

Cryptic or mystic? Glacial tree refugia in northern Europe

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Here, we examine the evidence for tree refugia in northern Europe during the Late Pleniglacial (LPG) interval of maximum tree-range contraction. Our review highlights the often equivocal nature of genetic data and a tendency to overestimate potential tree distributions due to warm climate-model bias, and also reveals a convergence of macrofossil and pollen evidence. What emerges is the absence of temperate trees north of 45°N and a west–east (W–E) asymmetry in boreal tree distribution, with a treeless Western Europe north of 46°N, while restricted boreal populations persisted in Eastern Europe up to 49°N, and higher latitudes east of the Fennoscandian ice-sheet. These results have implications for current thinking on European genetic diversity patterns, species migration capacity, and conservation strategies.

Paradigm shift?

According to the classic southern refugia (Box 1) paradigm, during glacial extremes, small temperate and boreal tree populations persisted in southern Europe (south of the Alps), while restricted boreal populations might have also survived farther north [1–3]. This has been challenged by the notion of northern cryptic glacial refugia of boreal and temperate trees with disjunct distributions that were well north of southern regions [4–6]. This hypothesis has gained substantial momentum, resulting in a shift in the way that glacial tree distributions in Europe are being considered, with potentially significant rethinking of: (i) postglacial migration histories; (ii) the spatial organization of genetic diversity; and (iii) conservation priorities to ensure long-term sustainability of temperate and boreal ecosystems. Specifically, northern refugial tree populations would have provided nuclei for postglacial recolonization and enhanced genetic diversity patterns in northern Europe [7]. By extension, original estimates of migration rates [2] would need to be significantly reduced to take into account the spread from northern refugia [7,8]. Importantly, this implies that species migration capacity would fall

substantially short of requirements to keep pace with projected anthropogenic climate change, although local expansion from small isolated pockets could partly compensate for that [9].

Evidence to support the case for northern refugia comes from: (i) plant macrofossils; (ii) pollen records; (iii) genetic data; and (iv) potential glacial tree distributions. Here, we review this evidence with reference to the LPG interval 15 000–24 000 calendar years before present (ka) [~13 000–20 000 radiocarbon years before present (¹⁴C yr BP)], representing the most extreme conditions of the Last Glacial and, by extension, the maximum contraction of tree populations (Box 2).

Plant macrofossils

Willis and van Andel [6] reviewed the fossil-charcoal record predominantly from Upper Paleolithic sites in loess sequences in Central and Eastern Europe and, on the basis of ‘151, ¹⁴C-dated and identified pieces of macrofossil charcoal wood’ ([6] p. 2369), concluded that, during the last glacial, this region was partly covered by taiga forests with pockets of temperate trees. There are two issues complicating their inference of northern refugia: (i) most of these records precede the LPG; and (ii) the majority of the charcoal pieces have not been dated directly, but by association with dates on the cultural layer within which they have been found (often on unidentified charcoal or sometimes on unspecified material). Given the problem of remobilized charcoal from post-depositional reworking or intrusive movement during archaeological excavations, there is a distinct possibility of assemblages containing material of disparate ages. This has been demonstrated most vividly by undertaking separate radiocarbon determinations on charcoal of temperate taxa found among assemblages dominated by boreal taxa at Kostienki in Russia: whereas *Picea* charcoal was dated to 28 500 ± 140 ¹⁴C yr BP, two charcoal pieces of *Quercus* from the same cultural layer yielded dates of 1340 ± 50 and 1400 ± 40 ¹⁴C yr BP [10].

In view of these issues, we re-examined the charcoal record, considering only LPG dates (Table S1A in the supplementary material online). Ideally, sites should have direct dates on identified charcoal, but only Cosautsi, Moldavia shows the continued presence of trees throughout the LPG with 17 dates on *Picea* and *Pinus cembra* charcoal [11]. Information from sites with unspecified

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Box 1. Refugia terminology

In recent years, there has been a proliferation of refugia-related terms. We have paleoreugia and neoreugia [51], macrorefugia and microrefugia (and within the latter, distal, widespread, and proximal) [52], nunatak, peripheral, and lowland glacial refugia for alpine plants, and also *in situ* and *ex situ* refugia [53]. In Europe, we have classic southern and cryptic northern glacial refugia for temperate species, polar and cryptic southern interglacial refugia for cold-adapted species, and also continental interglacial refugia along longitudinal gradients [50]. Although these modifiers may add precision to the term, the ever-growing list of refugia types runs the risk of approaching scientific relativism (refugia everywhere!), with any reduced distribution qualifying for consideration as a refugium.

Some of these terms may appear superfluous upon closer inspection. The distinction between 'macrorefugium' (the main distribution area) and 'microrefugium' ('a small area...in which small populations can survive outside...the macrorefugium' [52] pp. 482–483) appears unnecessary, at least within a European context, where the paleobotanical record from the LPG does not indicate a main distribution area of forest, but rather small fragmented populations. Similarly, the distinction between paleoreugia for Tertiary relicts and neoreugia for Quaternary species has been questioned, because areas with higher buffering capacity from climate extremes today might have harbored species for long periods, perhaps extending into the Tertiary [54]. A corollary of this is that, because phylogenetic lineages have a long history, these areas should not simply be viewed as 'glacial refugia', but rather as 'long-term' [55,56] or 'cumulative' [54] refugia.

Bennett and Provan [57] found the term 'refugium' wanting and proposed to replace it with 'bottleneck', where changes in abundances are being considered. This has some merit in underlining continuity through time, but does not satisfy the main conceptual need of a refugium as a location that provides suitable habitats for the long-term persistence of populations, representing a reservoir of evolutionary history. By extension, the identification of a site supporting a population of a temperate species during one of many range-contraction phases (e.g., a stadial of the Middle Pleniglacial) may be of biogeographical interest, but does not constitute a refugium if that population was subsequently extirpated. Ideally, persistence ought to be documented over several glacial–interglacial cycles, which is possible to infer from genetic evidence, but only rarely from paleobotanical evidence, given the dearth of long fossil records. For the latter, we therefore rely on sites covering the most recent interval of extreme glacial conditions, representing the maximum contraction phase of a species.

radiocarbon dates on cultural layers but with quantitative charcoal data is also useful, so that the most abundant taxa (rather than single finds) can be used. These show the LPG presence of *Betula*, *Salix*, *Pinus*, *Juniperus*, and also *Quercus* and *Abies* in southern France and Cantabria, and *Pinus cembra* and *Pinus sylvestris* in Hungary. Wood charcoal has not been found in LPG loess sediments in northwest Europe [11]. At La Grotte Walou, Belgium, charcoal is present until $29\,800 \pm 180$ ^{14}C yr BP [12]. This feature is reproduced at several sites across Europe, where wood charcoal is present before the LPG, but then disappears [11]. This is not an artifact of sites being abandoned, because Paleolithic occupations continue through the LPG and, therefore, reflect the scarcity of wood in the surrounding regions.

Tree-ring research, with over 8000 tree megafossils recovered in Europe, provides another valuable source of evidence [13]. The only sites with megafossils of LPG age are in northern Italy (70 *Larix* trees and one *Picea* trunk) and Romania (one *Pinus* log) (Table S1B in the supplementary material online). North of the Alps, megafossils of

boreal trees have only been found after the onset of the Lateglacial Interstadial (LGI; 14.6–12.9 ka). Finally, plant macrofossils of LPG age have also been reported from lake and peat sediments (Table S1C in the supplementary material online). The northernmost sites show Arctic treeless assemblages or the presence of dwarf shrubs, whereas sites in Eastern Europe and northern Italy show the presence of boreal and/or montane trees.

Pollen evidence

A recurring theme in recent literature is that pollen analysis is not well suited to detecting glacial tree refugia because of decreased pollen productivity and methodological difficulties in interpreting low pollen percentages [6,7]. Thus, it has been proposed that low temperatures, aridity, and low CO₂ concentrations (the latter has not been experimentally demonstrated) would have suppressed pollen production during glacials, resulting in palynologically 'silent' trees [4,7]. Given that these conditions persisted for thousands of years, tree populations would have been maintained through asexual reproduction [8]. Nonetheless, pollen records have also been invoked to support the existence of northern refugia [6,7], but the examples are from sites that pre-date or post-date the LPG (Appendix 1 in the supplemental material online). More relevant is the long and well-dated sequence from Galich Lake in Russia, with abundant *Picea* pollen during the entire LPG [14], undermining claims of palynological silence.

In addition, the interpretation of low tree pollen finds in glacial-age sediments dominated by herb pollen is complicated by two factors.

(i) Taphonomical biases. Reworking of older pollen grains through slope instability and erosion, associated with periglacial processes and incomplete vegetation cover, can significantly bias pollen spectra. Pollen of thermophilous trees in LPG sediments was traditionally treated as reworked, but recently there has been a reversal of this trend, especially in European-wide data compilations where all pollen grains are taken at face value (e.g., [15]). Neither approach is correct when applied uncritically. The presence of pre-Quaternary pollen grains and pollen preservation are often clues to reworking, but less frequently reported lately. A more utilitarian approach is consideration of pollen-stratigraphical trends in the context of climate changes. A hallmark of refugial populations is low pollen values during the LPG followed by increases at the onset of the LGI in response to warming, as in Galich Lake [14]. By contrast, the record from Lake Kurjanovas, Latvia, shows low LPG pollen percentages of thermophilous taxa, alongside pollen and macrofossil indicators of a tundra-like environment [16]. All pollen grains of thermophilous taxa disappear at the onset of the LGI and all are reported as degraded compared to pollen of other taxa, pointing to redeposition.

(ii) Distinguishing small local populations from long-distance pollen transport. Although critical pollen percentages have traditionally been used to establish the local arrival of a taxon (or, more precisely, its local population expansion [3]), these 'cut-off' values can vary through time and are often unable to address taphonomical biases. Pollen-stratigraphical trends can usually assist

in establishing general presence in the region, on the basis of quasi-continuous pollen percentages through the LPG interval and increases at the onset of the LGI (Appendix 2 in the supplemental material online).

When pollen-stratigraphical criteria are applied to records in Eastern Europe, the pollen data converge with macrofossil evidence from the same region in inferring the presence of *Pinus*, *Picea*, and *Larix* (Tables S1 and S2 in the supplemental material online), suggesting that the inadequacies of the pollen record have been exaggerated. Examination of pollen sites across Europe reveals the following patterns (Figure 1; Table S2 in the supplementary material online): (i) the northwestern sector (north of 45°N, west of 10°E) shows the presence of boreal dwarf shrubs and a general absence of conifers north of 46°N; (ii) the southwestern sector (south of 45°N, west of 15°E) reveals *Pinus*, *Betula*, and *Juniperus* with *Abies*, *Corylus*, and *Quercus* appearing at approximately 44/45°N and other temperate trees and Mediterranean sclerophylls at lower latitudes and elevations; (iii) in the northeastern sector (north of 45°N, east of 10°E), boreal trees are absent immediately south of the Fennoscandian ice-sheet, but present on its eastern side. Sites south of 49°N in Central and Eastern Europe point to the presence of *P. sylvestris* and/or *mugo*, *P. cembra*, *Larix*, *Picea*, *Betula*, *Salix*, *Alnus*, and *Juniperus* populations. Similar boreal and/or montane assemblages emerge from the southern pre-Alps and the Po plain; and finally (iv) in the southeastern sector (south of 45°N, east of 15°E) *Pinus*, *Juniperus*, and *Betula* are widely encountered; diverse assemblages of montane and temperate species are found at mid-altitude sites and Mediterranean elements at lower latitudes and elevations.

Genetic evidence

Proposals for the existence of northern refugia have used genetic data as supporting or primary evidence. Interpretation is usually equivocal, which is a consequence of the combined effects of range-shift dynamics and the genetic

signals that they produce, and the genetic markers used and their information content.

Genetic signals of refugia

Putative refugia are expected to show higher genetic variability compared with surrounding recolonized regions. This is because populations surviving several glacial cycles should accumulate genetic variation, but postglacial colonization does not necessarily involve all molecular variants within a refugial population and serial bottlenecks is expected to further reduce genetic variation within recolonized populations [17]. Thus, molecular variation within northern refugia would be expected to contain related and, in some cases, locally endemic alleles, distinct from surrounding regions and other refugial areas (see also [18]). It would also be expected that ancestral alleles would be more frequent within refugial areas, with mutationally younger alleles more frequent in recolonized areas [19]. However, several demographic factors may complicate the interpretation of these signals [17,20]: (i) genetic variation could be retained in a phalanx colonization to the north; (ii) distinct lineages and alleles that have colonized north may not yet have been discovered (or may have been extirpated) in southern areas; (iii) high local diversity might be produced by admixture between colonizing lineages in the north; (iv) the Younger Dryas cold reversal might have reduced and mixed colonizing lineages in the north to produce subsequent high-diversity expansions; and (v) distinct gene patches might be produced in the north by leading-edge dynamics and gene surfing.

Genetic markers

Genetic data of various sorts have been used to explore the geographical history of populations. Each has its advantages and disadvantages, with DNA sequences particularly informative due to the ability to extract temporal information in the form of ancestral and derived allelic states, facilitating the testing of temporal hypotheses

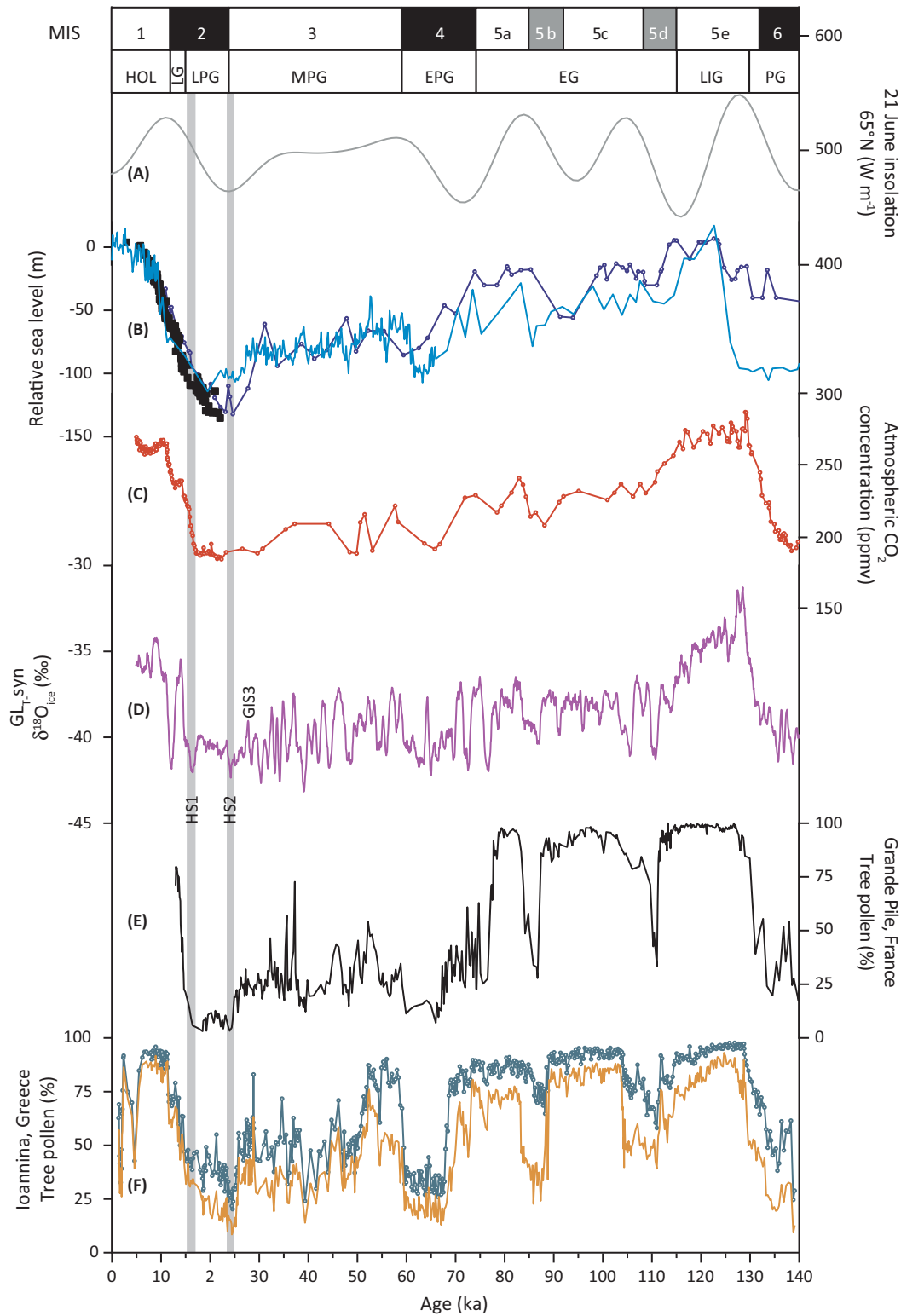
Box 2. When was the 'last glacial'?

Much ambiguity regarding climato- and chronostratigraphic nomenclature pervades the refugia literature. Terms such as 'last glacial', 'last full glacial', and 'last glacial maximum' are often used interchangeably, when in fact they represent distinct, though overlapping, intervals of time. The Last Glacial (Weichselian Stage in Europe) is the interval from the end of the Last Interglacial to the onset of the Holocene (114–11.6 ka). It comprises [1]: (i) the Early Glacial [equivalent to Marine Isotopic sub-Stages (MIS) 5d, 5c, 5b, and 5a; 114–74 ka]; (ii) the Pleniglacial (or Full Glacial) (74–14.6 ka), subdivided into Early (MIS4; 74–59 ka; EPG), Middle (MIS3; 59–24 ka; MPG) and Late (early MIS2; 24–14.6 ka; LPG) Pleniglacial; and the Lateglacial (late MIS2; 14.6–11.7 ka), subdivided into the LGI and the Younger Dryas (Figure 1).

A clear statement of the temporal interval of interest is important because its specific environmental conditions will have a direct bearing on the range and abundance of tree populations. For example, the loose use of the term 'full-glacial populations' is uninformative with respect to the refugia question because it conflates different climatic states, ranging from glacial maximum to interstadial warm intervals. Whereas the MPG is characterized by a succession of interstadials and stadials, the LPG represents the interval of most extreme glacial conditions devoid of major oscillations [1].

More specifically, after Greenland Interstadial 3, sea-level reconstructions [58,59] indicate an accelerated expansion of land-

ice 27.5–24 ka (Figure 1). This interval marks a decoupling between high and low–middle latitudes with Greenland and subpolar North Atlantic records indicating a return to cold conditions, whereas subtropical North Atlantic and European records show that relatively warm conditions persisted until 24 ka [60]. This led to steeper meridional temperature gradients and increased atmospheric transport from lower to high latitudes, providing the moisture supply for ice-sheet growth. The divergent climatic conditions between high and low–middle latitudes persisted until Heinrich Stadial (HS) 2 at 24 ka, when iceberg discharges disrupted the Atlantic meridional overturning circulation (AMOC) and led to widespread cooling, signaling the LPG onset. HS2 was followed by the Last Glacial Maximum interval (21 ± 2 ka [61]) of the lowest sea-level stand (–120–135 m) [59,62] and minimum atmospheric CO₂ concentrations [63] of the Last Glacial. Initial warming at 19 ka led to melting of ice-sheets, iceberg discharges, and further disruption of the AMOC (HS1, equivalent to the Oldest Dryas of northwest Europe). Full AMOC resumption at 14.6 ka signaled the onset of the LGI, although some records show an earlier warming. Thus, the LPG extended from 24 ka to approximately 15 ka and this is supported by precise dating of speleothems [64], showing a cessation of calcite growth during this interval of coldest and driest conditions.



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Figure 1. Climate changes and vegetation responses during the past 140 000 years (kyr). (A) 21 June insolation 65°N [65]; (B) Sea-level reconstructions (light-blue line: [58]); dark-blue line: [59]; black squares: [62]; (C) atmospheric CO₂ concentration in Antarctic ice cores [63]; (D) reconstructed δ¹⁸O composition of ice in Greenland synthetic (GL_Tsyn) record [66]; changes in arboreal pollen (AP) percentages in the Grande Pile record, Vosges Mountains, France [67]; changes in temperate (orange) and pioneer (*Pinus*, *Betula*, and *Juniperus*) pollen percentages in the Ioannina 284 record, northwest Greece [68]. Marine Isotopic Stages and Substages (MIS) are indicated. Also indicated are climato- and chronostratigraphic units: Penultimate Glacial (PG), Last Interglacial (LIG), Early Glacial (EG), Early Pleniglacial (EPG), Middle Pleniglacial (MPG), Late Pleniglacial (LPG), Lateglacial (LG), and Holocene (HOL). Heinrich Stadials 1 and 2 (HS1 and HS2) are shown by vertical bars and the Greenland Interstadial 3 (GIS3) is also shown.

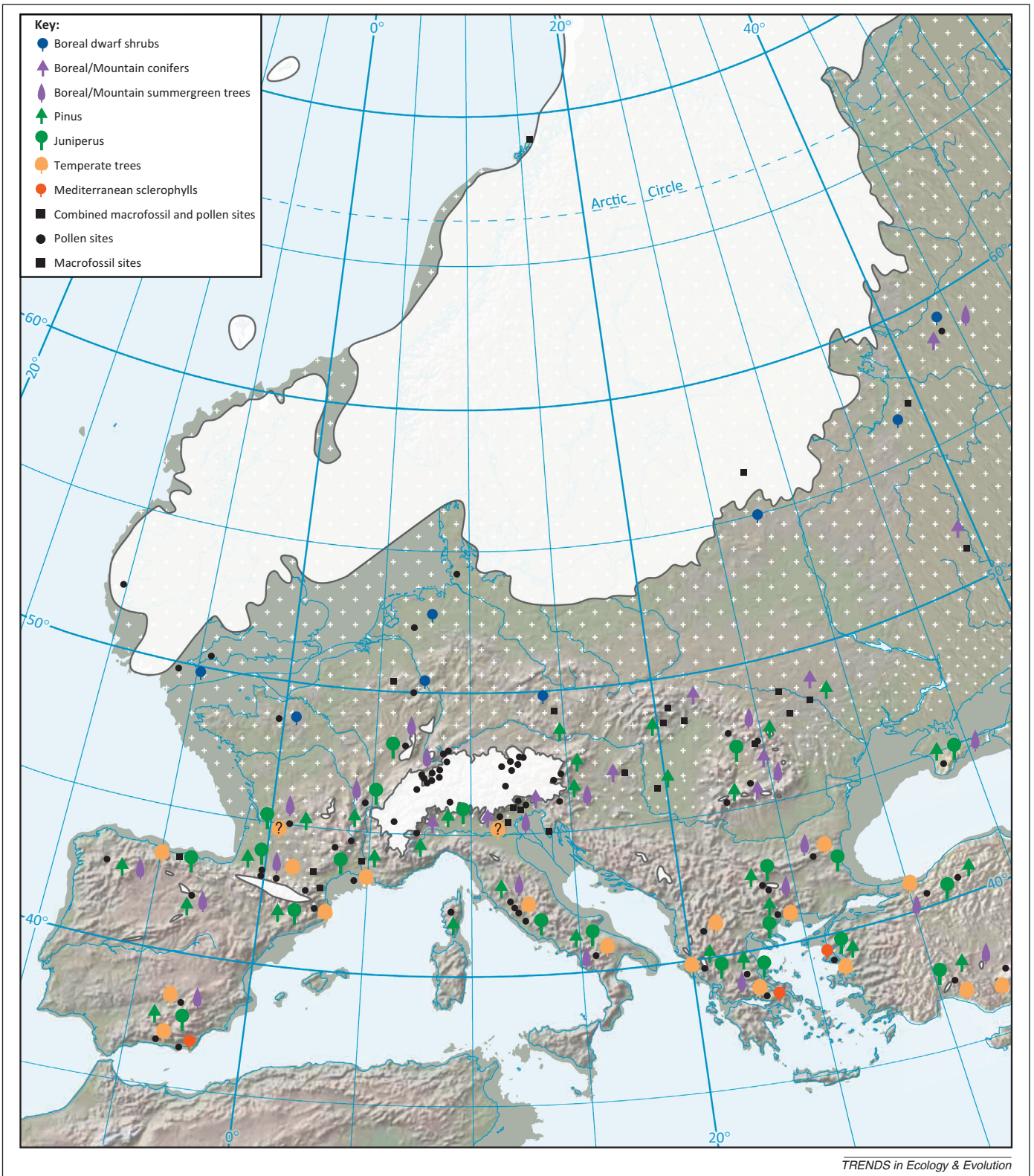


Figure 1. European paleoenvironments during the Late Pleniglacial. Maximum extent of ice (white) [69,70] and continuous and discontinuous permafrost (large and small crosses, respectively) [46] is shown. Also shown is the distribution of macrofossil and pollen sites and inferred tree presence (Tables S1 and S2 and Figure S1 in the supplementary material online): boreal dwarf shrubs: *Betula nana* (dwarf birch) and *Salix* (willow); boreal and/or mountain conifers: *Picea* (spruce) and *Larix* (larch); boreal and/or mountain summergreen trees: *Betula* (birch), *Populus* (poplar), *Salix*, and *Alnus* (alder); *Pinus* (pine); *Juniperus* (juniper); temperate trees: deciduous and evergreen *Quercus* (oaks), *Ulmus* (elm), *Corylus* (hazel), *Tilia* (lime), *Fraxinus* (ash), *Vitis* (vine), *Carpinus betulus* (hornbeam), *Ostrya* (hop hornbeam), *Castanea* (sweet chestnut), *Fagus* (beech), *Abies* (fir), *Cedrus* (cedar), and *Alnus*; Mediterranean sclerophylls: *Olea* (olive), *Phillyrea*, and *Pistacia* (lentisc and terebinth). Question marks over vegetation symbols denote uncertainty (see footnotes in Table S2 in the supplementary material online).

regarding refugial versus recolonized areas (e.g., [21,22]). mtDNA has been used effectively in Late Quaternary evolutionary dynamics of animals [23]. The slow mutation rate of mtDNA within plants has seen chloroplast (cp) DNA used for plant phylogeographic studies. Although cpDNA typically yields more intraspecific variation compared with plant mtDNA, its low mutation rate means that information content is low compared with animal mtDNA. Consequently, many plant studies have used cp-PCR-RFLP, cp microsatellites, and mitochondrial minisatellites to generate more variation (e.g., [24–26]). However, their evolution is less clear and, hence, data are phylogenetically less informative. This lack of phylogenetic information means that, although differentiation among populations may be quantifiable, a more refined understanding in terms of source (refugia) and sink (recolonized area) relationships may be more difficult to infer. The problems of relatively uninformative genetic markers should soon be over. Increasingly economical high-throughput DNA sequencing technology offers the promise of longer and, thus, mutationally more informative, cpDNA sequence matrices, and reduced representation nuclear genome sequencing (RAD sequencing) will soon enable many nuclear loci to be analyzed within species [27,28].

Tree refugia

When these considerations are applied to the available genetic data on temperate trees (Table S3 in the supplementary material online), they provide support for southern refugia in Iberia, Italy, Balkans, and near Alps, but are often equivocal. There is no support for northern refugia of temperate trees. Boreal and/or montane species give less clear genetic signals, but suggest more northeastern refugia for *Picea abies* (Table S3 in the supplementary material online).

Attempts to reconstruct the postglacial migration of different components of present-day forests have increasingly used a combination of paleobotanical and molecular data, with *Fagus sylvatica* [29] a much-cited case for northern refugia. Although testimony to the advantages of a combined approach, the study also underlines the limitations with the identification of glacial refugia: several refugia were proposed in southern Europe along with a refugium in Moravia-Bohemia. The paleobotanical case for the northernmost refugium was not based on any evidence for LPG presence, but on the early Holocene appearance of *Fagus* approximately 9 ka. This is also consistent with long-distance founding events since the start of the LGI, 6000 years earlier. On the genetic side, the study sampled allozyme and chloroplast markers across approximately 600 populations, but revealed little phylogeographic structure across central and northern Europe (Table S3 in the supplementary material online). The data are also consistent with colonization from refugia in northern Iberia and the Balkans alone. More informative genetic markers are needed such that the spatial distributions of alleles can be interrogated with phylogenetic and ancestor–descendant relations.

Recent technological advances in the use of ancient DNA from fossils and sediments are providing data on possible refugia for Pleistocene animals and plants [30],

including trees [31]. Using ancient sedimentary cpDNA and modern mtDNA, this latter study proposed that *Picea* and *Pinus* were present during the LPG in ice-free refugia of coastal northwestern Norway. However, the study has been questioned on the grounds of contamination or reworking of ancient DNA and the need for more discriminating modern genetic data to reject alternative explanations [32,33]. We note that locally endemic derived haplotypes are described in Scandinavia ([31,34]; Table S3 in the supplementary material online), and suggest that competing population genetic hypotheses for their origin (pre-LPG, post-LPG mutation, and post-LPG immigration) should be tested with additional genetic data.

Potential tree distributions

Paleoclimate model simulations have been used to gain insights into the potential vegetation at the Last Glacial Maximum (LGM; 21 ka). One approach is to combine simulations from global climate models (GCMs) with estimates of climatic requirements of trees to derive potential LGM distributions [35,36], or use species-distribution modeling to estimate the climate niches of trees, which are then projected onto GCM simulations to generate potential LGM distributions [37]. Another approach involves dynamic vegetation models, incorporating physiological and biogeochemical processes, which use the GCM output to generate potential vegetation [38] or primary productivity [39]. The LGM reconstructions show boreal species present in southern regions and also in Central and Eastern Europe, whereas temperate trees were largely restricted to southern Europe, but extended north of 45°N in Eastern Europe. However, low net primary productivity values suggest that tree populations were spatially restricted to sites with favorable microclimatic conditions [39].

Although these approaches provide rigorous reconstructions of potential vegetation, they also come with their own set of limitations: (i) the physiological effects of low CO₂ concentrations, leading to lower photosynthetic rates and reduced water-use efficiency of plants [40], have not been incorporated in some studies [35–37]; and (ii) a long-known feature of LGM climate simulations is that they underestimate the degree of cooling. Comparison with reconstructed temperatures from stable isotopes in ice-cores [41] and borehole measurements [42] show that models reproduce only approximately half the magnitude of LGM Greenland cooling [43]. This warm-bias could arise from not incorporating the effects of aerosol loading in the atmosphere [41] or the use of pre-industrial conditions at the start of model runs [43]. Moreover, the GCM experiments are equilibrium ‘snapshot’ runs of a few hundred years, representing the response of the climate system to instantaneous forcings. Incorporating the long-term effects of forcings over transient 100-kyr simulations might reproduce the magnitude of cooling, as suggested by recent experiments [44]. Although the underestimation of the temperature anomalies in LGM snapshot simulations is probably larger at high latitudes compared with mid-latitudes, the implication of the warm-bias is that the reconstructed vegetation would still overestimate European tree distribution and abundance.

Temporal trends and spatial patterns

Examination of MPG and LPG pollen and plant macrofossil records reveals a long-term decline in tree populations, superimposed on millennial-scale oscillations; an important threshold appears to have been crossed at the time of Heinrich Stadial [HS] 2 (24 ka) when tree populations crashed and never quite recovered until the end of HS1 (approximately 15 ka) (see Figure 1 in Box 2). Summer insolation reached a minimum at 24 ka, curtailing the amount of accumulated growing-season warmth. Water stresses on plants were exacerbated by minimum CO₂ concentrations and by the presence of permafrost. Boreal tree species can grow on continuous permafrost today, but soil texture, depth of the active layer, and timing of the spring–summer thaw determine the amount of water available for the growing season and influence species distributions [45]. Mapping of LGM permafrost distribution based on periglacial evidence [46] places the southern limit of continuous permafrost at 47°N and of discontinuous permafrost at 45–44°N. Taken together, conditions during the LPG would have exerted significant water stresses on trees and limited their growth to sites where moisture was available. Thus, in contrast to previous proposals of extensive taiga woodland in Central and Eastern Europe [4,6], we envisage a restricted distribution of boreal trees to favorable microhabitats within the area of continuous permafrost. Temperate trees would be confined to areas south of discontinuous permafrost, in agreement with the pollen and macrofossil data. The paleobotanical evidence also points to a W–E asymmetry in tree distribution, with a treeless Western Europe north of 46°N and an Eastern Europe with small boreal tree populations persisting up to approximately 49°N in the Carpathians and higher latitudes east of the ice-sheet. The distribution of mountainous regions providing microhabitats can, to some extent, account for this asymmetry, but not for refugial presence on the East European Plain (Figure 1). An additional explanation is provided by climate simulations, which show lower summer temperatures in Western Europe, arising from the proximity to a cold ocean, compared with continental Eastern Europe [36,38]. Despite warm-bias issues, this W–E temperature gradient is a robust model feature and suggests a greater amount of growing-season warmth in Eastern Europe, which would have also led to increased permafrost thaw and water availability.

It is important to note that the European situation might be different from that of Eastern North America, where the presence of boreal and also temperate species in close proximity to the ice-sheet has been proposed [47]. Compared with the southern limit of the Fennoscandian ice-sheet (approximately 53°N), the Laurentide ice-sheet penetrated to such lower latitudes (approximately 40°N) that temperature gradients were steeper and conditions warmer relative to those near the European ice-sheet margin [48].

Wider implications and future work

The absence of LPG refugia of temperate trees north of 45°N and of extensive taiga forests in northern Europe implies that: (i) present-day populations of temperate

trees in northern Europe are essentially young in age and, thus, are unlikely to present novel allelic variation; (ii) long-term maintenance of temperate tree species in Europe depends on the persistence of southern populations; (iii) calls to reduce original estimates of postglacial migration rates of temperate trees by an order of magnitude are premature. Thus, average migration rates of 200–500 m yr⁻¹ [2] for most temperate taxa continue to appear robust. This might give cause for guarded optimism in relation to projected velocities of temperature change [49], although migration potential may not translate to actual future rates, given habitat fragmentation and degradation or lack of past dispersal agents (e.g., megaherbivores). Finally, from a paleoclimate perspective, the overall scarcity of tree cover in northern Europe has implications for model simulations, because of the significant difference between tundra and forest land-surface albedo feedbacks (e.g., [49]).

On balance, the northern refugia concept has been very useful in cementing a consensus over the presence of boreal tree populations in Eastern Europe. However, it is worth remembering that the original formulation of this hypothesis referred to temperate rather than boreal species [5] and that inclusion of species such as *Pinus sylvestris* ‘...was already stretching the definition of a cryptic northern refugium’ ([50] p. 664). This highlights that the pursuit of these topics is not best served by the polarization of refugia into northern and southern. A more productive approach is to ask: (i) what was the spatial structure of the northern parts of a species LPG range; (ii) what are the postglacial colonization dynamics from this; and (iii) what are the genetic consequences. Combined paleobotanical and genetic studies are needed, with both strands providing independent and secure evidence, such as direct dates on macrofossils, well-dated LPG pollen records, and geographically comprehensive genetic sampling with phylogenetically informative genetic markers.

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Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2013.09.001>.

References

- 1 van der Hammen, T. *et al.* (1971) The floral record of the late Cenozoic of Europe. In *The Late Cenozoic Glacial Ages* (Turekian, K.K., ed.), pp. 391–424, Yale University Press
- 2 Huntley, B. and Birks, H.J.B. (1983) *An Atlas of Past and Present Pollen Maps for Europe: 0–13,000 Years Ago*, Cambridge University Press
- 3 Bennett, K.D. *et al.* (1991) Quaternary refugia of north European trees. *J. Biogeogr.* 18, 103–115
- 4 Willis, K.J. *et al.* (2000) The Full-Glacial forests of central and southeastern Europe. *Quat. Res.* 53, 203–213
- 5 Stewart, J.R. and Lister, A.M. (2001) Cryptic northern refugia and the origins of the modern biota. *Trends Ecol. Evol.* 16, 608–613

- 6 Willis, K.J. and van Andel, T.H. (2004) Tree or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* 23, 2369–2387
- 7 Birks, H.J.B. and Willis, K.J. (2008) Alpines, trees, and refugia in Europe. *Plant Ecol. Divers.* 1, 147–160
- 8 Bhagwat, S.A. and Willis, K.J. (2008) Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *J. Biogeogr.* 35, 464–482
- 9 Pearson, R.G. (2006) Climate change and the migration capacity of species. *Trends Ecol. Evol.* 21, 111–113
- 10 Damblon, F. and Haesaerts, P. (2002) Anthracology and radiocarbon chronology of the Upper Pleistocene in the loessic areas of Eurasia. In *Charcoal Analyses. Methodological Approaches, Palaeoecological Results and Wood Uses. Proceedings of the Second International Meeting of Anthracology, Paris 2000* (Thiébaud, S., ed.), pp. 65–71. *BAR Int. Ser.* 1063
- 11 Haesaerts, P. *et al.* (2010) Charcoal and wood remains for radiocarbon dating Upper Pleistocene loess sequences in Eastern Europe and Central Siberia. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 291, 106–127
- 12 Damblon, F. *et al.* (2011) Les analyses anthracologiques dans la séquence de la grotte Walou. In *La grotte Walou à Trooz (Belgique), Fouilles de 1996 à 2004* (Vol. 2) (Drailly, C., ed.), pp. 132–145. *Les Sciences de la vie et les Datations*
- 13 Kaiser, K.F. *et al.* (2012) Challenging process to make the Late glacial tree-ring chronologies from Europe absolute: an inventory. *Quat. Sci. Rev.* 36, 78–90
- 14 Velichko, A.A. *et al.* (2001) Late Quaternary palaeogeography of the North-East of Europe (based on the complex study of the Galich Lake sediments). *Izv. Akad. Nauk SSR Ser. Geogr.* 3, 42–54 (in Russian)
- 15 Di Domenico, F. *et al.* (2012) *Buxus* in Europe: Late Quaternary dynamics and modern vulnerability. *Perspect. Plant Ecol. Evol. Syst.* 14, 354–362
- 16 Heikkilä, M. *et al.* (2009) Rapid Late glacial tree population dynamics and ecosystem changes in the eastern Baltic region. *J. Quat. Sci.* 24, 802–815
- 17 Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* 58, 247–276
- 18 Provan, J. and Bennett, K.D. (2008) Phylogeographic insights into cryptic glacial refugia. *Trends Ecol. Evol.* 23, 564–571
- 19 Emerson, B.C. and Hewitt, G.M. (2005) Phylogeography. *Curr. Biol.* 15, R367–R371
- 20 Hewitt, G.M. and Nichols, R.A. (2005) Genetic and evolutionary impacts of climate change. In *Climate Change and Biodiversity* (Lovejoy, T.E. and Hannah, L.L., eds), pp. 176–192. Yale University Press
- 21 Emerson, B.C. *et al.* (2006) Testing phylogeographic predictions on an active volcanic island: *Brachyderes rugatus* (Coleoptera: Curculionidae) on La Palma (Canary Islands). *Mol. Ecol.* 15, 449–458
- 22 Miraldo, A. *et al.* (2011) Phylogeography and demographic history of *Lacerta lepida* in the Iberian Peninsula: multiple refugia, range expansions and secondary contact zones. *BMC Evol. Biol.* 11, 170
- 23 Hewitt, G.M. (2011) Mediterranean peninsulas: the evolution of hotspots. In *Biodiversity Hotspots* (Zachos, F.E. and Habel, J.C., eds), pp. 123–147. Springer-Verlag
- 24 Petit, R.J. *et al.* (2002) Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *For. Ecol. Manage.* 156, 49–74
- 25 Maliouchenko, O. *et al.* (2007) Comparative phylogeography and population structure of European *Betula* species, with particular focus on *B. pendula* and *B. pubescens*. *J. Biogeogr.* 34, 1601–1610
- 26 Tollefsrud, M.M. *et al.* (2008) Genetic consequences of glacial survival and postglacial colonization in Norway spruce: combined analysis of mitochondrial DNA and fossil pollen. *Mol. Ecol.* 17, 4134–4150
- 27 Brito, P. and Edwards, S.V. (2009) Multilocus phylogeography and phylogenetics using sequence-based markers. *Genetica* 135, 439–455
- 28 Thomson, R.C. *et al.* (2010) Genome-enabled development of DNA markers for ecology, evolution and conservation. *Mol. Ecol.* 19, 2184–2195
- 29 Magri, D. *et al.* (2006) A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.* 171, 199–221
- 30 Hofreiter, M. *et al.* (2012) Ancient biomolecules in Quaternary palaeoecology. *Quat. Sci. Rev.* 33, 1–13
- 31 Parducci, L. *et al.* (2012) Glacial survival of boreal trees in northern Scandinavia. *Science* 335, 1083–1086
- 32 Birks, H.H. *et al.* (2012) Comment on ‘Glacial survival of boreal trees in northern Scandinavia’. *Science* 338, 742
- 33 Vorren, T.O. *et al.* (2013) Palaeoenvironment in northern Norway between 22.2 and 14.5 cal. ka BP. *Boreas* 42, 876–895
- 34 King, R.A. and Ferris, C. (1998) Chloroplast DNA phylogeography of *Alnus glutinosa* (L.) Gaertn. *Mol. Ecol.* 7, 1151–1161
- 35 Leroy, S.A.G. and Arpe, K. (2007) Glacial refugia for summer-green trees in Europe and south-west Asia as proposed by ECHAM3 time-slice atmospheric model simulations. *J. Biogeogr.* 34, 2115–2128
- 36 Arpe, K. *et al.* (2011) A comparison of climate simulations for the last glacial maximum with three different versions of the ECHAM model and implications for summer-green tree refugia. *Clim. Past* 7, 91–114
- 37 Svenning, J.-C. *et al.* (2008) Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *J. Ecol.* 96, 1117–1127
- 38 Strandberg, G. *et al.* (2011) High-resolution regional simulation of last glacial maximum climate in Europe. *Tellus* 63A, 107–125
- 39 Allen, J.R.M. *et al.* (2010) Last glacial vegetation of northern Eurasia. *Quat. Sci. Rev.* 29, 2604–2618
- 40 Cowling, S.A. and Sykes, M.T. (1999) Physiological significance of low atmospheric CO₂ for plant-climate interactions. *Quat. Res.* 52, 237–242
- 41 Masson-Delmotte, V. *et al.* (2006) Past temperature reconstructions from deep ice cores: relevance for future climate change. *Clim. Past* 2, 145–165
- 42 Dahl-Jensen, D. *et al.* (1998) Past temperatures directly from the Greenland ice sheet. *Science* 282, 268–271
- 43 Singarayer, J.S. and Valdes, P.J. (2010) High-latitude climate sensitivity to ice-sheet forcing over the last 120 kyr. *Quat. Sci. Rev.* 29, 43–55
- 44 Smith, R.S. and Gregory, J. (2012) The last glacial cycle: transient simulations with an AOGCM. *Clim. Dyn.* 8, 1545–1559
- 45 Utkin, I.A. (1965) *Forests of Central Yakutia*, Nauka (in Russian)
- 46 Vandenberghe, J. *et al.* (2012) Eurasian permafrost instability constrained by reduced sea-ice cover. *Quat. Sci. Rev.* 34, 16–23
- 47 McLachlan, J.S. *et al.* (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86, 2088–2098
- 48 O’ishi, R. and Abe-Ouchi, A. (2013) Influence of dynamic vegetation on climate change and terrestrial carbon storage in the Last Glacial Maximum. *Clim. Past* 9, 1571–1587
- 49 Loarie, S.R. *et al.* (2009) The velocity of climate change. *Nature* 462, 1052–1055
- 50 Stewart, J.R. *et al.* (2010) Refugia revisited: individualistic responses of species in space and time. *Proc. R. Soc. B* 277, 661–671
- 51 Nekola, J.C. (1999) Paleorefugia and neorefugia: the influence of colonization history on community pattern and process. *Ecology* 80, 2459–2473
- 52 Rull, V. (2009) Microrefugia. *J. Biogeogr.* 36, 481–484
- 53 Holderegger, R. and Thiel-Egenter, C. (2009) A discussion of different types of glacial refugia used in mountain biogeography and phylogeography. *J. Biogeogr.* 36, 476–480
- 54 Médail, F. and Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *J. Biogeogr.* 36, 1333–1345
- 55 Tzedakis, P.C. (1993) Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature* 364, 437–440
- 56 Tzedakis, P.C. (2009) Museums and cradles of Mediterranean biodiversity. *J. Biogeogr.* 36, 1033–1034
- 57 Bennett, K.D. and Provan, J. (2008) What do we mean by refugia? *Quat. Sci. Rev.* 27, 2449–2455
- 58 Siddall, M. *et al.* (2003) Sea-level fluctuations during the last glacial cycle. *Nature* 423, 853–858
- 59 Thompson, W.G. and Goldstein, S.L. (2006) A radiometric calibration of the SPECMAP timescale. *Quat. Sci. Rev.* 25, 3207–3215
- 60 Tzedakis, P.C. *et al.* (2007) Placing late Neanderthals in a climatic context. *Nature* 449, 206–208
- 61 Mix, A. *et al.* (2001) Environmental processes of the ice age: land, oceans, glaciers (EPILOG). *Quat. Sci. Rev.* 20, 627–657
- 62 Lambeck, K. and Chappell, J. (2001) Sea level change through the last glacial cycle. *Science* 292, 679–686

- 63 Lüthi, D. *et al.* (2008) High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* 453, 379–382
- 64 Genty, D. *et al.* (2005) Apport des stalagmites pour l'étude de la grotte Chauvet: datations absolue U/Th (TIMS) et reconstitution paleoclimatique par les isotopes stable de la calcite. *Bull. Soc. Préhist. Fr.* 102, 45–62
- 65 Berger, A. (1978) Long-term variations of caloric insolation resulting from the earth's orbital elements. *Quat. Res.* 9, 139–167
- 66 Barker, S. *et al.* (2011) 800,000 years of abrupt climate variability. *Science* 334, 347–351
- 67 de Beaulieu, J.-L. and Reille, M. (1992) The last climatic cycle at La Grande Pile (Vosges, France) a new pollen profile. *Quat. Sci. Rev.* 11, 431–438
- 68 Tzedakis, P.C. *et al.* (2002) Buffered vegetation changes in a Quaternary refugium: evolutionary implications. *Science* 297, 2044–2047
- 69 Ehlers, J. and Gibbard, P.L., eds (2004) *Quaternary Glaciations—Extent and Chronology, Part I: Europe*, Elsevier
- 70 Clark, C.D. *et al.* (2012) Pattern and timing of retreat of the last British–Irish Ice Sheet. *Quat. Sci. Rev.* 44, 112–146