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Trees or no trees? The environments of central and eastern Europe during the Last Glaciation

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Abstract

The location and survival of trees in the coldest stages of the last full-glacial has long been of interest to palaeoecologists, biogeographers, archaeologists and geneticists alike. In particular, where species survived in isolated refugia and the influence that this has had upon the long-term ancestry of the populations, remain key research questions. However, the exact location of refugia during the coldest stages of the full-glacial still remains illusive for many species of fauna and flora, with different lines of evidence often being at odds. This is particularly true for Europe. Emerging evidence from various fossil proxies, palaeoclimatic modelling and genetic research is starting to suggest that the traditional paradigm that trees were restricted to southern Europe and in particular the three southern peninsulas (Balkan, Italian and Iberian) during the full-glacial is questionable. This is backed by increasing evidence, including 151 ^{14}C-dated and identified pieces of macrofossil charcoal wood from 40 localities in central and eastern Europe to indicate that during the last full-glacial populations of coniferous and some deciduous trees grew much further north and east than previously assumed. This paper reviews the fossil evidence and considers it alongside genetic and palaeoclimatic evidence in order to contribute towards a newly emerging synthesis of the full-glacial refugial localities in Europe and their influence upon the ancestry of European species. Plotted against a new high-resolution millennial time-scale for the interval ~32–~16 ka BP in Greenland our evidence shows that coniferous as well as some broadleaf trees were continuously present throughout those interstadial/stadial cycles for which there are adequate data.

1. Introduction

Ever since it was first suggested that during the coldest periods of the last full-glacial (~37–16 ka BP), the most probable location for cold-stage refugia of temperate tree taxa was in southern Europe (Frenzel and Troll, 1952), many researchers have looked to these locations for evidence of refugial populations (e.g. Huntley and Birks, 1983; Bennett et al., 1991; Willis, 1992; Tzedakis, 1993; Willis, 1994; Follieri et al., 1998; Carrión, 2002; Tzedakis et al., 2002). The theory that southern Europe and the Near East provided conditions suitable for refugia of temperate tree taxa is based on a number of assumptions relating to the full-glacial environments of those regions and their ability to supply the necessary conditions for growth. Those included an ice-free and in most places permafrost-free terrain, a soil able to support woody vegetation, and a climate with extremes that did not exceed the physiological capabilities of the tree taxa. There was plenty of evidence to support such a model given little or no geomorphological evidence for permafrost below 45°N (Washburn, 1979) and palaeoclimatic modelling (COHMAP, 1988; Wright et al., 1993) indicating that a steep climatic gradient existed across southern Europe at 21 ka BP).[1] This modelling

[1]The notation ka BP stands for calendar dates (ice-core, U–Th, TL, OSL and ESR) and calibrated ^{14}C dates in millennia (cal ka) before present (BP). Where appropriate ^{14}C years are appended in brackets (xx ± xxx ^{14}C yr b.p.) to specific dates. Calibration with CalPal (Jöris and Weninger, 2000) available from the CalPal website; http://www.calpal.de.

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therefore predicted that in the southern peninsulas of Europe January temperatures would have been no less than 0 °C and precipitation 2–4 mm/day (Wright et al., 1993), well within the physiological extremes of most European temperate tree taxa (Kienast, 1987; Prentice and Helmisaari, 1991; Nikolov and Helmisaari, 1992; Larcher, 1995).

Although the original refugial model implied that 'forests' could have survived in southerly locations during the cold stages of the Quaternary, extensive populations of trees have never been detected. Instead, palaeoecological sequences from the Near East and the three southern peninsulas of Europe (Balkan, Italian and Iberian) indicate that temperate tree taxa possibly survived in small pockets at microenvironmentally favourable locations with usually only a few tree taxa detected in low concentrations in any one place. Aridity was probably a significant limiting factor for tree growth, a fact supported by evidence for an increased presence of trees in mid-to-high altitude sites during the full and Lateglacial where there would have been more orographical precipitation (e.g. Wohlfarth et al., 2001; Carrión, 2002; Björkman et al., 2003; Wick et al., 2003). In many of the lowland regions, however, trees also survived and a number of pollen sequences extending back through multiple glacial–interglacial cycles show a small but persistent presence of mesophilous and thermophilous tree pollen throughout the cold stages. This full-glacial vegetation has commonly been described as 'open parkland' (van Andel and Tzedakis, 1996, 1998; Tzedakis et al., 1997; Follieri et al., 1998; Tzedakis et al., 2002; Davies et al., 2003).

The idea that southern Europe and the Near East provided full-glacial refugia for flora (and associated fauna) is now well established in the literature and constitutes an important biogeographical basis for a number of molecular phylogenetic studies into the ancestry of populations (e.g. Hewitt, 2000, 2004; Willis and Whittaker, 2000; Petit et al., 2003; Kadereit et al., 2004; Lascoux et al., 2004). The isolationary aspect of refugia is of particular interest because it provides a mechanism for allopatric speciation whereby the genetic differences apparent in present-day populations are attributed to cold-stage refugial isolation (e.g. Taberlet and Bouvet, 1994; Konnert and Bergmann, 1995; Demesure et al., 1996). It is this isolationary aspect of the refugia model however, that now appears to be coming under closer scrutiny (Petit et al., 2003; Lascoux et al., 2004; Willis and Niklas, 2004).

A key assumption associated with the southern European refugia model is that further north and east into central Europe the palaeolandscape was tree-less. The tree populations in southern refugia were therefore 'isolated' for long intervals and it was during these periods of isolation that genetic differences became established between them. The suggestion that central and eastern Europe remained tree-less during the full-glacial is based primarily on the assumption that the greater environmental extremes in these regions, would have restricted tree growth severely.

No long palaeoecological sequences from central and eastern Europe (east of 10°E) exist to support this interpretation. Instead, there is increasing evidence from macrofossil charcoal records that the interpretation of a tree-less full-glacial central and eastern European landscape may not be correct. In addition, new palaeoclimatic simulations of the Stage 3 Project suggest that full-glacial conditions in central and eastern Europe were not nearly as severe as previously anticipated (Barron and Pollard, 2002; Barron et al., 2003; Pollard and Barron, 2003).

Pollen-based "tree-less tundra" models for Europe north of the transverse mountain ranges of the Pyrenees, Alps and Carpathians (e.g. Frenzel, 1992; Alfano et al., 2003; Huntley et al., 2003) have repeatedly been questioned by researchers of the Late Pleistocene Mammalian fauna such as Guthrie (1990, 2000), Guthrie and van Kolfschoten (1999), Lister and Sher (1995), Yurtsev (2001) and Stewart and Lister (2002), because the carrying capacity adequate to feed numerous large herbivores such as mammoth, woolly rhinoceros, reindeer, giant deer, bison or auerochs demands a very productive environment (named "steppe-tundra" or "mammoth steppe" by Guthrie, 1990). This is not the place to go deeply into this issue, but the arguments, generally dismissed or ignored by palynologists, have gained considerable strength from the mammalian evidence contained in the environmentally oriented Mammalian database of the Stage 3 Project (Stewart et al., 2003) and from hitherto rather neglected central and eastern European data compiled by Musil (2003). The large number of Upper Palaeolithic sites spread across much of central and eastern Europe north of the mountain barrier (Musil, 2003; van Andel et al., 2003) bears witness that animal resources were plentiful.

This paper sets out to review the macrofossil charcoal evidence alongside other fossil evidence in the context of our current understanding of the climates and climate changes of the time, and to consider all in the light of the traditional 'southern European refugial model'. We shall do this in four ways. First, we review published macrofossil charcoal evidence for full-glacial trees from 40 localities (in 7 countries) that are north and east of the traditional 'southern refugia' localities. Second, we examine other lines of fossil evidence that appears to support this macrofossil charcoal evidence. Third, we review recent palaeoclimatic modelling for central and eastern Europe and consider whether tree growth was possible under those climatic conditions. Finally, we briefly consider the macrofossil charcoal evidence alongside recent genetic evidence to address the question whether a new interpretation of the full and Lateglacial environments for central and eastern Europe is needed.

2. Trees or no trees: the macrofossil charcoal evidence

Macrofossil charcoal is a term used to describe organic plant material (fragments >2 mm diameter) preserved in the fossil record through the process of burning and charcoalification (Schweingruber, 1978, 1990). It is a particularly useful record for the identification of fossil wood because the level of preservation is often good enough to examine the transverse and longitudinal ring structures and thus identify the tree to genus (and in some cases species) level.

Traditionally, macrofossil charcoal analysis has been a tool used by archaeologists for the identification of charcoal from occupation layers for ^{14}C dating and to understand the use of local materials in subsistence. ^{14}C dating of charcoal is often suggested as the most reliable material for dating from archaeological sites because of its high inert carbon content and the least risk of chemical contamination (Damblon and Haesaerts, 1997). Surprisingly, however, it has rarely been used in a comprehensive way for palaeoenvironmental reconstructions although there are notable exceptions (e.g. Badal et al., 1994; Damblon, 1997; Hansen, 2001; Rudner and Sümegi, 2001; Damblon and Haesaerts, 2002; Figueiral and Terral, 2002; Ntinou, 2002). One reason for the apparent lack of use of this technique in mainstream palaeoenvironmental research is that it does not provide a continuous stratigraphic sequence (unlike, e.g. pollen analysis from lake sediments). Rather, it represents a 'snapshot' of the vegetation in and around the site during the time of occupation. In environments where continuous sequences of lake sediments are available, macrofossil charcoal analysis is therefore not the first choice of technique. There are also concerns over lack of stratigraphic control, possible downward movement through the sequence, or introduction from elsewhere. However, there are many sites now where stratigraphic control is paramount to the research and numerous pieces of charcoal have been identified and dated from clearly defined stratigraphic horizons.

As to the suggestion that the material may have been brought into the archaeological site from elsewhere, it is obvious that this is often true for some of it. The question that really needs to be addressed, however, is how far woody material will be carried/dragged by humans and/or other transportation agents? Research into the transportation of woody material for burning on hearths suggests that in almost all cases it is probably from a radius of no more than 2 hours walking (<10 km) from the site (Vita-Finzi and Higgs, 1970; Bailey, 1997; Hansen, 2001; Bailey, 2004). Finding macrofossil charcoal at an occupation site, therefore, may not prove that it was growing in immediate proximity to the site, but it can be assumed that it was growing somewhere in the region and that dating this charcoal gives an age for its presence. In some sites, however, the evidence for local growth is compelling since silhouettes of tree trunks plus roots marked out in charcoal have been discovered (Willis et al., 2000) that indicate in situ growth and burning.

To counter some of the above concerns regarding macrofossil charcoal evidence only samples from sites with good temporal and stratigraphic control have been included in this review. These sites should have clearly identifiable and well-dated occupation horizons with ^{14}C dates based on identified pieces of charcoal. Ideally the site should also have material cross-dated from more than one laboratory.

In order to examine the coldest periods of the last glaciation but within the confines of reliable radiocarbon dating, this review includes published sites in central and eastern Europe that contained macrofossil charcoal evidence for woody plant species dated between ~42 and 19 ka BP (see footnote 1). Countries included in the review are Austria, Czech Republic, Croatia, Hungary, Moldova, Poland, and Romania (Fig. 1)—all regions traditionally described as being beyond the full-glacial refugial localities for tree taxa. Therefore, they provide an interesting west–east transect in which to examine the distribution of woody vegetation during the last full-glacial. The macrofossil charcoal evidence from each region will be briefly described.

2.1. Austria

Macrofossil charcoal assemblages from two Upper Palaeolithic sites in Austria have been included in this review (Table 1) namely Willendorf II and Schwallenbach (Haesaerts et al., 1996; Damblon, 1997; Damblon and Haesaerts, 1997). Both sites are situated on the banks of the Danube (Fig. 1) and have well-defined occupation layers contained within loess sequences. Willendorf was occupied between 44 and 26 ka BP (42,000–23,000 ^{14}C yr b.p.) and Schwallenbach between 43 and 35 ka BP (40,000–29,500 ^{14}C yr b.p.).

In Willendorf, six main occupation layers have been identified with 25 ^{14}C dates on macrofossil charcoal wood ranging between 44 and 26 ka BP (42,000–23,000 ^{14}C yr b.p.: Table 1) (Haesaerts et al., 1996; Damblon and Haesaerts, 1997). Species identified are predominantly needle-leaved (*Pinus cembra, Pinus*, *Picea-Larix*) although there are also several deciduous taxa including *Betula* and *Salix*. The presence of tree species in all six occupation layers leads the authors to conclude that they were an important element of the full-glacial palaeolandscape in this region (Haesaerts et al., 1996; Damblon, 1997).

The site of Schwallenbach is also located on the Danube, approximately 1 km upstream from Willendorf

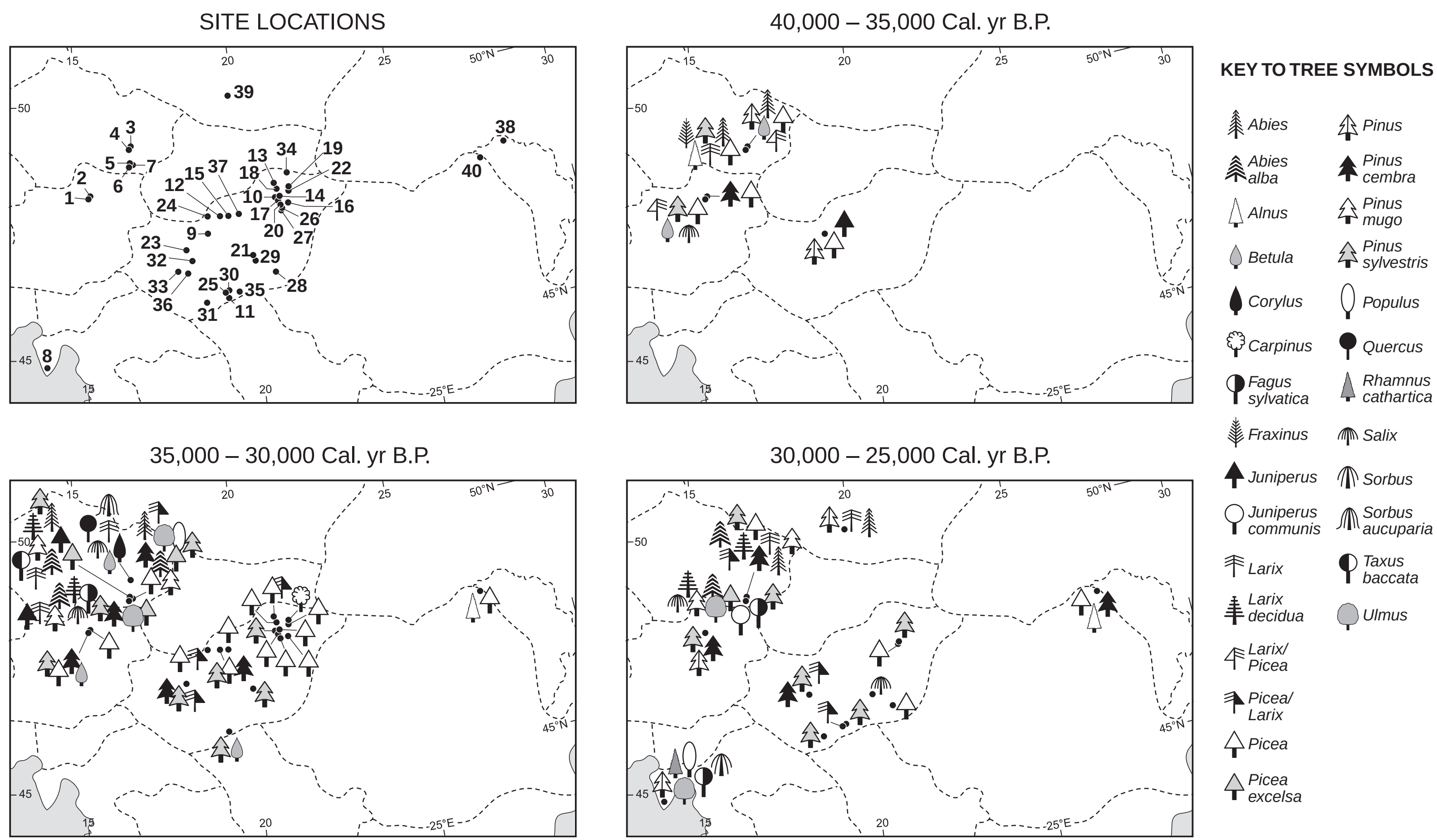

Fig. 1. Location of the 40 full-glacial macrofossil charcoal sites plus the tree species/genera identified at each site for the time intervals 40,000–35,000, 35,000–30,000 and 30,000–25,000 ka BP (full citation to sites is given in text and Tables 1–7). Numbers correspond to site names that are detailed in Tables 1–7.

Table 1
Identification of tree species/genera in macrofossil charcoal layers from sites in Austria and ^{14}C dates (based on the identified macrofossil charcoal wood within these layers)

Site number (with reference to Figs. 1 and 2): Site location: longitude (E)/latitude (N) Site name	Site type containing macrofossil charcoal layers[a]	Tree species/genera identified in macrofossil charcoal layers	Published ^{14}C dates (uncalibrated yr b.p.)[a]	Lab. code	Cal yr BP	References to source of data
(1) 15°24′/48°19′ Willendorf II	Occupation layers situated upon loess	*Pinus cembra* type, *Pinus* sp., *Picea* sp.	23,200±140 23,400±190 23,670±120	GrA-893 GrA-493 GrA-494	26,270±210 26,400±220 26,580±210	Haesaerts et al. (1996), Damblon and Haesaerts (1997), Damblon (1997)
		Pinus cembra type, *Pinus sylvestris*, *Picea* sp.	24,710±180 25,230±320 25,660±350 25,400±170 25,400±170 25,800±800	GrA-894 GrN-17801 GrN-17802 GrN-21690 GrN-20767 GrN-11191	28,010±780 28,710±1000 29,290±960 28,970± 910 28,970±910 29,230±1330	
		Pinus cembra type, *Picea* sp.	23,830±200 23,990±130	GrA-491 GrA-492	26,720±270 26,840±280	
		Pinus cembra, *Pinus sylvestris*, *Picea* sp.	26,500±480 26,150±110	GrN-20768 GrA-1016	30,440±640 30,300±450	
		Pinus sylvestris, *Pinus cembra*, *Picea* sp.	28,560±520	GrN-17804	32,550±700	
		Betula sp., *Pinus sylvestris*, *Picea* sp.	30,500±900 32,000±3000	GrN-11193 H-246/231	34,460±1000 36,270±3250	
		Pinus sylvestris, *Picea* sp.; *Betula* sp.	31,210±260 31,700±1800 32,060±250	GrA-501 H-249/1276 GrN-1273	35,060±520 36,320±2280 36,610±1400	
		Picea sp., *Salix* sp.	37,930±750 38,800±1530	GrA-896 GrN-17805	41,710±280 42,120±670	
		Picea sp., *Picea-Larix*	39,500±1500 41,600±4000	GrN-11190 GrN-17806	42,510±740 44,360±2900	
		Picea-Larix	>36,000 41,700±3700	GrN-17807 GrN-11195	— 44,360±2900	
(2) 15°24′/48°19′ Schwallenbach	Occupation layers situated upon loess	*Picea* sp.	29,530±800	GrA-5219	33,300± 890	Haesaerts et al. (1996)
		Picea sp.	31,680±290	GrA-6899	35,410±570	
		Picea sp.	39,000±2600	GrA-5221	41,780±2110	
		Picea sp.	37,400±2600	GrA-5222	39,840±2500	
		Pinus cembra, *Picea* sp.	39,920±1300	GrN-21801	42,660±690	

[a]Spaces between dates indicate different occupation layers.

II (Damblon, 1997). Here seven occupation layers have been identified in the loess sequence with dates ranging between 43 and 33 ka BP (~40,000–29,000 ^{14}C yr b.p.; Table 1). Of the five ^{14}C dates obtained on macrofossil charcoal from this site all were based on charcoal remains of *Picea* and *P. cembra,* providing further evidence for the regional presence of these coniferous trees during the coldest stages of the last full-glacial.

2.2. Czech Republic

In the Czech Republic at least four Upper Palaeolithic sites that contain well-dated macrofossil charcoal

Table 2
Identification of tree species/genera in macrofossil charcoal layers from sites in the Czech Republic and ^{14}C dates (based on identified macrofossil charcoal wood within these layers)

(3) 16°40′/49°11′ Stránska skàlà	Occupation layers situated upon loess	*Pinus* sp. cf. *Pinus*, *Abies* sp. cf. *Abies*, *Picea* sp.	41,300±3100 38,500±1400 38,200±1100	GrN-12606 GrN-12298 GrN-12297	44,160±2150 41,940±570 41,810±410	Svoboda and Svoboda (1985)
		cf. *Picea*, *Betula* sp., *Salix*, *Larix*, *Picea–Larix*, *Pinus* cf. *sylvestris*, *Pinus* sp. *Picea* sp., *Sorbus aucuparia*, *Corylus* sp., *Quercus* sp.	30,980±360 32,350±900 32,600±1700	GrN-12605 GrN-14829 GrN-16918	34,910±570 36,810±1590 37,250±2260	Musil (2003); Damblon et al. (1996)
(4) 16°35′/49°10′ Bohunice	Occupation layer situated upon loess	*Abies* sp., *Picea* sp., *Larix* sp., *Pinus sylvestris*, cf. *Alnus* sp., *Fraxinus* sp.	36,000±1100 40,173±1200 41,400±1400 42,900±700	GrN-16920 Q-1044 GrN-6802 GrN-6165	39,910±1350 42,750±680 43,550±1010 44,290±800	Svoboda and Svoboda (1985); Damblon et al. (1996); Musil (2003)
(5) 16°38′/48°53′ Dolní Věstonice II	Occupation layers situated upon loess	*Larix* sp., *Juniperus* sp., *Taxus baccata*	26,390±270	ISGS-1744	30,510±450	Mason et al. (1994)
		Abies alba, *Abies* sp., *Larix decidua*, cf. *Larix* sp., *Picea excelsa*, cf. *Picea* sp., *Picea-Larix*, *Pinus sylvestris*, *Pinus cembra*, *Pinus mugo*	24,470±190 28,220±370 29,940±300 27,600±80 25,570±280 25,740±210 26,390±270 26,640±110 26,920±250 27,070±300 26,550±160 26,970±160 27,070±170 27,080±170 27,900±550 26,970±200 26,390±190 26,100±100 24,560±640	GrN11003 GrN-11196 GrN-10525 GrN-13962 GrN-15276 GrN-15277 ISGS-1744 GrN-14831 GrN-15279 GrN-15278 GrN-15325 GrN-15326 GrN-15324 GrN-15327 GrN-15280 GrN-21122 GrN-21123 GrN-14830 GrN-20392	27,710±730 32,260±590 33,830±420 31,590±310 29,200±930 29,600±710 30,510±450 30,800±310 30,980±330 31,100±340 30,720±340 31,040±290 31,110±280 31,120±280 32,050±670 31,030±300 30,560±400 30,230±470 28,110±1110	Opravil (1994); Damblon et al. (1996); Damblon (1997)
(6) 16°38′/48°52′, Dolni Vestonice I	Occupation layers situated upon loess	*Abies alba*, *Larix decidua*, *Picea excelsa*, *Pinus sylvestris*, *Pinus cembra*, *Pinus mugo*, *Salix* sp., *Ulmus* sp., *Juniperus communis*, *Fagus sylvatica*	25,790±320 25,820±170 26,430±190 20,270±210 27,790±370 29,180±460 31,700±1000 32,850±660 25,950±600	GrN-6857 GrN-1286 GrN-10524 GrN-11004 GrN-6859 GrN-6860 GrN-11189 GrN-6858 GrN-18189	29,580±830 29,780±630 30,600±380 23,820±380 31,880±530 33,030±680 36,310±1710 37,340±1280 29,510±1130	Opravil (1994); Damblon et al. (1996); Damblon (1997); Slaviková-Veslá (1950)
(7) 16°40′/48°52′ Pavlov I	Occupation layer situated upon loess	*Abies alba*, cf. *Abies* sp., *Picea excelsa*, cf. *Picea* sp., *Picea-Larix*, *Pinus sylvestris*, *Pinus cembra*, *Pinus mugo*, *Pinus* sp., cf. *Pinus* sp., *Ulmus* sp., *Populus* sp.	26,000±350 26,650±230 26,170±170 26,580±460 30,010±460	GIN-104 GrN-19539 GrN-20391 KN-1286 KN-286	29,880±760 30,780±360 30,300±480 30,570±570 33,880±550	Opravil (1994); Damblon et al. (1996); Damblon (1997)

[a]Spaces between dates indicate different occupation layers.

assemblages indicating a full-glacial presence of trees (Table 2). The most extensive record is from Dolní Věstonice I, and II (Fig. 1), a cluster of adjacent sites that were settled between ~33 and 28 ka BP (~29,000–24,500 ^{14}C yr b.p.). These sites have undergone extensive investigation and recently detailed examination and revision of the earlier dating of these sequences has resulted in a detailed Upper Palaeolithic record with excellent temporal and stratigraphic resolution (Damblon et al.,1996; Damblon, 1997). From Dolní Věstonice I, and II over 3000 pieces of macrofossil charcoal have been identified, with site descriptions of parts of trunks up to 40 cm in length and 30 cm in diameter (Opravil, 1994; Musil, 1997, 2003). Species include both needle-leaved (*Picea excelsa, Pinus sylvestris, P. cembra, Pinus mugo, Larix decidua, Juniperus communis, Taxus baccata*) and broad-leaved trees (*Fagus sylvatica, Ulmus, Populus, Salix* and *Betula*) (Mason et al., 1994; Opravil, 1994) although it is noted that up to 80% of the material appears to be from conifers (in particular pine and spruce). Results from this site led several authors to conclude that former interpretations of this region as being a tree-less steppe during the full-glacial are probably incorrect and that it was a cold-forest steppe dominated by coniferous trees with deciduous trees surviving in more protected areas (Slaviková-Veslá, 1950; Mason et al., 1994; Opravil, 1994; Damblon, 1997; Musil, 2003).

In further support of this interpretation are macrofossil charcoal records from three other Upper Palaeolithic sites, namely Pavlov I, Bohunice and Strànska skàlà (Fig. 1; Table 2) dated to ~30 ka BP (~26,000 ^{14}C yr b.p.), ~43 ka BP (40,000 ^{14}C yr b.p.) and ~42–37 ka BP (~38,000–32,000 ^{14}C yr b.p.), respectively. Again these represent occupation layers in loess sequences where the stratigraphy is well determined and numerous ^{14}C dates have been obtained from identified pieces of macrofossil charcoal with cross-dating carried out by several laboratories (Damblon et al., 1996). Thus even though each of these sites only represents snapshots in time, viewed as a whole they provide a convincing record of the full-glacial presence of trees in the Czech landscape, and depict an environment between 43 and 24 ka BP (~40,000–20,000 ^{14}C yr b.p.) most closely described as cold-forest steppe (Damblon, 1997). With the presence of various temperate taxa including *Quercus, Fraxinus, Fagus* and *Taxus* at Bohunice, Stránská skála and Dolní Věstonice there is again the suggestion that these regions may have been refuges for some temperate deciduous taxa (Damblon, 1997).

2.3. Croatia

The site of Šandalja II is a karst cave near Pula in Croatia (Fig. 1) with evidence of Upper Palaeolithic occupation from ~29 to 12 ka BP (27,800 ± 850–10,830 ± 70 ^{14}C yr b.p.). Analysis and dating of macrofossil charcoal samples from several hearths (Table 3) in the cave indicates a full-glacial presence of *Pinus, Abies, Sorbus* sp., *F. sylvatica, Ulmus, Populus* and *Rhamnus cathartica* between ~28 and 24 ka BP (~25–21,00 ^{14}C yr b.p; Culiberg and Sercelj, 1995). The authors interpret these findings as representing trees in close proximity to the caves occurring in dispersed groups or communities in ecological niches (microrefugia) (Culiberg and Sercelj, 1995).

2.4. Hungary

A review of macrofossil charcoal sites in Hungary incorporating both data from Upper Palaeolithic archaeological sites and palaeosols in loess sequences (Table 4) has revealed over 29 sites containing macrofossil charcoal assemblages spanning the time interval 29–25 ka BP (~31,500–16,500 ^{14}C yr b.p.) (Willis et al., 2000). Macrofossil charcoal wood identified from these sites includes *Pinus, Picea, Larix, Betula, Juniperus, Salix* and at one site *Carpinus betulus* with again a predominance of coniferous wood but also the presence of broad-leaved deciduous trees at many of the sites. An advantage of this Hungarian data is that not all of the assemblages have been obtained from archaeological sites, but are records of tree growth that have been preserved within loess sequences. Since these records are

Table 3
Identification of tree species/genera in macrofossil charcoal layers from sites in Croatia and ^{14}C dates (based on identified macrofossil charcoal wood within these layers)

Site number (with reference to Figs. 1 and 2): Site location: longitude (E)/latitude (N) Site name	Site type containing macrofossil charcoal layers	Tree species/genera identified in macrofossil charcoal layers[a]	Published ^{14}C dates based on macrofossil charcoal (uncalibrated yr b.p.)*	Lab. code	Cal yr BP	Reference to source of data
(8) 13°53/44°54 Šandalja II	Occupation layers in karst cave	*Fagus sylvatica*	21,740 ± 45	Zg	25,260 ± 240	Culiberg and Sercelj (1995)
		Sorbus sp. *Pinus* sp.	23,540 ± 180	GrN	26,490 ± 220	
		Rhamnus cathartica	22,660 ± 460	Zg	25,890 ± 380	
		Fagus sp., *Ulmus* sp., *Populus* sp.	25,340 ± 170	GrN	28,870 ± 930	

[a]Spaces between dates indicate different occupation layers.

Table 4
Identification of tree species/genera in macrofossil charcoal layers from sites in Hungary and ^{14}C dates (based on the identified macrofossil charcoal wood within these layers)

Site number (with reference to Figs. 1 and 2) Site location: longitude (E)/latitude (N)	Site type containing macrofossil charcoal layers	Tree species/genera identified in macrofossil charcoal layers	Published ^{14}C dates based on macrofossil charcoal (uncalibrated yr b.p.)	Lab. code	Cal yr BP	References to source of data
(9) 18°50′/47°35′	Loess deposit	*Pinus* sp., *Picea* sp., *Juniperus* sp.	32,500±2,170	Hv-1776	37,070±2570	Geyh et al. (1969)
(10) 21°05/48°05′	Loess deposit	*Pinus sylvestris*	30,174±1,101	Deb-4347	34,070±1250	Willis et al. (2000)
(11) 19°10′/46°05′	Loess deposit	*Pinus sylvestris*, *Betula* sp.	29,828±554	Deb-3058	33,640±670	Willis et al. (2000)
(12) 19°15′/47°50′	Loess deposit Occupation layer	*Pinus sylvestris-Pinus cembra*, *Picea* sp.	29,800±600 27,200±1400	Mo-422 Deb-3035	33,600±710 30,810±1830	Geyh et al. (1969) Willis et al. (2000)
(13) 21°15′/48°20′	Loess deposit	*Picea-Larix*, *Picea* sp.	28,700±3000 26,316±365	GXO-195 Deb-3051	32,480±3470 30,330±590	Krolopp (1977) Willis et al. (2000)
(14) 21°20′/48°05′	Occupation layer	*Picea* sp.	28,225±360	Deb-3035	32,270±590	Willis et al. (2000)
(15) 19°25′/47°45′	Loess deposit	*Picea* sp.	27,700±300	Deb-1901	31,770±470	Willis et al. (2000)
(16) 21°25′/47°55′	Loess deposit	*Picea* sp.	27,323±644	Deb-2657	31,430±730	Willis et al. (2000)
(17) 21°10′/48°00′	Loess deposit	*Picea* sp.	27,491±362	Deb-3034	31,560±460	Willis et al. (2000)
(18) 21°10′/48°15′	Loess deposit	*Picea* sp.	27,251±288	Deb-4345	31,260±350	Willis et al. (2000)
(19) 21°30′/48°10′	Loess deposit	*Carpinus* sp.	26,962±657	Deb-5052	30,900±700	Willis et al. (2000)
(20) 21°15′/47°55′	Loess deposit	*Picea* sp.	26,851±398	Deb-3049	31,950±560	Willis et al. (2000)
(21) 20°05′/46°55′	Loess deposit	*Pinus sylvestris*	26,736±629	Deb-4346	30,600±740	Willis et al. (2000)
(22) 21°25′/48°10′	Loess deposit	*Picea* sp.	26,618±532	Deb-3042	30,420±810	Willis et al. (2000)
(23) 18°00/47°10′	Loess deposit	*Picea-Larix*, *Pinus sylvestris-Pinus cembra*	26,350±3111	Hv-1777	30,030±3270	Geyh et al. (1969)
(24) 18°50/47°50′	Loess deposit	*Picea-Larix*, *Picea* sp.	21,165±865 24,030±317	Hv-5426 Deb-3353	24,530±860 27,180±600	Pécsi (1977) Willis et al. (2000)
(25) 19°05′/46°10′	Loess deposit	*Pinus sylvestris*	23,749±494	Deb-3064	26,990±670	Willis et al. (2000)
(26) 21°20/47°50′	Loess deposit	*Picea* sp.	23,571±486	Deb-1562	26,660±480	Willis et al. (2000)
(27) 21°15/47°45′	Loess deposit	*Picea-Larix*	20,350±470	Hv-1775	23,850±620	Geyh et al. (1969)
(28) 20°50′/46°30′	Lake gytta	*Picea* sp.	23,519±494	Deb-4350	26,600±460	Willis et al. (2000)
(29) 20°10′/46°50′	Loess deposit	*Salix* sp.	23,290±285	Deb-4572	26,330±260	Willis et al. (2000)
(30) 19°15/46°15′	Loess deposit	*Pinus sylvestris*	22,110±300	Deb-1562	25,520±320	Willis et al. (2000)
(31) 18°30′/46°00	Loess deposit	*Pinus sylvestris*	21,937±252	Deb-3104	25,400±310	Willis et al. (2000)
(32) 18°10′/46°55′	Occupation layer	*Picea-Larix*, *Pinus sylvestris-Pinus cembra*	21,740±320 21,725±560	Hv-4189 Hv-2590	25,200±280 25,130±550	Krolopp (1977) Marosi and Szilárd (1974)
(33) 17°50′/46°45′	Occupation layer	*Pinus sylvestris-Pinus cembra*, *Picea-Larix*	18,900±100	GrN-1783	22,210±270	Vogel-Waterbolk (1964)
(34) 21°30′/48°30′	Occupation layer	*Pinus sylvestris-Pinus cembra* *Picea-Larix*	18,700±1900 17,050±350	A-518 GrN-4038	21,700±2180 19,980±660	Vértes (1964)
(35) 19°30′/46°10′	Occupation layer	*Pinus sylvestris-Pinus cembra*, *Picea-Larix*	18,080±405	Hv-1619	21,170±580	Dobosi (1967)
(36) 18°00′/46°40′	Loess deposit	*Pinus sylvestris-Pinus cembra*, *Picea-Larix*	17,760±150	GrN-1957	20,940±410	Gaborí-Csánk (1960)
(37) 19°15′/47°50′	Occupation layer	*Pinus sylvestris-Pinus cembra*, *Picea-Larix*, *Betula* sp.	16,750±400	—	19,560±680	Geyh et al. (1969)

not just associated with dates of human occupation, this has important implications for understanding the temporal extent of trees on the eastern European landscape during the full-glacial. Evidence from 34 ^{14}C dates clearly indicates the presence of trees in Hungary during each 1000-year time-slice between 37 and 20 ka BP (35,500–16,500 ^{14}C yr b.p.) with no obvious clustering of dates during the warmer Dansgaard/Oeschger (D/O) events. In addition, at several sites there is evidence for in situ growth of trees with charcoal silhouettes of tree trunks and extensive tree root systems in the cleaned loess face. Conclusions drawn from this study suggest that the full-glacial and lastglacial maximum (LGM) landscape was probably a mixture of forest-steppe—the nearest present-day equivalent being open boreal-type forest (Willis et al., 2000). Other data associated with this study to support this interpretation included fossil molluscan assemblages at many of the sites containing a number of species that at present occupy a woody habitat.

2.5. Moldova

The site of Cosautsi is an Upper Palaeolithic site located on the west bank of the Dniester river in north-east Moldova. It comprises an 18.5 m thick stratigraphic sequence in loess with occupation layers indicating that the site was occupied for approximately 3000 years between ~23 and 18 ka BP (~19,500–16,000 ^{14}C yr b.p). Numerous ^{14}C dates have been obtained for these occupation layers, with many based on macrofossil charcoal fragments. Most recently a new dating project was carried out on the Cosautsi sequence (Haesearts et al., 1998) involving detailed identification of the macrofossil charcoal to be dated and also cross-dating of all these samples with dates on bone fragments found in the same stratigraphic layers. Fourteen dates on macrofossil charcoal were obtained (Table 5) with the majority of the fragments identified as *Picea* sp. although in two of the layers *P. cembra* and *Salix* sp. were also noted. The predominance of *Picea* in this macrofossil charcoal record, plus the lack of any temperate tree taxa and a somewhat depauperate flora in comparison to records from other Upper Palaeolithic sites further west has led to the suggestion that although there were trees in the vicinity of this site during the full-glacial, the environment was harsh and unable to provide refugia for temperate flora (Damblon, 1997).

2.6. Poland

The site of Spadzista in Southern Poland is another Upper Palaeolithic occupation sequence situated in loess. Occupation at this site occurred between 28 and 26 ka BP (~24,000–23,000 ^{14}C yr b.p.: Damblon et al., 1996; Musil, 2003). There is also a date from a humic soil further down in the sequence ~36 ka BP (~32,000 ^{14}C yr b.p.). Macrofossil charcoal fragments identified from these two layers on which the dates were based include *Pinus, Larix* and *Abies* (Table 6), indicating a full-glacial presence of these species in Southern Poland.

2.7. Romania

The Upper Palaeolithic site of Mitoc Malu Galben is situated east of the Carpathians on the river Prut (Fig. 1) and is comprised of three main occupations

Table 5
Identification of tree-species/genera in macrofossil charcoal layers from Cosautsi, Moldova and ^{14}C dates (based on the identified macrofossil charcoal wood within these layers)

Site number (with reference to Figs. 1 and 2): Site location: (longitude E/latitude (N) Site name	Site type containing macrofossil charcoal layers	Tree species/genera identified in macrofossil charcoal layers	Published ^{14}C dates based on macrofossil charcoal (uncalibrated yr b.p.)	Lab. code	Cal yr BP	References to source of data
(38) 28°18′/48°30′ Cosautsi	Occupation layer situated upon loess	*Picea* sp., *Pinus cembra*, *Salix*	16,050 ± 170	GrA-4209	18,520 ± 240	Damblon and Haesaerts (1997); Haesaerts et al. (1998)
			17,130 ± 180	GrA-5217	20,060 ± 480	
			17,230 ± 140	GrN-217792	20,210 ± 450	
			17,620 ± 210	GrN-21793	20,720 ± 490	
			17,910 ± 80	GrN-21360	21,210 ± 280	
			18,030 ± 150	GrN-21359	21,330 ± 280	
			17,780 ± 190	GrA-7554	20,940 ± 440	
			17,950 ± 100	GrN-21794	21,260 ± 270	
			18,260 ± 210	GrA-5218	21,560 ± 270	
			19,200 ± 130	GrN-21361	22,560 ± 360	
			19,120 ± 100	GrA-7555	22,470 ± 340	
			19,440 ± 100	GrA-6746	22,800 ± 380	
			19,070 ± 100	GrA-7557	22,410 ± 330	
			19,410 ± 100	GrN-21795	22,770 ± 380	

Table 6
Identification of tree species/genera in macrofossil charcoal layers from Spadzitsta Street, Southern Poland and ^{14}C dates (based on the identified macrofossil charcoal wood within these layers)

Site number (with reference to Figs. 1 and 2): Site location: longitude (E)/latitude (N)	Site type containing macrofossil charcoal wood	Tree species/genera identified in macrofossil charcoal layers	Published ^{14}C dates based on macrofossil charcoal (uncalibrated yr b.p.)	Lab. code	Cal yr. BP	Sources of data
(39) 19°55′/50°03′ Spadzitsta Street	Occupation layer situated upon loess	*Pinus* sp., *Larix* sp., *Abies* sp.	23,040 ± 170 24,380 ± 180	GrN-6636 GrN-11006	26,170 ± 220 27,590 ± 700	Damblon et al. (1996); Musil (2003)

Table 7
Identification of tree species/genera in the macrofossil charcoal layers from Mitoc Malu Galben, Romania and ^{14}C dates (based on the identified macrofossil charcoal wood within these layers)

Site number (with reference to Figs. 1 and 2): Site location: longitude (E)/latitude (N) Site name	Site type containing macrofossil charcoal layers[a]	Tree species/genera identified in macrofossil charcoal layers	Published ^{14}C dates based on macrofossil charcoal (uncalibrated yr b.p.)[a]	Lab. code	Cal yr BP	References to source of data
(40) 27°02′/48°07′ Mitoc Malu Galben	Occupation layers situated upon loess	*Picea* sp.	20,300 ± 700	GrN-14031	23,720 ± 850	Damblon et al. (1996); Damblon (1997)
		Picea sp., *Alnus* sp.	23,850 ± 100	GrA-1353	26,700 ± 220	
		Picea sp. *Picea* sp.	23,390 ± 280 23,830 ± 330	GrN-20438 GrN-14034	26,390 ± 260 26,820 ± 400	
		Picea sp., *Pinus cembra*	23,990 ± 250	GrN-20439	26,960 ± 410	
		Picea sp., *Alnus* sp. *Picea* sp., *Alnus* sp.	25,610 ± 500 26,180 ± 290	GrN-20440 GrN-18811	29,120 ± 1120 30,220 ± 580	
		Picea sp. *Picea* sp. *Picea* sp., *Alnus* sp. *Picea* sp. *Picea* sp. *Picea* sp. *Picea* sp.	26,500 ± 460 26,020 ± 650 26,380 ± 600 26,300 ± 450 25,080 ± 500 26,110 ± 1050 28,910 ± 480	GrN-18815 GrN-18880 GrN-18881 GrN-18879 GrN-18882 GrN-18883 GrN-12636	30,470 ± 610 29,550 ± 1170 30,120 ± 900 30,210 ± 720 28,570 ± 1080 29,460 ± 1510 32,810 ± 700	
		Picea sp., *Alnus* sp.	25,380 ± 120	GrA-1355	28,950 ± 900	
		Picea sp.	31,850 ± 800	GrN-12637	36,410 ± 1610	
		Picea sp.	31,000 ± 330	GrA-1648	34,920 ± 550	
		Picea sp. *Picea* sp. *Picea* sp. *Picea* sp.	31,100 ± 900 30,240 ± 470 31,160 ± 570 30,920 ± 390	OxA-1646 GrN-20443 GrN-20770 GrN-20442	35,090 ± 940 34,180 ± 570 35,060 ± 670 34,870 ± 580	
		Picea sp.	31,160 ± 550 32,730 ± 220	GrN-20444 GrA-1357	35,060 ± 660 37,250 ± 1100	

[a]Spaces between dates are used to indicate different occupation layers.

phases between 37 and 33 ka BP (33,000–29,500 ^{14}C yr b.p.), 30–28 ka BP (27,500–25,000 ^{14}C yr b.p.) and 27–26 ka BP (24,000–23,000 ^{14}C yr b.p.) (Damblon et al., 1996). Similar to the majority of sites described above, this is a loess sequence containing well-determined stratigraphic horizons for the occupation layers. This site has been described as one of the most dated in Central Europe (Damblon et al., 1996) with over 46 ^{14}C determinations. Recent scrutiny of these dates plus the provision of additional 14 dates has led to a well-constrained temporal sequence containing 23 dates carried out on identified pieces of macrofossil charcoal assemblages (Damblon, 1997; Table 7). Similar to the records from Moldova the majority of the macrofossil charcoal obtained from this sequence was *Picea* with *Alnus* charcoal fragments found in five samples and *P.*

cembra in one sample. These results have led to the suggestion that spruce was the main tree species in the woody component of the landscape near Mitoc for the period between 37 and 26 ka BP (~32,000–23,000 ^{14}C yr b.p.) with local occurrences of alder growing along the river Prut (Damblon, 1997). The lack of temperate deciduous trees in the macrofossil charcoal assemblage from this site, again similar to the record from Moldova, is taken to suggest that this full-glacial environment of this region was too harsh to provide refugia for temperate elements of the flora.

In summary, there is now macrofossil charcoal evidence from at least 40 sites in central and eastern Europe (Figs. 1 and 2) to indicate the presence of trees growing either in situ or in close proximity to the sites during the full-glacial between 44 and 19 ka BP (~41,000–16,000 ^{14}C yr b.p.). At all of these sites, the macrofossil charcoal assemblages have been used to identify the trees present and provide the material for ^{14}C dating. Over 20 different tree taxa have been identified and 151 ^{14}C dates (often cross-dated with bone material from the same sequence) obtained from seven different dating laboratories (Tables 1–7). Although the majority of the wood identified in this macrofossil charcoal record is from coniferous trees there is also a notable presence of broad-leaved temperate deciduous trees including *Fagus, Ulmus, Quercus, Corylus, Sorbus, Carpinus, Rhamnus* and *Populus* at some sites (Figs. 1 and 2). The absence of these types from other sites is probably due to more severe climatic conditions although in some cases it might also be due to a sampling bias. In several site reports, e.g. it is stated that pieces of temperate deciduous taxa were identified in the assemblages but discarded from further analyses and dating since it was presumed that they must represent contamination of the sample (see, e.g. Damblon et al., 1996, 1997).

3. Trees or no trees: other lines of fossil plant evidence

At many of the sites described above, pollen has been identified in the same loess/cave sequences as the macrofossil charcoal. These records, however, have not been included in this review. This is due to the inherent problem of obtaining a stratigraphically meaningful pollen record in such sediments (Turner, 1985; but see Carrión et al., 1999; Navarro Camacho et al., 2000). Lake or peat sediments containing pollen sequences and extending back to the full-glacial are

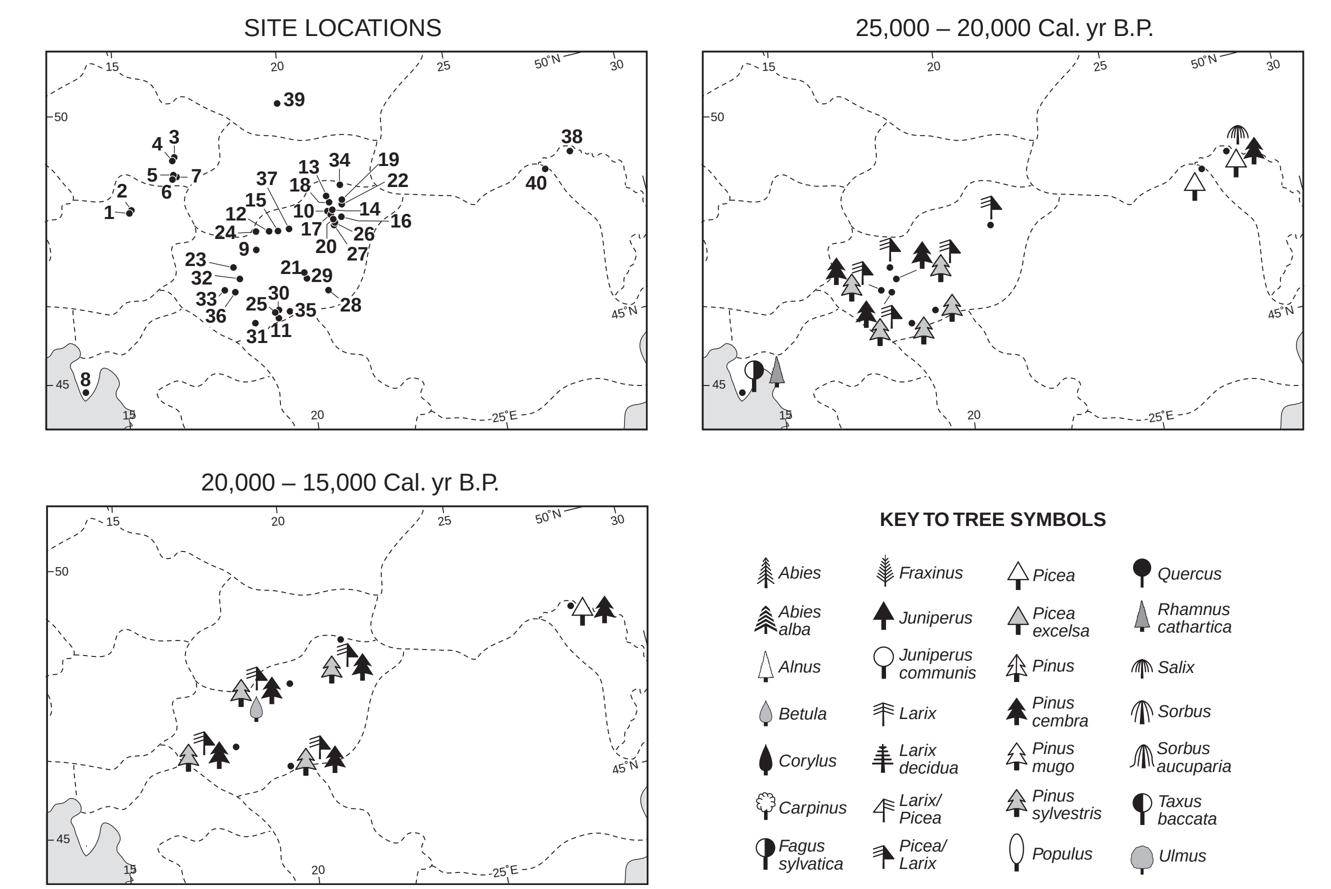

Fig. 2. Location of the 40 full-glacial macrofossil charcoal sites plus the tree species/genera identified at each site for the time intervals 25,000–20,000 and 20,000–15,000 ka BP (full citation to sites is given in text and Tables 1–7). Numbers correspond to site names that are detailed in Tables 1–7.

more stratigraphically secure, but are rare in central and eastern Europe (see, e.g. the coverage of sites in Huntley et al., 2003). However, there are several notable exceptions that add further support to the findings described above regarding a presence of trees in central and eastern Europe during the full-glacial. The most notable of these is from Bulhary in the Czech Republic where pollen and macrofossil analyses have been carried out on a buried peat dated to ~28 ka BP (25,657 ± 2750 ^{14}C yr b.p.) (Rybníčková and Rybníček, 1991). The pollen diagram indicates a coniferous forest containing *P. sylvestris, Pinus* cf. *mugo, P. cembra, Picea, Larix, J. communis* and *Betula.* There is also evidence for the scattered presence of temperate deciduous trees including *Ulmus, Acer, Corylus, Quercus* and *Tilia*. Plant macrofossils obtained from these peat deposits, which from numerous other studies are known to be a reliable indicator of a very local presence (Birks, 2003), include leaves, seeds and wood of *Betula* cf. *pubescens* and *Salix* sp.

Three lake sites that contain pollen diagrams extending back into the end of the LGM at ~20 ka BP (~18,000 ^{14}C yr b.p.) are Švarcenberk in the Czech Republic (Pokorný and Janlovská, 2000), Sarret in Hungary (Willis et al., 2000) and Steregoiu in NW Romania (Björkman et al., 2002, 2003). In all three cases the pollen diagrams indicate an open-forested vegetation during the LGM (with tree pollen accounting for over 60% of the total pollen). The pollen diagrams indicate that *Pinus* and *Betula* were predominant in this environment but there was also (in Hungary) a low but persistent presence of other tree taxa including *Juniperus, Salix, Alnus,* and *Larix.* In Švarcenberk plant macrofossils have been obtained from the same sequence indicating *Betula nana* seeds and *Salix* wood during the LGM. From the Czech Republic and Poland numerous finds of *Larix, Betula, P. excelsa* and *P. cembra* seeds and needles in early Lateglacial lake sediments (Alleröd: ~14,000 BP) (Jankovská, 1988, 1998) led to the suggestion that the Lateglacial vegetation of this area of eastern Europe bore a close analogy to the present-day Siberian boreal (taïga) forest zone (Jankovská, 1998). In addition, pine megafossils (logs) dating to ca 17,000 ka BP have been recently found at Magherus in Northwestern Romania (B. Wohfarth pers. comm., 2004).

4. Trees or no trees: the genetic evidence

Another line of evidence used in the interpretation of former distributions of vegetation is that of genetics. This involves the extraction and amplification of genetic signatures (DNA or other genetic markers) from present-day species in order to understand their ancestry, past movement of populations, and present-day patterns of genetic diversity. Much of this work is based on the assumption that in consequence of prolonged isolation during glacial periods, extant tree populations situated close to refugia should be highly divergent with a declining diversity away from the refugia indicating post-glacial colonization and successive founder events (Hewitt, 1996, 2000, 2004). Over the past 10 years, there have been a number of important publications examining the genetic legacy of European tree species including, e.g. *Quercus, Fagus,* and *Abies alba* (Konnert and Bergmann, 1995; Demesure et al., 1996; Dumolin-Lapégue et al., 1997) with the results from a number of these studies suggesting that indeed clear genetic differentiation between different populations of the same species exist. In many cases this genetic differentiation appears to have a distinct geographical coverage in southern Europe and is often used in conjunction with the fossil evidence to argue for the importance of refugia in their genetic diversification (e.g. Taberlet and Bouvet, 1994; Hewitt, 1996, 2000; Taberlet and Cheddadi, 2002; Tzedakis et al., 2002).

Amongst all the evidence supporting the southern European refugial model there is, however, an increasing amount of genetic evidence that indicates a somewhat different full-glacial distribution of some tree types and subsequent post-glacial migration routes. In particular, it has been demonstrated that several taxa including *Picea abies, Betula, Alnus, Populus* and *Salix* (Lagercrantz and Ryman, 1990; Palmé et al., 2002, 2003a, b; Petit et al., 2003; Lascoux et al., 2004) do not conform to a southern European refugial pattern but demonstrate a more northerly and diffuse distribution. Such results have led to the suggestion that this is a reflection of full-glacial survival of these species during the LGM in northerly refugia including central and eastern Europe (Palmé and Vendramin, 2002; Stewart and Lister, 2002; Palmé et al., 2003a, b; Petit et al., 2003; Lascoux et al., 2004).

5. Trees or no trees: could the trees identified in the macrofossil charcoal record have survived the full-glacial and Lateglacial environments of central and eastern Europe?

The records of full-glacial tree growth in central and eastern Europe presented in this review are clearly at odds with the most recent landscape reconstructions based on long-sequence pollen-based biomes which suggest an open, essentially tree-less environment (see, e.g. Alfano et al., 2003; Huntley et al., 2003). It is therefore not surprising that palynologists have tended to discount occasional dated macrofossil charcoal records from one site or another. However, as a whole those records (Figs 1 and 2; Tables 1–7) alongside equally piecemeal evidence from macrofossils and pollen provide a convincing case for the survival of trees in many parts of central and eastern Europe throughout the cold stages of the full and Lateglacial (~42–18 ka BP). So could trees have withstood the predicted climatic extremes of the full and Lateglacial in central and eastern Europe? Or were these climates too severe to have allowed trees in all but a few small microenvironmentally favourable locations? In order to address these questions we need to examine both the climatic simulations for the full and Lateglacial in central and eastern Europe and the physiological tolerances of the trees identified in the macrofossil charcoal record.

Recently, high-resolution climate simulations have been obtained for the early full-glacial and LGM climates as part of the Stage 3 Project (Barron and Pollard, 2002; van Andel, 2002; Barron et al., 2003; Pollard and Barron, 2003) to provide millennium-scale 'snapshot' simulations representing the main states of the glacial climate by means of: a ''modern'' state tested satisfactorily against modern data, a ''warm state'' typical for the 45–38 ka BP interval, and a ''LGM cold state for the acme of the LGM (27-~18 ka BP).

The European climate then—as it does today, displayed two main continental-scale regions in addition to the Mediterranean zone: a north–south gradient from arctic to cold temperate climates north of the trans-European mountain barrier and a west–east transition from the maritime Atlantic climate to the continental climate of eastern Europe; both are clearly reflected in the snapshot simulations (Barron et al., 2003). The 'LGM cold simulation', for example predicted winter (December, January, February) surface temperatures that were significantly cooler than the modern simulation, with much of northern Europe 10–20 °C cooler, southern Europe and parts of central Europe 7–10 °C, and only Spain and the area around the Black Sea a mere 2–4 °C cooler (Barron and Pollard, 2002). Winter and summer precipitation also had a strong east–west gradient, bringing to central and eastern Europe more precipitation than to the three southern peninsulas of Europe. In general, the 'early warm' and 'LGM cold' simulations are therefore much as they had been expected from previous anecdotal information.

The climate simulated for the interval between the early warm and LGM cold states (~38–27 ka BP), however, predicted temperature and precipitation regimes for central and eastern Europe quite different than those permitted in the tree-less tundra concept suggested by the Stage 3 pollen-based biomes; predicted temperatures and precipitation regimes for central and eastern Europe were much warmer than anticipated with, for example winter temperatures only 4–7 °C cooler (Fig. 4: Barron and Polard, 2002; Pollard and Barron, 2003); it also suggested that central and eastern Europe had much more rainfall both during the winter and summer than southern Europe. Since this simulation did not fit with the pollen evidence of a tree-less tundra, the climate simulation for ~38–27 ka BP was rejected (Barron and Pollard, 2002; Alfano et al., 2003; Barron et al., 2003). It is interesting to note however that the palynological data used in the Stage 3 Project and the underlying tree-less tundra concept, covered only the maritime and Mediterranean regions and not continental Europe with the exception of one site in Estonia at 39°E, 56°N (Liivrand, 1990, 1991).

So could the trees identified in the macrofossil charcoal records have survived the extremes of the simulated full and Lateglacial climates? Environmental factors that potentially could have limited tree growth include low temperatures, reduced amounts of precipitation, cold podzolic soils with permafrost in some regions, shorter growing seasons and low atmospheric CO_2 concentrations. Dealing with the latter point first, laboratory experiments have demonstrated that the physiological effects of CO_2 limitation only become predominant when other nutrients, water and light are available at high levels (Tilman, 1993). Therefore, although lower atmospheric CO_2 during the LGM may have had an important influence on low-latitude environments (e.g. Street-Perrott et al., 1997; Cowling et al., 2001; Harrison and Prentice, 2003), its impact on mid-to-high latitude vegetation would have been much less pronounced (Bennett and Willis, 2000). When considering the impact of the other environmental factors (reduced temperature, precipitation and cold podzolic soils), it is interesting to note the present-day tolerances in central and northern Europe and the Eurasian boreal forest of many of the species identified in the macrofossil charcoal record (Table 8; Kienast, 1987; Ellenberg, 1988; Prentice and Helmisaari, 1991; Nikolov and Helmissari, 1992; Larcher, 1995). All could have coped with the conditions predicted by the rejected 38–27 ka BP simulations but more importantly, also the cold conditions predicted for the LGM (27–18 ka BP) (Table 8). A reduced growing season and permafrost might have caused more limitations to temperate tree growth but it is probable that such conditions would not have had a significant impact on the physiological capabilities of the hardened boreal species.

Neither climatic scenario, the LGM cold nor the rejected 38–27 ka BP snapshots can therefore be used to assert that taïga-forests could not have existed in central and eastern Europe between ~40 and ~20 ka BP. In fact, the coupled climate vegetation model (Haxeltine and Prentice, 1996) for the 38–27 ka BP interval shows as a dominant vegetation type in central and northern Europe evergreen taïga/montane forest (Alfano et al., 2003: Fig. 6) as our data also suggest. Nonetheless, the simulation for 37–28 ka BP remains contentious and the pollen data continue to be seen as demanding a predominantly stepic herbaceous vegetation of low productivity for central and eastern Europe (Huntley

Table 8
Present day tolerances of minimum growing temperature, drought and nutrient availability for tree species/genera recognised in the macrofossil charcoal record (Tables 1–7)

Tree species/genus recognised in macrofossil charcoal record[a]	Tcold (°C)[b]	Drought resistance (1: very low to 5: very high)	Ability to grow on poor soils[c] (1 = tolerant, 2 = intermediate, 3 = intolerant)
Needle-leaved			
Abies alba	**−5**	3	—
Abies sibirica	*−35*	2	2
Juniperus communis	—	3	1
Larix decidua	**−10**	2	—
Larix gmelinii	*−45*	4	1
Larix sibirica	*−33*	5	1
Larix sukaczewii	*−22*	3	1
Picea abies	*−17*	1	2
Picea ajanensis	*−38*	2	2
Picea obovata	*−40*	1	2
Pinus cembra	**−10**	5	—
Pinus mugo	—	5	1
Pinus pumila	*−45*	2	1
Pinus sibirica	*−35*	2	2
Pinus sylvestris	*−40*	5	1
Taxus baccata	*−4*	4	1
Broad-leaved			
Acer platanoides	*−15*	3	3
Alnus incana	—	1	1
Alnus glutinosa	*−15*	1	1
Betula pendula	*−40*	5	1
Betula pubescens	*−40*	1	1
Betula verrucosa	—	2	2
Carpinus betulus	*−8*	3	2
Corylus avellana	*−15*	—	2
Fagus sylvatica	*−3*	2	1
Fraxinus excelsior	*−16*	2	3
Populus tremula	*−40*	4	1
Populus nigra	—	1	1
Quercus robur	*−16*	5	1
Quercus petrea	*−4*	3	2
Salix alba	—	1	1
Sorbus aria	—	4	1
Sorbus aucuparia	—	4	1
Tilia cordata	*−18*	3	3
Ulmus glabra	*−15*	—	3
Ulmus scabra	—	3	1

— Data not available.
[a]Where taxa are only recognised to genera in the macrofossil charcoal record, species of this genera presently growing in central and northern Europe and the Eurasian boreal forest (for which there are data available), (Ellenberg, 1988; Keinast, 1987; Prentice and Helmisaari, 1991; Nikolov and Helmisaari, 1992) are included for comparison.
[b]Numbers in bold represent lowest possible average January temperature for species (from Keinast, 1987); those in italics represent mean temperature of the coldest month at the border of the species' geographical range (from Prentice and Helmisaari, 1991; Nikolov and Helmisaari, 1992).
[c]Estimate based on tolerance to low nitrogen availability.

et al., 2003; Huntley and Allen, 2003), in direct conflict with the other evidence presented in this paper as well as the well-documented mammalian fauna of the period (van Andel, 2003b).

6. The temporal and spatial distribution of trees and the high-frequency oscillations of the Lateglacial climate

We regard the evidence presented in Tables 1–8 as conclusive for the existence during the last glaciation of a wide range of tree species in central and eastern Europe, so compelling a substantial revision of current views on the glacial landscape, its resources and its capacity to support human exploitation in continental Europe. This raises a number of important questions. Was the presence of trees limited to warm phases of the D/O oscillations, retreating at each stadial and returning at the next interstadial? Did trees occur only in small enclaves in favoured locations or gallery woodland along rivers or did extensive open woodland (taïga) exist? What were the glacial climate variations indicated by the mix of some nine coniferous and 20 broadleaf tree species recorded for the interval ~40–16 ka BP at various time and locations (Figs. 1 and 2)? And what are the consequences of the presence of trees for the carrying capacity in human terms of the full-glacial landscape.

Those questions and many others are beyond the scope of our paper or even beyond currently available evidence, except for the question as to whether the presence of trees was limited to short, warm D/O events or was continuous. A manuscript on high-resolution calibration of the Greenland time-scale generously made available to us by Nick Shackleton (Shackleton et al., 2004) has enabled us to distinguish with some confidence those macrofossil charcoal dates that are from warm interstadials from those present in cold stadials for Greenland Interstadials 2–7 (GIS: Shackleton et al., 2004; Fig. 2). Beyond GIS 7, the sparse data do not permit this determination.

Table 9 shows all sites with large sets of charcoal dates and a few others for comparison, plotted against a millennial time-scale for the late Oxygen Isotope Stage 3 and the LGM (32–~16 uncal. ka BP). Because of differences between the ^{14}C calibration method used in this paper and that of Shackleton et al. (2004), all charcoal and D/O cycle dates are uncalibrated. The sites listed in Table 9 are all south of the 49°N parallel and east of 15°E and therefore well within the continental climate region. Because the transitions from interstadial to stadial and back are steep (see Shackleton et al., 2004: Fig. 2), spanning at most a few centuries, the numbers in each category can be reasonably estimated except very near boundaries.

Table 9
Chronological distribution across Dansgaard/Oeschger oscillations of ^{14}C-dated charcoal samples on ^{14}C time scale; GIS (Greenland Interstadial) interstadial bases are also in uncalibrated ^{14}C time

Age uncal. ka BP	Interstadial Base	A	B	C	D	E	F	G
<19.9		–	–	–	–	6	14	–
.	GIS 2 19.9							
20.0 –.9		–	1	–	–	1	–	1
21.0 –.9		–	–	–	1	4	–	–
22.0 –.9		–	–	–	1	1	–	–
23.0 –.9		5	–	–	1	1	–	4
24.0 –.4		–	–	–	–	–	–	–
.	GIS 3 24.5							
		2	2	–	1	–	–	2
	GIS 4 25.3							
25.4 –.9		4	5	–	–	–		
26.0 –.9		2	8	4	–	6	–	6
27.0 –.9		–	6	–	–	5	–	–
28.0 –.4		–	1	–	–	1	–	–
	GIS 5 28.5							
		1	1	–	–	2	–	1
	GIS 6 29.5							
29.6 –.9		–	1	–	–	2	–	–
30.0 –.9		1	1	1	–	1	–	2
31.0 –.8		2	–	–	–	–	–	4
	GIS 7 31.9							
32.0 –.9		1	1	–	–	1	–	1

Site codes: A: Willendorf; B: Dolní Vestonice I + II; C: Pavlov; D: Šandalja; E: Hungarian region; F: Cosautsi; G: Mitoc Malu Galben.
Dated boundaries labelled GIS are the interstadial bases 2–7 (after Shackleton et al., 2004: Table 1). Interstadials shaded.

From our best data set (Table 9) the overwhelming majority of dates are found in cold events. Among the 121 dates for the seven sites displayed, only 16 are securely located within interstadials—as expected, given the difference in duration of stadials and interstadials. It is obvious that the presence of coniferous as well as broadleaf trees was continuous throughout the interval for which there are adequate data (~35–20 uncal. ka BP). The trees did not migrate northward during warm D/O events, only to perish during the subsequent cold event; they were always there. A decline in numbers towards the LGM would be expected and can indeed be seen in most sites together with a northward increase in the dominance of coniferous over broadleaf trees (Figs. 1 and 2; Table 9). The Hungarian region and the Cosautsi site in Moldavia, however, are striking exceptions that indicate a milder LGM there.

7. Conclusions

A review of the published macrofossil charcoal evidence from 40 localities in central and eastern Europe has revealed evidence for the presence of at least 20 different tree types growing in this landscape during the last full-glacial interval. In total, 151 ^{14}C dates have been obtained from the macrofossil charcoal assemblages that date these samples between ~42 and 19 ka BP. Identified tree types are predominantly needle-leaved, including *Picea, Pinus, Larix, Juniperus*, although broad-leaved types including *Salix, Betula, Fagus, Ulmus, Quercus, Corylus, Sorbus, Carpinus, Rhamnus* and *Populus* have been found at some localities. Additional data from plant macrofossils and pollen in lake sequences, although much less extensive in temporal and spatial coverage, adds further support to suggestion of the full-glacial presence of trees in central and Eastern Europe. In addition, genetic evidence from extant European tree populations suggests that many boreal tree types do not have a genetic distribution pattern that conforms to a model predicting full-glacial isolation in southern European refugia.

The evidence presented in this paper makes it difficult to support a European full-glacial refugial model that excludes trees from central and Eastern Europe. It is even more difficult, however, to establish from the fossil evidence alone whether the trees grew in isolated pockets on an otherwise open tundra landscape or in an open-taiga forest. Recent palaeoclimatic and biome model simulations for the last full-glacial, however, indicate that, contrary to previous interpretations, the central and eastern European landscape could have supported taïga forest, called "a speculative model" by Huntley and Allen, 2003: Fig. 6.12). The evidence presented in this paper fully supports these model interpretations and leads to the undoubtedly somewhat controversial suggestion that during the last full-glacial interval the central and eastern European landscape was partly covered by taïga/montane woodland, which in some regions also contained isolated pockets of temperate trees.

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