Fire on ice and frozen trees? Inappropriate radiocarbon dating leads to unrealistic reconstructions

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The questions as to where and how trees survived the Quaternary ice ages are key for understanding climate-driven range expansion processes (Clark, 1998; Giesecke et al., 2017) and the influence of ice-age legacies on current mid- and high-latitude biodiversity patterns (Willis & Whittaker, 2000). Such questions have long intrigued plant ecologists, biogeographers and palaeoecologists (Bennett et al., 1991; Kaltenrieder et al., 2009) and have recently become the focus of combined molecular-ecological and biogeographical studies (Magri et al., 2006; Wagner et al., 2015).

The classic southern-refugia paradigm (van der Hammen et al., 1971; Tzedakis et al., 2013) postulates treeless landscapes in central Europe and at the margins of the continental and Alpine ice-sheets for the time of the Last Glacial Maximum (LGM; c. 23 000–19 000 calendar years before present (cal yr BP, where 0 cal yr BP = AD 50), that is, the interval representing the most extreme conditions of the Last Glacial). Widespread cold-adapted alpine and arctic plants and boreal dwarf shrubs are documented to have occurred north of the Alps (Birks & Willis, 2008; Tzedakis et al., 2013), while small populations of temperate and boreal trees persisted in southern European peninsulas (Iberia, Italy, and the Balkans) (Bennett et al., 1991). Boreal and mountain conifers (e.g. Larix decidua Mill. and Pinus cembra L.) occurred at more northerly locations (up to c. 46°N) in eastern Europe, and grew closer to the southern margin of the Alpine and Carpathian ice-caps than temperate trees (Willis, 2000; Vescovi et al., 2007; Kuneš et al., 2008). This view has been challenged by the alternative interpretation that temperate plant species could have survived the LGM further north in locally favourable conditions as small populations that may be hard to detect with palaeoecological tools (e.g. Stewart & Lister, 2001; Heikkilä et al., 2009; Välimäki et al., 2011).

Recently, Carcaill et al. & Blarquez (2017) presented evidence for the occurrence of an LGM ‘tree refugium’ located at c. 2200 m above sea level (asl) on a nunatak (a mountain top or peak emerging from or at the edge of an ice sheet or glacier) on the western flank of the European Alps. The reported presence of L. decidua and P. cembra plant macrofossils during the LGM in sediments from Lake Miroir, a site located close to modern treeline altitude (TLA), challenges the consensus on the LGM distributions of trees in Europe. The authors further provided evidence of fire occurrence on the nunatak during the LGM, which they suggest demonstrates that ‘a glacial climate does not prevent the ignition of biomass and fire spread’. Finally, they concluded that their findings support the hypothesis of western Alpine glacial refugia of P. cembra and L. decidua (Mosca et al., 2012). The study uses the powerful approach of plant-macrofossil analysis (Birks & Birks, 2000) to determine the occurrence of trees in a high-alpine environment. Being located on a ridge rather than at the bottom of a cirque basin, it is possible that the LGM glacier did not cover the studied lake. Thus, this site may bear sediments older than typical Alpine glacial-cirque lakes, where organic sediment accumulation generally started not earlier than the onset of the Holocene (e.g. Tinner & Theurillat, 2003). Moreover, given the evidence for tree occurrences at elevations above glacier fronts nowadays (e.g. Lüdi, 1950), the occurrence of trees on nunataks in the past is a reasonable hypothesis. However, the hypothesis should be critically assessed because modern treeline is located significantly below the snowline (roughly the elevation of the 0°C isotherm of the warmest month), above which the ground remains snow covered throughout the year (Körner, 2003).

Claiming an LGM refugium on a nunatak for tree species in modern treeline environments requires strong evidence. First, the evidence for a nunatak around Lake Miroir is poorly supported because the LGM glacier-cover reconstruction referred to by Carcaillet & Blarquez (2017) is at the scale of the whole Durance-valley glacier (Cossart, 2008; Cossart et al., 2012). A detailed description of local glacial/periglacial landforms (e.g. trimlines, roches moutonnées, erratics) around the lake would be needed to firmly constrain the existence of a nunatak. Second, historical biogeography depends on reliable age assessments of sediment sequences, and here we argue that the choice of material used for radiocarbon ($^{14}$C) dating led to unsupported conclusions. To estimate the ages of sediments deposited before the Holocene, Carcaillet & Blarquez (2017) used $^{14}$C dates of total organic carbon extracted from lacustrine sediments (hereafter ‘bulk dates’). There are several studies (see for instance Björck & Wohlfarth, 2001, and references cited therein) that demonstrate that in many cases bulk dates yield older ages than the actual sediment deposition time due, for instance, to (1) contamination by $^{14}$C depleted (dead) fossil carbon from pre-Quaternary sediments/bedrocks and from Quaternary glacial till (Walker et al., 2001; Hägvar & Ohlson, 2013; van Mourik et al., 2013), and to (2) the well-known ‘hard-water reservoir effect’ (Deevey et al., 1954). The latter effect arises in areas with calcareous bedrock, soils, or aeolian input of carbonate-rich dust (Grimm et al., 2009) because aquatic organisms take up dead carbon from dissolved carbonates and incorporate it into their tissues, thereby leading to overestimations of the sediment ages based on samples consisting entirely or partly of aquatic organic matter. While early-Holocene plant-macrofossils and bulk $^{14}$C
dates at 710–715 cm provided nearly the same ages (see table 1 in Carcaillet & Blarquez, 2017) suggesting little or no early-Holocene hard-water effects, discrepancies are expected to increase down-core in sediments with low organic content (Fowler et al., 1986), because it is reasonable to assume that low organic content mostly reflects low terrestrial productivity. In down-core sequences such ages can become rapidly older with age, down to $^{14}$C exhaustion, while their sequence still displays a regular, yet fatal, stratigraphic consistency. Both biases are relevant in critically assessing the chronology of the sediments analysed by Carcaillet & Blarquez (2017) because Lake Miroir is located in a catchment dominated by biogenic-limestone bedrocks (Fig. 1), which in this context is important information that was not mentioned in the article.

Because such potential biases are well known, bulk dates or dates of aquatic-plant macrofossils are usually avoided (Marty & Myrbo, 2014) or rejected (Andree et al., 1986; Grimm et al., 2009; Giesecke et al., 2014; Hubay et al., 2018), particularly if they differ from those expected according to other sources of information. The justification given by Carcaillet & Blarquez (2017) for using bulk dates is weak, especially because conifer needles were found in the lower part of the Lake Miroir sediment core. Using a different sampling device able to retrieve larger sediment volume, or taking repeated parallel cores would have significantly increased the chance of finding sufficient terrestrial plant-macrofossils for AMS $^{14}$C dating (Tinner & Theurillat, 2003). Alternatively, the chronology could have been supported with other dating methods such as, for instance, tephrochronology (Lane et al., 2012) or by applying pollen-biostratigraphical marker horizons to detect well-known regional vegetation changes during the Lateglacial ($c. 14,700–11,650$ yr BP, where $0$ yr BP = AD 1950; Magyari et al., 2012; Giesecke et al., 2014; Heiri et al., 2014).

Here, we provide an alternative interpretation of the results based on available geomorphological and palaeoecological data. The modern equilibrium-line altitude (ELA), which broadly coincides with the snow line altitude and separates the zones of net accumulation and net ablation on glaciers (Bakke & Nesje, 2011), is located at $3,000 \pm 200$ m asl in the western Alps (Cossart et al., 2012; Rabatel et al., 2013; Fig. 2a). The LGM-to-modern ELA rise

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**Legend (selected symbols only)**

- **Ez**: Gravitational mass-movement deposits: talus
- **EG**: Glacial and periglacial deposits: active and inactive rock glaciers
- **EG**: Glacial and periglacial deposits: Würm
- **c-e**: Limestone (‘Calcaires planctoniques’ upper Cretaceous-Eocene)
- **IG(b)**: Gypsum (‘Trias carbonaté’)
- **ImC-D**: Limestones and dolomites (‘Trias carbonaté’)

**Fig. 1** Excerpt from the geological map of France (no. 871, scale 1/50 000) showing the bedrock geology and surface deposits around Lake Miroir (‘Lac Miroir’ in French; Kerckhove et al., 2005).
Fig. 2 (a) Modern and Last Glacial Maximum (LGM) equilibrium line altitude (ELA, indicated by a snowflake) and treeline altitude (TLA, indicated by a tree) based on geomorphological, palaeoclimatological, and ecological data. Modern ELAs are based on Cossart et al. (2012) (dark blue bar) and Rabaté et al. (2013) (light blue bar); LGM ELAs are based on Cossart et al. (2012), and on the difference between modern ELA as from Rabaté et al. (2013) and LGM ELAs, following Broecker & Denton (1990) and Federici et al. (2017) (light blue bar). Modern local TLA (yellow bar) is between 2200 and 2400 m above sea level (asl) (Caracillet & Barzaghe, 2017), and LGM TLA (orange bar) south of the Alps was c. 200–400 m asl (Tinner & Vescovi, 2005), corresponding to an LGM-to-modern treeline rise of c. 2000 m (Marta et al., 2013). Modern and LGM ELA-estimated TLAs (green bars) were inferred based on the elevation of the ELA and the modern altitudinal difference (ΔZ = 900 ± 100 m) between ELA and TLA (Körner, 2003). LGM TLA was also estimated using chironomid-inferred July-air temperatures from Lago della Costa (Samartin et al., 2016), July temperatures of 7.5 to 9.5°C necessary for tree growth and lapse rates of 6°C km⁻¹ (brown bar). The altitudinal position of Lake Miroir is shown with a horizontal dashed line. (b) Mean July-air temperature scenarios for the LGM to present estimated for the altitude of Lake Miroir using two chironomid-based temperature reconstructions from the Alpine region (Lago della Costa, Samartin et al., 2016; Lago di Origlio, Samartin et al., 2012), and a chironomid-inferred stacked Alpine temperature record representing temperature in the northern and central Swiss Alps (Heiri et al., 2015). Temperatures were corrected assuming a constant modern temperature lapse rate of 6°C km⁻¹ (Livingstone & Lotter, 1998). The Origlio record is only shown for the older section (c. 14000 cal yr BP, where 0 cal yr BP = AD 1950). Current July-air temperatures are shown for the area of Lake Miroir (horizontal red bar) based on WorldClim 2.0 (Fick & Hijmans, 2017). In addition, historical (c. 1755–2017) 30-yr moving average July-air temperature measurements from Basel Binningen (black line) are displayed, corrected to the altitude of Lake Miroir. ELA, TLA and alpine vegetation temperature thresholds are inferred from today’s observations in space (Körner, 2003; Landolt, 2003). All three temperature scenarios indicate that Lake Miroir was located well above the TLA and, for two scenarios, even above the limit of alpine vegetation during the LGM and the end of the last glaciation > 14 700 cal yr BP.

has been estimated to c. 1000 m (Broecker & Denton, 1990; Federici et al., 2017). This is a conservative estimate, given that greater ELA rises (c. 1300–1400 m) have been suggested, for instance, for the Durance valley itself (Cossart et al., 2012) and as far south as Montenegro (Bavec et al., 2004). Thus, if we assume an ELA 1000–1400 m lower than present this would lead to permanent snow and ice accumulation during the LGM at an altitude of c. 1600–2000 m asl, an elevation well below Lake Miroir (Fig. 2a). Lake Miroir, even as a nunatak, would thus have been perennially frozen and snow-covered, making tree or shrub growth impossible. Furthermore, snowline and treeline co-vary in space and are separated today by an altitudinal difference (ΔZ) of c. 800–900 m in the Alps (Körner, 2003; Landolt, 2003). If the modern ΔZ was used to infer the upper limit of LGM tree growth, the TLA would have been at 800–1300 m asl (Fig. 2a).

Quantitative vegetation-independent palaeotemperature reconstructions (Fig. 2b) as well as palaeoclimatic simulations show that LGM mean July-air temperatures were 10–12°C lower than today in the south-eastern sector of the Alps (Samartin et al., 2016) and that the western Alpine sector was likely colder than the eastern sector (Heyman et al., 2013). At the upper treeline tree growth is mainly temperature limited (Körner, 2003), and the upper treeline in the Alps is located at mean July temperatures of 7.5 to 9.5°C (Landolt, 2003). Assuming a lapse rate of 6°C km⁻¹ close to modern conditions (Livingstone & Lotter, 1998; Becker et al., 2016), a 10–12°C drop would result in c. 0°C mean July temperatures at Lake Miroir. This temperature estimate agrees well with estimated ELAs and supports the argument that during the LGM the area was covered by snow, ice, and permafrost (Osterkamp & Burs, 2003), making tree growth or persistence impossible (Körner, 2003; MacDonald et al., 2008; Kruse et al., 2016).

Obtaining a mean July-air temperature of 8°C at Lake Miroir on the basis of the reconstructed palaeotemperature records (Fig. 2b) would require an unrealistic summer-temperature lapse rate of c. 2°C km⁻¹. Such low lapse rates, however, are not needed to model the LGM Alpine ice cap (Becker et al., 2016). Instead, TLA depressions of c. 1400–1700 m are in much better agreement with both theoretical (models) and empirical evidence (pollen, plant macrofossils), which suggest LGM TLA depressions south of the Alps > 2000 m (Tinner & Vescovi, 2005; Marta et al., 2013), resulting in realistic TLA reconstructions (e.g. of L. decidua) below 500 m asl (Kaltenrieder et al., 2009; Monegato et al., 2015), that is > 1500 m below Lac Miroir. Taken together, the available evidence suggests that even if Lake Miroir was located on a nunatak at the margin of valley glaciers, it was most likely permanently covered by snow or ice, thus unsuited for tree growth, and far above treeline.
The picture does not change when considering single trees in sheltered microhabitats (e.g. rocky slopes) that are located today c. 200–300 m above the treeline (Körner, 2003).

The evidence clearly argues in favour of a more conservative interpretation than that proposed by Carcaillet & Blarquez (2017), implying that the macrofossils assigned to the LGM actually were deposited either during the early Holocene (< 11 650 cal yr BP) or during the Bolling-Allerød Late Glacial Interstadial (c. 14 700–12 850 cal yr BP). An early-Holocene age would fit with evidence attesting that the spread of L. decidua in the western sector of the Alps occurred later than in the eastern sector (Wagner et al., 2015). By contrast, a Bolling-Allerød age would be truly a novel palaeoecological finding showing the establishment of modern treeline before the Holocene. This finding would be conceivable on the basis of (1) the lowermost plant-macrofossil 14C date (9980 ± 50 14C yr BP), and (2) palaeotemperature records (i.e. the chironomid-inferred mean July temperatures shown in Fig. 2b). Both scenarios would show that L. decidua populations spread fast at high altitudes. Thus, the presence of tree refugia on nunataks is not required to explain the genetic differentiation of western and eastern populations (Mosca et al., 2012). Because charcoal-accumulation rates strongly depend on the sediment-accumulation rates that are inferred from the depth-age model, the charcoal-inferred fire history presented by Carcaillet & Blarquez (2017) is also poorly supported. Moreover, to obtain a more robust charcoal-inferred fire history presented by Carcaillet & Blarquez (2017) remain unsupported and in conflict with the data with inputs from O.H., A.R. and C.M-M. W.F., C.S., W.T. discussed the results and contributed substantially to the final manuscript.

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