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# Keep your feet warm? A cryptic refugium of trees linked to a geothermal spring in an ocean of glaciers

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## Abstract

Up to now, the most widely accepted idea of the periglacial environment is that of treeless ecosystems such as the arctic or the alpine tundra, also called the *tabula rasa* paradigm. However, several palaeoecological studies have recently challenged this idea, that is, treeless environments in periglacial areas where all organisms would have been exterminated near the glacier formed during the Last Glacial Maximum, notably in the Scandinavian mountains. In the Alps, the issue of glacial refugia of trees remains unanswered. Advances in glacier reconstructions show that ice domes did not cover all upper massifs, but glaciers filled valleys. Here, we used fossils of plant and malacofauna from a travertine formation located in a high mountain region to demonstrate that trees (*Pinus*, *Betula*) grew with grasses during the Late-glacial-Holocene transition, while the glacier fronts were 200–300 m lower. The geothermal travertine started to accumulate more than 14,500 years ago, but became progressively more meteorogenic about 11,500 years ago due to a change in groundwater circulation. With trees, land snails (gastropods) associated to woody or open habitats and aquatic mollusc were also present at the onset of the current interglacial, namely the Holocene. The geothermal spring, due to warm water and soil, probably favoured woody glacial ecosystems. This new finding of early tree growth, combined with other scattered proofs of the tree presence before 11,000 years ago in the western Alps, changes our view of the tree distribution in periglacial environments, supporting the notion of tree refugia on nunataks in an ocean of glaciers. Therefore, the *tabula rasa* paradigm must be revisited because it has important consequences on the global changes, including postglacial plant migrations and biogeochemical cycles.

## KEYWORDS

ecosystem, geothermal spring, glacial refugia, Lateglacial–Holocene climate, mollusc, nunatak, palaeoecology, tree

## 1 | INTRODUCTION

Theoretically, glacial environments are not suitable for trees. The *tabula rasa* paradigm characterizes such treeless environments in glacial areas where all organisms have been exterminated near, north or

above the glacier (Dahl, 1987). This paradigm applies both to the periglacial environments of the current interglacial, namely the Holocene starting 11,700 calibrated years before present (hereafter referred to as "cal BP"; Walker et al., 2009), and to past environments notably during the Last Glacial Maximum (LGM) that definitely ended 14,500 cal BP (Clark et al., 2009).

However, for some years now, shrubs and trees have started to invade arctic and alpine tundras or steppes (Hallinger, Manthey, & Wilmking, 2010; Myers-Smith et al., 2015), leading important global changes on fire, hydrology and biogeochemical budget at the tree-tundra transition (Abbott et al., 2016). Furthermore, several palaeoecological studies have recently challenged the *tabula rasa* paradigm. Indeed, subfossils supported by environmental DNA have demonstrated that trees have survived the LGM in Scandinavia (Kullman, 2008; Parducci et al., 2012) or in Alaska (Brubaker, Anderson, Edwards, & Lozhkin, 2005; Edwards, Armbruster, & Elias, 2014), and grew in periglacial steppes of the upper Pleistocene in central Canada (Bélanger, Carcaillet, Padbury, Harvey-Schafer, & Van Rees, 2014) or northern Siberia (van Geel et al., 2017).

Despite several decades of investigations, it remains controversial as to whether trees and associated fauna survived the glaciation in lowest European latitudes, for example, the southern peninsulas only (Petit et al., 2002), or also in *cryptic* refugia situated near ice sheet fronts (Birks & Willis, 2008; Quinzin, Normand, Dellicour, Svenning, & Mardulyn, 2017; Tzedakis, Emerson, & Hewitt, 2013) due to exceptional physiographical characteristics acting as climate refugia (Hampe, Rodriguez-Sanchez, Dobrowski, Hu, & Gavin, 2013). A climate refugia is a location where taxa survived periods of adverse climate (Gavin et al., 2014). Theoretically, cryptic climate refugia can exist above glaciers on *nunataks*, that is, an isolated mountain above the surface of a glacier. The *nunatak* theory hypothesizes that unglaciated reliefs existed in glacial areas where biota survived the LGM (Dahl, 1987). In general, cryptic refugia including on *nunataks* would be locations protected from glacial conditions (wind, summer, frost, etc.), with exceptional physiography (warm soil or freshwaters), and well exposed to sunlight (solar irradiance), favouring biogeochemical processes required for tree growth and their associated biota, for example, in Europe on the north Italian plain (Kaltenrieder et al., 2009; Ravazzi et al., 2006), on the southwest French plain (de Lafontaine, Amasifuen Guerra, Ducouso, & Petit, 2014) or in central Europe (Carcaillet & Vernet, 2001; Juříčková, Horáčková, & Ložek, 2014). Interestingly, advances in glacier reconstruction in the Alps have shown that ice domes did not cover all upper mountains during the LGM, but glaciers filled valleys (Buoncristiani & Campy, 2004; Cossart, Fort, Bourles, Braucher, & Siame, 2012), supporting the possibility of *nunataks* and thus climate refugia for biota, notably trees. In the inner Alps, the issue of climatic refugia of trees during glacial times (here after "glacial refugia") is challenged with a recent discovery (Carcaillet & Blarquez, 2017), while these mountains are at lower latitudes than Scandinavia that already evidenced the occurrence of glacial refugia (Kullman, 2008; Öberg & Kullman, 2011; Parducci et al., 2012).

In cold mountains, local warm conditions might result from geothermal groundwater and hot springs. Springs from geothermal groundwater, as well as from meteogene groundwater, can produce travertines, that is, a calcareous tufa (Pentecost, 2005). A travertine is a calcareous formation resulting from chemical processes in a spring, notably degassing of surfacing CO<sub>2</sub>-rich groundwater containing calcium carbonates followed by carbonate precipitation (Cantonati et al., 2016; Pentecost, 2005). They often contain fossilized plants or mollusc shells, and the chronology of these formations is usually based on Th/U ratio (Ghaleb & Falguères, 2017). We hypothesize that such soil warmed by geothermal groundwater and springs might have offer local conditions for glacial refugia for plants and animals.

Here, we have selected a travertine formation with expected age from the early Holocene at least and located in a high mountain region with geothermal groundwater, to test whether trees could grow in this site, while the glacier melting were late during the early Holocene. The museum of the University of Grenoble Alpes archived tree fossils collected during the 19th century from a travertine formation (Kilian, 1894) located in the Lautaret pass (45°2'11"N-06°23'55"E). This formation is several metres thick. Due to this impressive thickness and its unusual altitude (2,100 m a.s.l.) in a treeless modern environment overlooking slope glaciers and high summits, we examined it with modern methods for its biotic composition, the environmental context and chronology using bio- and geo-proxies. Biotic analyses were based on plant imprints and mollusc shells to characterize dominant ecosystems. During the initial survey, we observed that the lower part of the travertine displays an abrupt colour change, which could be linked to a change of water source and could explain environmental processes, that is, thermogene groundwater (geothermal spring) or meteogene (linked to precipitation). The geochemistry of carbonates based on  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  served to determine the groundwater origin of the travertine (Andrews, 2006).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study site is situated on a south-facing slope (2,100 m a.s.l.), above the Lautaret pass (Figure S1). The travertine is near the botanical garden of the Joseph Fourier research field station, run by the University of Grenoble Alpes. This travertine was quarried during the 19th century in order to build the church in the nearby village of Villar d'Arène. The scientific significance of this travertine was first reported in late-19th century (Kilian, 1894), supported with palaeobotanical identification (Fliche, 1904). The remaining travertine formation is, thus, a small fraction of the original that existed before it was quarried.

The travertine lies on limestone bedrock dating from the Lias, but the modern groundwater flows through Pleistocene deposits and Jurassic or Triassic limestone bedrock. The spring water temperatures are cold and stable, varying from 6.5°C (January) to 6.9°C (July). The pH is 7.1, with a HCO<sub>3</sub><sup>-</sup> concentration of 224 mg/L.

Currently, the  $\delta^{18}\text{O}$  value is  $-13.8\text{‰}$ . The high concentrations of  $\text{SO}_4^{2-}$  (677 mg/L) indicate that this groundwater flows through gypsum deposits and Triassic dolomitic limestone.

The surrounding vegetation is characterized by treeless subalpine meadows grazed in summer by domestic animals (Lavorel et al., 2017), and was, traditionally, mown for hay production. The meadows are dominated by Poaceae and Cyperaceae, with scattered small broadleaved trees (i.e., *Salix* spp. or *Alnus alnobetula*) and dwarf shrubs (*Daphne striata* Tratt., *Dryas octopetala* L., *Juniperus sibirica* Lodd. Ex Burgsd.).

## 2.2 | Global and regional climate and atmospheric framework

Globally, the LGM ended at 18,000 cal BP, but glacial climatic conditions prevailed until 14,500 cal BP in the North Hemisphere (Clark et al., 2009). The transition between the Lateglacial and the Holocene, which is the current interglacial period, is dated at 11,650 cal BP (Walker et al., 2009). The last cold event before the beginning of the Holocene is the Younger Dryas, from 12,900 to 11,700 cal BP. However, in mountain areas, cold conditions lasted longer due to the delayed melting of glaciers. The exact local climatic values during the early Holocene still remain unknown, while they represent an issue to understand the functioning of ecosystems during the first millennia of the Holocene, and could explain some delays between plain and mountain environments.

The regional climatic framework in the Alps or the western Europe is based on reconstructions inferred from pollen as temperature or precipitation proxy, and chironomids for temperature. From 12,000 to 9,000 cal BP, precipitation was lower by 200–400 mm (Ortu et al., 2008), that is, when trees grew at the Lautaret pass with summer regional temperatures between  $2^\circ\text{C}$  and  $4^\circ\text{C}$  below the modern values (Davis, Brewer, Stevenson, & Guiot, 2003; Heiri, Tinner, & Lotter, 2004).

Additional climatic features are provided by solar insolation simulations resulting from orbital forcing and from  $\text{CO}_2$  atmospheric concentration. The optimal solar irradiance was reached in June at 12,000 years BP, in July at 10,000 years BP and in August at 8,000 years BP (Berger & Loutre, 1991). The mean  $\text{CO}_2$  atmospheric concentration were low (ca. 189 ppmv) at 17,000 cal BP, and increased to attained values of ca. 238 ppmv between 13,800 and 12,300 cal BP, and ca. 265 ppmv between 11,100 and 10,500 cal BP, that is, during the first centuries of the Holocene (Monnin et al., 2001). The concentration attained the lowest Holocene values 260 ppmv ca. 8,000 cal BP before to increase almost linearly during 7,000 years attaining 285 ppmv (Indermühle et al., 1999). The low  $\text{CO}_2$  concentrations during the Lateglacial should conduct to lower the photosynthetic rate and the water-use efficiency.

Global and regional temperatures, precipitations and  $\text{CO}_2$  concentrations define a harsh environment unfavourable for tree growth before 9,000 cal BP. However, the eventual warmed geothermal freshwaters combined with an exposition on a south-facing slope and the high summer solar irradiances may have partially

counterbalanced the regional climatic pattern during the Lateglacial or the early Holocene by creating local microclimatic and stand conditions favourable for trees and other organisms.

## 2.3 | Sampling

Sampling took place during the summers of 2008, 2009 and 2010. A trench was hand-cut to a depth of 160 cm, on an undisturbed part of the travertine, the top of which was visible at ground level. The trench revealed a cascading travertine. From the 160 cm deep trench, the rest of the sampling was carried out using a rock corer down to a depth of 800 cm.

## 2.4 | Th/U dating

Thirteen  $^{230}\text{Th}/^{234}\text{U}$  radiometric datings were carried out at eight different depths.  $^{230}\text{Th}/^{232}\text{Th}$  ratios were measured along the travertine profile to detect any contamination by elemental migration through the travertine layers. Generally, older migration events are at the top of the trench and younger events deeper down (Eikenberg et al., 2001). We used  $^{232}\text{Th}$  as an index and assumed a typical crustal Th/U ratio, with  $^{234}\text{U}/^{238}\text{U}$  and  $^{230}\text{Th}/^{238}\text{U}$  activity ratios almost at secular equilibrium. In our model (Ludwig & Paces, 2002), the isotope and the activity ratios used were  $1.21 \pm 50\%$  for  $^{232}\text{Th}/^{238}\text{U}$ ,  $1.0 \pm 10\%$  for  $^{234}\text{U}/^{238}\text{U}$  and  $1.0 \pm 10\%$  for  $^{230}\text{Th}/^{238}\text{U}$ . The half-times used for the computation of ages were 245,250 years for  $^{234}\text{U}$  and 75,690 years for  $^{230}\text{Th}$ . Th/U measurements can be directly compared with the calendar chronology because there is no reservoir effect affecting  $^{14}\text{C}$  dating (Ghaleb & Falguères, 2017).

## 2.5 | $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes

As the surrounding valleys contain geothermal springs and active thermogene travertines, the spring water of the travertine was tested to see if it was ever meteogenic as it is at present. Indeed, travertine results from chemical processes occurring at a limestone-precipitating spring, notably the degassing of surfacing  $\text{CO}_2$ -rich groundwater containing calcium carbonate, followed by carbonate precipitation (Cantonati et al., 2016; Pentecost, 2005). Groundwater containing carbonate deposits mainly originates from two processes producing either meteogene or thermogene travertine. Thermogene travertine is linked to geothermal groundwater that is often associated with high  $\text{CO}_2$  concentration, thus making the water capable of dissolving a large amount of rock. In this case, the isotopic signature ( $\delta^{13}\text{C}$ ) is typically between  $-3\text{‰}$  and  $+8\text{‰}$ . These geothermal spring waters are not necessarily hot, although they are often above  $37^\circ\text{C}$  (Cantonati et al., 2016). Such geothermal springs exist at lower altitudes in the nearby Guisane river valley. Meteogene travertine is closely linked to the precipitation flux and to the capacity of the soil to concentrate organic acids that enrich the groundwater and dissolve bedrock. These meteogene groundwaters are often cold, and the  $\delta^{13}\text{C}$  signature is generally around  $-10\text{‰}$  (Andrews, 2006; Pentecost, 2005). If the  $\delta^{13}\text{C}$  is directly connected to the type of

groundwater (thermogene: between  $-3\text{‰}$  and  $+8\text{‰}$ ; meteogene: ca.  $-10\text{‰}$ ),  $\delta^{18}\text{O}$  is useful for characterizing the rate of calcification due to significant evaporation linked to water temperature (Andrews, 2006). Less negative values of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  would indicate disequilibrium processes, that is, rapid calcification and intense  $\text{CO}_2$  degassing, and *vice versa* when values are depleted (Andrews, 2006).

The isotopes were measured by Isotope Tracer Technologies Inc., Waterloo, Ontario.  $\Delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  were measured for 20 samples taken from between 350 and 750 cm depth, evenly distributed around the depth of colour change situated at 580 cm.

## 2.6 | Plant imprints

Plants imprints are classically observed in travertine, notably in the Alps. These imprints can reveal leaves and needles, cones, seeds, branches and, on rare occasions, fruits. The first collection of imprints from the Lautaret pass travertine, identified by Fliche (1904), is archived at the University of Grenoble Alpes. These old materials were not used in the present study due to the difficulty in cross-referencing the stratigraphical information reported by Kilian (1894) to our new samples.

The plant imprints were carefully extracted from travertine blocks using a hammer and chisel. The quality of the taxonomic identification depends on the preservation of leaf imprints and their margin and rib details. Imprints were drawn using a stereomicroscope ( $\times 12\text{--}50$ ) and a camera lucida. These morphological features generally permit accurate taxonomic identifications. For identification of conifer cones, cone moulds were created using silicon liquid, allowing morphological analyses of *Pinus* cone traits to determine the species (Fauvart et al., 2012). Indeed, among diploxylon pines, three species grow in the Alps: *Pinus mugo* (dwarf pine), *P. sylvestris* (Scots pine) and *P. uncinata* (mountain pine). Although *P. sylvestris* is currently found mostly at lower elevations up to around 2,000 m a.s.l., *P. mugo* and *P. uncinata* grow at subalpine elevations. Identification between these species is based on simple morphological analyses of cones, using measurements of their apophyses when necessary (Fauvart et al., 2012). *P. cembra* is also another subalpine species growing in the area, but it is a haploxylon pine. To distinguish the haploxylon (*P. cembra*) from the three diploxylon species, transversal cross-sections of needles were examined: *P. cembra* has triangular-shaped needles, whereas diploxylon pines have semi-circular needles.

## 2.7 | Malacofauna remains

Shell remains were manually collected in the field, from coherent travertine which did not allow bulk sampling and sieving of the sediment. The zoological nomenclature used is that of Welter-Schultes (2012).

## 2.8 | Data availability

All fossils will be stored at the museum of the University of Grenoble Alpes (<http://collections.obs.ujf-grenoble.fr/>).

# 3 | RESULTS

## 3.1 | Stratigraphy and chronology

The total thickness of the profile was 800 cm. The travertine is established on the Lias limestone bedrock with no evidence of morainic material (Figure 1a). The first 40 cm of the travertine (level AA28) are laminated, grey and dense, containing bedrock fragments. No Th/U measurement was possible from the first few 70 cm. The first dating was obtained at 725 cm ( $14,470 \pm 472 \text{ Th/U BP}$ ; Table 1), 75 cm above the base of the travertine; it corresponds to the early Lateglacial period. The level AA27 (760–570 cm) is a monotonic dense laminated travertine with a grey colour that progressively becomes beige near the transition with the AA26 level, which begins at 580 cm. The first 2 m (AA28 and AA27) are grey and azoic (no apparent fossils). Another dating was obtained at 630 cm, but the large uncertainty ( $\pm 9,527$ ) associated with the early Lateglacial date ( $17,789 \text{ Th/U BP}$ ; Table 1) prevents its use for interpretation of the stratigraphy.

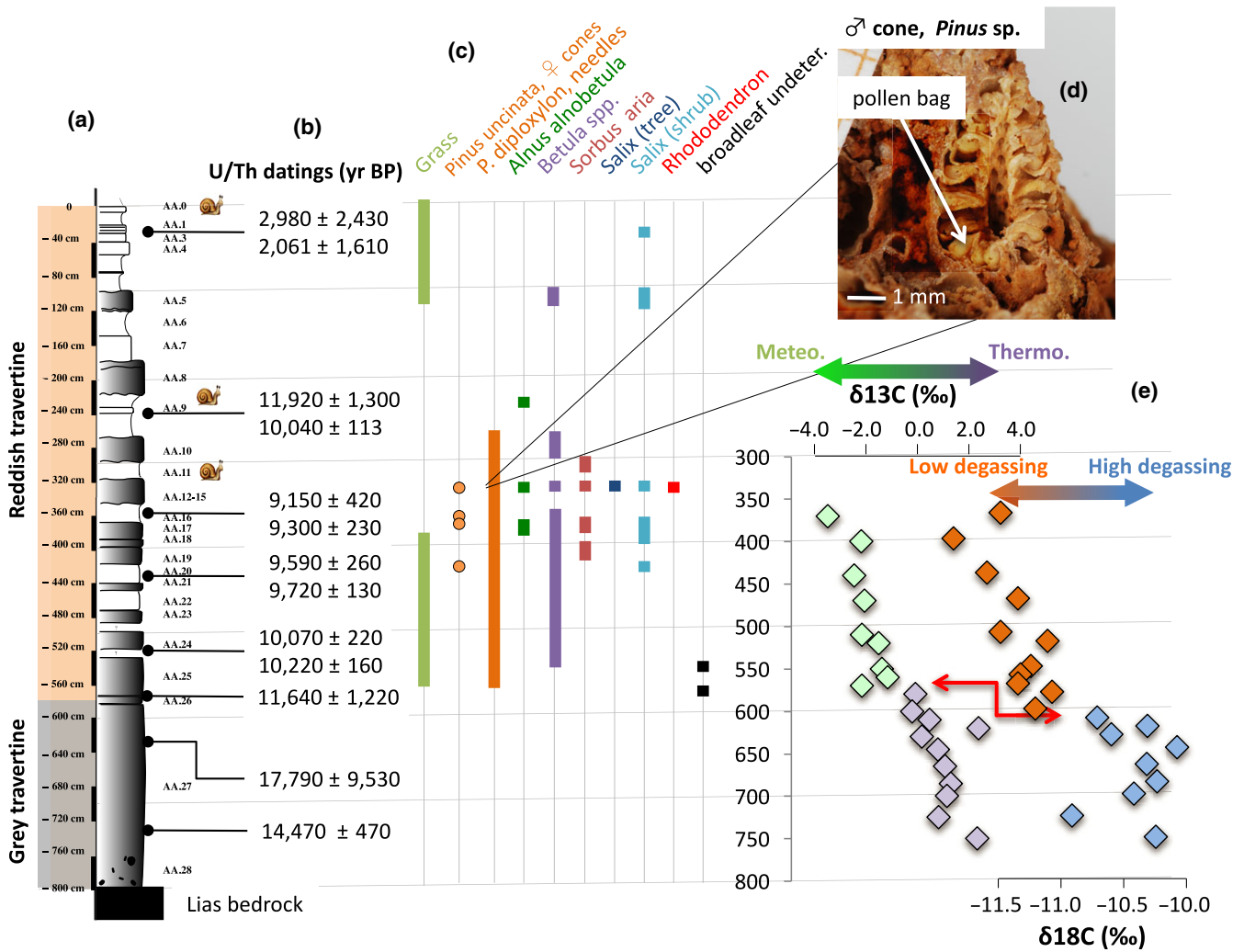
The dense layer AA26 (10 cm thick) is situated at about 580 cm. It becomes abruptly reddish-orange due to iron oxides. These changes in geochemical composition might suggest changes in the water sources supplying dissolved iron, or the occurrence of iron-oxidizing bacteria, which were not present before. The AA26 layer is dated to  $11,640 \pm 1,215 \text{ Th/U BP}$  (Table 1), which is synchronous with the beginning of the Holocene period, despite the large uncertainty in the dating. The rest of the travertine up to the uppermost layers remains an orange-red colour, rich in plant and mollusc fossils. Between AA25 and AA10, being about 300 cm of material, the accumulation rate increases, occurring between around 11,000 and 9,000  $\text{Th/U BP}$  (6 accurate dates associated with small uncertainties; Table 1). All these levels are orange-rust coloured and contain abundant needles or leaf imprints. These imprints attest to the presence of plants around the travertine. From AA9, the dating involves large uncertainties, but there is a good indication that there was a significant reduction in sedimentation up to the summit of the travertine.

## 3.2 | Isotope profiles

Between 800 and 300 cm,  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values covary and show monotonic decreases (Figure 2).  $\Delta^{13}\text{C}$  values were positive in the oldest and grey sediments (mean  $\pm \text{SE}$ :  $0.78 \pm 0.21\text{‰}$ ) and became progressively negative ( $-1.67 \pm 0.19\text{‰}$ ). The  $\delta^{18}\text{O}$  became more negative with the aggradation of carbonates. However, even though  $\delta^{13}\text{C}$  records a transition between 580 and 570 cm,  $\delta^{18}\text{O}$  shows a break between 610 and 600 cm (Figure 1). The  $\delta^{13}\text{C}$  depletion coincides with the colour change of the travertine, from grey to orange-rust (Figure 2).

## 3.3 | Palaeobotany

Plant macrofossils first appear in AA26 (Table 2). They are regular and abundant until the AA10 layer. From AA9 to AA6, there are



**FIGURE 1** Schematic stratigraphy of the travertine formation and, the geo- and bio-proxies, Lautaret pass, France. The colour of the sediment is indicated on the left, grey from 800 to 580 cm and orange from 580 cm to the top due to iron oxides (a); the grey sediments were azoic (no apparent fossils). The dates are based on Th/U ratio (b details in Table 1). Stratigraphic levels containing mollusc fauna are indicated with a shell symbol (details in Table 2). Palaeobotanical data are summarized (c, details in Table 1) with a photograph of a fossilized male cone of pine with visible pollen bags (d, in insert); plant names: *Pinus uncinata* (mountain pine), *Alnus alnobetula* (green alder), *Betula* sp. (birch), *Sorbus aria* (whitebeam), *Salix* sp. (willow), *Rhododendron* sp. (rhododendron). Isotopic measurements (e) characterized the origin of groundwater, from thermogene to meteogene ( $\delta^{13}\text{C}$ ) with an indication of the degassing intensity ( $\delta^{18}\text{O}$ )

almost no fossils. The topmost layers (120–0 cm) contain fewer macrofossils than between layers AA26 and AA10.

From layers AA26 to AA10, there were a diverse number of plants identified, including grass (graminoid-shape plants) and woody taxa, notably needleleaf and broadleaf species (Figure S2). Graminoid could not be identified. Needleleaf species fossils only included material from diploxylon pine (*Pinus* sp.) remains, including female cones, male cones and needles. All the mature female cones correspond to only one taxa, *Pinus uncinata* or mountain pine. At level AA14, male cones of *Pinus* were recorded clearly showing pollen bags (Figure 1d).

The broadleaf species included frequent and abundant leaves of *Betula pendula* and *B. pubescens* (white and silver birches, respectively), irregular occurrences of *Alnus alnobetula* (green alder), *Rhododendron* (one layer), *Sorbus aria* (whitebeam, several layers), and *Salix*

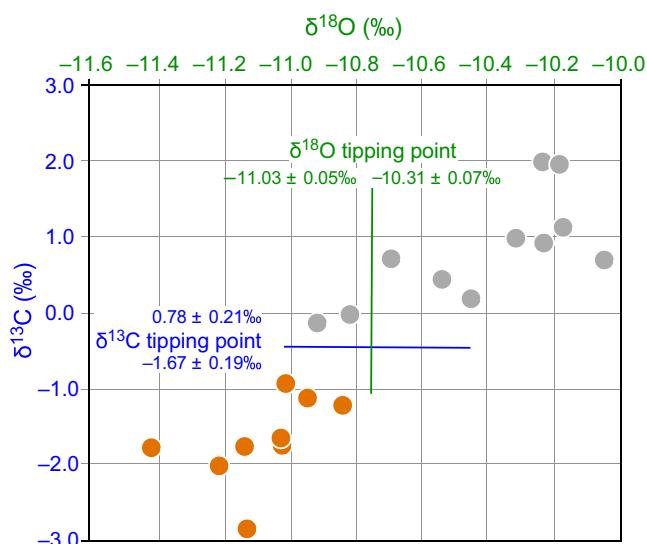
spp. (willow). Among the willow identified, one tree species was found (*S. caprea*) along with several shrubs: *S. arbuscular*, *S. helvetica*, *S. cinerea*, *S. myrsinifolia*, *S. myrtilloides*, *S. repens* (Table 2; Figure S2).

### 3.4 | Malacofauna

Only three layers provided material appropriate for mollusc (malacofauna) identification, AA11, AA9 and AA0 (Figure 1a, Table 3, Figure S3). As few shells were actually found, the ecological characteristics associated with specific species can only provide additional information to portray the past ecosystems (Table 3). Furthermore, the layers containing mollusc material were too disjointed to allow the temporal dynamics of these communities to be assessed. They all contain species from freshwater or swampy environments (Table 3), likely linked to the travertine spring. However, the oldest

**TABLE 1** Th/U measurements and datings of stratigraphical layers. Th/U measurements were carried out at IFM-Geomar, Kiel, Germany, and GEOTOP, Montreal, Canada. Corrected  $^{Th/U}BP$  ages are equivalent to calibrated years before present (cal BP)

Sample layer	Sample no.	$^{230}Th/^{232}Th$	Uncorrected age ( $^{Th/U}BP$ )	Corrected ages ( $^{Th/U}BP$ )	Lab
AA1 30 cm	1	$1.352 \pm 0.020$	$7,360 \pm 112$	$2,981 \pm 2,430$	IFM-Geomar
	2	$1.379 \pm 0.025$	$4,974 \pm 89$	$2,061 \pm 1,609$	
AA9 240 cm	1	$5.237 \pm 0.023$	$13,971 \pm 79$	$11,915 \pm 1,303$	IFM-Geomar
	2	$10.832 \pm 0.116$	$10,044 \pm 113$	$10,041 \pm 113$	
AA16 360 cm	1	$10.012 \pm 0.039$	$9,920 \pm 43$	$9,146 \pm 419$	IFM-Geomar
	2	$20.127 \pm 0.230$	$9,674 \pm 113$	$9,299 \pm 231$	
AA20 435 cm	1	$16.872 \pm 0.121$	$10,054 \pm 77$	$9,589 \pm 260$	IFM-Geomar
	2	$47.741 \pm 0.514$	$9,879 \pm 103$	$9,717 \pm 134$	
AA24 520 cm	1	$20.421 \pm 0.113$	$10,473 \pm 61$	$10,074 \pm 222$	IFM-Geomar
	2	$29.942 \pm 0.168$	$10,494 \pm 65$	$10,222 \pm 159$	
AA26(C12) 580 cm		$4.813 \pm 0.091$	$13,831 \pm 314$	$11,640 \pm 1,215$	GEOTOP
AA27(C20) 630 cm		$1.530 \pm 0.032$	$34,526 \pm 850$	$17,789 \pm 9,527$	GEOTOP
AA27(D8) 725 cm		$16.054 \pm 0.287$	$15,182 \pm 279$	$14,470 \pm 472$	GEOTOP



**FIGURE 2** Progressive change from thermogene to metogene groundwater. Biplot distribution of  $\delta^{18}O$  and  $\delta^{13}C$  measurements on grey azoic layers (grey dots) and orange and fossil rich layers (orange dots); tipping point correspond to significant differences ( $p < 0.0001$ ; Wilcoxon test). Less negative values (top right) indicate environmental conditions with vigorous degassing of  $CO_2$  linked to higher water temperatures and resulting in a higher calcification rate (Andrews, 2006). Higher water temperature can result from seasonal variability between summer and winter, or changes in water type. Geothermal waters favour higher degassing

sample, AA11, contained shells of Clausiliidae, a taxon usually associated with woody communities, and *Nesovitrea petronella*, a land snail found in humid open or humid woody ecosystems. In the lower AA9 level, the occurrence of *Aegopinella nitens* attested to the presence of woody communities, while *Candidula unifasciata* is linked to dry grassland.

## 4 | DISCUSSION

We found that mountain pine and birch colonized the Lautaret pass at 11,650  $^{Th/U}BP$ , at least, coinciding with the date of the transition between the Lateglacial and the Holocene (Walker et al., 2009), while the glaciers were still present at lower altitudes in the valleys (Buoncristiani & Campy, 2004) with their fronts at 1800–1900 m a.s.l. (Cossart et al., 2012). Unidentified grasses were associated with the first occurrences of mountain pine and birch. The other broadleaf trees, that is, willows, green alder and whitebeam, first occurred around 9,700–9,500  $^{Th/U}BP$ , clearly during the early Holocene (Table 1). These broadleaf trees occurred sporadically, while mountain pine and birch were more regular all along the profile from 11,650  $^{Th/U}BP$  until 9,100  $^{Th/U}BP$ . This difference in the record between species can have taphonomical or ecological origins: (i) taphonomically, the thin structure of leaves might limit their fossilization and, (ii) ecologically, the trees were not present around the spring during the Lateglacial–Holocene transition when mountain pine trees were abundant. As the numbers of birch leaf imprints were high (same thin leaf structures than the other broadleaf trees recorded later), we assumed that the taphonomic problem could be ruled out, and the scarcity of broadleaf species excepted birch was ecological.

The scarcity of willows, whitebeam and alder between 11,650 and 9,100  $^{Th/U}BP$  mirrors the composition of woodlands dominated by pines and birches. Furthermore, the abundance of fragile graminoid leaves from around 11,650 to 9,400  $^{Th/U}BP$  supports the evidence for mountain pine communities with grass understories, perhaps a tree-covered steppe ecosystem. Ericaceae (e.g. *Rhododendron*, *Vaccinium*), which generally abound in modern subalpine forests or alpine tundras, are generally missing from the travertine record (only one layer). Molluscan assemblages strengthened palaeobotanical observations indicating that, before 9,000  $^{Th/U}BP$ , woody

**TABLE 2** List of plant identification based on imprints (see pictures in Figure S3). Number of *Salix* species: (1) *S. arbuscula*; (2) *S. caprea*; (3) *S. cinerea*; (4) *S. helvetica*; (5) *S. myrtilloides*; (6) *S. myrsinifolia*; (7) *S. repens*; mc, male cone; nd, needle

Sample	Herbs Graminoid- shape plants	Needleleaf tree		Broadleaf trees and shrubs						
		<i>Pinus uncinata</i> # Female cone	<i>Pinus diploxylon</i> # Male cone (mc) # Needle (nd)	<i>Alnus alnobetula</i>	<i>Betula pendula</i> (a) <i>Betula pubescens</i> (b) <i>Betula sp.</i> (c)	<i>Rhododendron ferrugineum</i>	<i>Salix</i> (tree)	<i>Salix</i> (shrub)	<i>Sorbus aria</i>	Broadleaf, undetermined
AA0	●									
AA3	●							5		
AA5	●				b			3		
AA9				●						
AA10			nd		b					
AA11			nd						●	
AA12			nd						●	
AA13			nd							
AA14		●	mc nd	●	a	●	2	1 4	●	
AA15			nd							
AA16		●	nd		a					
AA17		●	nd	●	a b			4 7	●	
AA18	●		nd		b			6		
AA19	●		nd		b				●	
AA20	●	●	nd		b			4		
AA25-C1	●		nd		c					
AA25-C2	●		nd							●
AA25-C4	●		nd							
AA25-C5	●		nd							
AA25-C6	●		nd							
AA25-C7	●		nd							
AA25-C8	●		nd							
AA25-C9			nd							
AA25-C10			nd							
AA26-C12										●

communities dominated the environment around the travertine (AA11 and AA9), although gastropod species like *Candidula unifasciata* attest also the occurrence of dry grassland, suggesting an environment with both woodlands and grasslands. The lack of common high-altitude conifers (larch, cembra pine) is very intriguing because most macro-remain-based palaeoecological records in the Alps show that larch and cembra pine always dominated the treed communities at these altitudes since 11,000 cal BP at least (e.g. Blarquez, Carcaillet, Mourier, Bremond, & Radakovitch, 2010; Gobet, Tinner, Bigler, Hochuli, & Ammann, 2005; Tinner & Kaltenrieder, 2005) and even since 20,000 cal BP in a site situated 30 km further southeast (Carcaillet & Blarquez, 2017).

After ca. 9,100 <sup>Th/U</sup>BP, records of plant imprints disappeared from the travertine all over the middle Holocene (AA9-AA6) and reoccurred during the late Holocene with only few occurrences of broadleaved woody species, i.e., white birch, willows (*Salix cinerea*,

*S. myrtilloides*), but with a continuous record of grass (Figure 1, Table 2). This supports the idea that the present treeless environment of the Lautaret pass was created very early during the Holocene.

#### 4.1 | Interactions with groundwater and the climate dynamics

The first occurrence of trees was synchronous with the change in the source of the water that transported dissolved carbonates before sedimentation. Since the creation of the travertine before 14,500 <sup>Th/U</sup>BP (i.e., during the late LGM; Clark et al., 2009), carbonate precipitation had been from geothermal waters ( $\delta^{13}\text{C}$  values lower than  $-1\text{‰}$  before 570 cm); however, this progressively changed towards meteoric groundwater type. The first 2 m of travertine (800–580 cm) are grey and apparently azoic. Intriguingly, the onset of the



**TABLE 3** Malacofauna (fossils) of the Lautaret pass travertine; all the species are gastropods, excepted *Pisidium* that is a freshwater bivalve

Species	Main habitat	AA11	AA9	AA0
<i>Radix labiata</i>	Aquatic, small ponds or streams			●
<i>Aegopinella</i> cf. <i>nitens</i>	Humid woodland or rocky habitats		●	
<i>Candidula unifasciata</i>	Dry grassland		●	
<i>Quickella arenaria</i>	Low tree cover, swampy habitats	●	●	
<i>Vallonia pulchella</i>	Humid and swampy meadows	●	●	
<i>Nesovitrea petronella</i>	Alpine meadows or swamps; woodlands	●		
Clausiliidae undet.	Tree cover	●		
<i>Pisidium</i> sp.	Aquatic, freshwater	●		

Holocene (11,700 cal BP) was well characterized by an abrupt change in travertine colour due to iron oxides (orange), and a lowering in  $\delta^{18}\text{O}$  values between 610 and 600 cm, from  $-10.31 \pm 0.20\text{‰}$  to  $-11.03 \pm 0.17\text{‰}$  (mean  $\pm$  SD), that is, a few centuries earlier than the  $\delta^{13}\text{C}$  disruption. This pattern in  $\delta^{18}\text{O}$  is remarkable because it provides an indication of the water temperature, with the  $\delta^{13}\text{C}$  giving an indication of the main origin of water. When both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  show less negative values (Figure 2, top right), it indicates a vigorous degassing of  $\text{CO}_2$  linked to higher water temperatures, resulting in a higher calcification rate (Andrews, 2006). This mechanism took place in the oldest section of the travertine formation, that is, during the Lateglacial, which was mainly created from warm geothermal groundwater, but became progressively linked to colder meteogene groundwater (Figure 2, bottom left). The tipping point that marks the change in groundwater origin is around 11,650  $\text{Th}/\text{U}$ BP, oddly coinciding with the Holocene onset. However, the  $\delta^{18}\text{O}$  values decreased earlier than the  $\delta^{13}\text{C}$ , probably during the earlier colder climate period, namely the Younger Dryas (12,900–11,700 cal BP). Although the  $\delta^{18}\text{O}$  change suggests switch to colder waters, the  $\delta^{13}\text{C}$  values still remained in a range of geothermal groundwater (Andrews, 2006; Cantonati et al., 2016; Pentecost, 2005) until ca. 9,000 cal BP clearly indicating a mix of geothermal and meteogene waters, not an abrupt transition between one groundwater type to another. Today, the spring waters are cold but stable throughout year (from 6.5°C to 6.9°C) with depleted  $\delta^{13}\text{C}$  values clearly indicating meteogene groundwater. The progressive increase in meteogene groundwater ratio between 11,700 and 9,000 cal BP (Figure 1e) may be linked to the increase in precipitation during this period (ca. +300 mm/year; Ortu et al., 2008), although a tectonic mechanism changing the groundwater circulation cannot be ruled out.

The long period of woodland growth between around 11,700 and 9,100  $\text{Th}/\text{U}$ BP suggests growing limits of trees under climatic and atmospheric characteristics that are beyond the boundaries of their modern ecological niches. Indeed, precipitation was lower by 200–

400 mm (Ortu et al., 2008) when trees grew at the Lautaret pass with summer regional temperatures 2°C and 4°C below the modern values (Davis et al., 2003; Heiri et al., 2004). However, the lower temperatures were probably balanced by higher solar irradiance during summer time that reached their maximum for 21,000 years in June at 12,000 years BP, in July at 10,000 years BP and in August at 8,000 years BP (Berger & Loutre, 1991). Furthermore, the  $\text{CO}_2$  atmospheric concentrations attained their maximum (265 ppmv) since 21,000 cal BP (Monnin et al., 2001) that last until the Middle Age (Indermühle et al., 1999).

Geothermal groundwater providing unfrozen freshwaters and probably warming soils, high  $\text{CO}_2$  concentration and higher solar irradiance on a south-facing slopes would have initiated very comfortable conditions for tree growth despite the local presence of glaciers around the Lautaret pass (some glaciers are still present today in the landscape above 2,800 m a.s.l.) and unfavourable global temperatures.

## 4.2 | Evidences of glacial refugia in the western inner Alps

The following discussion is based only on plant macro- or gigarremains evidences, subfossils from lake sediments well dated based on AMS  $^{14}\text{C}$  or fossil imprints in travertine well dated based on  $\text{Th}/\text{U}$  on carbonates (synthesis in Figure 3). Pollen data are not used here because too much questionable due to long-distance transportation of most recorded taxa, which create serious doubt on their source area. Further, this review only focused on data from the inner Alps that were concerned by glacier extent.

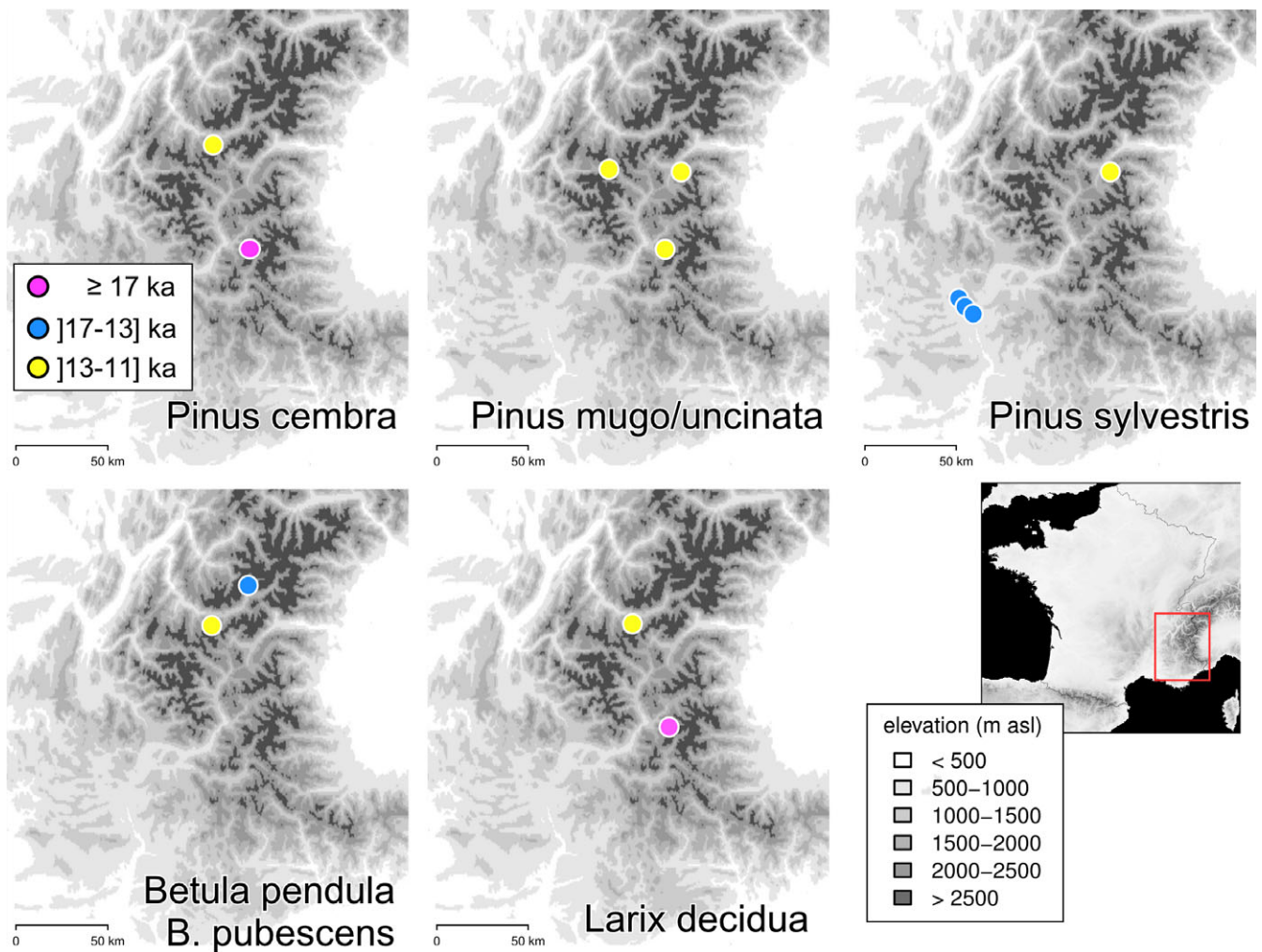
Trees obviously colonized high elevations above the valley glaciers, at the Lateglacial-Holocene transition, in a location with warm water and soil thanks to a geothermal spring. Interestingly, cembra pine and larch were not recorded in the Lautaret pass, although these taxa first occurred simultaneously 18 km further north ca. 11,700 cal BP (Blarquez et al., 2010), and earlier since the LGM 30 km further southeast (Carcaillet & Blarquez, 2017). The presence of birch was also found further 20 km northeast at around 14,700 cal BP during the last LGM (Carcaillet et al., 2009). This early tree occurrence combined with other scattered evidences of the presence of trees in the western central Alps before 11,000 cal BP on mountains (Ali et al., 2003) or valleys (Fauvart et al., 2012; Miramont, Sivan, Rosique, Edouard, & Jorda, 2000; Miramont et al., 2011) all supports the idea that the inner massifs sheltered glacial refugia of mountain and cembra pines, larch and birch (Figure 3). Excepted the valley sites that concerned only *P. sylvestris* (Fauvart et al., 2012; Miramont et al., 2000, 2011), all mountain data older than 11,000 cal BP are from sites above 2,030 m a.s.l. and concerned *P. cembra*, *P. uncinata*, *Larix decidua* or *Betula* sp. (Ali et al., 2003; Blarquez et al., 2010; present study). Some sites are on south-facing slopes (Ali et al., 2003; Carcaillet et al., 2009; present study) or on a small plateau well exposed to sunlight (Carcaillet & Blarquez, 2017). Only one is on a north-facing slope (Blarquez et al., 2010). However, the only site associated with geothermal spring is the Lautaret pass (present study).

These rare observations of early trees in high mountains match those from the central Alps in Switzerland (e.g. Lang & Tobolski, 1985; Tinner & Kaltenrieder, 2005) and in northern Italy (e.g. Leys et al., 2014; Ravazzi, Badino, Marsetti, Patera, & Reimer, 2012) and suggest a scattered pattern of cryptic refugia of trees in the inner Alps. As the upper valleys of the western Alps were filled with ice during the LGM (Buoncristiani & Campy, 2004; Cossart et al., 2012), these refugia were probably situated on *nunataks*, that is, mountain slopes above glaciers (Dahl, 1987). All this evidence suggests a scenario of scattered tree refugia in glacial environments in the inner Alps of France, of northern Italy and of Switzerland.

### 4.3 | Patch-scale physiographical ecosystem conditions supporting climatic refugia

In general, there are growing evidences that patch-scale physiographical conditions play a functional role on the survival of

organisms and diversity during glacial or interglacial times (Niskanen, Luoto, Väre, & Heikkinen, 2017; Valdés et al., 2015). Until now, the importance of such ecosystem processes for the preservation of biota during glacial times was underestimated due to the difficulties to find evidences based on palaeoecological methods (e.g. pollen that is the main used proxy is a poor predictor of stand-to-local vegetation composition due to several reasons; Birks & Birks, 2000), and because the spatial resolution of models was too coarse to detect and predict such rare and scattered conditions (review in Gavin et al., 2014). Topography and geology must, thus, be finely taken into account to detect potential climatic refugia for plants, animals and microorganisms, both by empirical field studies based on macrofossils and process-based models of species distribution. The study of environmental DNA offers new perspectives to investigate sediments from glacial periods when other classic approaches are partially or totally inoperative (Parducci et al., 2017).



**FIGURE 3** Synthesis of earliest occurrences of mountain trees. The occurrences are based on plant imprints in travertine formations (Figure 1; Ali et al., 2003; Fauvart et al., 2012), megafossils buried in alluvial deposits (Miramont et al., 2000), or macroremains from lake sediments (Blarquez et al., 2010; Carcaillet & Blarquez, 2017; Carcaillet et al., 2009) in the central western Alps earlier than 11,000 calibrated years before present (cal BP). These first occurrences on each site support a region of high mountains where trees survived the glaciation, while the valleys were filled with glaciers (Buoncristiani & Campy, 2004). *Pinus cembra* (cembra pine), *P. uncinata/mugo* (mountain pine), *P. sylvestris* (Scots pine), *Larix decidua* (European larch), *Betula pubescens* and *B. pendula* (white birch, silver birch)

Despite the inhospitable drier and colder regional climate during the Lateglacial–Holocene transition, trees and molluscs grew in the vicinity of a spring of geothermal groundwater. This woody habitat consisted of a climate refugium at the Lautaret pass probably because of the water's relative warmth, which maintained soil temperature and kept the water unfrozen, thus appropriate for plants and animals. Trees expanded during the early centuries of the Holocene with the increasing summer insolation when glaciers were still present under the Lautaret pass. This evidence changes our view of the tree distribution in periglacial environments, due to local favourable conditions producing optimal tree growth around a geothermal spring. Furthermore, this finding and the data scattered in the literature support the idea of tree climate refugia on nunataks in the Alps. The controversial paradigm of *tabula rasa* must be reconsidered.

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## AUTHOR CONTRIBUTION

SA and JLL originally formulated the idea to re-excavate the travertine formation after the discovery of the Kilian's collection from the 19th century; CC led the study; JLL carried out the excavations and the stratigraphic analyses. SA carried out the palaeobotanical analyses under the supervision of PR and AA, and FM and JLL carried out the molluscan identifications. BG took the Th/U measurements. SA, CC and JLL discussed the results. CC wrote the first draft and all authors contributed to the final version of the manuscript.

## CONFLICT OF INTEREST

The authors declare no competing interests.

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