Letter

Glacial refugia in the south-western Alps?

A response to Finsinger *et al.* (2019) 'Fire on ice and frozen trees? Inappropriate radiocarbon dating leads to unrealistic reconstructions'

Analyses of an array of biological and sedimentary proxies from Lake Miroir (altitude 2214 m above sea level (asl), latitude 44°38′03″N, longitude 6°47′31″E) supported by radiocarbon measurements revealed tree persistence and fire occurrences above valley glaciers during and after the end of the Last Glacial Maximum (LGM, 25 000 to 18 000 calendar yr before the present (cal yr BP)) in the western Alps (Carcaillet & Blarquez, 2017). Thus, although burning during the glacial times seems intuitively unlikely, conditions allowing the spread of fires were sometimes met in the region. In a recent *New Phytologist* article, Finsinger *et al.* (2018) have dismissed this finding, criticizing the fundamental elements of the analyses: the chronology, the fire and vegetation reconstructions, and treeline interpretation. Each of these criticisms is refuted here by new factual data or evidences from the literature. We welcome the opportunity to discuss our finding in relation to recent evidences regarding historical biogeography in a glacial context.

Dating, age–depth model and preliminary methodological studies

The criticized publication, Carcaillet & Blarquez, dates from 2017, but the finding dates back to 2006 during the coring of Lake Miroir, which is not a glacial-cirque lake from the LGM. The initial aim of the coring was to obtain Holocene sediments, which we expected to be no thicker than 300 cm, based upon information on this lake (Nakagawa, 1998) and other Holocene profiles in the region at such altitude. Of the +500 cm of sediments that were brought to the surface on the day of coring, *c.* 200 cm corresponded to the expected epoch (Holocene). While sampling to greater depth was possible, the coring device (10.5 m long corer) was at its maximum operating capacity with *c.* 500 cm of sediment beneath a *c.* 530 cm water column. The first dating of plant remains extracted from the presumed Holocene organic sediments (April 2007) corroborated our strong initial impression of an exceptional, substantially older than expected, depositional context.

To confirm or refute the unexpected finding we designed and conducted specific tests, focusing primarily on the chronology. Chronological tests were conducted in two carbon-14 (^{14}C) laboratories (LMC14, France and Poznan, Poland), with ongoing dialogue with the Poznan Laboratory regarding potential interference by old carbon from the carbonate basin. To avoid such interference, careful measurement and selection of datable material when sufficient terrestrial plant remains were lacking was required. A hard-water reservoir effect was tested by taking two ^{14}C measurements of both total organic carbon (TOC) extracted from bulk sediment and terrestrial plant macro-remains also extracted from bulk at the same depth (710–715 cm). The two acquired ^{14}C dates were identical (χ^2-test and t-test, $P = 0.95$, ddl = 1; 'Calib' program, 'Test Sample Significance' tool), indicating that no hard-water effect was present. It should be noted that technically, a ^{14}C measurement of TOC is not a 'bulk' measurement, contrary to an assertion by Finsinger *et al.* (2018). Carbonates (CO_3^{2-}, HCO_3^{-}) would be included in a bulk dating, but not in a TOC dating, although TOC was extracted from bulk sediment as well as terrestrial plant remains. In our chronology, the use of ^{14}C measurements of TOC resulted from substantial difficulties in obtaining sufficient organic carbon from terrestrial plant macro-remains (e.g. measurement SacA-6885 at 658–663 cm that was 'unproductive' according to the ^{14}C-laboratory despite 8.9 mg of *Larix* and *Pinus* needles), particularly from sediment deeper than 710 cm. These difficulties are likely due to the large size of this head-lake (0.7 ha), which impedes concentration of macro-remains, and probable sparsity of vegetation around the site during glacial times. We need to correct the lab-codes, and only the code, of three radiocarbon dates: SacA-27170, SacA-27171 and SacA-27172 instead of Poz-27170, Poz-27171 and Poz-27172 as reported in error in the Table 1 in Carcaillet & Blarquez (2017).

Whatever precautions are taken, the possibility of hard-water effect cannot totally be excluded. However, if the dating at 19 320 ± 100 ^{14}C BP is actually *c.* 14 700 or 11 700 cal yr BP as speculated by Finsinger *et al.* (2018), then an important part of the TOC would originally derive from the weathered and dissolved bedrock, which seems very unlikely. The best indicator of the chronology's validity is the coherence of the age–depth pattern, and its coherence with other age–depth patterns from similar lacustrine contexts. Thus, the chronology for Lake Miroir was compared with the chronology for another head-lake (Lake du Lait) at similar altitudes (2180 m vs 2214 m) dated to 21 000 cal yr BP in Carcaillet & Blarquez (2017). Their age–depth patterns are very similar, although Lake du Lait is located on acidic bedrock (granitoid crystalline composed of micaschists older than Permian or Stephanian; Debelmas, 1988) with no risk of a hard-water reservoir effect. These finding strongly support the validity of the Lake Miroir chronology, despite inclusion of four TOC-based ^{14}C dates among the nine used to establish it.

Other dating methods could not be applied. For instance, pollen biostratigraphy is not appropriate for establishing modern chronologies because it results in circular reasoning and impedes efforts to detect environmental inter-site variability. Further, pollen does not accurately reflect local vegetation in high mountain environments (e.g. Ortu *et al.*, 2006). In contrast, plant macro-remains are representative of stand vegetation, notably basal area (a tree-biomass proxy; Blarquez *et al.*, 2012). Remains of two dominant subalpine trees (*Larix decidua* Mill. and *Pinus cembra* L.) were well-represented in the Lake Miroir sediments, permitting estimations of their biomass. Concerning charcoal analyses, various statistics and transformations of time series have advocated to improve reconstructions of fire history. Instead, we proposed a consensual algorithm to minimize statistical disputes (Blarquez *et al.*, 2013). Regardless of the methodology selected for peak reconstructions, there is strong evidence that charcoal began accumulating either during or almost immediately after the LGM at Lake Miroir. The strength of these preliminary methodological results allowed us to create a local reconstruction of vegetation and fires covering the past 21 ka, although we admit being at the technical limits of reconstruction due to the thinness of sediments originating from between 21 and 11 ka.

Mountain tree refugia and glacial fires

In 2008, a second study commenced in the same region, *c.* 55 km northwest of Lake Miroir. This study focused upon travertine (calcareous tufa) containing fossil imprints of trees at 2100 m asl in a treeless and remote area. Fossil ages were determined from thorium/uranium (Th/U) ratios. The presence of trees was revealed at the Late-glacial–Holocene transition (Carcaillet *et al.*, 2018). The results were based upon archives, and chronological and paleobotanical methods differing from those employed by Carcaillet & Blarquez (2017), and support the idea of tree refugia in the south-western intra-alpine zone. The occurrence of fires was not reported. However, glacial conditions did not prevent accumulation of charcoals in sediments globally (Power *et al.*, 2008). Moreover, paleoecological and modern studies have demonstrated that fires could spread in periglacial contexts not only in northern Alaska (e.g. Higuera *et al.*, 2011; Mack *et al.*, 2011) but also in glacial central Canada (Bélanger *et al.*, 2014) and west Greenland (Anonymous, 2017).

Evidence of glacial tree refugia has been found in Scandinavian mountains and near seacoasts in Norway, including remains of trunks or cones (e.g. Kullman, 2008; Paus & Haugland, 2017) and sedimentary DNA, supported by population genetics (Parducci *et al.*, 2012). A very intriguing finding suggests that trees survived in a supraglacial ecosystem, i.e. on a stagnant LGM ice, based upon DNA found with plant remains (Zale *et al.*, 2018). Moreover, in northern Siberia or Canada, there are various lines of evidences (macro-remains, charcoal, DNA, pollen) that trees grew in a periglacial environment just before (e.g. Zazula *et al.*, 2006; Bélanger *et al.*, 2014; van Geel *et al.*, 2017), during (Willerslev *et al.*, 2014) or just after the LGM (e.g. Tarasov *et al.*, 2009; Zimmermann *et al.*, 2017). In mountain regions, nunataks (iceless slopes surrounded by ice) can provide favourable conditions for life during glacial times, as their soils are not frozen year-round. At the treeline, permafrost would form preferentially under a closed tree canopy where the sun cannot warm the soil (Körner, 2003). On a LGM nunatak, we would only expect scattered trees, likely prostrate, forming an open canopy, with the sun seasonally warming the soil, which would promote tree root growth and photosynthesis.

Modern treeline

Finsinger *et al.* (2018) presented speculations about the location of the current treeline in the south-western Alps relative to the current glacier equilibrium line altitude (ELA) that are problematic for several reasons. First, in paleoecology, the treeline is not physiognomically defined; it is only a limit of species occurrence. In studies of modern ecosystems, it is generally considered the maximum altitude line for erected trees at least 5 m tall. Second, it is not true that the ELA 'broadly coincides with the snowline altitude' (dixit) at fine topo-edaphic scale, where there are important spatiotemporal heterogeneities and complex relationships with winter precipitation and summer temperature as shown in the Alps by Rabatel *et al.* (2013) or Canada by Shea *et al.* (2013). For example, the ELA is at *c.* 2900–3300 m in the Écrins Massif of the southern French Alps, where there are many glaciers that trigger colder and wetter massif environment. In the French–Italian Queyras massif (the location of Lake Miroir) situated in the east, there are no glacier despite altitudes until 3841 m. Third, current relationships between treeline and permanent snowline differ between strongly human-modified Alps and relatively unmodified Canadian Cordillera or South American Subantarctic, where the differences between lines are smaller, as little as 300 m (Körner, 2003; pers. obser.). Fourth, the modern ELA monitored in the southern French Alps close to Lake Miroir is at *c.* 3000 m asl (Rabatel *et al.*, 2013), i.e. 300–400 m above the current observed upper treeline (Fig. 1), not 800–900 m as mentioned by Finsinger *et al.* (2018). Finally, while admitting that ELA is a proxy of snowline, the LGM value used by Finsinger *et al.* (2018) is an estimate by Cossart *et al.* (2012), while our data are measurements (datings and tree-remains).

Subalpine environments have been severely modified by land-use over millennia, notably by descending treelines. Nevertheless, land-use abandonment since the nineteenth century altered subsequent ecological dynamics, as evidenced by increases in the upper limit of the montane species *Abies alba* Mill. into the subalpine belt to: 2215 m near Lake Miroir (F. Guibal, pers. comm., August 2018); above 2150 m at Gran Bosco (Susa Valley, Italy); 2200 m near San Bernolfo (Stura Valley, Italy) (R. Motta, pers. comm., August 2018); and up to 2226 m in the Maurienne Valley, France (an increase of *c.* 250 m since the 1950s; Chauchard *et al.*, 2010). Land-use abandonment favoured pine and larch expansion well above 2400 m, occasionally reaching 2660 m (Fig. 1; Table 1) and even > 2700 m (B. Talon, pers. comm., December 2018). The best evidence that treeline in the western Alps near 45°N can attain very high elevations is the occurrence of *P. cembra* and *L. decidua* stands up to 2650 m and 2520 m, respectively, on the arid and rocky southern slopes of Mount Viso (Motta & Nola, 2001), and occasionally on cliff faces (Fig. 1). While these trees are often small (< 5 m tall), and sometimes prostrate, they can be 150- to 200-years-old (Motta & Nola, 2001). Such prostrate trees during

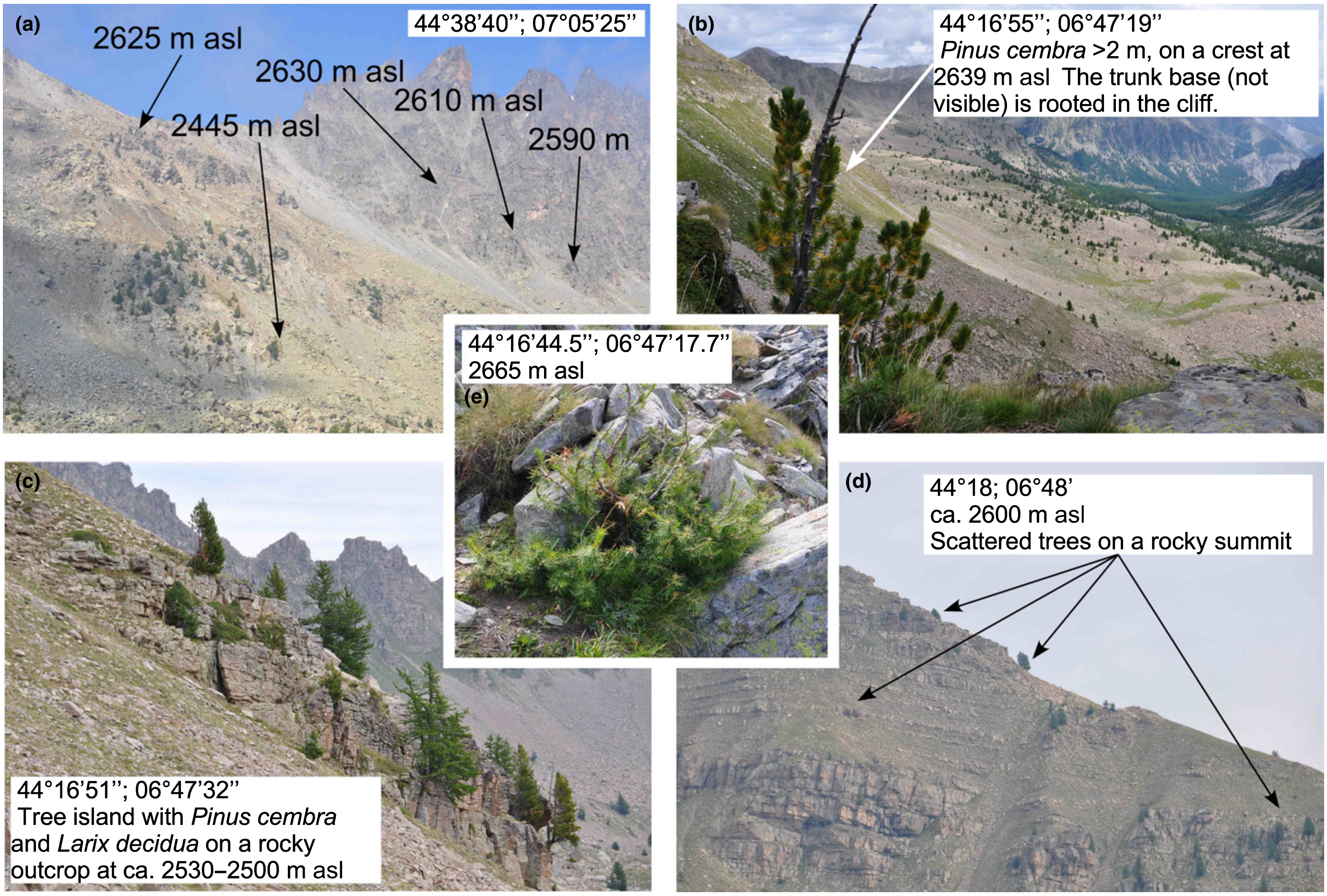

Fig. 1 (a) Positions of trees (arrows indicate elevations) on the south-facing slope of Mount Viso massif (Val Varaita, Italy); stands were located 25 km east of Lake Miroir. (b) Cembra pine (*Pinus cembra*) growing on a cliff top at 2639 m above sea level (asl), sheltering other pines and larches (not visible here) that are inaccessible to domestic ungulates; (c) tree island; (d) isolated trees on rocky crest; (e) isolated larch (*Larix decidua*) among boulders on a summit (b–e: Vallon de la Braïsse, France; 37 km south of Lake Miroir); Photograph credit: C. Carcaillet.

Table 1 Tree-limits recorded in the western Alps, from north to south, with indications of observed tree species.

Site name	Latitude Longitude	Altitude (maximum m asl)*	Bedrock	Slope exposure	Species
Aussois	45°15′44″N 6°43′59″E	*c.* 2500 m	Quartzite, mica schists, and limestone	South	*Larix decidua* *Pinus cembra* *Pinus uncinata*
Orgère	45′14′04″N 6°41′15″E	*c.* 2500 m	Quartzite	South	*Pinus cembra*
La Norma	45°11′05″N 6°43′40″E	*c.* 2535 m	Calcareous schists	North	*Larix decidua* *Pinus cembra*
Cristol	45°00′20″N 6°34′55″E	*c.* 2500 m	Acidic schists and sandstone	Northeast	*Pinus cembra* *Pinus uncinata* *Larix decidua*
Vallon des Granges	44°20′10″N 6°49′ 40″E	2570 m	Flysch and calcareous sandstone	West	*Larix decidua*
Vallon de la Braïsse	44°16′53″N 6°47′19″E	2665 m	Calcareous sandstone	West & East	*Larix decidua* *Pinus cembra*

*asl, above sea level.

the LGM have likely contributed to the observed macro-remains record at Lake Miroir.

In summary, the Lake Miroir chronology is sound and the pitfalls listed by Finsinger *et al.* (2018) in their critique were carefully addressed before publication. The chronology was established rigorously and meticulously using available material and techniques. The vegetation report is robust thanks to the use of macrofossils, which minimizes risks of misinterpretation as they are not transported long distances and, pre-calibration of basal area (in $m^2\ ha^{-1}$) as a biomass proxy. The vegetation was carefully reconstructed in terms of relative basal area (%), as absolute would have been inappropriate due to the large surface area of Lake Miroir (0.7 ha). Finally, fire reconstruction was parsimonious and consensual because it was based on a set of 130 simulations and five typical smoothing techniques. No claim was made about the density of tree cover during the LGM, except that enough biomass was present to support fire in a similar pattern to that in Alaskan tundra (Mack *et al.*, 2011).

It must be admitted that the actual upper treeline can be much higher in the Alps than the modern human-modified. Further, trees at the actual treeline likely differed physiognomically from those at the human-modified treeline, with prostrate habits – 'krummholz' – allowing resistance to low temperature, desiccation and wind. Such physiognomy helps decoupling of trees' micro-climate from the ambient climate (Körner, 2003). Our experience in high mountains, supported by the work of other field researchers (e.g. Motta & Nola, 2001), demonstrates that the treeline value used by Finsinger *et al.* (2018) is incorrect, which largely explains their methodological error in inferring past treelines relative to the present. There is no doubt that the Lake Miroir findings will seed future discussions on tree biogeography of glacial periods in temperate mountains.

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