

Letters

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; this issue of *New Phytologist*, pp. 715–729) 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) claiming 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 in 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 de Lafontaine *et al.* (2014), are plotted on Fig. 1, along with two palaeotemperature proxies, the $\delta^{18}\text{O}$ 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

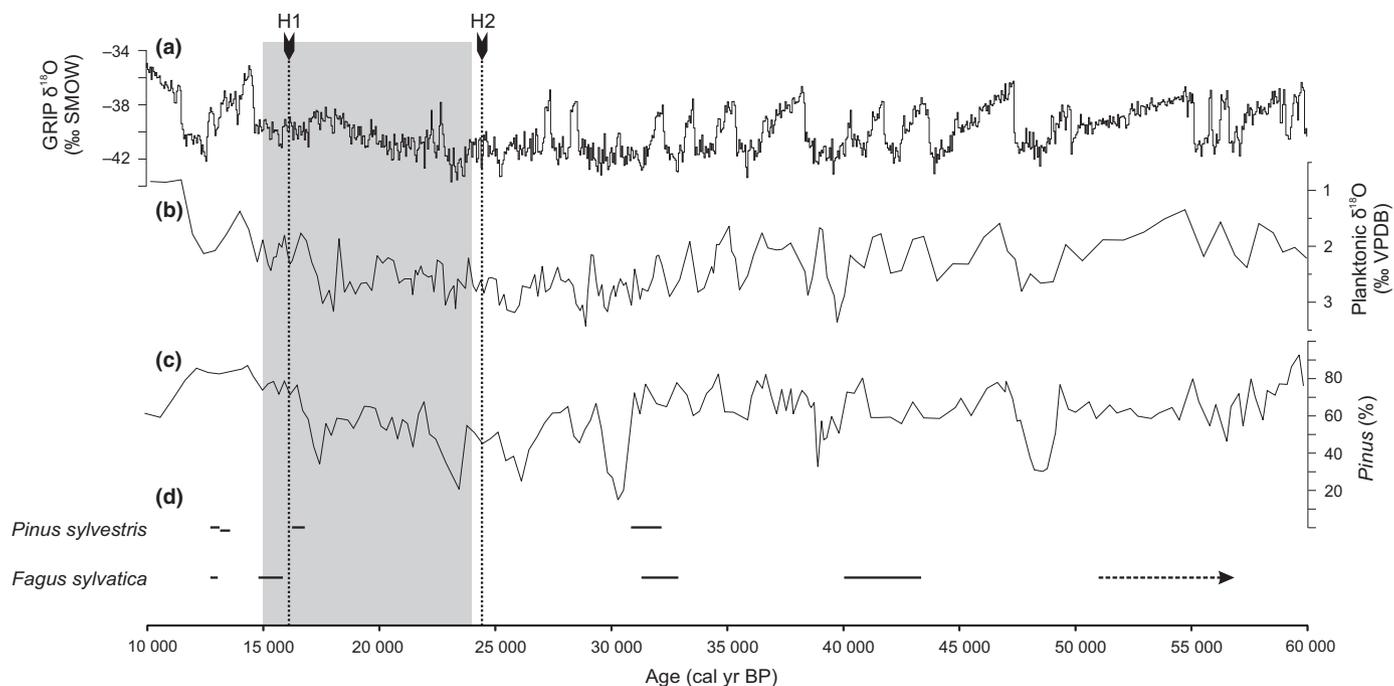


Fig. 1 Last glacial palaeoenvironment and charcoal evidence. (a) $\delta^{18}\text{O}$ record from the GRIP Greenland ice core (Johnsen *et al.*, 2001); (b) planktonic $\delta^{18}\text{O}$ record from marine core MD95-2039 taken off the coast of northwest Iberia (Roucoux *et al.*, 2005); (c) record 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; this issue of *New Phytologist*, pp. 715–729). (Note that the oldest dated sample for *Fagus sylvatica* gave an indefinite age of > 51 000 cal yr before present (BP).) Grey shading indicates the duration of the Late Pleniglacial (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. (a–c, redrawn from Roucoux *et al.*, 2005.)

(Roucoux *et al.*, 2005), and a regional palaeovegetation indicator, namely the relative abundance of *Pinus* pollen in the same marine core. Also shown in 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 Fig. 1 shows, although one of their fragments of *Fagus* charcoal does date from the very end of the LPG, it postdates 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 before present (BP; Fig. 1b), as it does in the GRIP ice core record (Fig. 1a), and corresponds to a general minimum in pollen of tree taxa (Fig. 1c), 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 with H1 (Fig. 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 the 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 range and abundance responses to the millennial climatic fluctuations that characterized the last glacial stage, as evidenced by long palynological records spanning the last glacial stage (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 recolonized the region rapidly as the 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 rejected this latter interpretation, principally on the grounds 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 *c.* 40 000 and 30 000–32 000 cal yr BP, and increases again briefly between *c.* 15 000 and 13 000 cal yr BP (Allen *et al.*, 2000), dates that 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 which they argue support the inference of long-term persistence of *F. sylvatica* in the Landes de Gascogne. First, they cite the species distribution modelling results of Svenning *et al.* (2008).

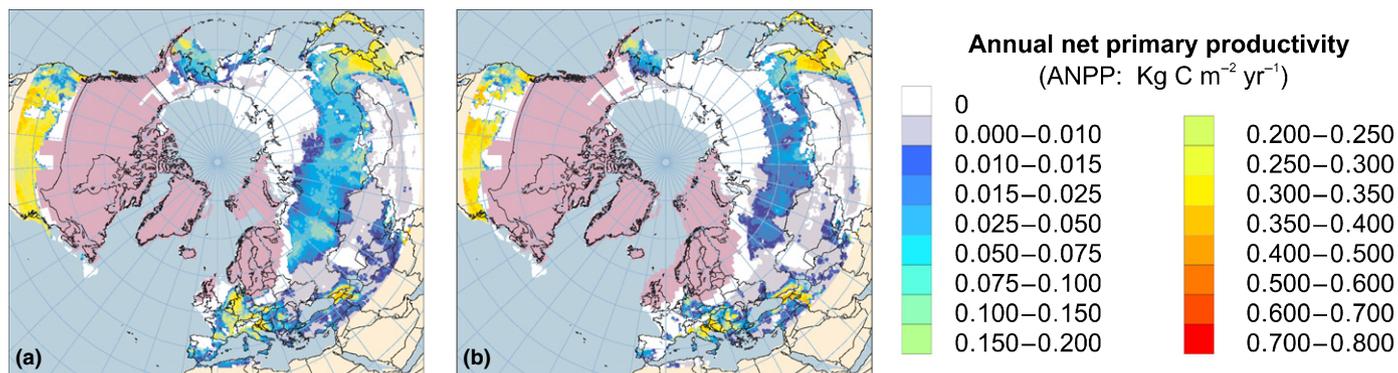


Fig. 2 Simulated annual net primary productivity of trees for Heinrich Events 1 and 2. Annual net primary productivity of trees simulated using the LPJ-GUESS dynamic vegetation model (Smith *et al.*, 2001) driven by palaeoclimatic conditions simulated for Heinrich Events H1 (a) and H2 (b) (Singarayer & Valdes, 2010; redrawn from Huntley *et al.*, 2013).

Whilst the latter study does simulate potential occurrence of *F. sylvatica* in southwest 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, at best, only very weak 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), which 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 a strong 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 Fig. 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 additional evidence 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 *c.* 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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Key words: *Fagus sylvatica* (beech), Heinrich Events 1 and 2, Landes de Gascogne, last glacial maximum, last glacial stage, Late Pleniglacial, soil charcoal.