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8 **Early-to-late-Holocene vegetation and fire dynamics at the treeline in the**
9 **Maritime Alps**

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20

21 **Abstract**

22 We used pollen, plant-macrofossil, and charcoal records to unfold local long-term timberline shifts and changes
23 in vegetation composition in relation to fire activity at the modern upper forest limit (ca. 2000 m asl) in the Mont
24 Bégo area. The area is an iconic place for Alpine archaeology because it bears thousands rock-art engravings
25 whose age cannot be directly assessed. Our new record confirms the occurrence of distinct land-use phases
26 (7450-7150, 6200-4900, and 4250-3700 cal BP), as suggested by prior studies based on rock-art typology.
27 Moreover, the macrofossil-inferred vegetation reconstruction (co-dominance of *Pinus* and *Betula*) suggests that
28 early-Holocene conditions were moister than in dry inner-alpine valleys, where *Larix decidua* played a more
29 important role, both in past as well as in modern timberline forests. After 8000 cal BP, the timberline shifted to
30 higher elevation and mixed *Abies alba* and *Pinus cembra* stands established around the study site. These fire-
31 sensitive tree populations were definitely replaced during the Bronze Age (around 4000 cal BP) by *L. decidua*
32 that still dominates the subalpine forests in the area today. Our study supports the notion that while the range (or
33 realized climatic niche) of *A. alba* has been reduced at the colder-end of its natural distribution that of *L. decidua*
34 has been widened by land-use changes and fire disturbances to create high-alpine pasture woodlands.

35

36 **Keywords:** Vegetation dynamics; mountain ecosystems; treeline ecotone; land-use phases; pasture woodlands; fires

37

38 **Introduction**

39 The altitudinal treeline ecotone is a prominent ecosystem boundary in mountain landscapes (Arno and Hammerly
40 1984) at the transition between the upper limit of closed forests (timberline, i.e. the upper limit of subalpine forests)
41 and open alpine meadows (beyond the upper tree species limit) (Körner 2003). While the species composition of the
42 treeline ecotone and of subalpine forests is mainly influenced by water availability, rainfall, soils, and disturbances
43 (Henne et al. 2011; Schwörer et al. 2014a), the upper limit of tree growth is primarily determined by temperature at
44 the regional scale (Körner and Paulsen 2004; Holtmeier and Broll 2005; Holtmeier 2009). Therefore, climatic
45 changes are expected to lead to both altitudinal shifts in its position and changes in species composition (Walther et
46 al. 2005; Heiri et al. 2006). However, in addition to being influenced by these factors, both the position and
47 composition of the timberline and of subalpine forests can be substantially modified by land use (Arno and
48 Hammerly 1984). In the European Alps, with its long history of land-use (Millennium Ecosystem Assessment 2005),
49 subalpine forests and treeline ecotones have been used and exploited for millennia to create pastures and grazing
50 meadows, often with the use of fire (Tinner 2007).

51 Palaeoecology provides long-term records of changes in timberline position and composition (Tinner 2007), and into
52 past trends of fire activity (Conedera et al. 2009). Such proxy-based reconstructions are relevant for estimating
53 vegetation responses to changing environmental conditions and land-use changes (Tinner 2007), thereby unfolding
54 cultural legacies on forested landscapes that are often viewed as ‘ancient’ (Willis and Birks 2006; Feurdean et al.
55 2009). As a result, a growing number of studies have focussed on long-term treeline dynamics in the European Alps
56 (e.g. Lang and Tobolski 1985; Tinner et al. 1996; Wick and Tinner 1997; Wick et al. 2003; Tinner and Kaltenrieder
57 2005; Lotter et al. 2006; Finsinger and Tinner 2007; Blarquez et al. 2010; Berthel et al. 2011; Rey et al. 2013;
58 Schwörer et al. 2014b) and elsewhere (e.g. Herring et al. 2018; Orbán et al. 2018; Finsinger et al. 2018).

59 In this study, we focus on treeline vegetation and fire dynamics from the Vallée des Merveilles and Mont Bégo
60 (2872 m asl) area, an iconic area in the Argentera Massif better known for the 36,000 rock arts distributed among c.
61 4200 rocks between 2000 and 2700 m asl that were already described in the 16th century (Arcà 2018) and more
62 intensely studied since the end of the 19th century (Bicknell 1913; Conti 1940, 1972; de Lumley 1984, 1995).
63 Recently, a chronological framework of land-occupation and land-abandonment phases has been proposed (Binder
64 et al. 2009; Huet 2017). However, because rock engravings could not be dated directly (they lack calcite crusts or
65 organic material), their ages were estimated based on rock-art typology, data from archaeological excavations and
66 surveys (Conti 1940; Louis and Ségui 1949; de Lumley 1995; Machu et al. 2007; Huet 2012), and evidence from

67 pollen records (increases of herb pollen such as *Artemisia*, Chenopodiaceae and Poaceae) (de Beaulieu 1977;
68 Kharbouch 2000). Moreover, with the exception of pollen from crops and adventive weeds, increases of herb pollen
69 in high-elevation lake sediments may also be indicative of climate-induced treeline shifts to lower elevations (Heiri
70 et al. 2006). In addition, fires can have a significant and long-lasting impact on vegetation structure and composition
71 by promoting open spaces and fire-resistant species, and disfavoured fire-sensitive species (Stähli et al. 2006; Leys
72 et al. 2014; Schwörer et al. 2015).

73 New taxonomically highly resolved palaeoecological records that include both plant macrofossils and charcoal
74 records may substantially improve knowledge on local vegetation and fire dynamics at the treeline ecotone in the
75 study area, thereby providing a better link between long-term vegetation dynamics, changing environmental
76 conditions, and findings of archaeological artefacts, rock engravings, and land-use phases. Both charcoal and plant-
77 macrofossil records may be relevant proxies in this study area, for at least three reasons. Firstly, in mountain settings
78 the combination of plant-macrofossil and charcoal records can allow apprehending past vegetation dynamics and
79 vegetation responses to changing environmental conditions and fire disturbances better than with wind-dispersed
80 pollen (Birks and Birks 2000). Secondly, pollen records (de Beaulieu 1977; Kharbouch 2000; Finsinger 2001; Ortu
81 et al. 2003) suggest that fire-sensitive *Abies alba* populations (Tinner et al. 1999) were more abundant during the
82 mid Holocene in the region. However, it is unclear at which elevation populations of this temperate tree species were
83 able to dominate, and how these populations responded to changing environmental conditions and disturbances
84 (including fires). Thirdly, the modern timberline is dominated by *Larix decidua* (Ozenda 1950; Barbero et al. 1973),
85 which is heavily under-represented in pollen records (Sjögren et al. 2008) but much better represented in plant-
86 macrofossil records because it sheds its needles in high numbers every year (Tinner and Theurillat 2003).

87 We selected as study site the Lac des Grenouilles (1994 m asl), which is located at about the modern timberline
88 (c. 2000 m asl; Ozenda 1950) and below the modern potential treeline in the Mont Bégo rock-art area (Fig. 1a).
89 Littoral sediments from this lake already have been analysed for pollen (Kharbouch 2000). However, that
90 sediment sequence was fragmentary (with hiatuses), and no plant-macrofossil and charcoal analyses were
91 conducted. Here we present novel temporally and taxonomically highly resolved pollen, spore, stomata, plant-
92 macrofossil, and charcoal records from sediments collected from the lake centre. Due to its small size (0.015
93 km²), the lake should collect sufficient plant macrofossils, thereby allowing the reconstruction of past vegetation
94 dynamics in the close surroundings. Because we were particularly interested in characterizing local-scale
95 changes in fire activity and vegetation dynamics prior to and during prehistoric land-use phases (7350-3700 cal

96 BP), we performed high-resolution macroscopic charcoal and plant-macrofossil analyses for early-to-late
97 Holocene sediments (Mesolithic - Early Bronze Age) sediments (10,000-3400 cal BP). In addition, we conducted
98 high-resolution palynological analyses for Neolithic to Early-Bronze Age sediments to investigate fire-vegetation
99 relationships using time-series analyses (Green 1981; Schwörer et al. 2014b).

100

101

102 **Materials and Methods**

103 *Study area*

104 Lac des Grenouilles (44°05'53" N, 7°29'07" E; 1994 m asl) is situated on the south-facing slope of the
105 Argentera Massif (Maritime Alps, southwestern Alps; Figure 1a) at the lower end of a hanging valley. Two small
106 seasonal streams feed the lake, and one outflow drains into the Vallon de Fontanalba, a tributary of the Vallon de
107 Casterino (Roya River basin). At the southeastern end of the Vallon is Mont Bégo, which separates that valley
108 from the Vallée des Merveilles. The majority of rock engravings is centred in the Vallée des Merveilles as well as
109 in the upper part of the Vallon de Fontalba (Figure 1a; Huet, 2017). Bedrock in the Mont Bégo area is dominated
110 by Permian granitoid and metamorphic rocks (Malaroda et al. 1970). However, Triassic-Jurassic calcareous and
111 dolomitic rocks and Grauwackes occur on the northern slope of the hanging valley (Faure-Muret 1967).

112 The study area lies at the edge of the inner-alpine zone (Figure 1b), which is characterised by higher
113 continentality (higher temperature seasonality and less rainfall) than the outer and intermediate
114 ("Zwischenalpen") zones (Ozenda 2002; Landolt 2003). Sub-alpine forests in the inner-alpine zone are
115 dominated by *Pinus cembra*, *L. decidua*, and *Pinus sylvestris* (Ozenda 1985, 2002; Landolt 2003). In the Mont
116 Bégo area, the treeline ecotone and the subalpine forests are dominated by open *L. decidua* pasture woodlands
117 with minor shares of *P. cembra*, *P. uncinata*, and *P. sylvestris*, and *Juniperus communis* and Ericaceae shrubs
118 (*Rhododendron hirsutum*, and *Vaccinium myrthillus*) characterize the forest understorey. While the timberline is
119 located at c. 2000 m asl, isolated *L. decidua* and *P. cembra* tree stands can be found up to c. 2300 and individual
120 trees (> c. 2m) up to 2400 m asl (Ozenda 1950; de Beaulieu 1977, own observations). On the northern, more
121 humid, slope of the Massif, the timberline is generally substantially lower (c. 1700 m asl) and *Fagus sylvatica* is
122 more abundant than on the southern slopes (Ozenda 1950). In the area trees can be found up to c. 2300-2400 m
123 asl (Barbero et al. 1973). *A. alba*-dominated forest stands occur few kilometres to the south of the study site
124 (Ponel et al. 2001) at altitudes of c. 900 to 1600 m asl (Barbero and Bono 1970), i.e. c. 400 m below the study

125 site at current timberline and c. 800 m below treeline. At Lac des Grenouilles, mean monthly temperatures are
126 around -2°C in winter, and 13°C in summer. The mean annual precipitation is about 1000 mm. Monthly rainfall
127 shows the influence of the Mediterranean climate with a bimodal distribution (maxima in spring and autumn
128 with c. 100-115 mm month⁻¹) and a comparatively drier summer (c. 50 mm month⁻¹) (Fick and Hijmans 2017).

129

130 *Fieldwork and sediment-core correlation*

131 A geomorphological survey was undertaken in the area around Lac des Grenouilles. The survey was particularly
132 focussed on glacial and periglacial landforms (Figure 1c). Two overlapping sediment cores (Gren-2 and Gren-3)
133 were collected in the year 2001 in 1-m long drives from a floating platform in the lake's centre with a modified
134 Livingstone piston cover (Merkt and Streif 1970) at 286 cm water depth. Core Gren-2 was collected with a
135 smaller-diameter barrel (5 cm) than core Gren-3 (8 cm). Sediment-core drives were longitudinally cut into halves
136 using an electro-osmotic guillotine (Sturm and Matter 1972), and photographed with a digital camera and
137 artificial-light equipment at the Institute of Plant Sciences (University of Bern). We subsequently used the
138 changes in lithology to correlate the sediment cores (Figure 2) and establish core depths for the 615 cm long
139 master core.

140

141 *Chronology*

142 The depth-age model is constrained by the following control points: the estimated age of the surface sediments
143 (c. the year of coring), 13 AMS radiocarbon (¹⁴C) dates extracted from core Gren-3 from terrestrial plant remains
144 (Finsinger et al. 2019), and a pollen-inferred age set to constrain the Younger Dryas/Holocene boundary
145 (following Giesecke et al. 2014) (Table 1). The two lowermost ¹⁴C dates were rejected because they provided
146 unrealistically young ages in comparison to all other age determinations, including regional biostratigraphy.
147 Radiocarbon ages were calibrated to calendar ages using the IntCal13 data set (Reimer et al. 2013) prior to fitting
148 a smoothing spline (Figure 2) using the CLAM v2.2 software (Blaauw 2010). Distinct turbidite layers, most
149 likely representing sediment deposition that occurred over a very short time span (hours, days), were excluded
150 from the depth-age model (Figure 2), following Heiri et al. (2003). Therefore, except where otherwise mentioned
151 all references to sediment depth hereafter refer to a corrected sediment depth that excludes turbidites.

152

153 *Pollen, spores, plant-macrofossils, and charcoal analyses*

154 Sediment samples (volume: 1 cm³; thickness: 1 cm) for pollen analysis were treated with standard physical and
155 chemical treatments (incl. HCl, KOH, sieving with a 500- μ m mesh and decanting, HF, and Acetolysis), coloured
156 with Fuchsin, and mounted in glycerine jelly. Pollen and spores were identified and counted using pollen keys
157 (Punt et al. 1976; Reille 1992; Moore et al. 1998) and the reference collection at the Institute of Plant Sciences
158 (University of Bern). Stomata were identified based on Trautmann (1953) and Finsinger and Tinner (2020) and
159 dung-fungi *Sporormiella* spores were identified based on Davis (1987). Results are presented as percentages of
160 the terrestrial pollen sum, which includes pollen from trees, shrubs, and herbs (spores and pollen of aquatic
161 plants were excluded; Figures 3a and 4). Sampling resolution was increased to one sample each 1-4 cm in the
162 portions between 298-387 cm and 392-450 cm depth. Pollen can be dispersed by wind over large distances and
163 generally integrates vegetation at extra-local to landscape scales (Sugita 1994). While the small area of the site
164 (0.015 km²) might suggest that the pollen source area could be substantially smaller (e.g. several hundred meters
165 to a few kilometres at most; Sugita 1994; Conedera et al. 2006), landscape-scale pollen from lower-elevation
166 areas may reach the site, which is located in an area with steep topography (Finsinger et al. 2007). By contrast,
167 stomata and *Sporormiella* spores should be considered local-scale indicators of the presence of the parent trees
168 (Ammann et al. 2014) and large herbivore density (Baker et al. 2013; Gill et al. 2013), respectively.

169 For plant macrofossils, sampling was mostly continuous between 284 and 460 cm depth. We measured sample
170 volume by water displacement (volumes vary between 12 cm³ and 19.25 cm³; median: 16 cm³). Samples were
171 soaked in a 10% NaP₂O₄ solution for 24 hours and sieved with water through a 250- μ m mesh. Identification of
172 plant macrofossils was performed under a dissecting microscope (7.5X) and achieved by comparisons with
173 reference collections stored at the Institute of Plant Sciences (University of Bern), at the University of
174 Montpellier, and atlases (Cappers et al., 2006; Schoch et al., 1988; Tomlinson, 1985). To account for varying
175 sample volumes, the results are presented as concentrations calculated with respect to a standard sediment
176 volume of 10 cm³ (Figure 3b). Plant macrofossils were grouped and summed by genus to compare them with the
177 pollen percentage records (Figures 3b and 4). Plant macrofossils are dispersed over substantially shorter
178 distances than pollen, and therefore better reflect local-scale vegetation within some decametres around the site
179 (Birks and Birks 2000; Birks and Bjune 2010).

180 For macroscopic charcoal analysis, contiguous samples (volume: 1 cm³; thickness: 1 cm) were taken between
181 283 and 460 cm depth. Samples were first soaked in a 10% NaP₂O₄ solution for 24 hours and then gently washed
182 through a 160- μ m mesh using a manual water spray. The remaining particles were subsequently bleached in a

183 2.6% NaOCl solution for a few minutes to distinguish charcoal from dark organic matter, following Genies et
184 al. (2012). The number and area of charcoal fragments were estimated under a dissecting microscope (at a
185 magnification of x6.3) connected to a digital camera and using image analysis software (Winseedle pro v.2007).
186 Charcoal concentrations (both as total number and area per sample) were converted to charcoal-accumulation
187 rates (hereafter denoted as CHAR) to account for variations in sedimentation rate (Whitlock and Larsen 2001).
188 Calibration studies suggest that charcoal particles larger than 600 μm might be of local origin, while smaller
189 particles can easily be dispersed over large distances (up to 30-50 km; Oris et al. 2014; Adolf et al. 2018).
190 Therefore, the low-frequency trends of the macroscopic charcoal record can be attributed to overall landscape-
191 scale fire activity (Marlon et al. 2008; Adolf et al. 2018). We estimated the low-frequency trend by fitting loess
192 smoothing (Cleveland and Devlin 1988) to the macrocharcoal influx values (Figure 4).

193 Pollen-assemblage zones were determined by optimal partitioning with square-root transformed percentage
194 values for pollen types included in the pollen sum (Birks and Gordon 1985). Statistically significant zones
195 (continuous lines in Figure 3) were assessed by comparison with the broken-stick model, following Bennett
196 (1996). Zonation was performed with Psimpoll v4.26 (Bennett 2008). The programs Tilia v2.6.1 and Affinity
197 Designer v1.7.0 were used to plot the pollen and plant-macrofossil diagrams (Figure 3).

198

199 *Time-series analyses*

200 To investigate leads and lags between fire activity (charcoal influx) and vegetation (pollen percentages), we use
201 cross-correlation analyses (Green 1981; Tinner et al. 1999; Rey et al. 2019). Analyses were restricted to the
202 higher-resolution section between 387 and 298 cm depth (6950-3750 cal yr BP) where the median sampling
203 resolution is of 48.5 years between samples (n. of samples: 49) and the median absolute deviation is 26.7 years
204 (Figure S1). This analysis requires homogeneously spaced time series sampled at the same time resolution
205 (Venables and Ripley 2002). Thus, we fitted a loess-smoothed line (span=0.15) to estimate pollen percentage
206 and charcoal influx values at 100-year intervals (Figure 4). Cross-correlation analyses were performed under the
207 R computing environment (R Core Team 2017). Cross-correlation coefficients are presented for maximum lags
208 of ± 4 corresponding to ± 400 years (Figure 5). As in our time series the loess-smoothed values are not entirely
209 independent, the 95% confidence intervals must be viewed with caution (Venables and Ripley 2002, p. 390).

210

211

212 **Results and interpretation**

213

214 *Geomorphological context*

215 Lac des Grenouilles is dammed by a prominent lateral moraine mantling the left flank of the Vallon de
216 Fontanalba (Figure 1c). According to regional reconstructions (Cossart 2008; Federici et al. 2012, 2017; Cossart
217 et al. 2012), the moraine formed during the Last Glacial Maximum (LGM) and the moraines mapped further
218 upvalley (around 2200-2300 m asl) were probably deposited during the Younger Dryas cold event (Egesen
219 stadial), as observed on the northern side of the Maritime Alps (Spagnolo and Ribolini 2019). The sparse glacial
220 debris in the area of Lac Ste Marie suggests the presence of relict ice bodies or glacierets also during the
221 Holocene cold events. Part of this debris, which is locally mixed with rock falls, experienced the formation of
222 permafrost. Permafrost creeping led to the formation of a rock glacier located around 2400 m asl. According to
223 permafrost-monitoring data in the Maritime Alps (Ribolini and Fabre 2006; Ribolini et al. 2007, 2010),
224 permafrost in the rock glacier could be still present.

225

226 *Vegetation and fire histories*

227 Three statistically significant pollen-assemblage zone boundaries were determined (Figure 3a). The zone at the
228 bottom (Gren-1; >467 cm; >10,700 cal BP) probably corresponds to the late-Glacial and early-Holocene because
229 pollen assemblages reflect a well-established pattern of late-Glacial pollen stratigraphies from the study area (de
230 Beaulieu 1977; de Beaulieu et al. 1994; Finsinger and Ribolini 2001). This chronological attribution is consistent
231 with the geomorphological context, with an LGM moraine that dammed Lac des Grenouilles. *Pinus*, *Artemisia*,
232 and *Poaceae* dominate pollen assemblages below 490 cm depth, with minor abundances of *Betula*, deciduous
233 *Quercus*, and *Juniperus* pollen. Around 12,000 cal BP, abundances of *Artemisia* and *Ephedra* pollen are higher
234 than in prior samples, and *Pinus* pollen abundance is lower, suggesting an opening of the vegetation that may
235 reflect the effects of the Younger Dryas cooling (12,850-11,650 cal yr BP; Rasmussen et al. 2014) in the Alpine
236 region (Larocque and Finsinger 2008; Samartin et al. 2012). Plant macrofossils (Figures 3b and 4) indicate that
237 *Larix* was present in the surroundings shortly prior to the onset of the Younger Dryas, and that *Dryas octopetala*
238 carpets briefly expanded at the Younger Dryas/Holocene transition. *Sporormiella* dung-fungi spores were
239 regularly found, suggesting the presence of large herbivores near the lake during the late Glacial. A shift to closer
240 vegetation with higher abundance of *Betula*, increasing arboreal pollen, a decrease of *Artemisia* and herb pollen,

241 and the first appearance of *Tilia* pollen characterizes the transition to the warmer Holocene.

242 The transition to zone Gren-2 (467-397 cm; 10,700-7450 cal BP) is marked by the rise of *Quercus* pollen
243 abundance, and the first appearance of *Corylus*, *Fraxinus*, *Alnus glutinosa*, and *Acer* pollen indicating that
244 thermophilous tree populations expanded, probably at lower elevation. The continuous presence of *Betula*
245 macrofossils and the rare occurrences of *Pinus mugo* and *Juniperus* needles suggest that the site was at the
246 treeline ecotone and that open *Betula-Pinus* stands were located in the surroundings. Rare occurrences of *Alnus*
247 *viridis* pollen and the absence of its macrofossils suggest that populations were either very sparse or distant. In
248 spite of decreasing *Pinus* pollen abundance, arboreal pollen abundance is highest (ca. 75-90%) in this zone. As
249 observed in other records (Tinner and Hu 2003; Finsinger et al. 2014), the two charcoal-influx records (by counts
250 and by area) are highly redundant ($r=0.912$, p -value <0.001 ; Figure S2). Thus, only the charcoal-influx record by
251 count is used in the following discussion. Fire activity was overall low (CHAR values <0.1 pieces cm^{-1} year $^{-1}$;
252 Figure 4).

253 Increasing abundance of *Abies* pollen and abundant finds of its plant-macrofossils in zone Gren-3 (397-330.5
254 cm; 7450-4700 cal BP) indicate the rise of the timberline and the establishment and expansion of a subalpine
255 forest in the surroundings. While light-demanding *Betula* populations shrank as shown by decreasing pollen and
256 macrofossil abundance, increasing pollen abundance and needle finds indicate that *P. cembra* populations
257 expanded. Pollen and plant macrofossil abundances of light-demanding *Larix* were low until c. 6000 cal BP,
258 when *Larix* populations started to expand. Increasing herb pollen abundance and charcoal influx values (CHAR
259 values >0.1 pieces cm^{-1} year $^{-1}$) suggest that forest cover decreased due to rising fire activity. Fire-sensitive *Abies*
260 populations, however, collapsed some 500 years later when a further rise in fire activity occurred.
261 Simultaneously, *Larix* populations further expanded and *Betula* pollen increased, indicating a major shift in the
262 composition of the subalpine forest cover. Between 4800 and 4300 cal BP (around transition into zone Gren-4:
263 330.5-220 cm; 4700-2000 cal BP) high arboreal pollen percentages suggest the partial recovery of forest cover
264 during a c. 500-years long period of low fire activity. Regular findings of plant macrofossils indicate that mixed
265 *Abies* populations re-expanded in the subalpine forest around the site. Around 4300 cal BP, fire activity increased
266 again and the composition of the subalpine forest shifted to a *Larix*-dominated forest. Decreasing *Betula* pollen
267 abundance and absence of plant macrofossils suggest that *Betula* stands, perhaps above the timberline, were
268 strongly reduced. *Abies alba* and *Pinus cembra* plant macrofossil abundances strongly decrease after 4300 cal
269 BP, pointing to local extinctions of the two species.

270 Variations in the relative abundance of cultural indicator pollen from crops and weeds as well as *Sporormiella*
271 dung-fungi spores document transient phases of human pressure. We found moderately higher values of
272 *Artemisia* and *Urtica* pollen, and of *Sporormiella* spores around 7450-7150 cal BP. *Sporormiella* spores'
273 abundance shows a local maximum around 6200-5500 cal BP, together with an increase of Poaceae and *Rumex*
274 pollen and the regular occurrence of Cerealia-type and *Plantago lanceolata*-type pollen. Similarly, Poaceae,
275 *Rumex*, *Veratrum*, *Trifolium pratense*-type, and *P. lanceolata*-type pollen, and *Sporormiella* spores abundance
276 increase after 4300 cal BP. In all of these three phases, arboreal pollen percentages are substantially reduced,
277 indicating transient openings of the subalpine forests in response to prehistoric land-use activities.

278

279 *Time series analyses*

280 Pollen percentages of herb pollen have significant positive correlations with charcoal influx (maximum
281 correlation at lag 0; Figure 5). The Poaceae illustrate particularly well the expansion of grasslands as a
282 consequence of forest-cover reduction in response to increasing fire activity, as also observed in other studies
283 (Rey et al. 2013, 2019). However, positive correlations of cultural indicators (*P. lanceolata* and *Urtica*) are
284 delayed, suggesting a gradual intensification of land use after fires, as also observed in another record from the
285 Alps (Gobet et al. 2003). By contrast, *Sporormiella* shows positive correlations at negative lags, suggesting that
286 grazing by large herbivores preceded increases in fire activity.

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

299 and Wasem 1997; Malowerschnig and Sass 2014).

300

301

302 **Discussion**

303 *Influence of climate on early-Holocene afforestation*

304 The late Glacial (c. 14,600-11,650 cal BP) vegetation was dominated by grasslands with *Artemisia* and Poaceae
305 (de Beaulieu 1977; this study), and *Pinus* probably occurred at lower elevation (de Beaulieu 1977). The absence
306 of *Betula* plant macrofossils suggests that these trees were either very sparse (de Beaulieu 1977) or locally
307 absent. The findings of *L. decidua* needles and pollen indicate the presence of this conifer tree in the
308 surroundings prior to the Younger Dryas. This corroborates the very rare findings of *Larix* pollen grains in late
309 Glacial sediments at Selle di Carnino (de Beaulieu 1977), a peaty depression at 1900 m asl few kilometres to the
310 east from Lac des Grenouilles. These two sites are among the highest-elevation Alpine sites where tree pollen,
311 stomata, and macrofossils suggest tree growth during the Bølling/Allerød (c. 14,600-12,800 cal BP) (Wagner et
312 al. 2015). For instance, the stomata findings of *Juniperus*, *Larix*, and *Pinus* at Simplon-Alter Spittel (1885 m asl)
313 a south-facing site in the Divedro Valley (southern Swiss Alps) showed the early establishment of trees during
314 the Allerød (13,900–12,800 cal. BP) (Welten 1982; Ammann et al. 2014). The substantial drop in summer
315 temperatures during the Younger Dryas cooling in the Alpine region (Heiri et al. 2014) likely led to a treeline
316 depression below Lac des Grenouilles, as no tree macrofossils were found. In other records from the Alpine
317 region treeline depressions of ca. 300-400 m were recorded (Tinner and Vescovi 2005; Gobet et al. 2005). Given
318 that sedimentation was not interrupted at Lac des Grenouilles, the Younger Dryas glacier advance did not reach
319 the site. This is in agreement with geomorphological evidences that suggest the location of Younger Dryas
320 moraines mostly above 2100 m asl (Brisset et al. 2015; Spagnolo and Ribolini 2019).

321 The plant-macrofossil record supports prior interpretations (de Beaulieu 1977; Ponel et al. 2001) suggesting that
322 treeline was close to 2000 m asl during the early Holocene in the study area. Specifically, an open *Betula* and
323 *Pinus* (probably *P. mugo*) dominated treeline with scattered *Juniperus* shrubs re-expanded around Lac des
324 Grenouilles in the early Holocene until c. 8000 cal BP, when the first *Abies* macrofossil was found. However,
325 due to the lack of ¹⁴C dates around the Younger Dryas/Holocene transition (Fig. 2), it is difficult to establish
326 precisely the afforestation lag in response to the early-Holocene warming for Lac des Grenouilles. Pollen-
327 independent temperature reconstructions show rapid warming of c. 2-4°C within a few decades after the Younger

328 Dryas (Lotter et al. 2000; Schwander et al. 2000; von Grafenstein et al. 2000; Larocque and Finsinger 2008;
329 Heiri et al. 2015) that likely led to a rapid early-Holocene treeline rise in the Central and Southern Alps, showing
330 the ability of treelines in tracking climate warming with decadal to centennial lags (Tinner and Kaltenrieder
331 2005). Conversely, other sites suggest that due to the regional setting (e.g. colder Northern Alps) or local
332 peculiarities (soils, aspect, moisture availability), today's treeline positions were only reached at ca. 10,000 cal
333 BP (Schwörer et al. 2014a) or even after 8200 cal BP (Finsinger and Tinner 2007). Nevertheless, we found a
334 short-term early-Holocene expansion of *Dryas octopetala*, a pioneer species of open, base-rich habitats
335 (Elkington 1971), prior to the expansion of *Betula* at 11,300 cal BP. This indirectly supports the chronology for
336 Lac des Grenouilles, because early-Holocene expansions of *D. octopetala* were also detected at Gouillé Rion and
337 at Lac de Fully, two sites above current timberline in the dry inner-alpine Valais (Kaltenrieder et al. 2005b;
338 Finsinger and Tinner 2007) as well as at Iffigsee and Lago Basso (Wick and Tinner 1997; Schwörer et al.
339 2014b).

340 Early-Holocene fire activity was substantially lower than during the mid-to-late-Holocene (Figure 4). We assume
341 that fire activity was limited by low biomass availability, as also observed elsewhere (Berthel et al. 2011; Gil-
342 Romera et al. 2014; Finsinger et al. 2018). Indeed, high early-Holocene insolation seasonality (Figure 4) likely
343 was a determining factor for climate-induced low biomass availability in high-elevation Alpine landscapes
344 (Schwörer et al. 2014a).

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

357 acknowledged when comparing past plant distributions from the currently moister northern Swiss Alps and the
358 currently drier inner-alpine valleys (Lotter et al. 2006; Schwörer et al. 2014b) and may explain the early-
359 Holocene dominance of *Betula* in the Scandes Mountains despite the presence of *Larix sibirica* (Kullman and
360 Öberg 2015).

361

362 *Highest timberline position during the Holocene*

363 At Lac des Grenouilles, *Betula* dominated the treeline ecotone with scattered *Pinus* stands (probably *P. mugo* as
364 suggested by the plant macrofossils) and *Juniperus* shrubs until ca. 8000 cal BP, when *Abies* expanded. The
365 timing of the *Abies* expansion is in good agreement with regional pollen data (de Beaulieu et al. 1994; Nakagawa
366 1998; Finsinger 2001). The dominance of temperate *Abies* at today's treeline elevation marks the highest
367 timberline position, which was reached around 7500-7000 cal BP. While the stacked Alpine temperature
368 reconstruction shows highest temperatures around 8500-8000 cal BP, this interpretation is in good agreement
369 with a chironomid-inferred temperature record from the Alps (Heiri et al. 2003) and from the northern the
370 northern Apennines (Samartin et al. 2017) as well as with Global Circulation Models (Renssen et al. 2009), all
371 showing ~1.5 °C higher-than-present temperatures during the Holocene Thermal Maximum (HTM) around 7500
372 cal BP. Some records also point to the establishment of progressively more oceanic conditions after 8000 cal BP
373 (Magny et al. 2011). Although the local establishment of *Abies* was suggested by the marked rise of pollen
374 percentages (Ponel et al. 2001), no *Abies* macrofossils were found in the nearby located Lac Long Inférieur at
375 2090 m asl (F. Damblon unpublished, see Finsinger 2001). This may suggest that *Abies* reached its upper limit at
376 about 2000-2100 m asl during the HTM in the study area. However, compared to other Alpine records, 2100 m
377 asl is a substantially lower mid-Holocene timberline elevation. Plant-macrofossil records document timberline c.
378 150-200 m above current timberline during the HTM to reach altitudes between c. 2300 and 2500 m asl (Tinner
379 and Theurillat 2003; Schwörer et al. 2014b). Thus, further plant-macrofossil records from sites at higher
380 elevation may be needed to constrain the position reached by the upper limits of the timberline and the treeline in
381 the study area during the Holocene.

382 The occurrence of mid-Holocene plant-macrofossil assemblages with both *A. alba* and *P. cembra* is striking
383 because at present these two species thrive together in very few and isolated locations, mainly in the inner-alpine
384 zone of the southwestern Alps. For instance, in the Valais (Switzerland) on steep and convex slopes around 1900-
385 2000 m asl (Lingg 1986), in the Susa Valley (Italy) at c. 1950 m asl (Dotta and Motta 2000) and in the

386 Maurienne Valley (France) at 1950-2000 m asl (Chauchard et al. 2010) *A. alba* occurs together with *P. cembra*,
387 *P. abies*, and *L. decidua*, and further east in the inner-alpine Italian Vinschgau Valley it occurs with *P. cembra*
388 (Mayer 1979). In these lower-subalpine stands, *A. alba*'s abundance is generally low in comparison to other
389 conifers, but there are clear signs of active regeneration (Lingg 1986; Dotta and Motta 2000) and even
390 population expansion in response to land-use abandonment after the 1950s (Lingg 1983; Chauchard et al. 2010).
391 It has been suggested that inner-(western)alpine populations (ecotypes) maintained a stronger adaptive potential
392 to drought stress and strong irradiation, if compared to provenances from the moister southern, eastern and
393 northern Alps (e.g. Marcet 1971, 1972; Mayer 1979; Kral 1989; Kral and Mayer 1993). However, there are still
394 critical knowledge gaps in this regard. For instance, while modern mtDNA maternal lineages and allozyme
395 clusters of *A. alba* show little differences among Alpine populations (Liepelt et al. 2009), distinct
396 interpopulational genetic variation (genetic distance, genetic differentiation) between stands within and outside
397 the Alpine region as well as between neighbouring populations may point to processes of adaptation to different
398 or specific environmental conditions (Hussendörfer 1999). It might be that the mtDNA and allozyme genomic
399 regions identifying the haplotypes (Liepelt et al. 2009) bear little connection with adaptive genes for drought-
400 stress response, which are starting to be uncovered (Behringer et al. 2015). Moreover, intraspecific variation in
401 drought sensitivity of *A. alba* is yet not very well constrained (George et al. 2015).

402 By contrast, there is a substantially larger consensus on the view that these isolated inner-alpine *P. cembra-A.*
403 *alba* (-*L. decidua*) mixed stands at very remote sites represent remnants of past and more widespread populations
404 (Lingg 1986; Kral and Mayer 1993; Tinner et al. 2013) whose occurrence is attested by mid-Holocene plant-
405 macrofossil and stomata records (Welten 1982; Wick et al. 2003; Schwörer et al. 2014b; this study). Similarly,
406 there is a large consensus indicating that *A. alba* populations declined due to increasing human pressure (fire
407 disturbances, pasture, logging) at high-elevation sites (e.g. Markgraf 1969; Lingg 1986; Tinner et al. 2013),
408 suggesting marked contraction of the realized climatic niche of the species in response to prehistorical land use.

409

410

411 *Relationships between vegetation dynamics and land-use phases*

412 We found evidence of higher abundance of large herbivores and intensified land use activities (Figures 3 and 4)
413 during previously identified rock-art phases (Table 2; Huet 2017). The Neolithic Cardial phase (7450-7150 cal
414 BP) is attested by the finding of a ceramic artefact at *Gias del Ciari* as well as in other rock shelters (Conti 1940;

415 Louis and Ségui 1949; Bianchi et al. 2011) in the study region. Based on this evidence, the first sign of human
416 occupation associated to agricultural activities in the area dates back to 7450-7150 cal BP, thereby attesting that
417 the Vallée des Merveilles was one of the first Alpine areas being visited during the Neolithic (Binder 2005).
418 Indeed, trade and transhumance across this sector of the Alps may already have started between 7000 and 6000
419 cal BP (Ricq-de Bouard and Fedele 1993; Huet 2017). At Lac des Grenouilles, this phase is only characterised by
420 higher *Urtica* pollen and *Sporormiella* spores' abundance, when fire activity remained low. Instead, the Copper
421 Age phase (Chassean period (6200-5500 cal BP), and the Recent Bell-Beaker and Early Bronze Age phase (c.
422 4250-3700 cal BP)) are also associated with the presence of Cerealia and other cultural indicator pollen types, a
423 rise of total herb pollen, and increasing charcoal influx values. An increase of cultural pollen during the most
424 recent phase was also detected at Lac Long Inférieur (de Beaulieu 1977; see Table 1 in Huet 2017).

425 Although we found a good match between the new pollen record and the rock-art phases, our results indicate that
426 the Chassean land-use phase lasted longer than suggested by Huet (2017). For instance, *Urtica* pollen abundance
427 actually increased at 5300 and remained high until 4900 cal BP, suggesting increasing nitrogen supply as e.g.
428 resulting from grazing activities. Similarly, charcoal influx and Poaceae pollen abundance did not decrease, and
429 overall arboreal pollen abundance did not increase until 4900 cal BP, suggesting that land use with the use of fire
430 continued until the end of the Copper Age. Yet, the Copper Age land-use phase did not have persistent
431 consequences on ecosystems. For instance, although at the landscape-scale (as inferred from the pollen record)
432 *Abies* did not recover, local-scale *Abies* populations (as attested by plant-macrofossils) were able to re-establish
433 during the low fire-activity period and land-abandonment phase that occurred between 4900 and 4300 cal BP.
434 This transient recovery ended with the Bronze Age land-use phase (4250-3700 cal BP), when *Abies* and *Betula*
435 collapsed locally (macrofossils) and *Betula* and *Pinus* regionally (pollen). Interestingly, the timing of this land-
436 use phase matches with a major deforestation and land-use phase detected elsewhere in and around the Alps
437 (Gobet et al. 2003; Tinner et al. 2003; Finsinger and Tinner 2006). This suggests that Bronze Age land use was
438 pervasive at both low and high elevations in the Alps, possibly leading to irreversible changes such as the
439 disappearance of *Abies alba* treeline communities.

440

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

442 In the Alps, the development of larch meadows ("Lärchenwiesen"), a form of wood pastures with *L. decidua*
443 stands and dense grass-dominated herbaceous under-storey (Garbarino et al. 2011), is associated in several

444 palaeoecological records to anthropogenic activities, in particular grazing after fire occurrence (Wagner et al.
445 2015 and references therein). *L. decidua* is considered as a species being favoured for livestock herding, because
446 its light canopy permits the growth of suitable foraging ground cover (Motta and Lingua 2005). Moreover, with
447 its great bark thickness on mature individuals, a key fire-tolerance trait (Pellegrini et al. 2017), and the ability to
448 produce new foliage each year, *L. decidua* is rather fire resistant (Sullivan 1994) also because mature individuals
449 show relatively low mortality rates (Dupire et al. 2019). Conversely, due to its physiology and its ability to
450 colonize raw soils (Garbarino et al. 2010), *L. decidua* is less limited by soil moisture availability than other
451 subalpine tree species (*A. alba*, *P. abies*, and *P. cembra*) (Schwörer et al. 2014a). However, although a decrease
452 in moisture availability might have been favourable for *L. decidua* at the expense of *A. alba*, there is no evidence
453 of a decrease in rainfall between 6000 and 4000 cal BP in lake-level records from the Alpine region (Figure 4),
454 which instead indicate higher precipitation between 4500 and the present when compared to mid-Holocene
455 (Magny et al. 2011, 2013). Based on this evidence and on the fact that *L. decidua* is the dominant tree species in
456 the Mont Bégo area today (Ozenda 1950; de Beaulieu 1977), it seems far more plausible to infer that the
457 expansion of *L. decidua* at Lac des Grenouilles was triggered by excessive human fire disturbance (see cross-
458 correlation analyses, Figure 5) while *A. alba* populations were strongly reduced. This interpretation regarding the
459 causes of paramount vegetation changes is consistent with prior studies, which indicate that under low-
460 disturbance conditions *A. alba* can dominate forests under colder temperatures than observed today (Wick et al.
461 2003; Lotter et al. 2006; Tinner et al. 2013).

462

463

464 **Conclusions**

465 We present the first palaeoecological study that includes pollen, plant-macrofossil, and charcoal records from the
466 modern timberline (c. 2000 m asl) in the Mont Bégo area (Maritime Alps). The area is an iconic place for Alpine
467 archaeology because it bears thousands rock-art engravings (Bicknell 1913; de Lumley 1995; Huet 2012) whose
468 age cannot be directly assessed. The new taxonomically highly-resolved palaeoecological record confirms most
469 of the land-use phases (7450-7150, 6200-5500, and 4250-3700 cal BP) inferred based on rock-art typology (Huet
470 2017), and in addition unfolds local long-term timberline shifts and vegetation-composition changes in relation
471 to environmental changes (land-use, fire disturbances, and climatic changes). The absence of *Larix* macrofossils
472 suggests that early-Holocene conditions were moister than in dry inner-alpine valleys, where *Larix* played a

473 more important role both in past as well as in modern timberline forests. After 8000 cal BP, the timberline shifted
474 to higher elevation and mixed *A. alba* and *P. cembra* stands established around the study site above c. 2000 m
475 a.s.l. during the Holocene Thermal Maximum (HTM), when the first rock-arts were probably engraved. At the
476 timberline, *Abies* populations were replaced during the Bronze Age (around 4000 cal BP) by *L. decidua*
477 dominated subalpine forests, which are still dominant today in the study area (Ozenda 1950; de Beaulieu 1977).
478 Thus, *A. alba* populations were reduced at the colder-end of their natural distribution (Tinner et al. 2013), and
479 populations of *L. decidua* expanded in response to past land-use (with the use of fire) that allowed the
480 establishment of pasture woodlands. This implies that modern forested landscapes are markedly shaped by
481 prehistorical legacies, even in high-alpine remote areas (Willis and Birks 2006; Feurdean et al. 2009).

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497 **Figure captions**

498

499 **Fig. 1** Maps showing (a) the location of Lac des Grenouilles in the Mont Bégou area (inset marks the location of
500 the Argentera Massif in Europe), and (b) the location of the study site (GREN) in relation to other sites discussed
501 in the text (BACH: Bachalpsee (Lotter et al. 2006); SÄG: Sägistalsee (Wick et al. 2003); IFF: Iffigsee (Schwörer
502 et al. 2014b); LdF: Lac de Fully (Finsinger and Tinner 2007); GR: Gouillé Rion (Tinner and Theurillat 2003;
503 Kaltenrieder et al. 2005a); CER: Lac de Cerin (Magny et al. 2011); LOUP: Lac du Loup (Blarquez et al. 2010);
504 LPA: Lago Piccolo di Avigliana (Finsinger and Tinner 2006); LLInf: Lac Long Inférieur (de Beaulieu 1977);
505 BAS: Lago Basso (Wick and Tinner 1997), and LSM: Lej da San Murezzan (Gobet et al. 2003)); ACC: Lago
506 dell'Accesa (Magny et al. 2011)). Panel (c) shows the mapped geomorphological features around the lakes'
507 catchment. The basemap in panel (b) shows the hygric continentality (Gams 1931, 1932; Ozenda 2002;
508 Holtmeier 2009) recalculated using the WorldClim2 dataset (Fick and Hijmans 2017)

509

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

513

514 **Fig. 3a** Abundances of selected pollen and spores, and *Sporormiella* spores (as percentages of the terrestrial
515 pollen sum) from Lac des Grenouilles. Grey horizontal bands indicate land-use phases as inferred from
516 archaeological data (see Table 2). Continuous horizontal lines indicate statistically significant pollen-assemblage
517 zones (LPAZ); the short-dashed line indicates the pollen-inferred Younger Dryas/Holocene boundary (see Table
518 1). Empty curves show 10× exaggerations

519

520 **Fig. 3b** Plant-macrofossil concentration record from Lac des Grenouilles. Grey horizontal bands indicate land-
521 use phases as inferred from archaeological data (Table 2). Continuous horizontal lines indicate statistically
522 significant pollen-assemblage zones (LPAZ); the short-dashed line indicates the pollen-inferred Younger
523 Dryas/Holocene boundary (Table 1)

524

525 **Fig. 4** Comparison of the main biotic and abiotic proxies for vegetation dynamics, fire, and climate. From top to
526 bottom: Lake-level changes in the Jura Mountains (Lake Cerin) and in Central Italy (Lake Accesa) (digitized
527 from Magny et al. 2011); mean December, January, February (DJF, blue line) and June, July, August (JJA, red
528 line) insolation at 65 °N (Laskar et al. 2004); stacked chironomid-inferred July-air temperatures for the Alpine
529 region (Heiri et al. 2015); selected data from Lac des Grenouilles: pollen percentages (raw data: coloured areas
530 (dark green: trees, light green: shrubs, yellow: herbs), interpolated and loess-fitted data (black lines) used for
531 cross-correlation analyses (see Fig. 5), and plant-macrofossil concentrations (summed by genera; black bars;
532 values 10×)); and charcoal-accumulation rate of charcoal counts (black bars; loess-fitted data: red lines). Vertical
533 shaded areas (grey) indicate the land-use phases based on archaeology (Table 2)

534

535 **Fig. 5** Cross-correlation of charcoal accumulation rates (CHARc) and pollen percentages (interpolated to 100-

536 year intervals) showing trends of taxon responses to changes in fire activity up to lags +/-4, corresponding to
537 time periods of +/-400 years
538

539 **Table 1:** Radiocarbon measurements of plant macrofossils used to establish the age-depth model (* = rejected
540 ¹⁴C measurement; † = master-core depth below water surface; § = corrected sediment depth that excludes
541 turbidites)

Lab-ID	Material dated	Age (¹⁴ C yrs BP)	Age (cal yrs BP)	Depth (cm)†	Depth (cm)§
Surface	/	/	-55±1	286	0
Erl-4375	Wood with bark	3521±69	/	587-586	301-300
Erl-4376	Wood with bark	3886±58	/	602-601	316-315
Erl-4377	Wood with bark	4066±66	/	609.5	323-322
SacA-25565	Plant macrofossils	4100±35	/	619-618	332-331
Erl-4378	Wood with bark	4860±58	/	638.7	351-350
SacA-25566	Plant macrofossils	4725±40	/	647-646	355-354
SacA-25567	Plant macrofossils	5810±45	/	676-675	380-379
Erl-4379	Wood with bark	7708±76	/	717-716	417-416
Erl-4380	Wood with bark	7600±68	/	719-718	419-418
Erl-4381	Wood with bark	8119±69	/	730-729	430-429
Poz-7822	Plant macrofossils	8990±50	/	759-758	459-458
	Pollen-inferred age	/	11500 ± 250	780-779	477-476
Poz-10812*	Plant macrofossils	1725±35	/	817	505
Poz-7907*	Plant macrofossils	2135±35		821-819	508-506

542

543 **Table 2:** Occupation phases determined based on archaeological findings in the Mont Bégo area (from Huet
 544 2017)

Archaeological period	Southwestern Alpine chronology	Age (cal yr BP)	Age (B.C.)	Source
Bronze Age	Recent Bell Beaker – Early Bronze Age I	4250-3700	2300-1750	Ceramic artefacts (de Lumley 1995; Bianchi et al. 2011; Huet 2012)
Copper Age	Early-Recent Chassean	6200-5500	4250-3550	Flint bladelet below the <i>Stele du Chef de Tribu</i> (de Lumley et al. 2010), ceramic and flint artefacts
Neolithic	Cardial	7450-7150	5500-5200	Ceramic artefact (de Lumley et al. 1991; de Lumley 1995; Binder et al. 2009)

545

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