline. *Dissertation Botanicae* 87: 209–228.
- Leys B, Carcaillet C. 2016. Subalpine fires: the roles of vegetation, climate and ultimately, land uses. *Climatic Change* 135: 683–697.
- Li MH, Kruauchi N, Dobbertin M. 2006. Biomass distribution of different-aged needles in young and old *Pinus cembra* trees at highland and lowland sites. *Trees—Structure and Function* 20: 611–618.
- Mack MC, Bret-Harte MS, Hollingsworth RN, Jandt RR, Schuur EAG, Shaver GR, Verbyla DL. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. *Nature* 475: 489–492.
- Moritz MA, Parisien M-A, Batllori E, Krawchuk MA, Van Dorn J, Ganz DJ, Hayhoe K. 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3: 49.
- Mosca E, Eckert AE, Di Pierro EA, Rocchini D, La Porta N, Belletti P. 2012. The geographical and environmental determinants of genetic diversity for four alpine conifers of the European Alps. *Molecular Ecology* 21: 5530–5545.
- Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmsking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC *et al.* 2015. Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change* 5: 887–891.
- Nebel B, Matile P. 1992. Longevity and senescence of needles in *Pinus cembra* L. *Trees—Structure and Function* 6: 156–161.
- Öberg L, Kullman L. 2011. Ancient subalpine clonal spruces (*Picea abies*): sources of postglacial vegetation history in the Swedish Scandes. *Arctic* 64: 183–196.
- Ortu E, Peyron O, Bordon A, de Beaulieu JL, Siniscalco C, Caramiella R. 2008. Lateglacial and Holocene climate oscillations in the South-western Alps: an attempt at quantitative reconstruction. *Quaternary International* 190: 71–88.
- Parducci L, Jorgensen T, Tollefsrud M, Elverland E, Alm T, Fontana SL, Bennett KD, Haile J, Matetovici I, Suyama Y *et al.* 2012. Glacial survival of boreal trees in Northern Scandinavia. *Science* 335: 1083–1086.
- Pausas JG, Ribeiro E. 2013. The global fire-productivity relationship. *Global Ecology and Biogeography* 22: 728–736.
- Payette S, Morneau C, Sirois L, Despons M. 1989. Recent fire history of the northern Quebec biomes. *Ecology* 70: 656–673.
- Prentice IC, Sykes MT, Cramer WA. 1993. simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling* 65: 51–70.
- Ravazzi C, Badino F, Marsetti D, Patera G, Reimer PJ. 2012. Glacial to paraglacial history and forest recovery in the Oglio glacier system (Italian Alps) between 26 and 15 ka cal BP. *Quaternary Science Reviews* 58: 146–161.
- Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Ramsey CB, Buck CE, Cheng H, Edwards RL, Friedrich M *et al.* 2013. INTCAL13 and MARINE13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55: 1869–1887.
- Rocha AV, Lorant MM, Higuera PE, Mack MC, Hu FS, Jones BM, Breen AL, Rastetter ED, Goetz SJ, Shaver GR. 2012. The footprint of Alaskan tundra fires during the past half-century: implications for surface properties and radiative forcing. *Environmental Research Letters* 7: 044039.
- Saulnier M, Talon B, Edouard JL. 2015. New pediaanthracological data for the long-term history of forest species at mid-high altitudes in the Queyras Valley (Inner Alps). *Quaternary International* 366: 15–24.
- Serre F. 1978. The dendroclimatological value of the European Larch (*Larix decidua* Mill.) in the French Maritime Alps. *Tree-Ring Bulletin* 38: 25–34.
- Simonsen TJ, Huemer P. 2014. Phylogeography of *Hepialus humilis* (L.) (Lepidoptera: Hepialidae) in Europe: short distance vs. large scale postglacial expansions from multiple Alpine refugia and taxonomic implications. *Insect Systematics & Evolution* 45: 209–250.
- Stephens FR. 1969. A forest ecosystem on a glacier in Alaska. *Arctic* 22: 441–444.
- Stuiver M, Reimer PJ. 1993. Extended <sup>14</sup>C data base and revised CALIB 3.0 14C age calibration program. *Radiocarbon* 35: 215–230.

- Sturm M, Racine C, Tape KD. 2001. Increasing shrub abundance in the Arctic. *Nature* 411: 546–547.
- Svenning J-C, Normand S, Kageyama M. 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *Journal of Ecology* 96: 1117–1127.
- Tinner W, Kaltenrieder P. 2005. Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. *Journal of Ecology* 93: 936–947.
- Tranquillini W. 1979. *Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps*. Berlin, Germany: Springer-Verlag.
- Tzedakis PC, Emerson BC, Hewitt GM. 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends in Ecology & Evolution* 28: 696–704.
- Willis KJ, Rudner E, Sumegi P. 2000. The full-glacial forests of central and southeastern Europe. *Quaternary Research* 53: 203–213.
- Zoller H. 1981. Gymnospermae. In: Hegi G, ed. *Illustrierte Flora von Mitteleuropa Band 1, Teil 2*. Berlin, Germany: Paul Parey, 11–148.
- Zumbrunnen T, Bugmann H, Conedera M, Burgi M. 2009. Linking forest fire regimes and climate—A historical analysis in a dry Inner Alpine Valley. *Ecosystems* 12: 73–86.

## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Pictures of Lake du Lait and Lake Miroir and, in the background, aerial picture of Lake Miroir with a sketch of the possible glacier cover during the LGM according to landform observations and geomorphological results.

**Fig. S2** Statistical elements of charcoal series analyses: signal to noise index and Kolmogorov–Smirnov goodness of fit.

**Fig. S3** Cumulative fire numbers at each date based on the 65 selected ensemble-member fire dates for Lake Miroir charcoal records.

**Fig. S4** The complete sediment profile, from the top-most centimeters to the bottom.

**Fig. S5** Six detailed views of sediment profile showing the laminations and the color of sediment.

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