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Trees in the subalpine belt since 11 700 cal. BP: origin, expansion and alteration of the modern forest

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Abstract: High altitude alpine ecosystems are likely to be highly sensitive to future climate change. Understanding long-term tree stand dynamics may be a key requirement for forecasting such changes. Here, we present a high resolution record of paleobotanical macroremains covering the last 11 700 years, from a small subalpine pond situated in the inner French Alps, at 2035 m a.s.l. The early presence of larch (*Larix decidua*), arolla pine (*Pinus cembra*) and birch (*Betula*) at this elevation, just after the end of the Younger Dryas cold transition, suggests the occurrence of either glacial tree-refugia located nearby in the northwestern Alps, or a previously unrecorded early and rapid tree migration. The 8200 cal. BP cooling event is characterized by a rapid and limited expansion of mountain pine (*Pinus mugo/uncinata* type). Mixed stands of larch, birch and arolla pine established at 8300 cal. BP and were present through the mid Holocene. After the Holocene climatic optimum, at 5600 cal. BP, recurrent fires led to the development of highly dynamic and more diversified forests, with larch, birch, arolla pine, mountain pine and fir (*Abies alba*). Natural and anthropogenic disturbances, e.g., fires, avalanches, slash-and-burn and other agricultural practices, influenced subsequent vegetation until the last millennium when tree-pasture established around the lake. The data indicate that the vegetation was progressively dominated by open larch woodland from 4000 years ago, and was clearly established during the Middle Ages (1250 cal. BP) up to the nineteenth century, when land began to be abandoned. The modern vegetation, dominated by larch and arolla pine and resulting from land abandonment, tends to resemble the communities that occurred from 8300 to 4000 cal. BP, before the postulated anthropogenic alteration of subalpine forest ecosystems. The plant macroremains analysis provides a unique and precise record of stand-to-local vegetation composition and dynamics that can bridge paleoecology and forest management.

Key words: Macroremains, *Larix decidua*, *Pinus cembra*, fire, climate, land uses, 8.2 ky, European Alps.

Introduction

In mountain ecosystems, understanding current changes in ecological conditions is a key research issue (Grace *et al*., 2002; Thuiller *et al*., 2005; Albert *et al*., 2008). Knowledge of past and present conditions is essential for forecasting future change (Gavin *et al*., 2007). Therefore, we need more studies on past vegetation changes in order to analyze future plant distribution and ecosystems dynamics (Peteet, 2000). This should provide useful information on which to plan sustainable management policies for mountain areas (Botkin *et al*., 2007).

In the western Alps, the Holocene subalpine vegetation was mainly dominated by arolla pine (*Pinus cembra*). However, at present, pure stands dominated by this pine are rare and extremely fragmented (review in Ali *et al*., 2005). The origin of the present-day mixed woodlands dominated by larch (*Larix decidua*) and

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spruce (*Picea abies*), in which arolla pine is scattered, is not accurately known. Pollen-based vegetation studies suggest that modern larch-dominated subalpine vegetation results from increasing human activities from the time of the Roman invasion, ie, since 1980 cal. BP (e.g., David, 1995; Nakagawa *et al*., 2000). Other studies indicate that land abandonment results in larch expansion within the subalpine belt (Didier, 2001; Albert *et al*., 2008). Conversely, the abundance of larch macroremains dated from 10 650 cal. BP in the central Alps (Gobet *et al*., 2003) brings into question whether larch-dominated communities in the inner western Alps are natural features. Paleoecology can resolve this question of naturalness by investigating the vegetation during the millennia prior to any human influences on the landscape of the mountains (>5000 cal. BP).

Here, we present a record of plant macroremains, with high temporal resolution, covering the last 11 700 cal. BP, ie, since the beginning of the Holocene according to the chronology of Walker *et al*. (2009). The source area for plant macroremains is limited to less than 100 m horizontal, which means that macroremains are an ideal representation of the stand-to-local vegetation (Warner, 1990; Birks and Birks, 2000). The sediments were collected from a small subalpine pond situated in the French Alps. This research strategy allows a combination of paleoecology and plant ecology to investigate the origin, the setting and the dynamics of the modern subalpine vegetation.

Material and methods

Study site

The Lac du Loup (45°11′15″N–6°32′16″E) is a small, north-facing pond (1400 m^2) situated at 2035m a.s.l. within the commune of Orelle in the upper Maurienne valley, Savoy (Figure 1a). This valley marks the southern edge of the Vanoise and the Grand Arc massifs, forming the boundary between the Mediterranean Alps to the south and the colder western Alps to the north. The following climate data were recorded at 1360 m a.s.l. at Saint-Michel-de-Maurienne for the period 1949–1999. The data depict a continental-type climate with mean annual precipitation of 947±184 mm. The mean annual temperature was 7.1±0.6°C, –0.2±2.2°C for January and 15.5±1.6°C for July. Less precise climate data were recorded at Bissorte dam (2150 m a.s.l., 3 km from the study site) for the period 1949–1955, giving a mean annual temperature of 2.9°C, 10.0°C for July and a mean summer precipitation of 250 mm (in Contini and Lavarello, 1982). The bedrock comprises permo-carboniferous schists and sandstones; soils are acidic and podzols occur under the mature forests (Mourier *et al*., 2008). Mixed stands of larch (*Larix decidua*) and arolla pine (*Pinus cembra*) dominate the present-day local vegetation from 1900 m to 2400 m a.s.l., with scattered spruce (*Picea abies*). The woody understorey is mostly composed of *Juniperus sibirica*, *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. vitis idaea*, *V. uliginosum*, *Arctostaphylos uva-ursi* and *Empetrum hermaphroditum*. Ancient pastures dominated by species of the Poaceae and Cyperaceae also occur on the surrounding slopes.

Sampling

Four parallel cores were extracted in March 2007 with a Russian corer. Two samples of the topmost water-saturated sediments (0–34 cm) were extracted with a Kajak-Brinkhurst sampler. Cores were sliced into 292 contiguous 1 cm samples. The samples were soaked in a hot 5% KOH solution to deflocculate the sediments. Macroremains were then extracted from each sample by water-sieving through a 160 μm mesh (Bhiry and Filion, 2001).

Macroremain identification, analysis and zonation

Plant macroremains were identified under a stereomicroscope (6.3–50×), by comparing fragments with our reference collection of modern material, and with published guides and atlases (e.g., Cappers *et al*., 2006). The distinction between pine species in the section *sylvestris* (*Pinus sylvestris, P. mugo* ssp. *mugo*, *P. mugo* ssp. *uncinata*) was performed by examining transverse sections of needles under a reflected-light microscope (100×, 200× and 500×). The height/width ratio of epidermal cells is >2 for *P. mugo* (ssp. *mugo* and ssp. *uncinata*) and is between 1 and 2 for *P. sylvestris* (Boratyńska and Bobowicz, 2001). Birch species were not differentiated in this study, as the identification of birch remains is highly dependent on the quality of their preservation in sedi-

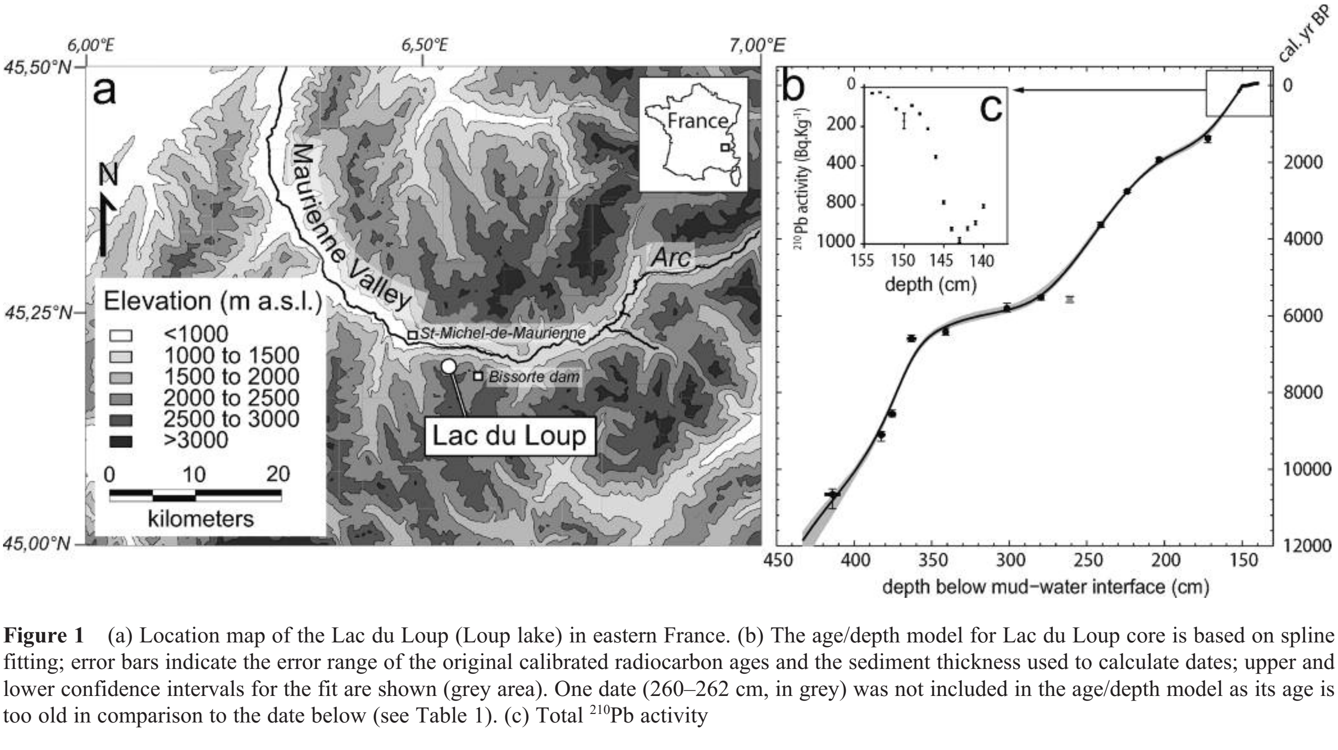

Figure 1 (a) Location map of the Lac du Loup (Loup lake) in eastern France. (b) The age/depth model for Lac du Loup core is based on spline fitting; error bars indicate the error range of the original calibrated radiocarbon ages and the sediment thickness used to calculate dates; upper and lower confidence intervals for the fit are shown (grey area). One date (260–262 cm, in grey) was not included in the age/depth model as its age is too old in comparison to the date below (see Table 1). (c) Total ^{210}Pb activity

Table 1 Results of macroremains ^{14}C dating: depth, codes, ^{14}C ages, material, median calibrated age inferred from the Monte Carlo resampling technique, upper and lower confidence intervals (see Material and methods)

Depth	Lab. code	^{14}C yr BP	Dated material	Median age (yr cal. BP)	Age: upper confidence interval	Age: lower confidence interval
170.0–174.0	Poz-22999	1490±35	*Larix decidua* N SE, *Pinus cembra* N	1370	1318	1478
202.0–205.0	Poz-18280	1985±30	*Larix decidua* N, *Pinus cembra* N, *Betula* SE *BS,* leaves fragments	1934	1883	1989
223.0–225.0	SacA-8347	2630±30	*Larix decidua* N, *Pinus cembra* N, leaves fragments	2754	2734	2781
240.0–242.0	SacA-6901	3385±30	*Betula* SE, leaves fragments	3629	3571	3689
260.0–262.0	SacA-8348	4850±35	*Larix decidua* N, *Pinus cembra* N, leaves fragments	5595	5491	5643
278.0–281.0	SacA-6902	4790±30	*Betula* SE, leaves fragments	5516	5476	5586
300.0–303.0	SacA-6900	5040±30	*Larix decidua* N, *Pinus cembra* N, leaves fragments	5810	5682	5890
340.0–342.0	SacA-6899	5640±40	*Larix decidua* N, *Pinus cembra* N, leaves fragments	6420	6327	6489
360.0–366.0	SacA-8349	5795±35	*Larix decidua* N, *Pinus cembra* N, *Abies alba* N, leaves fragments	6595	6509	6664
373.0–378.0	SacA-8350	7785±40	*Larix decidua* N, *Pinus mugo* N, *Pinus cembra* N, *Abies alba* N, leaves fragments	8562	8466	8623
380.0–385.0	Poz-18282	8160±50	*Larix decidua N, Pinus cembra N, Betula SE BS,* leaves fragments	9105	9021	9253
409.0–419.0	Poz-23000	9420±60	*Larix decidua* N, *Pinus cembra* N, *Betula* SE BS, leaves fragments	10 653	10 529	10 966

ments. These remains need further investigations based on biometric descriptors (van Dinter and Birks, 1996; Freund *et al.*, 2001), for instance geometric measurements (Terral and Mengüal, 1999; Terral *et al.*, 2004). The macroremain influx (= accumulation rate) is expressed as number per cm^2 per year (/cm^2 per yr). To highlight the temporal differences in macroremain assemblages, the diagram was numerically zoned using the CONISS program for stratigraphically constrained cluster analysis, after square root transformation of the data (Grimm, 1987). Differences between macroremain influxes were tested using the non-parametric Mann-Whitney rank test (U-test).

Dating

Twelve AMS ^{14}C measurements were obtained by dating terrestrial plant macroremains. All ^{14}C measurements were calibrated to calendar years before present using the IntCal04 database (Reimer *et al*., 2004) and the Calib 5.0.1 program (Stuiver and Reimer, 1993). Fifteen ^{210}Pb measurements helped to constrain the uppermost chronology, assuming −57 calibrated years BP (cal. BP) at the water/sediment interface, ie, AD 2007, the sampling year. The ^{210}Pb dates were computed using the CRSModel program (Appleby and Oldfield, 1983; ©Philip Higuera, U. Montana). Median ages for each date and confidence interval around it were determined using a Monte Carlo resampling approach, which in the case of ^{210}Pb picks each date randomly from a normal distribution and in the case of ^{14}C selects the date from the calibrated probability distribution. Subsequently, the importance of each age in the spline model was weighted based on its standard deviation, so that ages with larger associated errors had less influence in the model (Telford *et al*., 2004). This method was implemented using the freely available program MCAgeDepth (©Philip Higuera, U. Montana, http://webpages.uidaho.edu/phiguera/software/software.html).

Results

Stratigraphy and chronology

The 11 AMS ^{14}C datings and the 15 ^{210}Pb measurements were used to construct the spline-based age/depth model (Figure 1b, c; Table 1). One date (SacA-8348, 260–262 depth) was not used for the age/depth model, because it was too old when compared with the date below, probably the result of older macroremains being introduced into the sediments (Table 1).

The chronology starts at 11 738 cal. BP. One major change in the sediment accumulation rate is observed at a depth of 360 cm, resulting in the deposition time increasing from 31.7 yr/cm to 60.8 yr/cm. The sediment was composed of laminated clay from depths of 431 to 400 cm, alternating with gyttja from 400 to 378 cm (Figure 2). From 378 cm up to the water–sediment interface, ie, a depth of 140 cm, the sediment was composed of gyttja, rich in plant macroremains. There is a ^{210}Pb anomaly in the topmost 3 cm (Figure 1c). This could result from the current surrounding peat excavation by the lake-owner that may have disturbed the less compacted gyttja sediments.

Vegetation history

The CONISS cluster analysis identified six main zones on the macroremain diagram (Figure 2) as follows.

Loup-1 (431–378 cm, 11 740–8300 cal. BP)

This is a phase of plant establishment. The diversification of the woody cover starts at 11 740 cal. BP with the first occurrences of tree taxa, ie, *Larix decidua* and *Betula* sp. and later, *Pinus cembra*, *Juniperus sibirica*, *Abies alba* and *Pinus mugo/uncinata* types. The latter four dated from 11 285, 11 075, 10 240 and 9155 cal. BP, respectively. The total macroremain influx is extremely low, ie, 0.026±0.019 per cm^2 per yr.

Loup-2 (378–348 cm, 8300–6500 cal. BP)

The influx of *Larix* reaches 0.38±0.23 per cm^2 per yr (61±20% of the total macroremain influx). *Abies* macroremains, including needles and seeds, indicate that mature trees were present around the lake. New taxa appear, with the occurrence of *Vaccinium* shrubs and *Carex* amongst the herbs.

Loup-3 (348–289 cm, 6500–5600 cal. BP)

The sediment accumulation rate reaches 0.065±0.007 cm/yr. *Larix* is dominant with an influx of 1.90±0.80 per cm^2 per yr, ie, 53±8%

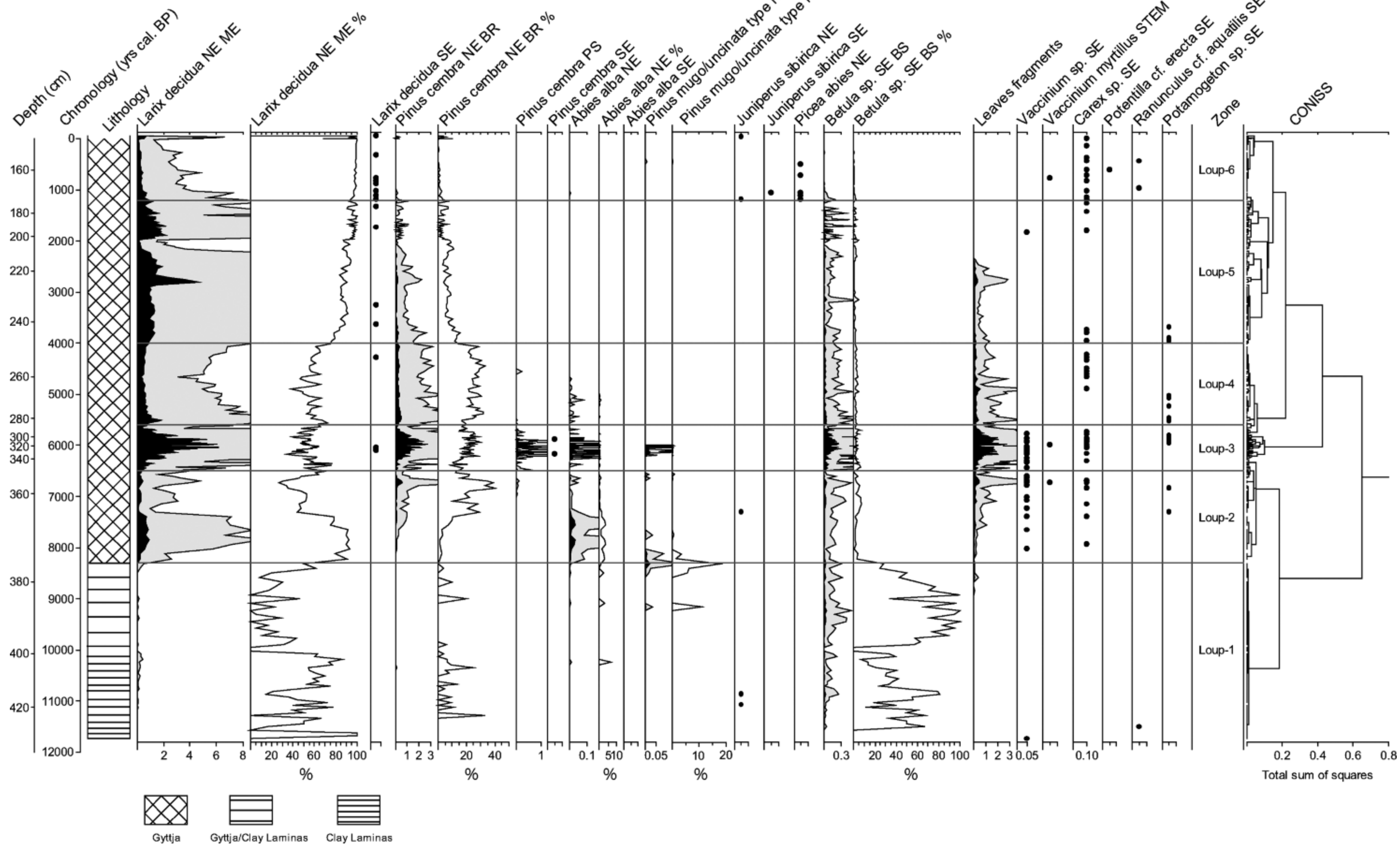

Figure 2 Macroremain diagram for the Lac du Loup sediments with influx values in black and percentages in white. Taxa representing less than 1% of the total influx are represented as presence/absence (dots). The 10× magnification is shown (grey area). N, needles; ME, mesoblasts (short shoot-bearing needles for *Larix decidua*, brachyblast equivalent); SE, seeds; BR, brachyblasts; PS, pollen sacs; STEM, stem

of the total. *Pinus cembra* occurs with an influx of 0.80±0.36 per cm^2 per yr, ie, 21 5% of the total. Numerous *Pinus cembra* pollen sacs and seeds indicate the presence of mature trees. *Pinus mugo/uncinata* type remains are no longer present after 6000 cal. BP.

Loup-4 (289–249 cm, 5600–4000 cal. BP)

After a mid-Holocene maximum in the influx of tree-remains, all taxa start to decline during this zone, e.g., from a rate of 0.80±0.36 to 0.30±0.10 per cm^2 per yr for arolla pine (p<0.01, U-test). *Vaccinium* sp. and *Abies* are almost completely absent after 5600 and 4600 cal. BP, respectively.

Loup-5 (249–169 cm, 4000–1250 cal. BP)

The transition at 4000 cal. BP is marked by a shift between *Larix* and the other trees. The *Larix* influx rises from 0.73±0.34 to 1.32±0.68 per cm^2 per yr (p<0.01, U-test), whereas the arolla pine influx decreases from 0.30±0.10 to 0.08±0.06 per cm^2 per yr (p<0.01, U-test). The *Betula* influx also declines from 0.027±0.014 to 0.013±0.012 per cm^2 per yr (p<0.01, U-test).

Loup-6 (169–140 cm, 1250–0 cal. BP)

Larix accounts for more than 98% of the total influx, but it declines from 1.32±0.68 to 0.35±0.27 per cm^2 per yr (p<0.01, U-test). This zone corresponds to the first occurrences of *Picea abies* at 1315 cal. BP, and some accumulations of *Abies*, *Pinus*, *Vaccinium myrtillus*, *Juniperus* and herbs such as *Ranunculus* cf. *aquatilis*, *Potentilla* cf. *erecta* and *Carex* sp.

Comparisons with fire, climate and archaeological chronologies

The first occurrences of trees at *c*. 11 700 cal. BP (Figure 3a) correspond exactly to the Younger Dryas/Holocene transition (Walker *et al*., 2009), a period marked, in central western Europe (CWE), by an increase in summer temperature anomalies (Davis *et al*., 2003; Ortu *et al*., 2006) and in δ^{18}Op (Oxygen-isotope ratios of precipitation, von Grafenstein *et al*., 1998) (Figure 3b). The Loup-2 zone coincides with an increase in CWE summer temperatures and δ^{18}Op that marks both the beginning of the Holocene climatic optimum (Figure 3b) and the transition from the Mesolithic to the Early Neolithic (Figure 3c). The Loup-2/Loup-3 transition is marked by maximum CWE summer temperature anomalies (Figure 3b), a decrease in the fire intervals (Figure 3d) inferred by Carcaillet *et al*. (2009) and closely corresponds to the early-Neolithic/middle-Neolithic transition (Figure 3c). Fires occurred during the Loup-3 zone or close to it (eight events, Figure 3d) and the period has a high variability of macroremain influxes. The Loup-3/Loup-4 and Loup-4/Loup-5 transitions correspond respectively to the middle-/late-Neolithic and late-Neolithic/Bronze Age transitions. During the Loup-5/Loup-6 transition (1250 cal BP), which falls in the mid Middle Ages, all macroremain anomalies are negative, and there is no evidence of any fires (Figure 3d).

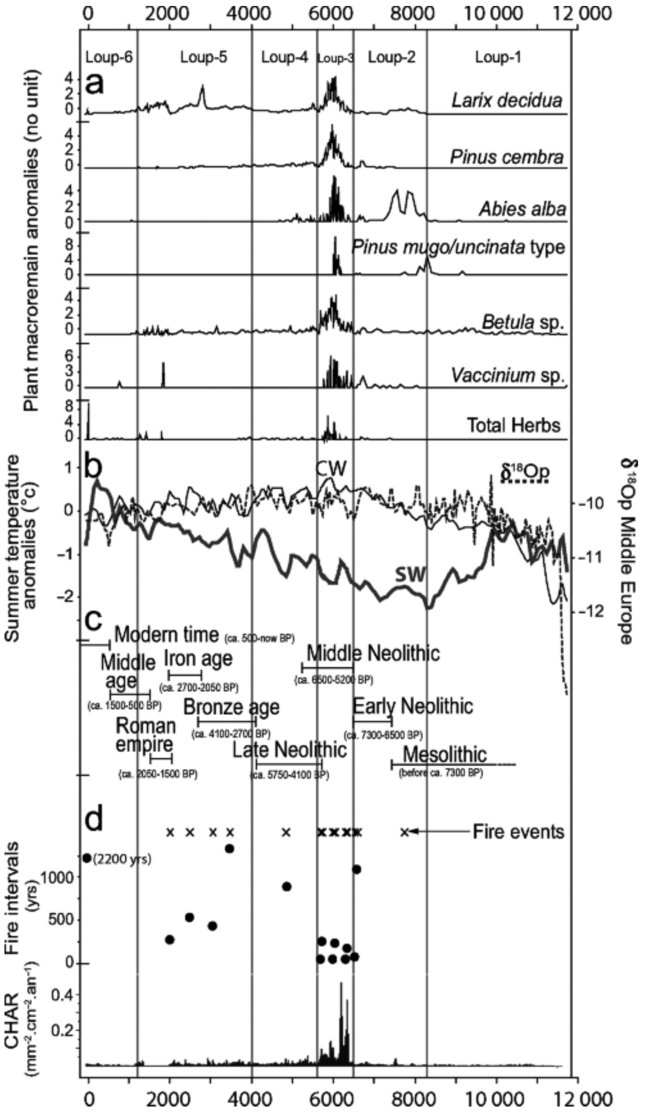

Figure 3 (a) Main plant macroremains anomalies obtained by influx normalization $x' = (x\bar{x}/)\sigma$. (b) Summer temperature anomalies for southwestern Europe (SWE, grey line) and central-western Europe (CWE, black line) (Davis *et al*., 2003). Both temperature anomalies are shown because the study site is close to the transition between central and southern Europe, but only CWE are used to compare with the macroremains, as they better match δ^{18}Op for mid-central Europe (dashed line, von Grafenstein *et al*., 1998). (c) Archeological regional periods after Bocquet (1997). (d) Fire intervals (dots), fire events (crosses) and CHarcoal Accumulation Rate: CHAR (bar chart) after Carcaillet *et al*. (2009)

Discussion

An exceptional presence of trees at the beginning of the Holocene

Based on the chronology, we found that trees were clearly present at the transition between the Younger Dryas cold period and the Holocene. These occurrences of *Larix*, *Pinus cembra* and *Betula* at 2035 m a.s.l. *c*. 11 700 cal. BP are exceptional, because conifers have never been recorded during this transition at such an elevation in the western Alps. This compares with evidence from the central Alps, where *Larix*, *Pinus cembra* and *Betula* have been shown to have been growing above 2000 m a.s.l. since 11 400 cal. BP (Lang and Tobolski, 1985). There is also an exceptional record for larch at 2350 m *c*. 11 350 cal. yr BP (Tinner and Kaltenrieder, 2005). In the western Alps, pollen-based studies have indicated that the upper treeline was at 700–1000 m a.s.l. during the Younger Dryas, 12 900–11 700 cal. BP (David, 1993), ie ~1000–1300 m below the altitude of our observations for 11 700 cal. BP. Our data, combined with other macroremains data from the central Alps (e.g., Lang and Tobolski, 1985; Tinner and Kaltenrieder, 2005) suggest that trees survived the Younger Dryas cooling at elevations close to, or above 2000 m, indicating that pollen-inferred reconstructions may be inaccurate. If conifers were present at 11 700 cal. BP at the beginning of the Holocene, then trees were probably present at the end of the warmer Lateglacial, ie, during the Allerød, which was over around 13 000–12 900 cal.

BP (chronology based on Alley, 2000). In the Maurienne valley, the oldest previous evidence of *Pinus cembra* remains was at 10 180 cal. yr BP and 14 460 cal. BP for *Betula*, in a site situated 2180 m a.s.l. (Carcaillet *et al*., 2009; Genries *et al*., 2009c). Our data strengthen the evidence of tree refugia in this valley or nearby and the occurrence of trees during the Lateglacial above 2000 m. These data from the upper Maurienne valley, combined with evidence from a massif situated 30 km to the south (Ali *et al*., 2003, 2005) and from Switzerland (Tinner and Kaltenrieder 2005; Gobet *et al*., 2005), provide support for the existence of early-Holocene subalpine woodlands composed of conifers (e.g., *Larix*, *P. cembra*, *P. mugo/uncinata*), birch or willows, depending on the site.

During the first millennia between 11 700 and 8300 cal. BP, tree macroremains did not abound, suggesting open vegetation containing scattered trees, with birch and larch being the most frequent species. It seems that the vegetation did not reflect the trend of global warming during the early Holocene (Figure 2) that has been described by von Grafenstein *et al*. (1998), Davis *et al*. (2003), Ortu *et al*. (2006) and Larocque and Finsinger (2008). This apparent inertia of the vegetation could be due to the presence of cold air masses, caused by the remains of glaciers in the alpine massifs (Joerin et *al.,* 2006). However, the inertia could also have been the result of the time needed for soil genesis.

At *c*. 8300 cal. BP, the vegetation transformed abruptly, with the expansion of mountain pine over a period of *c*. 200 years. This short-duration event perfectly matches, within the expected variability of dating and the age/depth model, the well-known ‘8200 cal. BP event’ initially pinpointed in Greenland cores (Dansgaard *et al.*, 1989). It appears that the vegetation transition was triggered by climatic changes, whatever the likely inertia in previous centuries. Surprisingly, the abrupt increase in mountain pine from 8300 to 8100 cal. BP matches the increase in pine-pollen observed in Switzerland (Tinner and Lotter, 2001), strongly indicating that large-scale processes were affecting alpine regions. The 8200 cal. BP climatic reversal promoted mountain pine, before subsequent expansion of silver fir, arolla pine and larch (Figure 3). Our 8300–8100 cal. BP event, characterized by an increase in mountain pine, appears to have been the result of drier rather than colder conditions, because mountain pine tends to occur on the drier mountains of southern Mediterranean Europe (Ozenda, 1985). Arolla pine and larch have the same altitudinal adaptations as mountain pine. Interestingly, the reconstructions of Ortu *et al*. (2006) include a drier event (a ~200mm decrease in annual precipitation) *c*. 8200 cal. BP in the southwestern Alps.

The sudden increase in influx of plant remains after 8300 cal. BP closely corresponds to a rise in summer temperatures and δ^{18}Op for mid Europe (von Grafenstein *et al*., 1998; Davis *et al*., 2003), which marks the beginning of the Holocene climatic optimum. This suggests that climate-driven vegetation dynamics produced a mixed larch/arolla pine/birch woodland with scattered mountain pines and firs that persisted through the climatic optimum, ie, up to 4000 cal. BP.

Middle- to late-Holocene vegetation changes

After 6500 cal. BP (Loup-3), the vegetation was affected by different factors. The site experienced 14 fire events between 7650 and 2150 cal. BP, with a maximum of eight fires between 6550 and 5600 cal. BP (Figure 3d). Fire may have promoted important transformations and fluxes in the vegetation between 6500 and 5600 cal. BP, a zone with an increase in total macroremain influx and variability (Figure 3a). This fire epoch corresponds with the Holocene climatic optimum, a period with high temperatures (Davis *et al.,* 2003). The decrease in fire occurrence after 5650 cal. BP (Figure 3d), corresponds with a lower total macroremains influx, probably reflecting an opening-up of the forest that lasted until 4000 cal. BP, a period of 1600 years. This episode closely resembles a fire–vegetation sequence observed a few kilometers away on the south-facing slopes of the same valley, where fires became rare from 6600 to 5000 cal. BP and the total pollen and macroremains influx dropped for 1600 years (Genries *et al*., 2009a). These two sequences are extremely similar, although they are from different locations. The sequences both follow an epoch of short fire intervals, so the role of fire as a key process is certainly likely. Gobet *et al*. (2003) have suggested that the opening-up of the vegetation in the Engadine region was related to permanent settlements during the Bronze Age (*c*. 3900 cal. BP). Although direct evidence of permanent settlements at this elevation in the Maurienne Valley is still lacking, possible human impact might explain the trend towards the opening-up of woody vegetation after 4000 cal. BP. This would have been the result of first slash-and-burn and later grazing activities at the Neolithic/Bronze age transition and again after the Roman Empire (Figure 3c). However, because arolla pine is the main fuel of subalpine fires (Genries *et al*., 2009a), the recurring short fire interval could have altered forest productivity and the regeneration capacity of the forest communities. Such a process has also been recorded in the same region but later, between 2500 and 1800 cal. BP, when fire frequency increased. This was before the total suppression of the arolla pine-forest 300 years later (1500 cal. BP) and its replacement by a grass-dominated ecosystem (Genries *et al*., 2009c). At our study-site, after 2150 cal. BP, the lack of fires (until the present), the continuous decrease in tree remains and the presence of herb remains during the Iron age and the Roman Empire (Figure 2), all suggest that grass biomass increased, although some trees still remained around the lake. The development of a grass-dominated ecosystem occurred well before the Middle Ages. The Middle Ages were characterized by total fire suppression, the first occurrences of spruce and a huge decrease in the abundance of tree remains, particularly *P. cembra*, which almost disappeared (Figures 2 and 3a). This indicates that open woodlands progressively dominated by larch date back from 1250 cal. BP until the nineteenth century, when land abandonment began (Didier, 2001). The modern vegetation dominated by larch and arolla pine, resulting from the land abandonment, tends to resemble the vegetation that occurred from 8300 to 4000 cal. BP.

Presence of *Larix decidua* woodland

Our results do not support a former assertion that larch stands expanded in the subalpine belt *c*. 2000 years ago, corresponding with the intensification of slash-and-burn practices dating from the period of the Roman Empire (e.g., David, 1995; Nakagawa *et al*., 2000). This assertion was constructed with no direct evidence of fire (no charcoal analyses were performed in these studies) and with chronologies poorly supported by ^{14}C measurements. In contrast, our data show that the mixed larch/arolla pine woodlands could have been present throughout the entire Holocene. Larch is a resilient species, commonly found in early successional stages or disturbed stands (Lingua *et al*., 2008; Genries *et al*., 2009b). The continuous presence of *Larix* since 11 700 cal. BP might have been the result of avalanches (Rixen *et al*., 2007). Indeed, the site topography is favourable to snow avalanches (e.g. >10 avalanches recorded during the twentieth century around the Lac du Loup pond). The absence of *Alnus viridis* macroremains in our record, a species well adapted to avalanches, needs further investigation. Indeed, its absence does not exclude the importance of avalanches in ecosystem function around Lac du Loup as *Alnus viridis* expansion in the Alps is highly dependent on current land-use abandonment (e.g., Didier, 2001; Anthelme *et al*., 2007): it grows in avalanche tracks, the location to which this species has been relegated by domestic grazing (Richard, 1990). In addition, we cannot rule out the effect of the northerly aspect of the slope, which would have favoured deciduous conifers, such as *Larix* (Muller *et al*., 2000). Severe disturbance, including avalanches and fires, may overcome the direct effect of climate changes on ecosystem composition during the Holocene and may have promoted larch woodlands.

Conclusion

The early presence of conifers and *Betula* 11 700 years ago at 2035 m a.s.l. is probably the result of unknown glacial refugia in the northwestern Alps, or an extremely rapid and early migration of trees that has not been recorded before in this area. Between 11 700 and 4000 cal. BP, the vegetation was affected by the global and regional climate, as subalpine vegetation primarily reacted to rapid climate warming after the 8.2 ky event. Larch/arolla pine woodlands that established around 8300 cal. BP persisted until 4000 cal. BP, then progressively declined, disappearing 1300 years ago. This supports the suggestion that the mixed larch/arolla pine stands that have expand around the study site since the nineteenth century are the natural vegetation. During the Holocene climatic optimum *c.* 6500–5600 cal. BP, macroremain fluctuations were probably related to disturbances such as fires, while snow avalanches or the northern exposure of the slope might explain the abundance of larch woodlands over the entire period. Plant macroremains analysis provides a unique and precise record of stand-to-local vegetation composition; its use should be encouraged to obtain better records of past dynamics in order to bridge the gap between paleoecology and forest management.

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