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# Holocene fires and a herb-dominated understorey track wetter climates in subalpine forests

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## Summary

**1.** Relationships between vegetation, climate and disturbance are likely to be altered in the near future as a result of changes in both climate and human impacts on ecosystems. These changes could trigger species losses and distribution shifts in sensitive (e.g. mountainous) ecosystems. Models project a 2.5–3 °C increase in global temperatures by the end of the 21st century, and combined with effects of current land-use abandonment (leading to the build-up of fuel material); these increases could cause future ecosystems to become similar to ecosystems of the first half of the Holocene when human impact was negligible.

**2.** A high-resolution macroremain record from a small subalpine lake in Italy allowed us to examine 8000 years of stand vegetation dynamics. Linkages between disturbance, vegetation and climate were deciphered by reconstructing local fire occurrence patterns from charcoal remains, characterizing plant species richness by rarefaction analysis, and regional climatic reconstructions in the light of the human archaeological context.

**3.** Before 5100 cal. year BP, forest ecosystems had fluctuating richness and an intermediate mean fire frequency. The climate was warmer and drier than today. From *c.* 5100 to 2200 cal. year BP when the climate became wetter, a higher fire frequency promoted the establishment of mixed ecosystems with several tree species, a herbaceous understorey and higher richness. The last 2200 years were characterized by a decrease in richness, a lower fire frequency, and lower temperatures and precipitation. Over the last 8000 years, the probability of fire has increased with time since the last fire, probably as a result of increased fuel-load or composition, which has assisted the spread of fire.

**4.** *Synthesis.* The fire frequency was higher when forest richness was higher, during periods of wetter climate. Temperatures had no correlation with the fire frequency and the ecosystem dynamics in the study region.

**Key-words:** charcoal, climate, disturbance ecology, fire, forest, Holocene, land-use history, palaeoecology, rarefaction analysis, richness

## Introduction

Natural disturbances are often long-term processes that affect vegetation structure, diversity and dynamics by influencing the abundance, composition and distribution of species and changing the physical features of ecosystems and the distribution of the resources they contain (Pickett & White 1985; Johnson & Miyanishi 2006). Previous studies have shown clear relationships between diversity and disturbance by fires (Glitzenstein, Streng & Wade 2003), windstorms (Hiura 1995), insect outbreaks (Stone & Wolfe 1996) and avalanches (Rixen *et al.* 2007). These relationships are dependent on the type, severity, frequency and location of the disturbances, and on the interactions between the disturbances, other features and processes that affect ecosystems (such as resilience), post-disturbance dynamics and nutrient cycling (McCullough, Werner & Neumann 1998; Veblen *et al.* 1994). Expected changes in climate and human activities could modify the linkages among ecosystem properties and disturbances, and disturbance regimes are likely to change following global warming (Schumacher & Bugmann 2006; Bergeron *et al.* in press).

Palaeoecology allows the long-term relations between disturbance and diversity to be assessed. During the Holocene climatic optimum (HCO, *c.* 8000–5000 cal. BP), Europe was *c.* 1–1.5 °C warmer than today (Renssen *et al.* 2009), and human impact was negligible at the time, although pre-historic

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man was already scattered across Europe. Climate scenarios project a 2.5–3 °C global temperature increase by the end of the 21st century (IPCC 2007), and combined with current and future land-use abandonment, this will probably cause some ecosystems to become comparable to those that prevailed during the HCO, excluding the expected fertilization effect of elevated $CO_2$ (LaMarche *et al.* 1984). Mountain ecosystems appear particularly sensitive to climate change (Thuiller *et al.* 2005; Dirnbock, Dullinger & Grabherr 2003) and have been subject to on-going land-use abandonment since the mid-19th or beginning of the 20th century (Chauchard, Carcaillet & Guibal 2007; Motta, Morales & Nola 2006). This process promotes the build-up of fuel in stands and increases forest landscape connectivity.

Understanding the past impacts of climate and disturbance on ecosystem dynamics and species richness is essential for predicting future changes, partly because ecosystems need centuries or more to reach equilibrium following major changes, so experimental analysis of their effects is impossible. Here we explore subalpine ecosystem plant species richness through the Holocene with respect to fire regimes and climate. Examination of the sedimentary macroremains from a subalpine pond over the last 8000 years allowed us to reconstruct the stand dynamics, since terrestrial plant macroremains reliably depict local vegetation (Birks & Birks 2000). Rarefaction analyses (Heck, Vanbelle & Simberloff 1975; Birks & Line 1992), here modified for macroremain records, allowed an assessment of macroremain record richness that is assumed to be related to floristic richness at the local scale. Fire regimes were identified by sedimentary charcoal analyses and the raw data were divided into background levels and peaks relating to fires (Higuera *et al.* 2009). Finally, regional reconstructions of temperature and precipitation (Davis *et al.* 2003; Ortu *et al.* 2008) were compared with the macroremain record. Combining these data sets provided an opportunity to decipher past vegetation dynamics and their linkages with climate and fire history. Although Carcaillet (1998) and Genries *et al.* (2009a) showed that fire is a natural feature of subalpine forest ecosystems, these authors ignored the relationship between this disturbance and floristic richness. In our study area, wildfires have been almost completely inhibited for centuries by man-made grasslands, on which there is little if any woody-fuel accumulation, and by active fire suppression. This study provides useful data for planning sustainable land management policies for ecosystems subjected to biodiversity alteration (Botkin *et al.* 2007).

## Materials and methods

### SITE DESCRIPTION: LAGO PERSO

Lago Perso (44°54′21″ N–6°47′50″ E) is a small north-facing lake (408 $m^2$, with a 0.27-$km^2$ watershed) located at 2000 m a.s.l. within the municipality of Cesana Torinese, in the Susa Valley, Italy (Fig. 1a). The site is situated near the Italian–French border in the western upper Susa valley, which marks the boundary between the Mediterranean Alps, the Queyras massif to the south and the continental Alps to the north. The site is in the internal Alps with a continental-type climate characterized by a mean precipitation of 881 mm $year^{-1}$. The bedrock of the region is composed of carbonated schist, underlying subalpine forest soils, typically Dystrochrepts with ochric orthimull-moder as the most frequent humus type (Motta & Lingua 2005).

The composition and structure of the forest around the lake have been described by Motta & Lingua (2005), based on observations of a permanent plot located nearby. The subalpine forest is mixed, composed of larch (*Larix decidua* Mill.) and arolla pine (*Pinus cembra* L.), with scattered mountain pine (*Pinus mugo* subsp. *uncinata* (DC.) Domin.). The local tree line extends from 2200 to 2300 m a.s.l.

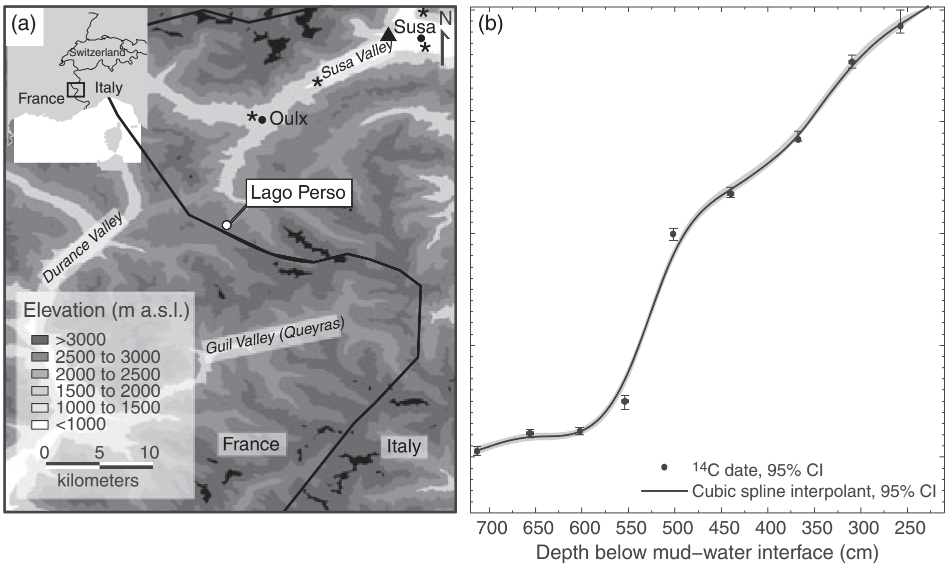

**Fig. 1.** (a) Site location map of Lago Perso, Italy, near the French–Italian border, showing (▲) Middle to Late Neolithic settlements and (*) occasional Neolithic archaeological findings (adapted from Rey & Thirault 1999). (b) The age-depth model for Lago Perso core is based on spline fitting; error bars indicate the error range of the original calibrated radiocarbon ages and the sediment thickness used to calculate dates, 95% upper and lower confidence intervals for the fit are shown (grey area).

The understorey is characterized by *Calamagrostis villosa* (Chaix) J.F.Gmel. and *Festuca paniculata* (L.) Schinz & Thell. The woody understorey is mostly composed of *Juniperus sibirica* Lodd. ex Burgsd., *Rhododendron ferrugineum* L., *Vaccinium myeartillus* L., and *V. vitis-idaea* L. At present, cattle graze the forest in summer.

### SAMPLING, DATING AND CALCULATION OF THE AGE-DEPTH MODEL

Four parallel overlapping sediment cores were extracted from the centre of the lake in January 2008 with a Russian corer (ø = 7.5 cm); the longest core (471 cm of sediment under a 225-cm deep water column) was used for charcoal (ø > 160 μm) and macroremain analyses. Two samples of the topmost water-saturated sediments (0–17 cm) were extracted with a Kajak–Brinkhurst sampler.

Accelerated mass spectrometry (AMS) radiocarbon dating was applied to terrestrial plant remains (Table 1). Each $^{14}$C date was then calibrated in years Before Present (hereafter cal. BP) by the CALIB program (Stuiver & Reimer 1993) version 5.0.1. An age-depth model was then calculated by the MCAgeDepth program (Higuera *et al.* 2009), which applies a Monte Carlo resampling technique to assess median ages and to generate confidence intervals (CI) around the fit based on the probability distribution of each date given by the CALIB program (Fig. 1b). The resulting spline-based age-depth model, associated with the CI from the Monte Carlo simulations, is more robust than those constructed on the basis of ages inferred from the median value of calibrated dates or by the line intersect method. This is because the model assumes a non-normal distribution of each $^{14}$C date, which is weighted in accordance with its standard deviation (e.g. Telford, Heegaard & Birks 2004).

### CHARCOAL ANALYSIS AND THE FIRE HISTORY RECONSTRUCTION

One cm$^3$ of sediment was extracted every 1 cm along the longest core and sieved to retrieve charcoal fragments. In total, a series of 488 contiguous samples was obtained from the core. The samples were soaked in a 5% KOH solution to deflocculate any particles and bleached in a 10% aqueous solution of NaOCl to distinguish charcoal from dark organic matter, then sieved through a 160-μm mesh. Particles larger than 160 μm were assumed to be of stand or local origin (Higuera *et al.* 2007). The area of each charcoal fragment was estimated under a 10× dissecting stereomicroscope equipped with a digital camera and image-analysis software (WinSeedle 2007; ©Regent Instruments Inc., Quebec, Canada). Measurements are reported as charcoal area concentration (mm$^2$ cm$^{-3}$). The age-depth model derived from $^{14}$C dating was applied to estimate charcoal accumulation rates (CHAR, mm$^2$ cm$^{-2}$ year$^{-1}$), from which fire events and intervals were reconstructed, by dividing the charcoal concentrations by the age span between consecutive samples at a constant time step (15 years), as this was the median resolution of the whole record. Since CHAR is highly sensitive to the sediment accumulation rate, we also assessed the extent to which different age-depth models influenced the CHAR reconstruction.

To identify fire events, we divided the CHAR series into CHAR-background and CHAR-peak categories using a locally weighted polynomial regression (LOWESS) smoother with a time window of 900 years, which was approximately three times the expected mean fire interval in the region (*c.* 300 years, Carcaillet *et al.* 2009). The CHAR-peak component was obtained by subtracting the CHAR-background, which represents the variation in overall charcoal production, sedimentation, mixing and sampling, from the CHAR series. Fire events were reconstructed by applying a local threshold to each sample given that the CHAR-peak series was composed of two sub-populations: CHAR-noise and fire; CHAR-fire exceeding the overall variation of CHAR-noise is probably induced by local fires. We assumed that the variability in the CHAR-peak series resulting from sediment mixing, sediment sampling and analytical noise varied on a time-scale > 500 years. Therefore, for each 500-year overlapping window, a Gaussian mixture model was used to evaluate the mean and variance of the CHAR-noise distribution, enabling us to break down the CHAR-peak series locally into CHAR-fire and -noise. For each 500-year window, CHAR-peaks exceeding the 99th percentile of the modelled CHAR-noise distribution were identified as fire events. A signal-to-noise index for threshold values at each interpolated sample was estimated using the following formula (eqn 1):

$$\mathrm{SNI} = \frac{\mathrm{var}(\mathrm{CHAR}_{\mathrm{fire}})}{\mathrm{var}(\mathrm{CHAR}_{\mathrm{fire}}) + \mathrm{var}(\mathrm{CHAR}_{\mathrm{noise}})}, \qquad \text{eqn 1}$$

where the dates of the reconstructed fire events were used to calculate the fire return interval (FRI), defined as the time between two consecutive fire events. The mean FRI over the sequence was estimated by fitting a two-parameter Weibull model—which passed a Kolmogorov–Smirnov goodness-of-fit test ($P > 0.10$)—to the FRI distribution. We estimated the 95% CI for the Weibull scale, *b*, and shape, *c*, parameters based on 1000 bootstrapped samples from the population, to obtain the mean FRI. We then smoothed the fire numbers per 1000 years using a LOWESS function to illustrate the trajectory of the fire frequency. The Weibull parameter *c* indicates whether fire risk

**Table 1.** Radiocarbon measurements on terrestrial plant macroremains and calibration results. The median calibrated ages are inferred from Monte Carlo resampling (see Materials and methods). N, needle; BR, brachyblast; SE, seed. The laboratory code beginning with Poz- indicates measurements carried out at the *Poznan radiocarbon laboratory*, Poland

| Depth (cm) | Laboratory code | $^{14}$C years BP | Dated material | Median age (years cal. BP) | Upper CI (years cal. BP) | Lower CI (years cal. BP) |
|---|---|---|---|---|---|---|
| 255–260 | Poz-25988 | 240 ± 30 | *Larix decidua* N, *Pinus cembra* N | 286 | 1 | 414 |
| 306–313 | Poz-28983 | 1010 ± 40 | *Larix decidua* N, *Pinus cembra* N BR | 928 | 803 | 1036 |
| 365–370 | Poz-25989 | 2290 ± 35 | *Larix decidua* N SE, *Pinus cembra* N BR | 2315 | 2168 | 2349 |
| 436–444 | Poz-28984 | 3060 ± 35 | *Larix decidua* N SE, *Pinus cembra* N BR | 3285 | 3171 | 3358 |
| 500–504 | Poz-25990 | 3675 ± 35 | *Larix decidua* N SE, *Pinus cembra* N BR | 4011 | 3904 | 4129 |
| 550–558 | Poz-27303 | 6120 ± 40 | *Larix decidua* N SE, *Pinus cembra* N BR | 7004 | 6894 | 7151 |
| 600–605 | Poz-26005 | 6670 ± 40 | *Larix decidua* N SE | 7536 | 7469 | 7604 |
| 652–660 | Poz-27304 | 6710 ± 40 | *Larix decidua* N | 7578 | 7502 | 7653 |
| 710–716 | Poz-26004 | 7070 ± 40 | *Larix decidua* N | 7895 | 7810 | 7966 |

has been increasing ($c > 1$), stable ($c \sim 0$) or decreasing ($c < 1$) with time since the last fire (Clark 1989; Johnson & Gutsell 1994).

### PLANT COMMUNITY COMPOSITION: THE MACROFOSSIL ANALYSIS

The longest core was sliced into 488 continuous 1-cm samples, and the volume of each sample was measured to calculate macroremain concentrations. The samples were then soaked in a hot 5% KOH solution to deflocculate them and macroremains were extracted from each sample by water-sieving through a 160-μm mesh (Birks 2001). Plant remains were identified under a stereomicroscope (6.3–50×) by comparing fragments with reference collections of modern plants and information in atlases (Cappers, Bekker & Jans 2006). It was not possible for us to differentiate between birch (*Betula* spp.) species formerly present around the lake, as the scope for identifying birch remains is highly dependent on the quality of their preservation in sediments. For taxonomic identification to species rank, birch remains need further investigation based on biometric descriptors (Freund, Birks & Birks 2001). The macroremain influx (accumulation rate) was expressed as the fragment numbers per $cm^2$ per year ($\# \ cm^{-2} \ year^{-1}$). To highlight the temporal differences in macroremain assemblages, a diagram was numerically zoned by the CONISS program for stratigraphically constrained cluster analysis, i.e. by square-root transformation (Grimm 1987).

To analyse plant population dynamics, macroremain influx values were then log-transformed to minimize the weighting of extreme values on the overall macroremain record (Mahaney *et al.* 2010) and then a min–max transformation (eqn 2) was performed to rescale the different taxa influxes (from 0 to 1) using:

$$x_i' = (x_i - \min(x_i - j))/(\max(x_i - j) - \min(x_i - j)), \qquad \text{eqn 2}$$

where $x_i'$ is the rescaled value of the $i$th sample $x_i$, and $min(x_{i\text{-}j})$ and $max(x_{i\text{-}j})$ are the minimum and maximum values of the $x_i$', respectively. Subsequently, a LOWESS smoother was applied to the record to illustrate the main trends in the trajectories of macroremain influx.

### RAREFACTION ANALYSIS: A RICHNESS INDEX

Trajectories of plant species richness were deduced using a rarefaction index [$E(T_n)$, eqn 3], commonly used to constrain sampling variability. This index is defined by the number of sampled taxa estimated under a constant sum of counted taxa for each record (Birks & Line 1992):

$$E(T_n) = \sum_{i=1}^{T} 1 - \left[ \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right], \qquad \text{eqn 3}$$

where $n$ is the number of individuals from a larger population of $N$ individuals containing $T$ taxa (Heck, Vanbelle & Simberloff 1975). However, this index is not directly applicable to macroremain records for which the minimum number of counted taxa is often equal to zero. This contrasts with pollen records, for which the minimum number of counted taxa is almost always greater than zero. To avoid bias caused by over- or under-estimation of the number of taxa, $E(T_n)$ was calculated separately for each plant zone, defined by the CONISS analysis. Due to the stochastic nature of $E(T_n)$, a LOWESS filter was used to fit the record.

### INDEPENDENT CLIMATE PROXIES

Temperature and precipitation anomaly reconstructions have been inferred from four pollen sequences from the subalpine belt in the south-western Italian Alps, which is close to our study area (Ortu *et al.* 2008). The climate reconstructions are based on the principle of the modern-analogue technique (Overpeck & Webb 1985), with a specific algorithm for each study. 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) for central Western Europe were also used for comparison with our local data, although this data set covers a large region from the Atlantic coast to central Europe.

## Results

### STRATIGRAPHY AND CHRONOLOGY

The spline-based age-depth model was based on the $^{14}C$ AMS dating, and in the absence of any $^{210}Pb$ dating we assumed a date of −58 cal. BP (i.e. AD 2008) at the sediment water interface (Fig. 1; Table 1). The chronology begins at 7900 cal. BP at 716 cm depth. Until 6840 cal. BP (560 cm depth, PER-1 zone, Figs 1 and 2) the sediment accumulation rate was extremely high, 0.37 ± 0.34 mm $year^{-1}$, providing high sampling resolution (6.8 ± 7.2 year $cm^{-1}$), with a maximum between 7890 and 7480 cal. BP (0.45 ± 0.33 cm $year^{-1}$, 3.5 ± 2.3 year $cm^{-1}$). The extreme accumulation rate in this part of the core is likely to be linked to the rapid production of macroremains in the watershed as this part of the core was composed of a gyttja extremely rich in terrestrial plant remains (382 ± 106 *Larix* $\# \ cm^{-3}$ from 716 to 560 cm depth, 7890–6840 cal. BP). From 6840 to −58 cal. BP the sediment accumulation rate decreased, with a mean value of 0.06 ± 0.02 cm $year^{-1}$ (deposition time: 20.8 ± 11.1 year $cm^{-1}$) and little variability according to the low standard deviations. The core was composed of macroremain-rich gyttja from 6840 cal. BP until the top-most sediments.

### FIRE HISTORY

Independently from the age-depth models, the high peaks of CHAR were preserved through the sequence and thus accurately reflect increases in charcoal accumulation that were not caused by chronological artefacts. Over the 7900 years, the fire reconstruction model identified 33 charcoal peaks corresponding to distinct fire events (Fig. 2a). These 33 high charcoal peaks were well differentiated from the charcoal background as the signal-to-noise indices were always greater than 0.5 (Fig. 2b) and thus did not reflect noise in the record, but represented fire events (Higuera *et al.* 2009; Ali *et al.* 2009).

The fire event reconstruction showed three main fire periods over the Holocene (Fig. 2c,d). During the first period, from *c.* 8000 to 5000 cal. BP, the fire frequency was low (3.5 ± 0.3 fires 1000 $year^{-1}$) and the mean fire return interval (FRI) was comparatively long (262 ± 149 year per fire). During the subsequent period, from *c.* 5000 to 2000 cal. BP, there was an increase in fire frequency (5.2 ± 0.6 fires 1000 $year^{-1}$), i.e. the

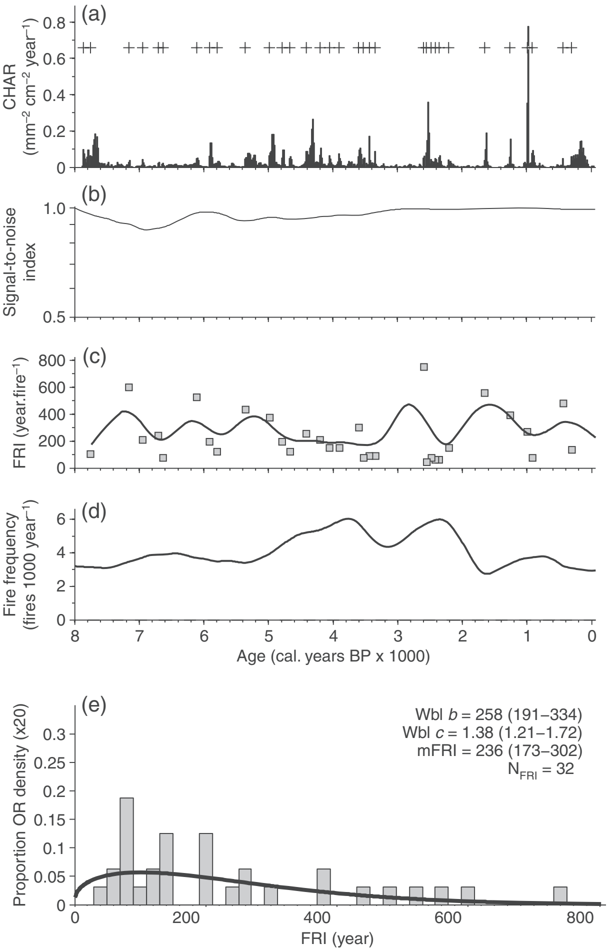

**Fig. 2.** Reconstruction of the fire frequency at Lago Perso, (a) charcoal accumulation rate (CHAR) and reconstructed fire events (+), (b) signal-to-noise index indicating the power of the reconstruction, (c) smoothed fire return intervals (FRI) using a LOWESS curve fitting, (d) smoothed fire frequency using a LOWESS curve fitting, (e) scores for the Weibull model parameters.

FRI became shorter (173 ± 171 year per fire). The most recent part of the record, covering the last two millennia, was marked by a lower fire frequency (3.7 ± 0.6 fires 1000 year$^{-1}$) and a longer FRI (317 ± 174 year per fire). The Weibull *b* parameter provided a mean FRI of 258 year per fire over the whole period with a 95% CI ranging from 191 to 334 year per fire (Fig. 2e). This was consistent with the expected *c*. 300 years mean FRI previously found in a valley situated north of the Susa valley (Carcaillet *et al.* 2009), although the cited mean was obtained using a different statistical method to our study. The parameter *c* of the Weibull model was $>1$ [(1.21–1.72); Fig. 2c], which indicates that the burning hazard increased with time since the last fire.

## VEGETATION HISTORY

The following five main vegetation zones (Fig. 3) were identified by the CONISS analysis.

PER-1 (716–560 cm depth, 7890–6840 cal. BP): from the beginning of the sequence, a tree community was present around the lake. *Larix* remains are abundant in the sediment (53.4 ± 86.7 # cm$^{-2}$ year$^{-1}$) and of diverse types, e.g. needles, seeds, mesoblasts. This suggests a forest composed of mature larch with an understorey composed of dwarf shrub species, including *Vaccinium myeartillus* and *Juniperus sibirica*. Some *Betula* and *Abies alba* remains were also found, indicating that they were present in the vicinity of the lake at this time. A single needle of *Pinus cembra* at *c*. 6950 cal. BP marks the first local occurrence of this taxon.

PER-2 (560–517 cm depth, 6840–5100 cal. BP): *Larix* macroremains still dominate the record, despite a decrease in influx from 53.4 ± 86.7 to 3.1 ± 2.3 # cm$^{-2}$ year$^{-1}$. This zone provides the first evidence of sexually mature *Pinus cembra* (seeds and pollen sacs) in the forest around the lake. *Abies alba* disappeared after 6200 cal. BP.

The main transition of remain assemblages, according to CONISS, occurred at *c*. 5100 cal. BP, corresponding to the transition between the PER-2 and PER-3 zones (Fig. 3). This abrupt transition, well depicted in the diagram by the sharp drop in *Larix* remains, is by far the main ecological transformation that occurred around Lago Perso over the past *c*. 8000 years.

PER-3 (517–365 cm depth, 5100–2200 cal. BP): this zone is characterized by a drop in *Larix* remains from 3.1 ± 2.3 to 0.5 ± 0.2 # cm$^{-2}$ year$^{-1}$and the frequent occurrence of *Potentilla* cf. *erecta*, *Carex* sec. *trisperma* and other *Carex* spp. These changes suggest that the abundance of larch/arolla pine forest increased, accompanied by the establishment of a mire surrounding the lake. *Betula* still occurred until *c*. 3100 cal. BP.

PER-4 (365–314 cm depth, 2200–1100 cal. BP): after a slight increase in *Larix* until *c*. 2200 cal. BP (PER-3), *Larix* then decreased along with *Pinus cembra* and other taxa that were well represented in the older records, most of which almost completely disappeared, including Ericacea, *Potentilla* cf. *erecta*, *Carex* sec. *trisperma* and *Carex* spp. This suggests an increased density of the tree canopy, thus limiting the herb understorey.

PER-5 (314–228 cm depth, from 1100 to –58 cal. BP): from 1100 cal. BP, the abundance of *Larix* and *Pinus cembra* remains in the record increases again from 0.99 ± 0.75 to 2.17 ± 3.29 and 0.05 ± 0.06 to 0.25 ± 0.72 # cm$^{-2}$ year$^{-1}$, respectively. In addition, a shift appears from an understorey dominated by *Vaccinium* species (PER-3 zone) to one characterized by *Arctostaphyllos uva-ursi* (L.) Spreng. and *Juniperus sibirica*. *Potentilla* cf. *erecta*, *Carex* sec. *trisperma* and *Carex* spp. were irregularly and poorly represented, while *Isoetes* spp., which generally grows in lake waters, was present, indicating the occurrence of a mire and shallow waters, probably resulting from sediment aggradation over millennia.

## PLANT POPULATION DYNAMICS

From *c*. 8000 to 6000 cal. BP the ecosystem was mainly characterized by *Larix*, *Abies*, *Betula* and *Vaccinium* species (Fig. 4). The first substantial shift in species dominance occurred at *c*. 6000 cal. BP with a decrease in the abundance of *Larix* and *Abies* that coincided with the first occurrence of *Pinus cembra*

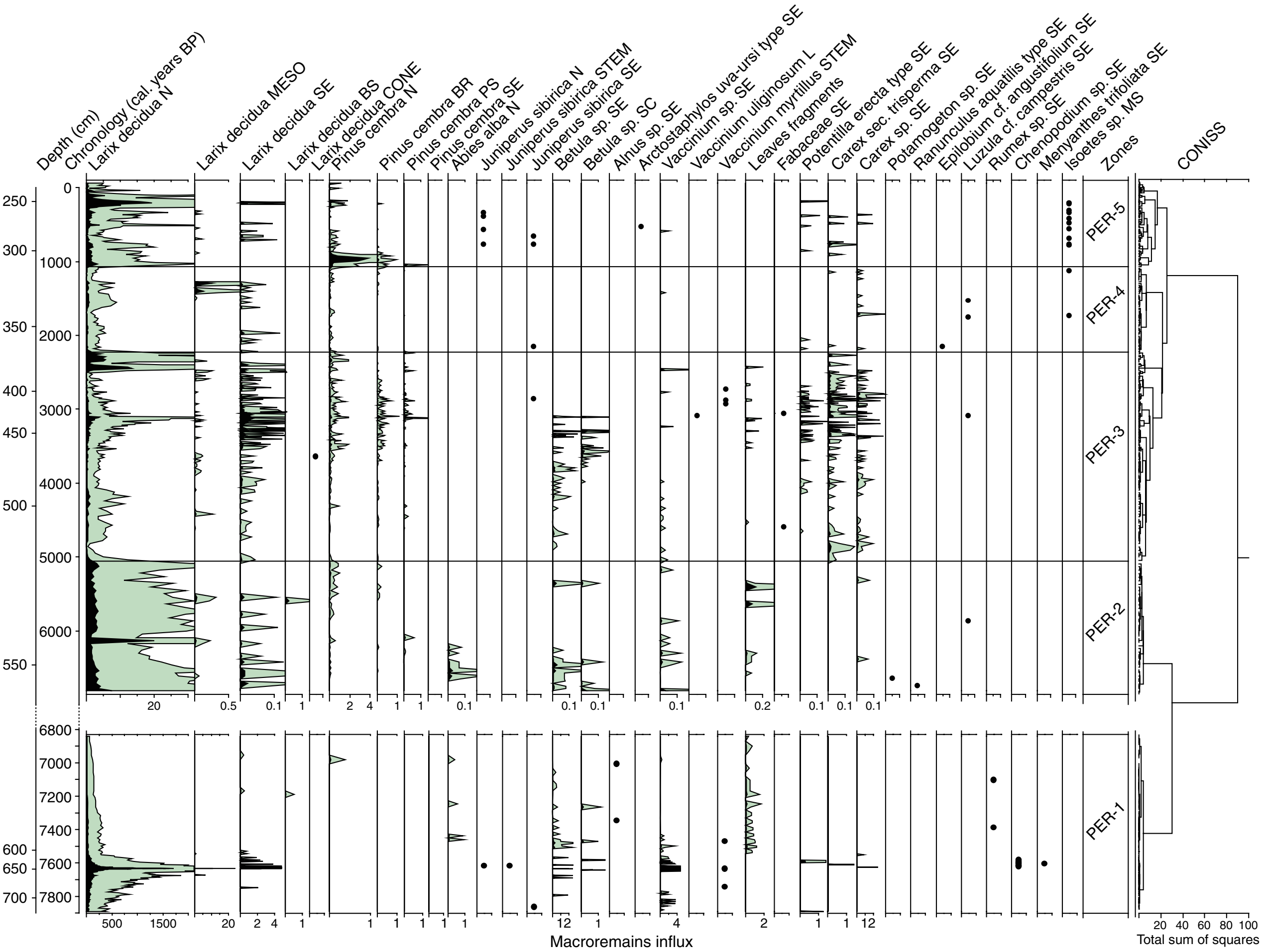

**Fig. 3.** Influx diagram of the terrestrial plant macroremains for Lago Perso sediments. Taxa representing less than 1% of the total influx are represented as presence/absence (dots). 10× exaggerations are shown (grey area). N, needles; ME, mesoblasts (short shoot-bearing needles for *Larix decidua*, brachyblast equivalent); SE, seeds; BR, brachyblasts; PS, pollen sacs; STEM, stem. The CONISS ordination tree is shown on the right. The figure is divided into two parts to highlight macroremains influx variations, influenced by the dramatic change in sediment accumulation rate at 6840 cal. BP, when the sediment accumulation rate decreased from 0.37 ± 0.34 to 0.06 ± 0.02 cm year$^{-1}$.

around the lake. However, the main plant population transformation occurred at 5100 cal. BP with a sharp increase in herb macroremains. Until *c.* 2000 cal. BP, abundant remains of herbs, *Betula* and *Pinus cembra* were the main features characterizing the terrestrial plant community. After 2000 cal. BP, the abundance of almost all of the taxa were below their Holocene mean abundances, except for temporary increases in *Larix*, *Pinus cembra* and *Juniperus sibirica,* indicating a less productive forest community.

### RICHNESS E(T$_N$) VARIATIONS

From 8000 to 5100 cal. BP, E($T_n$) values were almost always below the mean value observed over the whole record, except for a 500-year period around 6200 cal. BP. In contrast, from 5100 to 2200 cal. BP, the rarefaction index was almost always higher than the mean value, indicating that the ecosystem was more diversified during this period. From 2200 cal. BP until the present, $E(T_n)$ was almost always below its mean value except from 1500 to 900 cal. BP, but it remained lower than in the older period (Fig. 4).

### COMPARISON OF VEGETATION, CLIMATE, FIRE AND HUMAN ACTIVITY

Simplified macroremain anomalies (Fig. 5a) were plotted against: $E(T_n)$ (Fig. 5b); fire history (Fig. 5c); summer temperature and precipitation anomalies for the southern Alps from Ortu *et al.* (2008) (Fig 5d); temperature anomalies from Davis *et al.* (2003) for central Western Europe (Fig. 5d); and archaeological periods from (Bocquet 1997) and (Thirault 2004) (Fig. 5e).

The PER-1 zone showed elevated macroremain influxes for all taxa except arolla pine and herbs, while taxa richness, expressed by $E(T_n)$ scores, was highest in the PER-2 zone at *c.* 6500 cal. BP and decreased thereafter. Four fires occurred during the PER-1 period and six during the PER-2 period, leading to a median FRI of 309 ± 107 year per fire until 5100 cal. BP (Fig. 5c). These two zones cover the early, middle and beginning of the late Neolithic, when climatic reconstructions indicate that temperatures were higher and precipitation lower than today, corresponding to the Holocene climatic optimum.

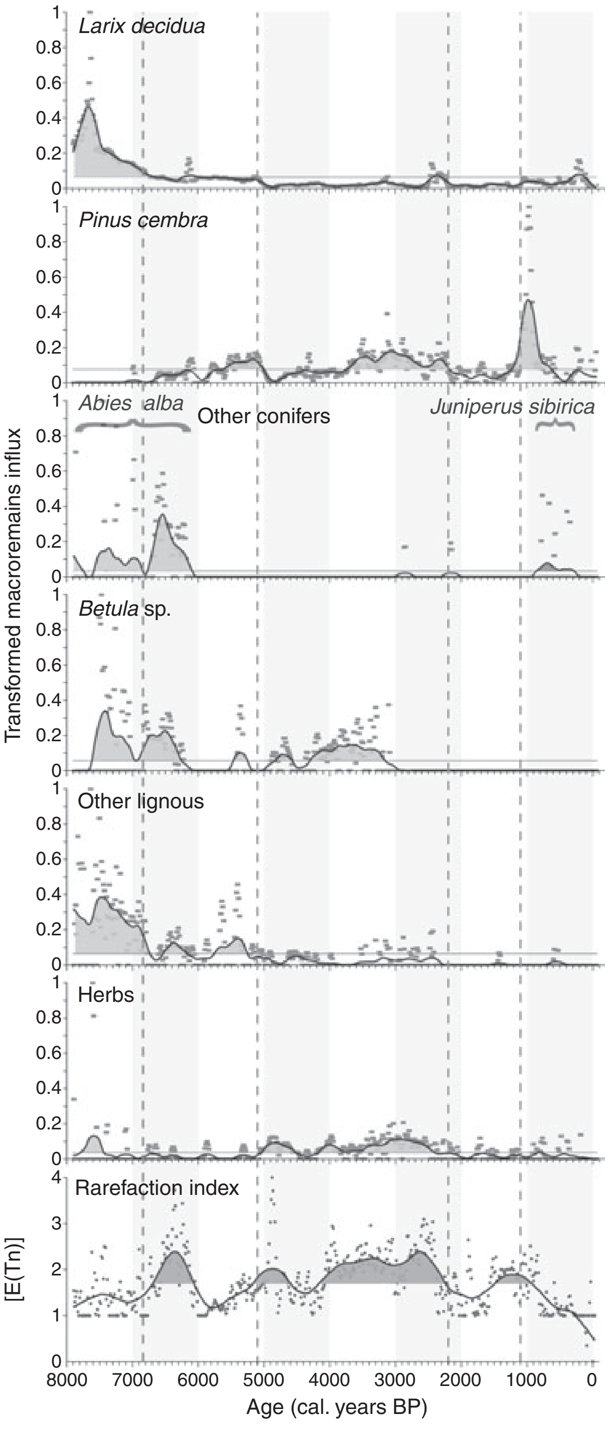

**Fig. 4.** Plant population dynamics inferred from transformed macroremain influxes of the main taxa (see Materials and methods for formula); influxes higher than the record mean value are indicated in grey Rarefaction index values [$E(T_n)$] (see Materials and methods for mathematical formula) and $E(T_n)$ smoothed using LOWESS curve fitting (black curve) are shown in the bottom panel.

The PER-3 zone matches the late Neolithic to the Iron Age period. The temperature reconstructions indicate that temperatures tended to decrease slowly from the end of the climatic optimum, whereas precipitation anomalies had higher values than previously. Conversely, fire frequency and $E(T_n)$ increased during this zone and reached a maximum during the Iron Age at 5.68 ± 0.29 fires 1000 $\text{year}^{-1}$. The increase in richness appears to be linked to the increases in understorey taxa, whereas trees, particularly larch, were less abundant.

During the period covered by the PER-4 zone, from Roman times to the early Middle Ages, the temperatures showed negative anomalies (Ortu *et al.* 2008) or a pattern of slowly decreasing temperatures (Davis *et al.* 2003), whereas precipitation anomalies continued to be mainly positive. This period was marked by lower total macroremains and fewer fires (2 fires 1000 $\text{year}^{-1}$).

During the last period, to modern times (PER-5), temperature and precipitation anomalies remained negative, but fires were less frequent (3.38 ± 0.32 fires 1000 $\text{year}^{-1}$) and the $E(T_n)$ was low, the lowest in the Holocene. These changes were accompanied by an increase and a maximum in influx of *Pinus cembra* between 1300 and 900 cal. BP.

## Discussion

### THE PARADOX OF A *LARIX*-DOMINATED FOREST ASSOCIATED WITH A MEDIUM FIRE FREQUENCY

Over the past 8000 years, *Larix decidua* (larch) has been continuously present around Lago Perso (Fig. 3), especially until 5100 cal. BP when the fire frequency was low with only 3.5 ± 0.3 fire 1000 $\text{year}^{-1}$ (Fig. 2). This is a surprising finding given that larch is a poor competitor and requires a seedbed without humus, or low levels of competition for light from herbs and shrubs. Larch seeds require mineral soil for regeneration and very low soil phenol concentrations for adequate growth and development, as phenols limit nitrogen availability (Hattenschwiler & Vitousek 2000). Larch is thus a generalist tree, matching the *expansionist model* (Barbero *et al.* 1990), colonizing abandoned land (Schulze *et al.* 2007). Disturbance is required to sustain the abundance of larch, otherwise it will be replaced after several decades by other species (Genries *et al.* 2009a). A possible explanation for the long period of larch dominance is that its regeneration may have been permitted by various disturbances in addition to fire, e.g. avalanches or uprooting. Lago Perso is situated along a gentle slope, which is unlikely to be affected by avalanches, so this disturbance is not considered further. Uprooting, which offers mineral soil contact for seedlings, caused by storms, snow or tree ageing is currently so infrequent in such ecosystems that its natural variability is unknown. However, the current low rate of uprooting might be linked to the juvenility of the forests, due to the recent land abandonment (Motta, Morales & Nola 2006), and if so, uprooting might have been more important in the past. A certain rate of uprooting associated with fires, combined with the longevity of larch species, could have sustained larch-dominated ecosystems.

In the western Alps, previous studies have suggested that larch stands expanded during the late Holocene, *c.* 2000 years ago, with the intensification of human activities during the Roman Empire for building-wood production and to create treed pasture for cattle and sheep (e.g. Nakagawa, Edouard &

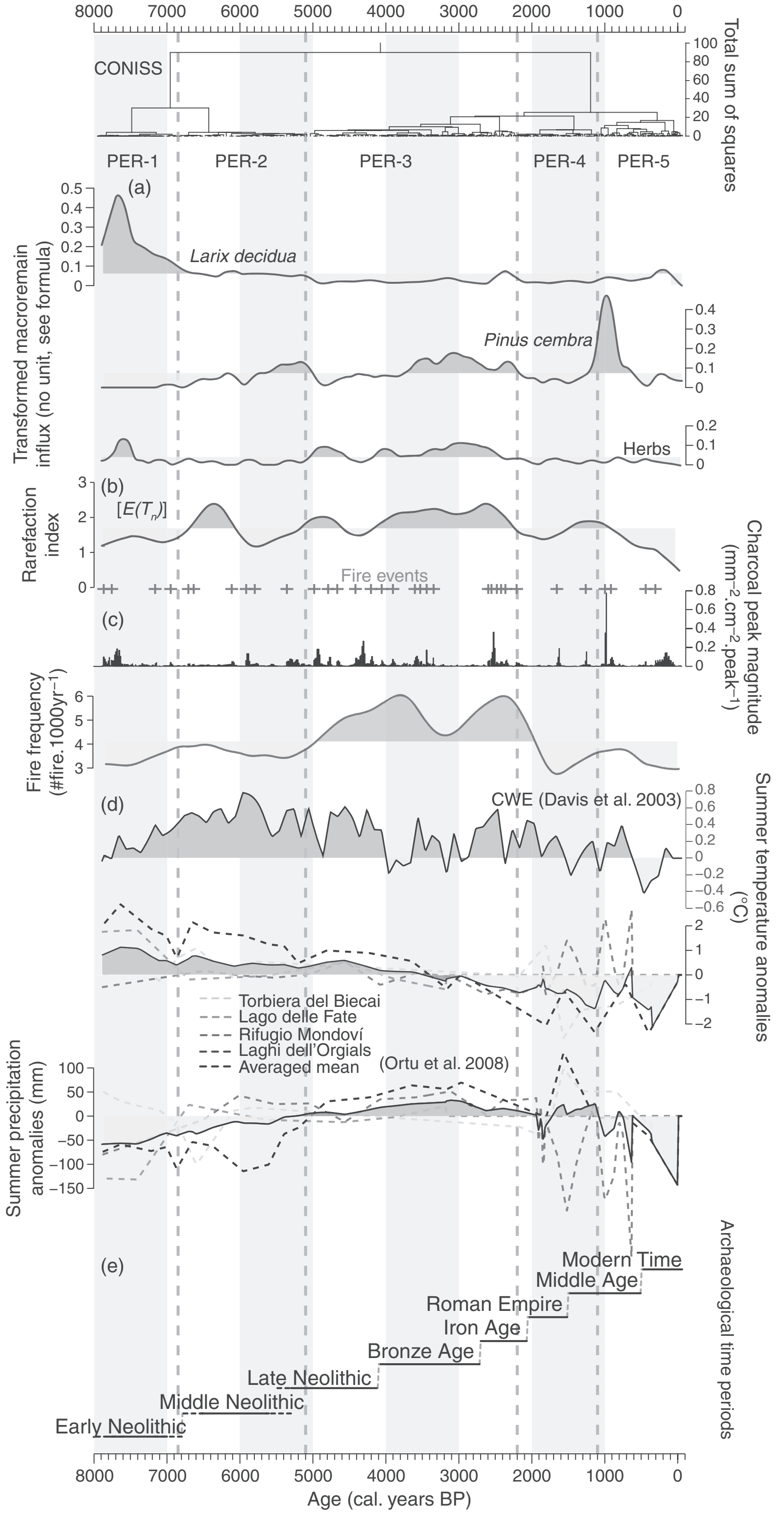

**Fig. 5.** Environmental synthesis. The vertical dotted lines indicate the vegetation periods identified by the CONISS analysis. (a) Smoothed macroremain influxes for the functional taxa (see Materials and methods for formula); influxes higher and lower than mean record values are shown in dark grey and light grey, respectively. (b) Smoothed rarefaction index $[E(T_n)]$, (c) reconstructed fire events and fire frequency, (d) Summer temperature anomalies for Central Western Europe [CWE, black line (Davis *et al.* 2003)], averaged summer temperature and precipitation anomalies from Ortu *et al.* (2008) (the black curve represents averages of the four reconstructions from Torbiera del Biecai, 1920 m a.s.l., Lago delle Fate, 2130 m a.s.l., Rifugio Mondoví, 1760 m a.s.l.and Laghi dell'Orgials, 2240 m a.s.l.; dotted lines from light grey to dark grey). (e) Archaeological periods from Bocquet (1997) and Thirault (2004).

de Beaulieu 2000). However, recent macroremain records have shown that larch has occurred since 11 700 BP at around 1900–2000 m a.s.l. in the region (Ali *et al.* 2006; Blarquez *et al.* 2010) and that larch-dominated communities expanded after the 8200 cal. BP cooling event (Blarquez *et al.* 2010). These results, together with other observations from the central Alps (e.g. Lang & Tobolski 1985; Thuiller *et al.* 2005; Gobet *et al.* 2005), support the evidence that ecosystems with scattered larch occurred since the end of the Late-Glacial period and the occurrence of natural larch-dominant woodlands since *c.* 8000 cal. BP.

Larch woodland with scattered silver firs (*Abies alba*) and birches (*Betula*) persisted until *c.* 6000 cal. BP (Fig. 3). Fir was never abundant although it is a stronger competitor than larch (Robakowski *et al.* 2004), probably because Lago Perso is near the historical upper limit of fir (Carcaillet & Muller 2005; Blarquez *et al.* 2010), thus limiting its capacity to develop. Fir and birch were substituted by arolla pine that expanded around 6500 cal. BP (Fig. 4). This expansion occurred earlier in valleys situated north and southward (Genries *et al.* 2009b; Ali *et al.* 2005; Blarquez *et al.* 2010), but these areas were within mountain ranges facing the western, more oceanic air-masses rather than the eastern Adriatic air-masses like the Susa Valley that encompasses Lago Perso. Interestingly, in the Susa Valley, arolla pine was already present 10 000–9500 cal. BP (Ali *et al.* 2006). Our records clearly indicate that conditions were not completely suited to the establishment of arolla pine at the elevation of Lago Perso.

Whereas silver fir completely disappeared after 6000 cal. BP, birch recovered from 5500 to 3000 cal. BP at the expense of larch and arolla pine, and then disappeared completely. It has been suggested that the decline in fir could have been driven either by an increase in fire frequencies in the northern Italian foothills at *c.* 5000 cal. BP (Tinner *et al.* 1999) or by a drier climate at 6200 cal. BP (Haas *et al.* 1998). However, since we found no evidence of changes in fire frequency around 6000 cal. BP (Fig. 2), or drier conditions (Fig. 5d), it is most likely that fir was out-competed by arolla pine and was disadvantaged by the harsh altitudinal conditions.

### VEGETATION, RICHNESS AND FIRE DYNAMICS

Plant species richness appears to have been closely linked to fire frequency (Figs 4 and 5), since increases in reconstructed fire frequencies occurred during periods with higher rarefaction scores, $E(T_n)$ (Fig. 4). Between 5100 and 2200 cal. BP (PER-3 zone) the fire frequency was high (Fig. 2) and the vegetation was mixed, being composed of arolla pine and larch with birch, and an understorey dominated by herbs and very few ericaceous species (Figs 3 and 4). The increase in fire frequency could explain the ecosystem transformation that occurred in the transition from the period before 5100 cal. BP, but alternatively the vegetation change could have caused the alteration in the fire regime via accompanying changes in fuel quality. This classic *chicken and egg* dilemma is difficult to resolve. However, the expansion of arolla pine after 5500 cal. BP (Fig. 5a), needles of which can promote fire (Genries *et al.* 2009a), appears to have preceded the change in fire frequency, at *c.* 5100 cal. BP (Fig. 5c), indicating that a change in fuel quality or abundance accounts for the change in fire frequency. This conclusion is also supported by the *c*-parameter of the Weibull model (1.38, Fig. 2), which suggests that the probability of burning increased with increases in time since the last fire, which can be explained by the need for a suitable fuel-load for fire to spread, a classic finding in palaeo-fire analyses (Clark 1989; Higuera *et al.* 2009; Carcaillet *et al.* 2001). These results agree with studies in other conifer-dominated ecosystems, suggesting that fire frequency is controlled by fuel availability (Hu *et al.* 2006; Higuera *et al.* 2008, 2009). Changes in fuel abundance or quality can thus explain the shifts in fire frequency. The frequency was low when the vegetation was mainly composed of larch and ericaceous taxa, notably *Vaccinium* (Fig. 3). An ericaceous understorey, especially if dominated by *Vaccinium*, preserves moisture on the ground and in the litter layer, a feature that hinders the spread of fire. Conversely, a herbaceous understorey offers a large amount of fuel, which becomes desiccated due to autumn frosts before snowfall. The scorched herbs, along with the arolla pine needles, then provide fire-promoting fuel.

### IS THE IRON AGE EQUIVALENT TO THE FIRE AGE?

In the upper Susa valley (Fig. 1a), several archaeological sites dating from the Middle to the Late Neolithic have been identified (Rey & Thirault 1999). Although human settlements were present in the valley since at least the Middle Neolithic, we have no evidence of direct human effects on the vegetation from before the Late Neolithic (when fire frequency began to increase) until the Iron Age, i.e. from 5100 to 2200 cal. BP (Fig. 5). The highest fire frequency was recorded during the Iron Age at *c.* 2500 cal. BP, which is consistent with fire patterns in the northern and southern Swiss Alps (Tinner *et al.* 1999, 2005) and in the inner French Alps (Carcaillet *et al.* 2009). Despite the lack of pollen studies reporting information on *cerealia* pollen grains in the upper Susa valley, it is possible that human activities during the Iron Age were responsible for ignition and forest clearance from 2500 cal. BP until the beginning of the Middle Ages. Indeed, cereals were cultivated at altitudes up to 2000 m a.s.l. during the Iron Age in the southern Swiss Alps (Jacomet *et al.* 1999). However, the high abundance of herbs and low influxes of trees were already established features around Lago Perso from the Late Neolithic, indicating that humans are unlikely to have been the ultimate cause of ecosystem transformation before 2500 cal. BP. Between 2200 and 1100 cal. BP, a period covering the Roman Empire and part of the Middle Ages, the low influx of woody species together with the occurrence of early successional species like *Epilobium* cf. *angustifolium* L. and *Luzula* cf. *campestris* (L.) DC. are indicative of a paroxysm of forest clearance.

### CLIMATE CHANGE THROUGH TIME

From 8000 to 5100 cal. BP, when the fire frequency was rather low, the climate was warmer and drier than today (Davis *et al.*

2003; Ortu *et al.* 2008; Fig. 5). The cited climatic reconstructions are based on pollen data and are consistent with chironomid-inferred temperature reconstruction in the Alps (Heiri *et al.* 2003, 2004) and $\delta^{18}O$ measurements of lake ostracods (Grafenstein *et al.* 1999). Hence, warmer and drier conditions did not favour higher fire frequency. Interestingly, the fire frequency increased when the climate became wetter, i.e. after 5000 cal. BP, whereas the temperature decreased slightly from 3500 to 2200 cal. BP (Ortu *et al.* 2008) they remained positive (Davis *et al.* 2003). In such dry regions of the Alps, the probability of fire rises when wet conditions predominate during the 3 years before a fire-year, which is marked by higher than usual temperatures (Zumbrunnen *et al.* 2009). This is because higher precipitation favours understorey fuel accumulation and hence promotes the spread of fire. Consequently, precipitation may be the main limiting climatic factor for subalpine fires. From 5100 to 2200 cal. BP, the changes in precipitation combined with the changes in fuel composition (more herbs, less *Vaccinium*) that occurred since 5500 cal. BP can explain the observed shift in fire frequencies. The reduced temperatures and drier conditions prevailing since 2200 cal. BP have resulted in lower ecosystem productivity and thus the observed lower fire frequency. However, we cannot rule out the possibility that impacts by humans through forest clearance and fire ignition since the Iron Age have contributed to the observed reductions in fires and consequent shifts in forest composition and richness.

## Conclusion

We have shown that periods of increased fire frequency (shorter fire return intervals) occurred during periods of higher plant richness over the last 8000 years at Lago Perso. Before 2500 cal. BP, the ecosystem was mainly influenced by natural processes (disturbance and climate) that maintained larch-rich forests for millennia before the appearance of the mixed larch and arolla pine ecosystem 5500 years ago. This change in fuel composition likely drove the main historical transformation, through a sharp increase in fire frequency from 5100 to 2200 cal. BP and the subsequent expansion of herbs at the expense of dwarf shrubs (i.e. *Vaccinium* spp. and *Juniperus sibirica*). These transformations were accompanied by a change to a wetter climate after 5100 cal. BP and the assumed development of Iron Age activities after 2500 cal. BP. This change in fire frequency co-evolved with the ecosystem dynamics and its richness up to the present day. If both the current land-use abandonment and global warming with droughts continue until the end of the 21st century, subalpine ecosystems might resemble those from 8000 to 6000 cal. BP, which were dominated by larch. However, anthropogenic impacts on these long-lived ecosystems might delay such responses to climate changes by promoting alterations in natural relationships between fire and climate.

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