Extreme temporal interpolation of sparse data is not a sufficient basis to substantiate a claim to have uncovered Pleistocene forest microrefugia

de Lafontaine et al. (2014) claim to have uncovered Pleistocene forest microrefugia in the Landes de Gascogne, western France, using radiocarbon dated charcoal fragments recovered from soils. In particular, they conclude that Fagus sylvatica (beech) “persisted in situ in several microrefugia through full glacial and interglacial periods up to the present day”. They cite genetic evidence of extant populations of F. sylvatica from this region and elsewhere (de Lafontaine et al., 2013) in support of their conclusion, stating that F. sylvatica populations in the Landes de Gascogne “belong to distinct endemic genetic lineages” (my emphasis). They also cite in support of their conclusions published evidence from species’ distribution models (Svenning et al., 2008) that claims to show that Fagus could have persisted in the region during the Late Pleniglacial (LPG) interval. Before the claims made by de Lafontaine et al. (2014) can be accepted, both their own evidence, and that which they cite in support of their conclusions, must be subjected to critical examination.

Careful examination of Table S2 of the Supporting Information that accompanies their paper reveals that de Lafontaine et al. (2014) obtained only nine pre-Holocene radiocarbon dates on pieces of charcoal, five of which were identified as F. sylvatica, one of which gave an effectively infinite age, and four of which were identified as Pinus sylvestris. The 2σ calibrated age ranges for these nine dates, as given in Table S2 of

![Figure 1: Last glacial palaeoenvironment and charcoal evidence](image_url)

(a) δ¹⁸O record from the GRIP Greenland ice core (Johnsen et al., 2001); (b) Planktonic δ¹⁸O record from marine core MD95-2039 taken off the coast of north-west Iberia (Roucoux et al., 2005); (c) Record of relative abundance of Pinus pollen from MD95-2039 (Roucoux et al., 2005); (d) Bars showing the 2σ ranges of the calibrated ages of all pre-Holocene charcoal fragments reported by de Lafontaine et al. (2014) (Note that the oldest dated sample for Fagus sylvatica gave an indefinite age of > 51,000 cal yr BP.) Grey shading indicates the duration of the LPG (after Tzedakis et al., 2013), whilst the ages of 16,118 and 24,419 cal yr BP determined for Heinrich Events H1 and H2, respectively, in ODP Site 976, Alboran Sea (Combourieu Nebout et al., 2002), are indicated by the dotted lines.
de Lafontaine et al. (2014), are plotted on Figure 1, along with two palaeo-temperature proxies, the δ¹⁸O records from the GRIP ice core (Johnsen et al., 2001) and from planktonic foraminiferans from the MD95-2039 marine sediment core obtained off the coast of north-west Iberia (Roucoux et al., 2005), and a regional palaeo-vegetation indicator, namely the relative abundance of Pinus pollen in the same marine core. Also shown on the figure are the extent of the LPG, following Tzedakis et al. (2013), and the ages determined for Heinrich Events H1 and H2 in ODP Site 976 (Combourieu Nebout et al., 2002).

An important plank of the argument advanced by de Lafontaine et al. (2014) is their claim to have recovered charcoal of *F. sylvatica* from “the coldest and driest interval of the LPG” in western Europe, which they consider to have been that corresponding to Heinrich Event H1. However, as Figure 1 shows, although one of their fragments of *Fagus* charcoal does date from the very end of the LPG, it post-dates the age typically assigned to the cold extreme of H1 in European marine records. Furthermore, this interval does not correspond to the coldest part of the last glacial stage in most records from Europe; instead in most cases the coldest interval occurs before 20,000 cal yr BP (Fig. 1(b)), as it does in the GRIP ice core record (Fig. 1(a)), and corresponds to a general minimum in pollen of tree taxa (Fig. 1(c)), including Boreal trees. Often, but not in all cases, the extreme coldest interval corresponds to Heinrich Event H2, dated to 24,419 cal yr BP in ODP Site 976 (Combourieu Nebout et al., 2002). Furthermore, as Huntley et al. (2013) showed, net primary productivity of trees simulated using a dynamic vegetation model is much reduced in western Europe during H2 compared to H1 (Figure 2).

Given that de Lafontaine et al. (2014) recovered no charcoal of any tree dating to between 30,845 and 16,784 cal yr BP, and no charcoal of *F. sylvatica* dating to between 31,295 and 15,839 cal yr BP, taking in all cases the extreme of the 2σ ranges for the ages obtained, there is an interval of 14,061 yr with no charcoal evidence, and of 15,456 yr with no evidence of *F. sylvatica*, that in each case spans the coldest interval of the last glacial stage when various lines of evidence indicate that trees were at their lowest ebb in western Europe (Huntley et al., 2013; Tzedakis et al., 2013). Using this charcoal evidence to infer continuous presence of *F. sylvatica* at favourable microsites requires temporal interpolation of the data across this lengthy interval. Given the plentiful evidence that European vegetation responded sensitively to millennial fluctuations during the last glacial stage (Fletcher et al., 2010), and that trees showed dynamic

**Figure 2:** Simulated annual net primary productivity of trees for Heinrich Events 1 and 2

Annual net primary productivity of trees simulated using the LPJ-GUESS dynamic vegetation model (Smith et al., 2001) driven by palaeoclimatic conditions simulated for Heinrich Events H1 (a) and H2 (b) (Singarayer & Valdes, 2010). (Re-drawn from Huntley et al., 2013)
range and abundance responses to the millennial climatic fluctuations that characterised the last glacial stage, as evidenced by long palynological records spanning the last glacial stage (e.g. Allen et al., 1999; 2000), a much more plausible interpretation of the charcoal data is that trees, and *F. sylvatica* in particular, were present in the Landes during favourable interstadials of Marine Oxygen Isotope (MOI) Stage 3, became regionally extirpated by the extreme cold climatic conditions that followed, but recolonised the region rapidly as climate warmed once again during late MOI Stage 2, probably from populations that had persisted through the coldest interval around the Pyrenees, in the Cantabrians and/or in southern France (Magri et al., 2006).

de Lafontaine et al. (2014) explicitly reject this latter interpretation on the grounds, principally, that the dates obtained for charcoal of *F. sylvatica* “do not match with intervals of major Atlantic deciduous forest expansion over Southwestern Europe” as reported by Fletcher et al. (2010) and Sánchez-Goñi et al. (2008). Given, however, that pollen of *Fagus* is hardly present after MOI Stage 5 in the only pollen record presented in detail in the latter paper, and is discussed principally in relation to long records from southern Europe in the former, this lack of correspondence seems a flimsy basis for rejecting this interpretation. Interestingly, at Lago Grande di Monticchio, southern Italy, *Fagus* pollen is relatively abundant during interstadials dated to around 40,000 and 30,000 – 32,000 cal yr BP, and increases again briefly between ca. 15,000 and 13,000 cal yr BP (Allen et al., 2000), dates that do coincide approximately with those finite dates obtained by de Lafontaine et al. for charcoal of *F. sylvatica*. This may suggest that the climatic conditions of those intervals were particularly favourable to *F. sylvatica*, albeit not necessarily to the majority of taxa included by Sánchez-Goñi et al. (2008) as components of the ‘Atlantic deciduous forest’. de Lafontaine et al. (2014) discuss two additional lines of evidence that they argue support the inference of long-term persistence of *F. sylvatica* in the Landes de Gascogne. Firstly, they cite the species’ distribution modelling results of Svenning et al. (2008). Whilst the latter study does simulate potential occurrence of *F. sylvatica* in south-west France at the last glacial maximum (LGM), the particular species’ distribution model used for this simulation also simulates potential occurrences of the species in central western Norway under the present climate, far to the north of its actual range today. Simulation of such potential areas of occurrence beyond a species’ actual range is a general feature of many species distribution modelling techniques that use presence only data. In particular, as Royle et al. (2012) showed, the Maxent model used by Svenning et al. (2008) systematically “overestimates occurrence probability in regions where the species was never detected”. Given the geographically marginal position of the Landes de Gascogne relative to the overall simulated LGM range for *F. sylvatica*, the result presented by Svenning et al. (2008) provides only very weak, at best, support for the conclusions reached by de Lafontaine et al. (2014)

The second additional line of evidence cited is from a study of the genetics of *F. sylvatica* populations in France and northern Spain (de Lafontaine et al., 2013) that de Lafontaine et al. (2014) state shows that populations from the Landes de Gascogne “belong to distinct endemic genetic lineages”. Nowhere in the text of the cited paper, however, do the authors reach such strong a conclusion, stating only that these “populations do not group together with other known refugia but instead form a distinct genetic cluster”. Even this more moderate conclusion, however, is not fully in accord with the evidence presented in Figure 3 of their paper. This shows differing clustering of the populations when different methods are applied,
and also shows geographical mixing of populations assigned to different clusters, with some populations in the Landes region forming part of clusters found predominantly elsewhere, and occurrences elsewhere of populations classified into the cluster that is principally restricted to the Landes. Such a lack of clarity tends to undermine the present authors’ extreme statement of the genetic results. Furthermore, given the highly dynamic last glacial environment, and the evidence that vegetation responded rapidly to these dynamics, it is questionable whether the present location of any given genetic lineage necessarily implies that lineage has a long history of occupying that location, as opposed to having persistently occupied locations generally different from those occupied by other lineages. This might readily occur if, as seems likely, different isolated populations have evolved different adaptive characteristics that lead them to occupy locations differing with respect to the environmental conditions offered.

It is thus necessary to conclude that neither the dated charcoal evidence presented by de Lafontaine et al. (2014), nor the further evidence that they cite in support of their conclusions, is a sufficient basis to substantiate their claim to have uncovered "Pleistocene forest microrefugia within a periglacial desert" as their title claims. Until such time as direct and compelling evidence is provided of the occurrence of temperate trees in regions such as the Landes during the critical coldest part of the last glacial stage, between ca. 24,000 and 19,000 cal yr BP, then, as Tzedakis et al. (2013) concluded, the available evidence indicates that temperate trees were restricted to more southern areas, for example in the Iberian and/or Italian peninsulas, during at least the coldest part of the last glacial stage.

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