



Early to late Holocene vegetation and fire dynamics at the treeline in the Maritime Alps

Walter Finsinger¹ · Quentin Vanel² · Adriano Ribolini³ · Willy Tinner⁴

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Abstract

We used pollen, plant macrofossil, and charcoal records to investigate local long-term timberline shifts and changes in vegetation composition in relation to fire activity at the modern upper forest limit (ca. 2,000 m a.s.l.) in the Mont Bégo area, Maritime Alps of France and Italy. The area is an important place for Alpine archaeology because it has thousands rock-art carvings whose age cannot be directly assessed. Our new record confirms the occurrence of distinct land use phases (7,450–7,150, 6,200–4,900, and 4,250–3,700 cal BP), as suggested by earlier studies of rock art typology. Moreover, the vegetation reconstruction from macrofossils, with co-dominance of *Pinus* and *Betula*, suggests that early Holocene conditions were moister than in drier inner Alpine valleys, where *Larix decidua* played a more important role, both in the past as well as in modern timberline forests. After 8,000 cal BP, the timberline shifted upwards and mixed *Abies alba* and *Pinus cembra* stands established around the study site. These fire sensitive trees were finally replaced during the Bronze Age (around 4,000 cal BP) by *L. decidua*, which still dominates the subalpine woodlands in the area today. Our study supports the notion that while the range of *A. alba* has been reduced at the colder end of its natural distribution, that of *L. decidua* has been widened by land use changes and fire disturbances to create high alpine wood pastures.

Keywords Vegetation dynamics · Mountain ecosystems · Treeline ecotone · Land use phases · Wood pasture · Fires

Introduction

In mountain landscapes, the altitudinal treeline ecotone marks a prominent ecosystem boundary (Arno and Hammerly 1984) between the upper limit of subalpine closed

forest (the timberline or forest line) and open alpine meadows above stands of stunted trees (*Krummholz*) and tree seedlings (tree species line) (Körner 2003). While the species composition of the treeline ecotone and of subalpine forests is mainly influenced by water availability, rainfall, soils and disturbances (Henne et al. 2011; Schwörer et al. 2014a), the upper limit of tree growth is primarily determined by regional temperature (Körner and Paulsen 2004; Holtmeier and Broll 2005; Holtmeier 2009). Therefore, climatic changes are expected to lead to both altitudinal shifts in its position and changes in species composition (Walther et al. 2005; Heiri et al. 2006). However, in addition to being influenced by these factors, both the position and composition of the timberline and of subalpine forests can be substantially modified by human activities (Arno and Hammerly 1984). In the European Alps, with their long history of land use (Millennium Ecosystem Assessment 2005), subalpine forests and treeline ecotones have been used for millennia to create pastures for grazing, often with the use of fire (Tinner 2007).

Palaeoecology provides long-term records of changes in timberline position, composition and past trends of fire

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✉ Walter Finsinger
walter.finsinger@umontpellier.fr

¹ ISEM, University of Montpellier, CNRS, EPHE, IRD, Montpellier, France

² Ecosphère, Agence Nord-Ouest, 28 rue du Moulin, 60490 Cuvilly, France

³ Dipartimento di Scienze della Terra, Università di Pisa, 56126 Pisa, Italy

⁴ Oeschger Centre for Climate Change Research and Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

activity (Tinner 2007; Conedera et al. 2009). Such proxy-based reconstructions are relevant for estimating vegetation responses to changes in environmental conditions and land use (Tinner 2007), thereby revealing cultural legacies of forested landscapes that are often viewed as ancient (Willis and Birks 2006; Feurdean et al. 2009). As a result, there have been a growing number of studies on long-term tree-line dynamics in the European Alps (for example, Lang and Tobolski 1985; Tinner et al. 1996; Wick and Tinner 1997; Wick et al. 2003; Tinner and Kaltenrieder 2005; Lotter et al. 2006; Finsinger and Tinner 2007; Blarquez et al. 2010; Berthel et al. 2012; Rey et al. 2013; Schwörer et al. 2014b) and elsewhere (for example, Herring et al. 2018; Orbán et al. 2018; Finsinger et al. 2018).

In this study, we discuss treeline vegetation and fire dynamics in the Vallée des Merveilles and Mont Bégo (2,872 m a.s.l.) area, an area in the Argentera Massif between France and Italy which is especially known for the 36,000 examples of rock art distributed among ca. 4,200 sites between 2,000 and 2,700 m that were described as early as in the 16th century (Arcà 2018) and have been more intensively studied since the end of the 19th century (Bicknell 1913; Conti 1940, 1972; de Lumley 1984, 1995). Recently, a chronology of the phases of land occupation and abandonment represented by this rock art has been proposed (Binder et al. 2009; Huet 2017). However, because rock carvings cannot be dated directly as they lack calcite crusts or organic material, their ages are estimated by their typology, by data from archaeological excavations and surveys (Conti 1940; Louis and Ségui 1949; de Lumley 1995; Machu et al. 2007; Huet 2012), as well as evidence from pollen records with increases of herb pollen such as *Artemisia*, Chenopodiaceae and Poaceae (de Beaulieu 1977; Kharbouch 2000). Moreover, with the exception of pollen from crops and weeds introduced with agriculture, increases of herb pollen in high elevation lake sediments may also be indicative of climate-induced treeline lowering (Heiri et al. 2006). In addition, fires can have a significant and long-lasting impact on vegetation structure and composition by promoting open spaces and fire resistant species over fire sensitive ones (Stähli et al. 2006; Leys et al. 2014; Schwörer et al. 2015).

New taxonomically detailed palaeoecological records that include both plant macrofossil and charcoal records may substantially improve knowledge of local vegetation and fire dynamics at the treeline ecotone in the study area, thereby providing a better link between long term vegetation dynamics, changing environmental conditions and findings from archaeological artefacts, rock carvings and land use phases. Both charcoal and plant macrofossil records may be relevant sources of proxy evidence in this study area, for at least three reasons. First, in mountain settings the combination of plant macrofossil and charcoal records can show past vegetation

dynamics and responses to changing environmental conditions and fire disturbances better than wind-dispersed pollen results (Birks and Birks 2000). Secondly, pollen records (de Beaulieu 1977; Kharbouch 2000; Finsinger 2001; Ortu et al. 2003) suggest that fire-sensitive *Abies alba* (Tinner et al. 1999) was more abundant in the region during the mid Holocene. However, it is unclear at which altitude *A. alba* was able to dominate, and how these trees responded to changing environmental conditions and disturbances, including those from fires. Thirdly, the modern timberline is dominated by *Larix decidua* (Ozenda 1950; Barbero et al. 1973), which is heavily under-represented in pollen records (Sjögren et al. 2008), but much better represented by macrofossils because it sheds needles in large numbers every year (Tinner and Theurillat 2003).

We selected as our study site the Lac des Grenouilles (1,994 m), which is a small lake located at about the modern timberline, ca. 2,000 m (Ozenda 1950) and below the modern potential treeline in the Mont Bégo rock art area (Fig. 1a). Sediments from the shore of this lake have already been analysed for pollen (Kharbouch 2000). However, that sediment sequence was fragmentary (with hiatuses), and no plant macrofossil or charcoal analyses were done. Here we present new temporally and taxonomically highly detailed pollen, spore, stomata, plant macrofossil and charcoal records from sediments collected from the lake centre. Due to its small size (0.015 km²), the lake should collect sufficient plant macrofossils, thereby allowing the reconstruction of past vegetation dynamics in its close surroundings. Because we were particularly interested in local changes in fire activity and vegetation dynamics before and during prehistoric land use phases (7,350–3,700 cal BP), we performed high resolution macroscopic charcoal and plant macrofossil analyses of the early to late Holocene sediments dating from 10,000 to 3,400 cal BP and representing the Mesolithic to early Bronze Age. In addition, we carried out high resolution palynological analyses of the Neolithic to early Bronze Age sediments to investigate relationships between fire and vegetation, using time series analyses (Green 1981; Schwörer et al. 2014b).

Materials and methods

Study area

Lac des Grenouilles (44°05'53"N, 7°29'07"E; 1,994 m) is situated on the south-facing slope of the Argentera Massif in the Maritime Alps, southwestern Alps, at the lower end of a hanging valley (Fig. 1a). Two small seasonal streams feed the lake and one outflow drains into the Vallon de Fontanalba, a tributary of the Vallon de Casterino, in the Roya river basin. At the southwestern end of the valley is Mont

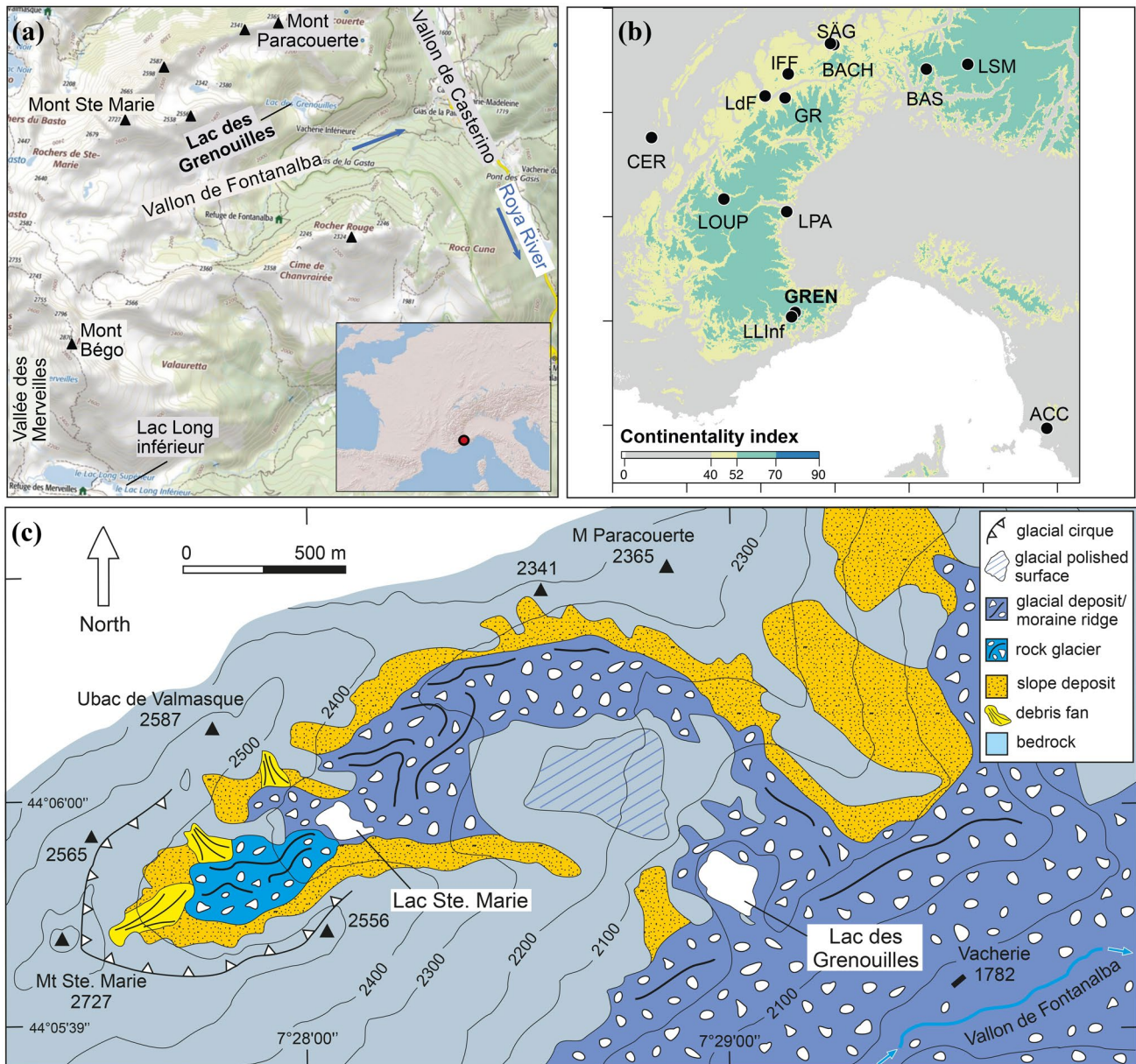


Fig. 1 Maps showing **a**, the location of Lac des Grenouilles in the Mont Bégo area. The inset marks the location of the Argentera Massif in Europe; **b**, the location of the study site (GREN) in relation to other sites discussed in the text; BACH: Bachalpsee (Lotter et al. 2006); SÄG: Sägistalsee (Wick et al. 2003); IFF: Iffigsee (Schwörer et al. 2014b); LdF: Lac de Fully (Finsinger and Tinner 2007); GR: Gouillé Rion (Tinner and Theurillat 2003; Kaltenrieder et al. 2005); CER: Lac de Cerin (Magny et al. 2011); LOUP: Lac du Loup (Blar-

quez et al. 2010); LPA: Lago Piccolo di Avigliana (Finsinger and Tinner 2006); LLInf: Lac Long Inférieur (de Beaulieu 1977); BAS: Lago Basso (Wick and Tinner 1997) and LSM: Lej da San Murezzan (Gobet et al. 2003); ACC: Lago dell'Accesa (Magny et al. 2011); the base map shows the hygric continentality (the ratio of altitude to annual precipitation; Gams 1931, 1932; Ozenda 2002; Holtmeier 2009) recalculated using the WorldClim2 dataset (Fick and Hijmans 2017); **c**, geomorphological features around the catchment of the lake

Bégo, which separates the Vallon de Fontanalba from the Vallée des Merveilles. The majority of rock carvings are in the Vallée des Merveilles as well as in the upper part of the Vallon de Fontalba (Fig. 1a; Huet 2017). The geology of the Mont Bégo area is dominated by Permian granitic and metamorphic rocks (Malaroda et al. 1970). However,

Triassic-Jurassic calcareous and dolomitic rocks and greywacke sandstones occur on the northern slope of the hanging valley (1967).

The study area lies at the edge of the inner Alpine zone, which has a more continental climate with higher temperature seasonality and less rainfall than the outer and

intermediate *Zwischenalpen* zones (Fig. 1b; Ozenda 2002; Landolt 2003). The sub-alpine forests in the inner Alpine zone are dominated by *Pinus cembra*, *Larix decidua* and *Pinus sylvestris* (Ozenda 1985, 2002; Landolt 2003). In the Mont Béggo area, the treeline ecotone and the subalpine woods are dominated by open *L. decidua* wood pastures with small amounts of *P. cembra*, *P. uncinata* and *P. sylvestris*, with a shrub understorey of *Juniperus communis*, *Rhododendron hirsutum* and *Vaccinium myrthillus*. Although the timberline is located at ca. 2,000 m, isolated *L. decidua* and *P. cembra* tree stands grow up to ca. 2,300 m and individual stunted trees > ca. 2 m tall up to 2,400 m (Ozenda 1950; de Beaulieu 1977, own observations). On the northern moister slope of the massif, the timberline is generally substantially lower at ca. 1,700 m and *Fagus sylvatica* is more abundant than on the southern slope (Ozenda 1950). Trees can be found growing in this area up to ca. 2,300–2,400 m (Barbero et al. 1973). Stands dominated by *Abies alba* occur few kilometres to the south of the study site (Ponel et al. 2001) at altitudes of ca. 900 to 1,600 m (Barbero and Bono 1970), ca. 400 m below the study site and the current timberline and ca. 800 m below the treeline. At Lac des Grenouilles, mean monthly temperatures are around $-2\text{ }^{\circ}\text{C}$ in winter and $13\text{ }^{\circ}\text{C}$ in summer. The mean annual precipitation is about 1,000 mm. Monthly rainfall shows the influence of the Mediterranean climate with a bimodal distribution of maxima in spring and autumn with ca. $100\text{--}115\text{ mm month}^{-1}$ and a comparatively drier summer with ca. 50 mm month^{-1} (Fick and Hijmans 2017).

Fieldwork and sediment core correlation

A geomorphological survey was undertaken in the area around Lac des Grenouilles, which concentrated particularly on glacial and periglacial landforms (Fig. 1c). Two overlapping sediment cores (Gren-2 and Gren-3) were collected in 2001 in 1 m long sections from a floating platform in the centre of the lake with a modified Livingstone piston corer (Merkt and Streif 1970) at 286 cm water depth. Gren-2 was collected with a smaller diameter corer barrel (5 cm) than Gren-3 (8 cm). The core sections were cut longitudinally into halves using an electro-osmotic guillotine (Sturm and Matter 1972) and photographed with a digital camera and artificial light equipment at the Institute of Plant Sciences, University of Bern. We then used the changes in lithology to correlate the cores and establish depths for a 615 cm long master core (Fig. 2).

Chronology

The depth-age model is based on the following control points, the estimated age of the surface sediments at around the year of coring, 13 AMS radiocarbon dates obtained from

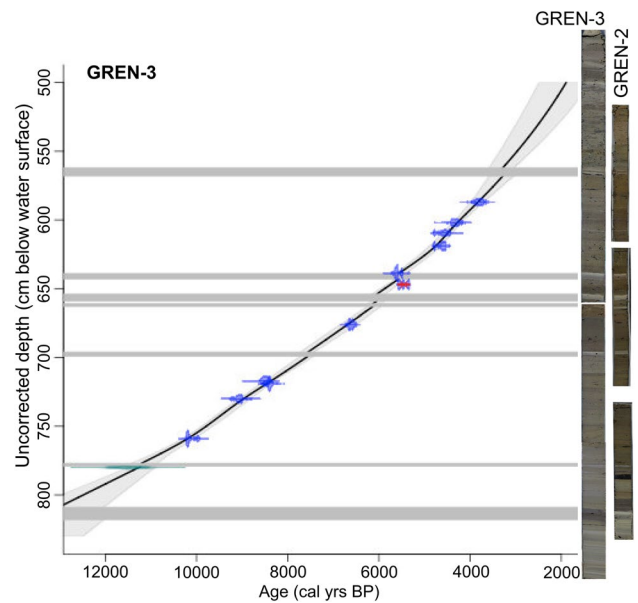


Fig. 2 Depth-age model for the Lac des Grenouilles cores plotted against depth below the water surface. Grey horizontal bands indicate turbidites that were excluded from the model. Images of the two parallel and overlapping sediment cores are shown on the right

terrestrial plant remains in Gren-3 (Finsinger et al. 2019) and biostratigraphic dating by pollen for the Younger Dryas/Holocene boundary (Table 1; following Giesecke et al. 2014). The two lowermost ^{14}C dates were rejected because they provided unrealistically young ages in comparison to all other age determinations, including regional biostratigraphy. The radiocarbon ages were calibrated to calendar dates using the IntCal13 data set (Reimer et al. 2013) before fitting a smoothing spline using CLAM v. 2.2 software (Fig. 2; Blaauw 2010). Distinct turbidite layers, most probably representing sediment deposition that occurred over a very short time span of hours or days, were excluded from the depth-age model (Fig. 2), following Heiri et al. (2003). Therefore, except where otherwise mentioned, all references to sediment depth hereafter refer to the corrected sediment depth that excludes turbidites.

Pollen, spore, plant macrofossil and charcoal analyses

Sediment samples for pollen analysis, 1 cm^3 and 1 cm thick were treated with standard physical and chemical treatments including HCl, KOH, sieving through a $500\text{ }\mu\text{m}$ mesh and decanting, HF treatment and acetolysis, stained with fuchsin and mounted in glycerine jelly. Pollen and spores were identified and counted using pollen keys (Punt et al. 1976–96; Reille 1992; Moore et al. 1998) and the reference collection at the Institute of Plant Sciences, University of Bern. Stomata were identified using Trautmann (1953) and Finsinger

Table 1 Radiocarbon dates of plant macrofossils used to establish the age-depth model

Lab-ID	Material dated	Age (^{14}C yr BP)	Age (cal yr BP)	Depth (cm) ^b	Depth (cm) ^c
Surface	/	/	-55 ± 1	286	0
Erl-4375	Wood with bark	$3,521 \pm 69$	/	587–586	301–300
Erl-4376	Wood with bark	$3,886 \pm 58$	/	602–601	316–315
Erl-4377	Wood with bark	$4,066 \pm 66$	/	609.5	323–322
SacA-25565	Plant macrofossils	$4,100 \pm 35$	/	619–618	332–331
Erl-4378	Wood with bark	$4,860 \pm 58$	/	638.7	351–350
SacA-25566	Plant macrofossils	$4,725 \pm 40$	/	647–646	355–354
SacA-25567	Plant macrofossils	$5,810 \pm 45$	/	676–675	380–379
Erl-4379	Wood with bark	$7,708 \pm 76$	/	717–716	417–416
Erl-4380	Wood with bark	$7,600 \pm 68$	/	719–718	419–418
Erl-4381	Wood with bark	$8,119 \pm 69$	/	730–729	430–429
Poz-7822	Plant macrofossils	$8,990 \pm 50$	/	759–758	459–458
Pollen-inferred age	/	/	$11,500 \pm 250$	780–779	477–476
Poz-10812 ^a	Plant macrofossils	$1,725 \pm 35$	/	817	505
Poz-7907 ^a	Plant macrofossils	$2,135 \pm 35$	/	821–819	508–506

^aRejected ^{14}C measurement; ^bdepth of the master core below water surface; ^ccorrected sediment depth that excludes turbidites

and Tinner (2020), and *Sporormiella* dung fungus spores were identified from Davis (1987). The results are presented as percentages of the terrestrial pollen sum, which includes pollen from trees, shrubs and herbs, but excludes spores and pollen of aquatic plants (Figs. 3a, 4). Sampling resolution was increased to one sample each 1–4 cm in the portions between 298–387 cm and 392–450 cm depth. Pollen can be dispersed by wind over large distances and generally represents vegetation at extra-local to landscape scales (Sugita 1994). While the small area of the site (0.015 km²) might suggest that the pollen source area might be substantially smaller, several hundred metres to a few kilometres at most from the site (Sugita 1994; Conedera et al. 2006), pollen from the vegetation in the landscape lower down may have reached the site, which is located in an area with steep topography (Finsinger et al. 2007). By contrast, stomata should be considered local indicators of the presence of the parent trees (Ammann et al. 2014) and *Sporormiella* spores of large herbivore density (Baker et al. 2013; Gill et al. 2013).

For plant macrofossils, sampling was mostly continuous between 284 and 460 cm depth. We measured sample volume by water displacement (volumes vary between 12 cm³ and 19.25 cm³; median = 16 cm³). Samples were soaked in a 10% NaP₂O₄ solution for 24 h and sieved with water on a 250 µm mesh. Identification of plant macrofossils was done with a stereo microscope at 7.5× and by comparisons with reference collections at the Institute of Plant Sciences, University of Bern, at the University of Montpellier, and with publications (Tomlinson 1985; Schoch et al. 1988). Since sample volumes varied, the results are presented as concentrations representing a standard sediment volume of 10 cm³ (Fig. 3b). Plant macrofossils are grouped by genera to

compare them with the pollen record (Figs. 3b, 4). Plant macrofossils are dispersed over substantially shorter distances than pollen, and therefore better reflect local vegetation within some tens of metres around the site (Birks and Birks 2000; Birks and Bjune 2010).

For macroscopic charcoal analysis, contiguous samples of 1 cm³ and 1 cm thick were taken between 283 and 460 cm depth. The samples were first soaked in a 10% NaP₂O₄ solution for 24 h and then gently washed on a 160 µm mesh using a manual water spray. The remaining particles were then bleached in a 2.6% NaOCl solution for a few minutes to distinguish charcoal from dark organic matter, following Genies et al. (2012). The numbers and areas of the charcoal fragments were estimated using a stereo microscope at a magnification of 6.3×, connected to a digital camera using Winseedle pro v. 2007 image analysis software. Charcoal concentrations, both as total number of fragments and area per sample, were converted to charcoal accumulation rates (hereafter called CHAR) to account for variations in the sedimentation rate (Whitlock and Larsen 2001). Calibration studies suggest that charcoal particles larger than 600 µm might be of local origin, while smaller particles can easily be dispersed over large distances, up to 30–50 km (Oris et al. 2014; Adolf et al. 2018). Therefore, the low frequency trends of the macroscopic charcoal record can be attributed to fire activity in the surrounding landscape (Marlon et al. 2008; Adolf et al. 2018). We estimated the low frequency trend by fitting a locally estimated scatterplot smoothing (loess, Cleveland and Devlin 1988) to the macrocharcoal influx values (Fig. 4).

Pollen assemblage zones were determined by optimal partitioning with square root transformed percentage values

Fig. 3 a Pollen diagram of Lac des Grenouilles, showing abundances of selected pollen, spores and *Sporormiella* spores as percentages of the terrestrial pollen sum. Empty curves show 10× exaggerations. **b** Plant macrofossil concentration record from Lac des Grenouilles. Grey horizontal bands show land use phases indicated by archaeological data (Table 2). Continuous horizontal lines denote statistically significant pollen assemblage zones (LPAZ); the short-dashed line indicates the Younger Dryas/Holocene boundary, based on pollen data (Table 1). All palynological, plant macrofossil and charcoal data presented in this article is publicly available on the Neotoma Database (<https://www.neotomadb.org/>)

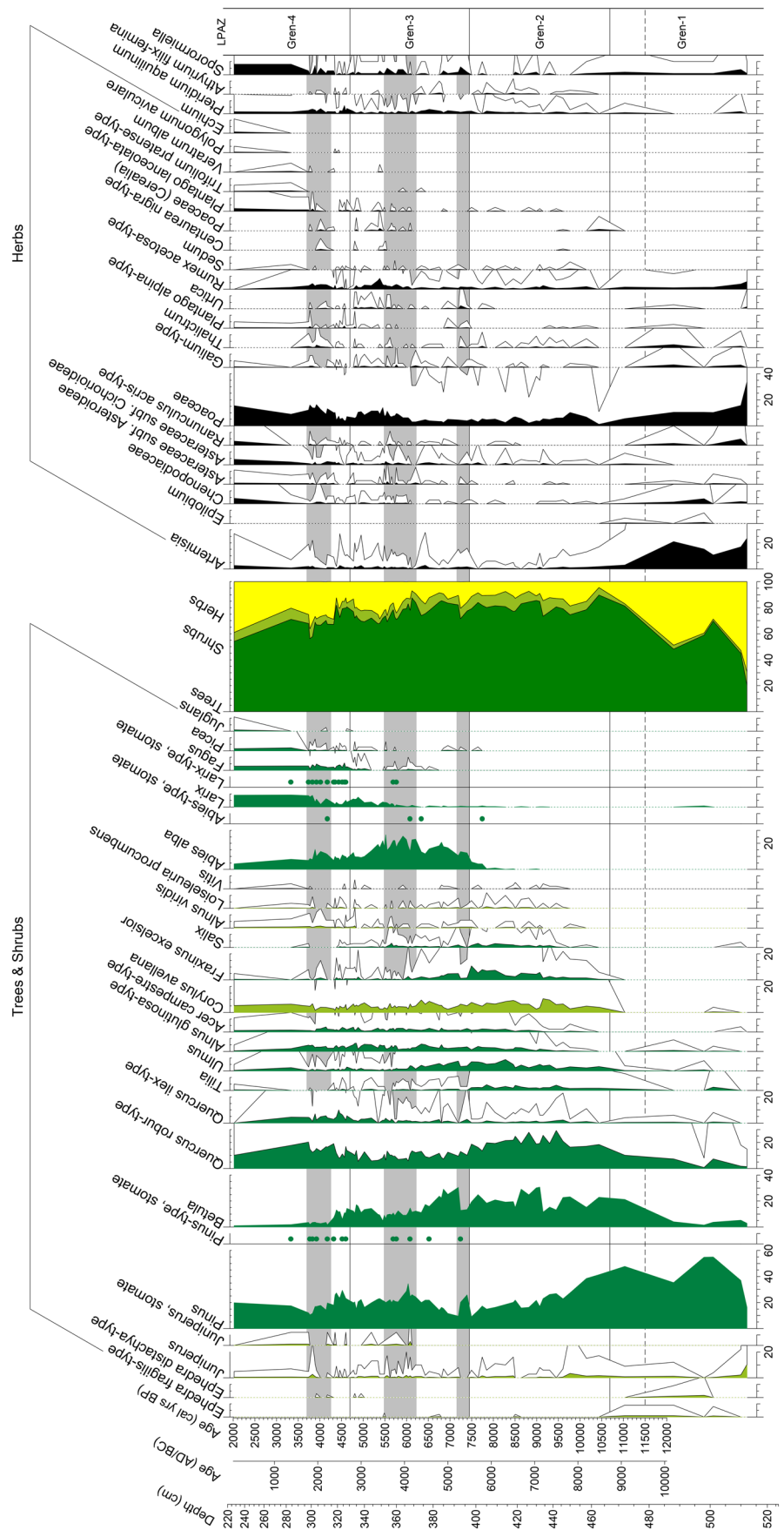
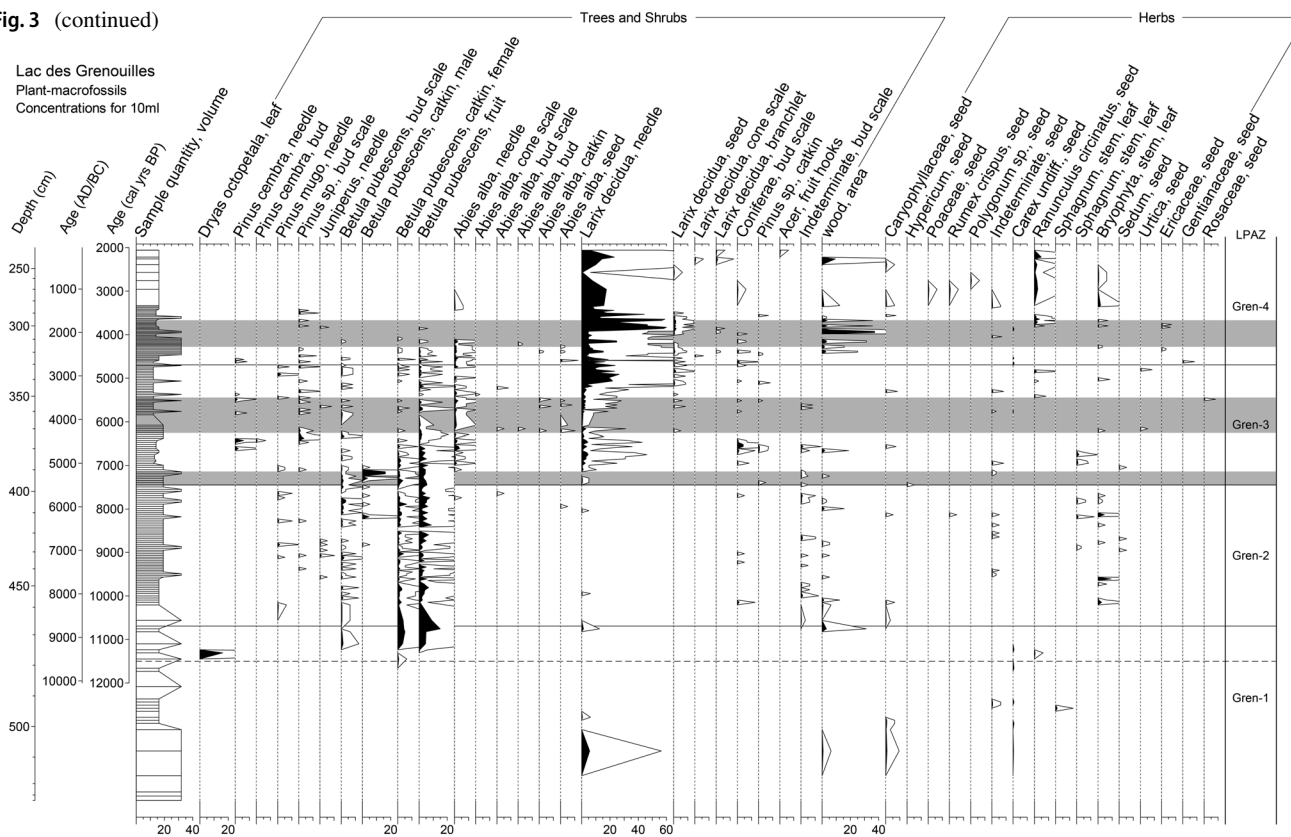


Fig. 3 (continued)



for pollen types included in the pollen sum (Birks and Gordon 1985). Statistically significant zones were assessed by comparison with the broken-stick model, following Bennett (1996). Zonation was done with Psimpoll v. 4.26 (Bennett 2008). Tilia v. 2.6.1 and Affinity Designer v. 1.7.0 were used to draw the pollen and plant macrofossil diagrams (Fig. 3a, b).

Time series analyses

To investigate the relationships between fire activity shown by charcoal influx and vegetation change by pollen percentages (leads and lags), we used cross correlation analyses (Green 1981; Tinner et al. 1999; Rey et al. 2019). Analyses were restricted to the higher resolution section between 387 and 298 cm depth (6,950–3,750 cal BP) where the median sampling resolution is 48.5 years between samples (49 samples) and the median absolute deviation is 26.7 years (ESM Fig. S1). To obtain evenly spaced time series (Venables and Ripley 2002), we fitted a loess smoothed line (span=0.15) to estimate pollen percentage and charcoal influx values at 100 year intervals (Fig. 4). Cross correlation analyses were done with the R computing environment (R Core Team 2017). Cross correlation coefficients are presented for maximum lags of ± 4 corresponding to ± 400 years (Fig. 5). The 95% confidence intervals must be viewed with caution

because the loess smoothed values are not entirely independent (Venables and Ripley 2002, p 390).

Results and interpretation

Geomorphological context

Lac des Grenouilles is dammed by a prominent lateral moraine which covers the left flank of the Vallon de Fontanalba (Fig. 1c). According to regional reconstructions (Cossart 2008; Cossart et al. 2012; Federici et al. 2012, 2017), the moraine formed during the Last Glacial Maximum (LGM) and the moraines mapped further up the valley at around 2,200–2,300 m were probably deposited during the Younger Dryas cold event (Egesen stadial), as observed on the northern side of the Maritime Alps (Spagnolo and Ribolini 2019). The sparse glacial debris in the area of Lac Ste Marie suggests the presence of relict ice bodies during the Holocene cold events. Part of this debris, which is locally mixed with rock falls, shows signs of permafrost formation. Permafrost creeping led to the formation of a rock glacier at around 2,400 m and permafrost could be still present in the rock glacier as suggested by monitoring data in the Maritime Alps (Ribolini and Fabre 2006; Ribolini et al. 2007, 2010).

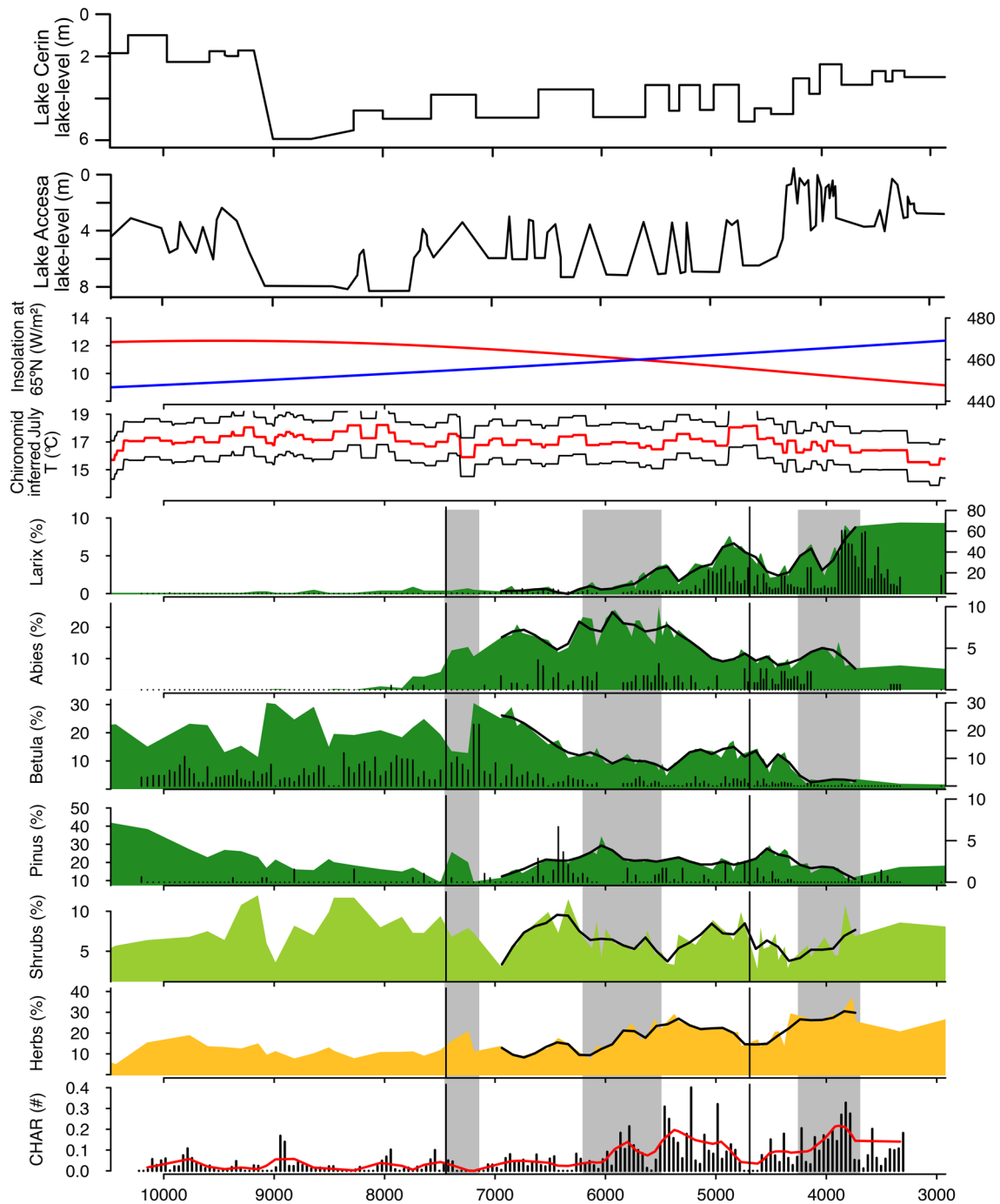


Fig. 4 Comparison of the main biotic and abiotic proxies for vegetation dynamics, fire and climate. From top to bottom, lake level changes in the Jura mountains (Lac de Cerin) and in central Italy (Lago dell'Accesa) (digitized from Magny et al. 2011); insolation at 65°N (Laskar et al. 2004), mean December, January, February (DJF, blue line) and June, July, August (JJA, red line); stacked July air temperatures for the Alpine region based on chironomids (Heiri et al.

2015); selected pollen data from Lac des Grenouilles, as raw percentage values (coloured areas) and interpolated and loess-fitted values (black lines) used for cross-correlation analyses (Fig. 5), together with plant macrofossil concentrations (summed by genera; black bars; values 10×); charcoal accumulation rate of charcoal counts shown as black bars; loess-fitted data, red lines. Vertical shaded grey areas indicate the land use phases based on archaeological data (Table 2)

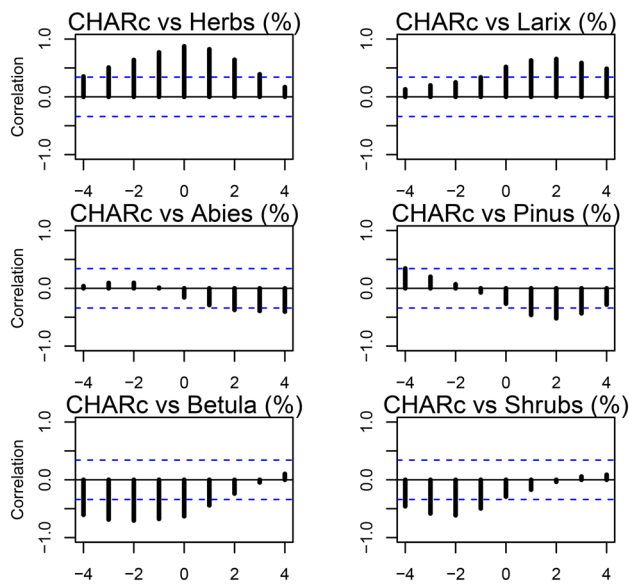


Fig. 5 Cross correlation of charcoal accumulation rates (CHARc) and pollen percentages (interpolated to 100 year intervals) showing trends of taxon responses to changes in fire activity up to time lags ± 4 , corresponding to time periods of ± 400 years. Dashed lines indicate the 95% confidence intervals

Vegetation and fire histories

Three statistically significant pollen assemblage zone boundaries were determined (Fig. 3a). The lowermost (Gren-1; > 467 cm; $> 10,700$ cal BP) probably corresponds to the late Glacial and early Holocene because the pollen assemblages reflect the well established pattern of late Glacial pollen stratigraphies from the study area (de Beaulieu 1977; de Beaulieu et al. 1994; Finsinger and Ribolini 2001). This chronology is consistent with the geomorphological context, with an LGM moraine that dammed Lac des Grenouilles. *Pinus*, *Artemisia* and Poaceae dominate the pollen assemblages below 490 cm, with minor abundances of *Betula*, deciduous *Quercus* and *Juniperus*. Around 12,000 cal BP, abundances of *Artemisia* and *Ephedra* pollen are higher than in earlier samples and *Pinus* abundance is lower, suggesting an opening of the vegetation that may reflect the effects of the Younger Dryas cooling (12,850–11,650 cal BP; Rasmussen et al. 2014) in the Alpine region (Larocque and Finsinger 2008; Samartin et al. 2012). Macrofossils indicate that *Larix* was present in the surroundings shortly before the start of the Younger Dryas and that *Dryas octopetala* carpets briefly expanded at the Younger Dryas/Holocene transition (Figs. 3b, 4). *Sporormiella* dung fungus spores were regularly found, suggesting the presence of large herbivores near the lake during the late Glacial. A change to more closed vegetation characterizes the transition to the warmer Holocene,

shown by a higher abundance of *Betula*, increasing arboreal pollen, a decrease of *Artemisia* and herb pollen, and the first appearance of *Tilia*.

The transition to zone Gren-2 (467–397 cm; 10,700–7,450 cal BP) is marked by the rise of *Quercus* pollen and the first appearance of *Corylus*, *Fraxinus*, *Alnus glutinosa* and *Acer*, indicating that thermophilous trees expanded, probably at lower elevations. The continuous presence of *Betula* macrofossils and the rare occurrences of *Pinus mugo* and *Juniperus* needles suggest that the site was at the treeline ecotone and that open stands of *Betula* and *Pinus* grew in the surroundings. Rare occurrences of *Alnus viridis* pollen, but the absence of its macrofossils, suggest that alders were either very sparse or distant. In spite of decreasing *Pinus* pollen abundance, arboreal pollen values are highest (ca. 75–90%) in this zone. As observed in other records, the two charcoal influx records (by counts and by area) are highly redundant ($r = 0.912$, p -value < 0.001 ; ESM Fig. S2) (Tinner and Hu 2003; Finsinger et al. 2014). Thus only the charcoal influx record by count is used in the following discussion. Fire activity was low overall, with CHAR values < 0.1 pieces $\text{cm}^{-1} \text{year}^{-1}$ (Fig. 4).

Increasing abundance of *Abies* pollen and abundant finds of its macrofossils in Gren-3 (397–330.5 cm; 7,450–4,700 cal BP) indicate the rise of the timberline and the establishment and expansion of a subalpine forest in the surroundings. While light demanding *Betula* shrank as shown by decreasing pollen and macrofossil abundance, *P. cembra* expanded, shown by increasing pollen abundance and needle finds. Pollen and macrofossil abundances of light-demanding *Larix* were low until ca. 6,000 cal BP, when larch started to expand. Increasing herb pollen abundance and charcoal influx values (CHAR values > 0.1 pieces $\text{cm}^{-1} \text{year}^{-1}$) suggest that forest cover decreased due to rising fire activity. Fire sensitive *Abies*, however, collapsed some 500 years later when a further rise in fire activity occurred. Simultaneously, *Larix* further expanded and *Betula* increased, indicating a major change in the composition of the subalpine forest cover. Between 4,800 and 4,300 cal BP around the transition to Gren-4 (330.5–220 cm; 4,700–2,000 cal BP), high arboreal pollen percentages suggest the partial recovery of forest cover during a ca. 500 year period of low fire activity. Regular finds of macrofossils indicate that *Abies* spread once more in the subalpine forest around the site. Around 4,300 cal BP, fire activity increased again and the composition changed to a *Larix*-dominated wood. Decreasing *Betula* pollen abundance and absence of macrofossils suggest that birch, perhaps above the timberline, was strongly reduced. *Abies alba* and *Pinus cembra* macrofossil abundances strongly decrease after 4,300 cal BP, pointing to local disappearance of the two species.

Variations in the relative abundance of cultural indicator pollen from crops and weeds as well as *Sporormiella*

spores indicate occasional phases of human pressure. We found moderately higher values of *Artemisia* and *Urtica* pollen and *Sporormiella* spores around 7,450–7,150 cal BP. There is a local maximum of *Sporormiella* around 6,200–5,500 cal BP, together with an increase of Poaceae and *Rumex* pollen and the regular occurrence of Cerealia-type and *Plantago lanceolata*-type. Similarly, Poaceae, *Rumex*, *Veratrum*, *Trifolium pratense*-type and *P. lanceolata*-type pollen, together with *Sporormiella* spores, increase after 4,300 cal BP. In all of these three phases, arboreal pollen percentages are substantially reduced, indicating temporary openings of the subalpine forests from prehistoric land use.

Time series analyses

Percentages of herb pollen have significantly positive correlations with charcoal influx (maximum correlation at lag 0; Fig. 5). The Poaceae record illustrates particularly well the expansion of grasslands as a consequence of woodland reduction from increasing fire activity, as also observed in other studies (Rey et al. 2013, 2019). However, positive correlations of cultural indicators (*P. lanceolata* and *Urtica*) are delayed, suggesting a gradual intensification of land use after fires, as also observed in another record from the Alps (Gobet et al. 2003). By contrast, *Sporormiella* shows positive correlations at negative lags, suggesting that grazing by large herbivores preceded increases in fire activity.

Most tree taxa (*Abies*, *Betula* and *Pinus*) show negative correlations with charcoal influx. *Abies* is negatively correlated at positive lags, suggesting either a slightly higher fire tolerance or less intense disturbance if compared to warmer lowland sites (Tinner et al. 2000), a finding that is in agreement with other high-resolution mountain studies (Rey et al. 2013; Schwörer et al. 2015). Similarly, *Pinus* is negatively correlated at positive lags. While this matches with the long-term fire ecology of *P. cembra*, a tree sensitive to prolonged fire disturbance (Gobet et al. 2003; Schwörer et al. 2015), the clear interpretation of this result is complex because the macrofossil record shows the local presence of *Pinus mugo* (Gobet et al. 2003; Stähli et al. 2006; Finsinger et al. 2018). Moreover, the contribution of pollen from other *Pinus* species growing at lower elevation is difficult to estimate. *Betula* and shrubs are also negatively correlated, but at negative lags. By contrast, *Larix* is positively correlated at positive lags, suggesting the gradual and delayed expansion of larch-dominated open woodlands. While this contrasts with results from the Engadin, which showed non-lagged negative correlations (Gobet et al. 2003), our results are consistent with evidence of fast post-fire regeneration by

Larix (Schöneberger and Wasem 1997; Malowerschnig and Sass 2014).

Discussion

Influence of climate on early Holocene afforestation

The late Glacial vegetation (ca. 14,600–11,650 cal BP) was dominated by grasslands with *Artemisia* and Poaceae (de Beaulieu 1977; this study), and *Pinus* probably occurred at lower elevation (de Beaulieu 1977). The absence of *Betula* macrofossils suggests that birches were either very sparse (de Beaulieu 1977) or locally absent. The finds of *L. decidua* needles and pollen indicate the presence of larch in the surroundings before the Younger Dryas. This corroborates the very rare finds of *Larix* pollen grains in late Glacial sediments at Selle di Carnino (de Beaulieu 1977), a peaty depression at 1,900 m, a few kilometres to the east of Lac des Grenouilles. These two sites are among the highest Alpine sites from which tree pollen, stomata and macrofossils suggest tree growth there during the Bølling/Allerød (ca. 14,600–12,800 cal BP) (Wagner et al. 2015). For instance, the stomata finds of *Juniperus*, *Larix* and *Pinus* at Simplon-Alter Spittel (1,885 m), a south-facing site in the Val Divedro (Simplontal) in the southern Swiss Alps showed the early establishment of trees there during the Allerød (13,900–12,800 cal BP) (Welten 1982; Ammann et al. 2014). The substantial drop in summer temperatures during the Younger Dryas cooling in the Alpine region (Heiri et al. 2014) probably led to a lowering of the treeline to below Lac des Grenouilles, as no tree macrofossils were found. In other records from the Alpine region, treeline lowerings of ca. 300–400 m have been recorded (Gobet et al. 2005; Tinner and Vescovi 2005). Given that sedimentation was not interrupted at Lac des Grenouilles then, the Younger Dryas glacier advance did not reach the site. This is in agreement with geomorphological evidence that suggests the location of Younger Dryas moraines mostly above 2,100 m (Brisset et al. 2015; Spagnolo and Ribolini 2019).

The macrofossil record supports previous interpretations suggesting that the treeline was close to 2,000 m during the early Holocene in the study area (de Beaulieu 1977; Ponel et al. 2001). Specifically, an open *Betula* and *Pinus* (probably *P. mugo*) dominated treeline with scattered *Juniperus* shrubs re-expanded around Lac des Grenouilles in the early Holocene until ca. 8,000 cal BP, when the first *Abies* macrofossil was found. However, due to the lack of ¹⁴C dates around the Younger Dryas/Holocene transition (Fig. 2), it is difficult to establish precisely the afforestation lag in response to the early Holocene warming at Lac des Grenouilles. Vegetation-independent temperature

reconstructions show a rapid warming of ca. 2–4 °C within a few decades after the end of the Younger Dryas (Lotter et al. 2000; Schwander et al. 2000; von Grafenstein et al. 2000; Larocque and Finsinger 2008; Heiri et al. 2015) that probably led to a rapid early Holocene rise in the treeline in the central and southern Alps, showing the ability of treelines to track climate warming with a delay of decades to centuries (Tinner and Kaltenrieder 2005). Conversely, other sites suggest that due to the regional setting, as in the colder northern Alps, or local features of soils, aspect or moisture availability, today's treeline positions were only reached at ca. 10,000 cal BP (Schwörer et al. 2014a) or even after 8,200 cal BP (Finsinger and Tinner 2007). Nevertheless, we found a short term early Holocene expansion of *Dryas octopetala*, a pioneer species of open, base-rich habitats (Elkington 1971), before the expansion of *Betula* at 11,300 cal BP. This indirectly supports the chronology for Lac des Grenouilles, because early Holocene expansions of *Dryas* were also detected at Gouillé Rion and at Lac de Fully, two sites above the current timberline in the dry inner Alpine Valais (Kaltenrieder et al. 2005; Finsinger and Tinner 2007), as well as at Iffigsee and Lago Basso (Wick and Tinner 1997; Schwörer et al. 2014b).

Early Holocene fire activity was substantially lower than during the mid to late Holocene (Fig. 4). We assume that it was limited by low biomass availability, as also observed elsewhere (Berthel et al. 2012; Gil-Romera et al. 2014; Finsinger et al. 2018). Indeed, high early Holocene seasonality of insolation (Fig. 4) was probably a factor which caused climate-induced low biomass availability in high elevation Alpine landscapes (Schwörer et al. 2014a).

The absence of *Larix* during the early and mid Holocene at Lac des Grenouilles is striking when compared to records from dry inner Alpine valleys. For instance, at Gouillé Rion, *Salix* and *D. octopetala* tundra preceded the expansion of a *Larix*-dominated subalpine forest around 11,000 cal BP (Tinner and Kaltenrieder 2005). Similarly, an early Holocene expansion of *Larix* has also been recorded from Lac de Fully, another site in the dry inner Alpine Valais (Finsinger and Tinner 2007), at Iffigsee in the northern Swiss Alps (Schwörer et al. 2014b), at Lej da San Murezzan in the Engadin and several other sites in the Swiss Alps (Gobet et al. 2005), as well as at Lac du Loup in the inner Alpine part of the French Alps (Fig. 1b; Blarquez et al. 2010). Indeed, light-demanding *Larix decidua* grows at present mostly in continental climates, with cold, dry and snowy winters (Da Ronch et al. 2016), whereas *Betula pendula* and *B. pubescens* have a greater tolerance of lower temperatures in the coldest months, and *B. pubescens* has greater tolerance to higher annual precipitation (Beck et al. 2016). Thus, the dominance of *Betula* together with the absence of *Larix* points to contrasting early Holocene moisture conditions in the Maritime Alps compared with the central Alps. The

importance of moisture conditions was also acknowledged when comparing past plant distributions in the currently moister northern Swiss Alps and the now drier inner Alpine valleys (Lotter et al. 2006; Schwörer et al. 2014b), and may explain the early Holocene dominance of *Betula* in the mountains of Sweden despite the presence of *Larix sibirica* (Kullman and Öberg 2015).

Highest timberline position during the Holocene

At Lac des Grenouilles, *Betula* dominated the treeline ecotone together with scattered *Pinus* stands (probably *P. mugo* as suggested by the macrofossils) and *Juniperus* shrubs until ca. 8,000 cal BP, when *Abies* expanded. The timing of the *Abies* expansion is in good agreement with regional pollen data (de Beaulieu et al. 1994; Nakagawa 1998; Finsinger 2001). The dominance of temperate *Abies* at today's treeline elevation marks the highest timberline position, which was reached around 7,500–7,000 cal BP. While the overall Alpine temperature reconstruction shows highest temperatures at around 8,500–8,000 cal BP, this interpretation is in good agreement with chironomid-inferred temperature records from the Alps (Heiri et al. 2003) and from the northern the northern Apennines (Samartin et al. 2017), as well as with global circulation models (Renssen et al. 2009), all showing temperatures ~1.5 °C higher than at present during the Holocene Thermal Maximum (HTM) around 7,500 cal BP. Some records also point to the establishment of progressively more oceanic conditions after 8,000 cal BP (Magny et al. 2011). Although the local establishment of *Abies* was suggested by the marked rise of pollen percentages (Ponel et al. 2001), no *Abies* macrofossils were found from nearby Lac Long Inférieur at 2,090 m (F. Damblon unpublished, in Finsinger 2001). This may suggest that *Abies* reached its upper limit of about 2,000–2,100 m during the HTM in the study area. However, other records from the Alps indicate that the timberline was ca. 150–200 m above its current altitude during the HTM, reaching up to 2,300–2,500 m (Tinner and Theurillat 2003; Schwörer et al. 2014b). Thus, macrofossil records from higher sites may be needed to find the upper limits of the timberline and the treeline in the study area during the Holocene.

The occurrence of mid Holocene macrofossil assemblages with both *A. alba* and *Pinus cembra* is striking because at present they grow together only in very few and isolated locations, mainly in the inner Alpine zone of the southwestern Alps, for instance in Valais, Switzerland, on steep and convex slopes at around 1,900–2,000 m (Lingg 1986), in Val Susa, Italy, at ca. 1,950 m (Dotta and Motta 2000) and in La Maurienne, a valley in France, at 1,950–2,000 m (Chauchard et al. 2010). *A. alba* occurs at these sites together with *P. cembra*, *P. abies* and *L. decidua*. Further east in the inner Alpine Italian Vinschgau (Val Venosta), Italy, it occurs with

P. cembra (Mayer 1979). Generally, the abundance of *A. alba* in these lower subalpine stands is low, but there are clear signs of active regeneration (Lingg 1986; Dotta and Motta 2000) and even expansion in response to abandonment of land use after the 1950s (Lingg 1983; Chauchard et al. 2010).

It has been suggested that inner and western Alpine populations of *Abies alba* maintained stronger adaptive potential to drought stress and strong irradiation than those in the moister southern, eastern and northern Alps (Marcet 1971, 1972; Mayer 1979; Kral 1989; Kral and Mayer 1993). However, there are still critical knowledge gaps for this, for instance, while modern mitochondrial DNA (mtDNA) maternal lineages and allozyme clusters of *A. alba* show little differences between Alpine populations (Liepelt et al. 2009), there is distinct inter-populational genetic variation with genetic distance and genetic differentiation between stands within and outside the Alpine region as well as between neighbouring populations, which may point to processes of adaptation to different or specific environmental conditions (Hussendörfer 1999). It might be that the mtDNA and allozyme genomic regions which identify the haplotypes (Liepelt et al. 2009) bear little connection to adaptive genes for drought stress response, which are starting to be uncovered (Behringer et al. 2015). Moreover, intraspecific variation in drought sensitivity of *A. alba* is not yet very well understood (George et al. 2015).

By contrast, there is a substantially larger consensus on the view that mixed stands of *P. cembra* and *A. alba*, sometimes including *L. decidua*, which today occur isolated at very remote sites, were more widespread in the past (Lingg 1986; Kral and Mayer 1993; Tinner et al. 2013), as shown by mid Holocene macrofossil and stomata records (Welten 1982; Wick et al. 2003; Schwörer et al. 2014b; this study). Similarly, there is a large consensus indicating that *A. alba* declined due to increasing human pressure with fire disturbances, grazing and tree felling at high elevation sites (Markgraf 1969; Lingg 1986; Tinner et al. 2013), suggesting a marked contraction of its realized climatic niche in response to prehistoric land use.

Relationships between vegetation dynamics and phases of land use

We found evidence of greater abundance of large herbivores and intensified land use during previously identified phases of rock art (Figs. 3, 4; Table 2; Huet 2017). The Neolithic Cardial culture (7,450–7,150 cal BP) in the study area is indicated by finds of pottery in rock shelters (Conti 1940; Louis and Ségui 1949; Bianchi et al. 2011). Based on this evidence, the first sign of human occupation associated with agriculture in the area dates back to 7,450–7,150 cal BP, thereby showing that the Vallée des Merveilles was one of the first Alpine areas being visited during the Neolithic (Binder 2005). Indeed, trade and transhumance in this part of the Alps may already have started between 7,000 and 6,000 cal BP (Ricq-de Bouard and Fedele 1993; Huet 2017). At Lac des Grenouilles, this phase is only characterised by higher *Urtica* pollen and *Sporormiella* spores, while fire activity remained low. In contrast, the Copper Age Chassey period (6,200–5,500 cal BP) and the early Bronze Age Culture Campaniforme (Recent Bell-Beaker) period (ca. 4,250–3,700 cal BP) are also associated with the presence of Cerealia and other cultural indicator pollen types, a rise of total herb pollen and increasing charcoal influx values. An increase of cultural pollen during the most recent phase was also detected at Lac Long Inférieur (de Beaulieu 1977; Huet 2017; Table 1).

Although we found a good match between the new pollen record and the rock art phases, our results indicate that the Chassey land use phase lasted longer than suggested by Huet (2017). For instance, *Urtica* abundance actually increased at 5,300 and remained high until 4,900 cal BP, suggesting increasing nitrogen enrichment maybe resulting from grazing. Similarly, charcoal influx and Poaceae pollen abundance did not decrease, and overall arboreal pollen abundance did not increase until 4,900 cal BP, suggesting that land use with fire continued until the end of the Copper Age. However, the Copper Age phase did not have persistent consequences on the local environment. For instance, although the pollen record shows that *Abies* did not recover in the surrounding landscape, macrofossils show that fir trees were able to re-establish locally during the period of land

Table 2 Occupation phases based on archaeological findings from the Mont Bégo area (from Huet 2017)

Archaeological period	Southwestern Alpine chronology	Age (cal yr BP)	Age (BC)	Source
Bronze Age	Recent Bell Beaker to Early Bronze Age I	4,250–3,700	2300–1750	Pottery (de Lumley 1995; Bianchi et al. 2011; Huet 2012)
Copper Age	Early to recent Chassey	6,200–5,500	4250–3550	Flint bladelet from below the Stele du Chef de Tribu (de Lumley et al. 2010), pottery and flint artefacts
Neolithic	Cardial	7,450–7,150	5500–5200	Pottery (de Lumley et al. 1991; de Lumley 1995; Binder et al. 2009)

abandonment with few fires that occurred between 4,900 and 4,300 cal BP. This temporary recovery ended with the Bronze Age land use phase (4,250–3,700 cal BP), when *Abies* and *Betula* collapsed locally and *Betula* and *Pinus* in the surrounding landscape. Interestingly, the timing of this land use phase matches a major phase of woodland clearance and land use detected elsewhere in and around the Alps (Gobet et al. 2003; Tinner et al. 2003; Finsinger and Tinner 2006). This suggests that Bronze Age land use was widespread at both low and high elevations in the Alps, possibly leading to irreversible changes such as the disappearance of *Abies alba* treeline communities.

From an *Abies*-dominated subalpine forest to a *Larix* wood pasture

In the Alps, the development of larch meadows (*Lärchenwiesen*), a form of wood pasture with *L. decidua* stands with a dense grass-dominated herbaceous understorey (Garbarino et al. 2011), is associated in several palaeoecological records with human activities, in particular grazing after burning (Wagner et al. 2015 and references therein). *L. decidua* is considered useful for grazing livestock, because its light canopy permits the growth of suitable ground cover for foraging (Motta and Lingua 2005). Moreover, with its great bark thickness on mature individuals, a key fire tolerance trait (Pellegrini et al. 2017), and the ability to produce new foliage each year, larch is rather fire resistant (Sullivan 1994), also because mature individuals show relatively low mortality rates (Dupire et al. 2019). Conversely, due to its physiology and its ability to colonize raw soils (Garbarino et al. 2010), *L. decidua* is less limited by soil moisture availability than the other subalpine trees, *Abies alba*, *Picea abies* and *Pinus cembra* (Schwörer et al. 2014a). However, although a decrease in moisture availability might have favoured *L. decidua* at the expense of *A. alba*, there is no evidence of a decrease in rainfall between 6,000 and 4,000 cal BP in lake level records from the Alpine region (Fig. 4), which instead indicate higher precipitation between 4,500 cal BP and the present when compared to the mid Holocene (Magny et al. 2011, 2013). Based on this evidence and upon the fact that *L. decidua* is the dominant tree in the Mont Bégo area today (Ozenda 1950; de Beaulieu 1977), it seems far more plausible to suggest that the expansion of larch at Lac des Grenouilles was caused by excessive human fire disturbance (see cross-correlation analyses, Fig. 5) while *A. alba* was strongly reduced. This interpretation of the causes of the main vegetation changes is consistent with earlier studies, which indicate that under conditions of low disturbance *A. alba* can dominate forests under colder temperatures than observed today (Wick et al. 2003; Lotter et al. 2006; Tinner et al. 2013).

Conclusions

We present the first palaeoecological study that includes pollen, plant macrofossil and charcoal records from the modern timberline (ca. 2,000 m) in the Mont Bégo area of the Maritime Alps. The area is an important place for Alpine archaeology because it has thousands rock art carvings whose age cannot be directly assessed (Bicknell 1913; de Lumley 1995; Huet 2012). The new taxonomically highly-resolved palaeoecological record confirms most of the land use phases (7,450–7,150, 6,200–5,500 and 4,250–3,700 cal BP) known from the rock art typology (Huet 2017), and in addition reveals local long term timberline shifts and transformation of vegetation composition in relation to environmental changes such as land use, fire disturbances and climatic changes. The absence of *Larix* macrofossils suggests that early Holocene conditions were moister than in drier inner Alpine valleys, where *Larix* played a more important role both in the past as well as in modern timberlines. After 8,000 cal BP, the timberline moved upwards and mixed stands of *A. alba* and *P. cembra* established around the study site above ca. 2,000 m during the Holocene Thermal Maximum (HTM), when the first examples of rock art were probably carved. At the timberline, *Abies* was replaced during the Bronze Age (around 4,000 cal BP) by *L. decidua* dominated subalpine woods, which are still dominant in the study area today (Ozenda 1950; de Beaulieu 1977). *A. alba* was thus reduced at the colder end of its natural distribution (Tinner et al. 2013) and *L. decidua* expanded in response to past land use with the use of fire that allowed the establishment of wood pastures. This implies that modern wooded landscapes are markedly shaped by prehistoric legacies, even in remote high-alpine areas (Willis and Birks 2006; Feurdean et al. 2009).

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