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The spread of deciduous *Quercus* throughout Europe since the last glacial period

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Abstract

For most of the last glacial period, which ended about 10 ka BP[2], the temperate forest species were restricted to small areas (termed refugia) with a milder climate, situated mostly along the Mediterranean borderlands and around the Black Sea. Species only started to expand from these glacial period refugia with the large-scale shifts in the global climate in the late-glacial (15–10 ka BP) and the beginning of the Holocene period (10 ka BP to present).

Fossil pollen data from sites across Europe have been used to reconstruct the location of refugia of the deciduous oak species, and the spread from these refugia into their current ranges. Three areas of southern Europe have been identified as refugia for deciduous *Quercus*: southern Iberian peninsula, southern Italian peninsula and the southern Balkan peninsula.

The spread of *Quercus* took place in two steps. First, in the late-glacial interstadial (13–11 ka BP) *Quercus* spread to the central European mountains from these refugia. Second, with the stabilisation of a climate favourable to deciduous trees species in the Holocene, oak spread into northern Europe, rapidly into the north–west, and more slowly into the centre and east, due to physical barriers. The earlier distribution changes are strongly correlated with the shifts in climate, whereas the

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[2] 1 ka BP = 1000 years before present. All ages given are in radiocarbon years, and differ from calendar years. See text for details.

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later changes are most strongly controlled by competition between species, landscape topography and other edaphic factors. By approximately 6 ka BP, the deciduous oak had reached its maximum extension in Europe.

Two types of refugia have been identified from the observed range expansion: primary, full glacial refugia; and secondary, temporary refugia, which supported populations of the oak during the short, climatically unfavourable late-glacial stadial.

Keywords: Post-glacial colonisation; Palynology; Refugia; *Quercus* spp.

1. Introduction

The climatic changes between glacial and interglacial periods during the course of the quaternary period have resulted in large-scale changes in the distribution of vegetation. In the current interglacial period, the Holocene, deciduous oak forests reach the Atlantic coasts between approximately 40°N and 60°N and extend east as far as 70°E (Hultén and Fries, 1986). The comprehensive comparison of climatic parameters and tree and shrub taxa distributions in North America (Thompson et al., 2000) indicates that on that continent, the principal limiting factors on the distribution of the *Quercus* group are winter temperature and available moisture (AE/PE). A comparison of the distribution maps of Hultén and Fries (1986) with the gridded climatic data of Huntley et al. (1995) suggest that in Europe, oak forests are limited to the north by temperature and to the south by drought, and are replaced at these limits by, respectively, coniferous forests and evergreen Mediterranean vegetation.

During the last 20,000 years, the climate has undergone a period of major change from a glacial period with a maximum ice volume between 18,000 and 15,000 years ago, termed the last-glacial maximum (LGM), to an interglacial warm period, with a minimal global ice cover between 9 and 6000 years ago (Walker, 1995). The climate of the glacial maximum was cold and dry. Ice sheets covered much of the northern European continent (Peltier, 1994), and the oceanic circulation had changed. The position of the North Atlantic Polar Front (NAPF), the boundary between the warm, saline-rich waters flowing north from the equator, and the cool, saline-poor waters flowing from the north pole, was displaced southwards, in comparison with its modern-day position, to approximately 40°N (Ruddiman and McIntyre, 1981). The Gulf stream, which presently brings heat and moisture to the western European continent, was depressed to the south. The vegetation was principally composed of herbaceous plants, e.g. *Artemisia* and many species of the Poaceae family, a landscape described by Pons (1984) as ‘‘l'état zéro’’ or the initial stage.

The prevailing climatic conditions of the glacial period had restricted the range of the deciduous forests to refugia, where favourable microclimates existed. Temperate species had either spread to favourable areas, or had their range reduced in these areas (Huntley and Birks, 1983; Bennett et al., 1991; Birks and Line, 1993) during the beginning of the glacial. Whilst short-lived warm periods early in the glacial may have allowed some expansion from these refugia (Behre, 1989; Tzedakis, 1993), the aridity and cold of the LGM would have severely limited the distribution of these temperate species to parts of Europe where favourable topography and microclimates existed (Huntley and Birks, 1983). During the LGM, temperatures in the north of Europe were reduced by 25–30 °C (Peyron et al., 1998). The Mediterranean region, where the reconstructed temperatures were 15 °C lower than today (Peyron et al., 1998), played a major role as a refugium for several temperate species. This region was relatively wetter than northern Europe. Following the end of the LGM (approximately 15 ka BP), the ice sheets began to melt and more water became available on the continent.

The change between the glacial and interglacial (Holocene) periods was by no means smooth or unidirectional. A series of rapid changes between cold and warm periods took place, as well as in the amount of available moisture (Walker, 1995; Isarin and Renssen, 1999). An initial warming took place at around 15 ka BP in the south–west of Europe (Walker, 1995). This was followed by a rapid increase of temperatures at around 13 ka BP, recorded in records of fossil Coleoptera (Atkinson et al., 1987), showing an increase of 8 and 20 °C in summer and winter temperatures, respectively. A thermal maximum is indicated by fossil proxy data between 13 and 12.5 ka BP in most of Europe, with temperatures equivalent to the modern day (Beaulieu et al., 1994; Walker, 1995). A short-lived climatic deterioration at around 12 ka BP (the "Older Dryas"), was followed by a period of higher but declining temperatures across Europe. Mean July temperatures rose to above 12 °C, then declined by as much as 5 °C (Atkinson et al., 1987; Walker, 1995). During the Younger Dryas period (10,950–10,150 yr BP; Hoek, 1997), a strong cooling had a marked effect on the development of the temperate forests. Temperatures in north-western Europe were 3–6 °C cooler than the present, and as low as 8 °C less than the present in the south (Walker, 1995; Isarin and Bohncke, 1999).

The increase of temperatures at the beginning of the Holocene period (10 ka BP) accelerated the melting of the ice sheets. In Europe, temperatures increased rapidly to values above those of the present day (Beaulieu et al., 1994; Walker, 1995). The Gulf Stream moved north, and the increased humidity transfer from the Atlantic Sea over the European continent resulted in higher precipitation. The increased temperature and precipitation provided favourable conditions for the colonisation of the temperate forest species. Non-climatic factors such as soil development and competition between species were also involved but at a shorter time-scale. Whitlock and Bartlein (1997) have proposed that climate changes are the cause of the millennial scale changes in vegetation. Where there are no large-scale changes in climate, such as those seen during the transition from glacial to interglacial period, ecosystem changes are better explained by interactions between the vegetation and its non-climatic environment (e.g. soils, competitive interactions).

Past distributions of elements of the deciduous forests can be reconstructed using fossil geological records, most notably fossil pollen sequences (Huntley and Birks, 1983). A large number of studies have been carried out on the European continent, covering all or part of the period between the LGM and the present. Many of these have been archived in the European Pollen Database (EPD), and these form the basis for the present study.

The purpose of the present paper is to: (1) locate the glacial period refugia for the deciduous oak; (2) reconstruct the general pattern of distribution of the deciduous oak at intervals of 500 radiocarbon years, regardless of any specific climatic event. The maps cover the period between 15 and 6 ka, and correspond to the most recent period of non-anthropogenic change in the distribution. By 6 ka, European oak species had largely reached their present-day limits. Later distribution changes may have been caused by human activities.

2. Methodology

2.1. Pollen analysis

Pollen analysis has been well-established as a means for reconstructing vegetational history, and the period between the end of the last glacial period and the present day is well documented (Berglund et al., 1996). The pollen grains and spores produced by plants preserve well in anoxic environments, e.g. lake sediments or peat bogs. They may be extracted from these deposits by sampling exposed sections, or more commonly, by taking sediment cores. The resulting sequences are sub-sampled along their length, to provide a stratigraphically ordered set of samples.

The variations of the pollen content between these samples (the pollen assemblages) reflect the past changes in the vegetation that surrounded the sample site. These variations are normally presented in the form of a pollen diagram, with the changes in pollen percentages of each taxon plotted against depth, thus enabling the temporal changes in the representation of individual taxa and in the makeup of the surrounding vegetation to be examined.

When interpreting the results of a pollen diagram, it is important to bear in mind the factors that influence the representation of any particular taxa in the sediments, e.g. the pollen production, transportation, the catchment area of the sample site. The transportation of the pollen grains varies from few metres to hundreds of kilometres and so pollen grains may be found of taxa that were not present locally or even regionally. Large open-system lakes have a larger pollen-catchment area, and thus receive a greater amount of pollen from long-distance transport (Jacobson and Bradshaw, 1981). Small, closed-basin lakes, or at the extreme, small forest hollows, receive pollen from a reduced area and so the nature of the recorded signal reflects vegetation changes on a more local scale. Studies on the representation of tree in sediments suggest that low percentages indicate either the presence of large populations at a distance greater than 20 km (Woods and Davis, 1989), or the installation of small scattered local populations (Bennett, 1988). Taking these factors into account, we have chosen a cut-off of 0.5%. Values lower than this are assumed to come from population at distances greater than 20 km, whereas a percentage greater than 0.5% indicates the presence of *Quercus* within this region. A cut-off higher than this may not detect populations that are under-represented due to site-specific variations (Davis et al., 1991). The pollen sum is the total number of pollen grains of tree, shrub and herbaceous taxa, counted for each level of each core. It therefore explicitly excludes aquatic plants, as these are often over-represented in pollen sequences, due to their proximity to pollen sites. These criteria should be kept in mind when interpreting the distribution maps of oak.

A further issue which is the representation of plant species in the fossil record is the identification of the pollen grains. The grouping "deciduous *Quercus*", as used here, includes pollen from 22 *Quercus* species listed in the flora Europeae (Tutin et al., 1964), including one evergreen species and three semi-evergreen (Huntley and Birks, 1983). Whilst distinction is occasionally made between the species of this group, this does not occur consistently or regularly. The maps presented here therefore include pollen derived from these 22 species.

2.2. Chronologies

For any pollen sequence, it is necessary to establish a time-scale on which to interpret the observed palynological changes. For a single site, this provides a means to examine the timing and rate of inferred vegetational changes at the site and to relate these to changes at a regional scale. In a study such as the one presented here where vegetational changes are examined on a continental scale, these chronologies play an essential role in allowing a correlation to be made between the network of sites. The chronology is based on the dates attributed to significant changes in the pollen assemblages, or on independent dating evidence.

The principal form of independent dating used for pollen sequences is radiocarbon measurements on the sediments or, preferably, plant remains derived from the same fossil record. A number of measurements are made throughout the core, and the chronology is obtained by interpolation between these dates, giving a date for each sample. The reliability of the chronology, therefore, depends on the number of available control dates. The radiocarbon dates may be supplemented by other control points, e.g. layers of volcanic ash derived from a known dated eruption.

There are, however, a number of problems in using radiocarbon dates, mainly contamination by inert carbon (see Bowman, 1990 or Lowe and Walker, 1997, Chapter 5 for more details), which must be taken into account when constructing a chronology. Also, it should be stressed that ages expressed in ^{14}C years, which are a measure of the ratio of $^{14}C/^{12}C$, are not equal to calendar ages due to variations in the atmospheric production of ^{14}C (Stuiver et al., 1998). However, sequences with some form of objective dates are preferable when studying time-dependent phenomena, such as the spread of a tree species. Where possible, undated sequences were omitted from the data-set. A few undated sites were retained in areas were no other information was available, principally the north of the Balkan peninsula. Dates for these sites were estimated by correlation with the nearest dated sites.

2.3. Database of pollen sequences

The EPD (http://medias.meteo.fr/paleo/epd/epd_main.html) was established in 1991 to archive, in a relational database, the original data from pollen analyses performed across Europe. Of the 875 sequences which are currently held in the EPD, 483 have chronologies based on radiocarbon dates as described above. These formed the basis of the data-set used to map the oak pollen percentages.

To this data-set, information was added from 50 sequences held in the Alpine Palynological Database (ALPADABA), covering Switzerland and Austria, plus several sequences supplied for use in this project. Finally, in areas where no original data were available for use in this project, the percentages of *Quercus* were digitised directly from the published pollen diagrams. The digitising method used to recover the data was tested on sites where the original

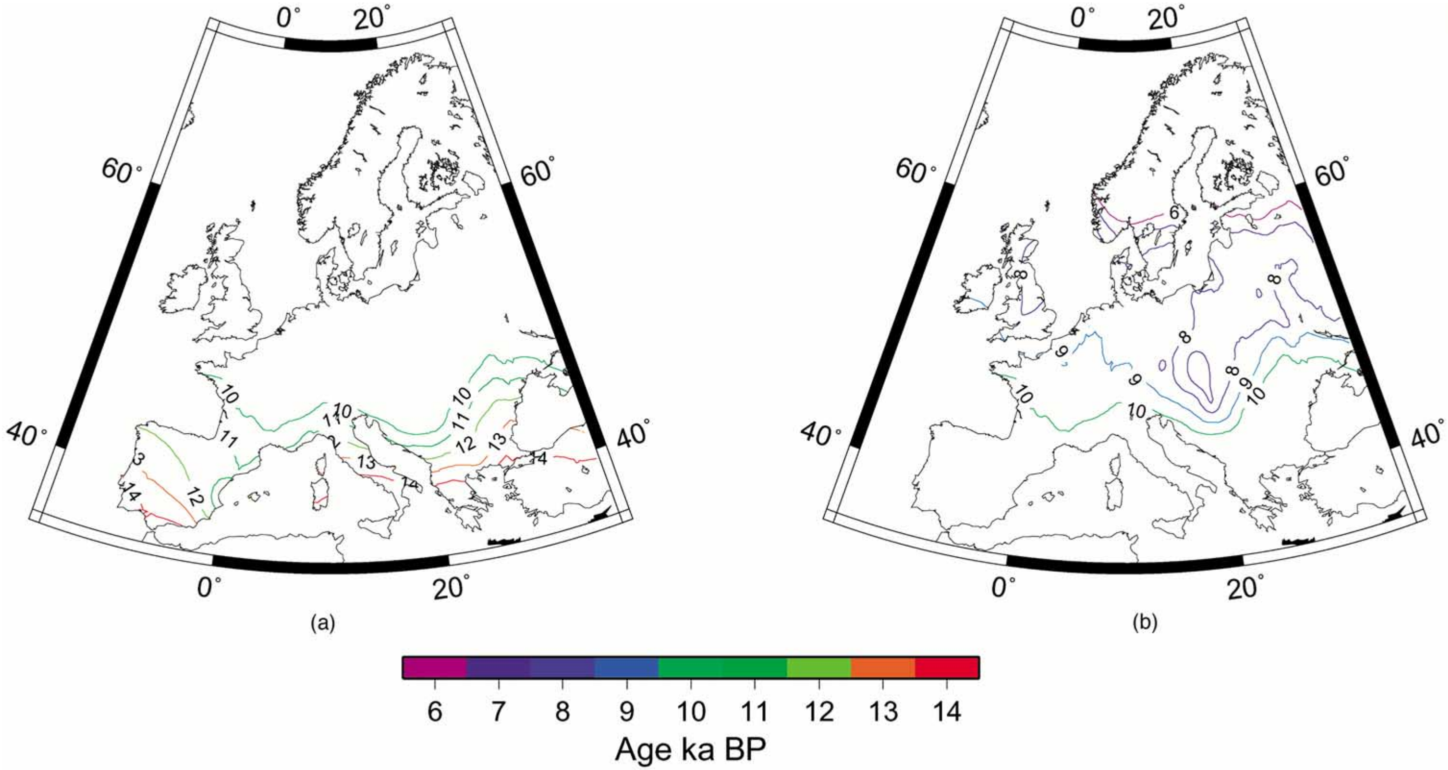

Fig. 1. Maps based on the time of first arrival of the oak from the pollen diagram. The maps show clearly the south to north direction of the spread, as well as the differences in rates of expansion between the west and east. (a) Range expansion of oak during the late-glacial period (15–10 ka BP). (b) Range expansion of oak during the Holocene period (10 ka BP to present). No contours are drawn after 6 ka, as by this time the oak had reached its range limit. (c) Map showing the standard deviations (95%) resulting from the interpolation process. The deviations are well contained in regions of high site density, but increase strongly in areas of little or no information. (d) Distribution of sites used in the mapping.

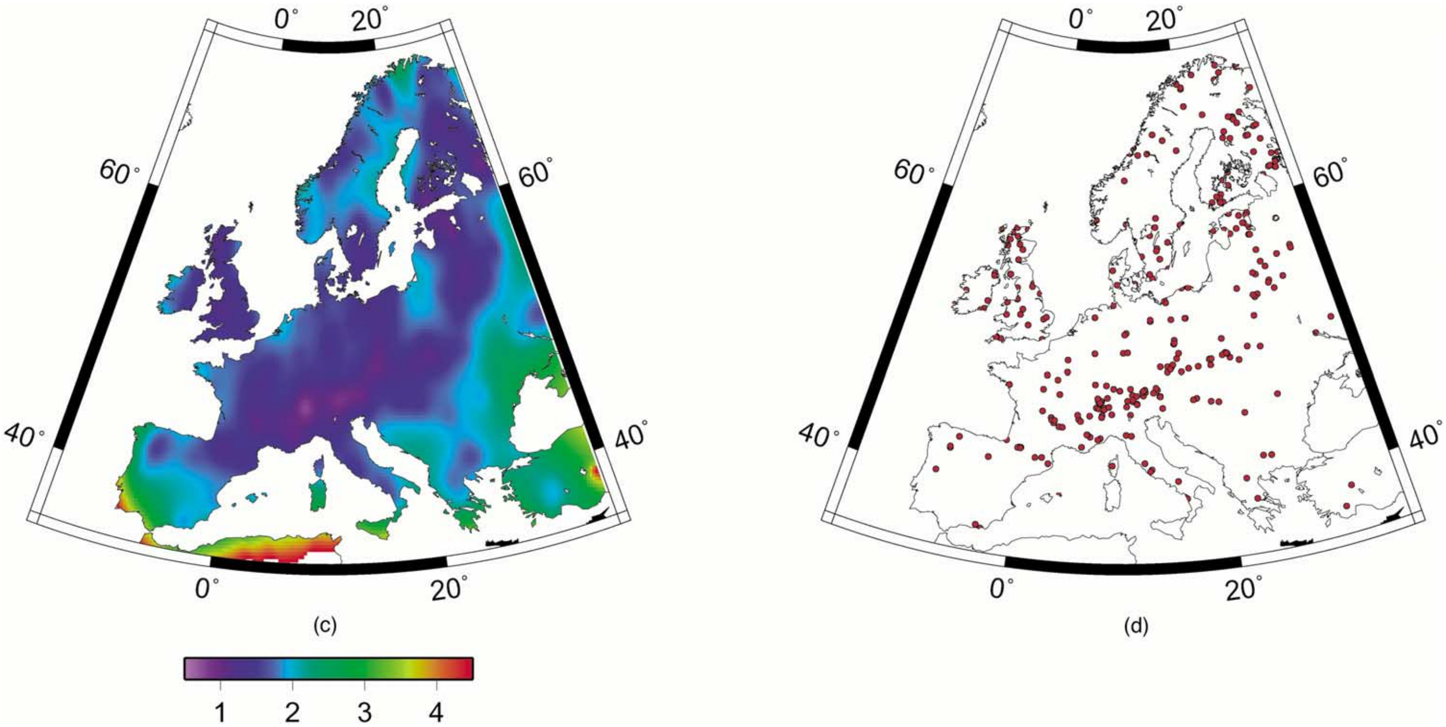

Fig. 1. (*Continued*).

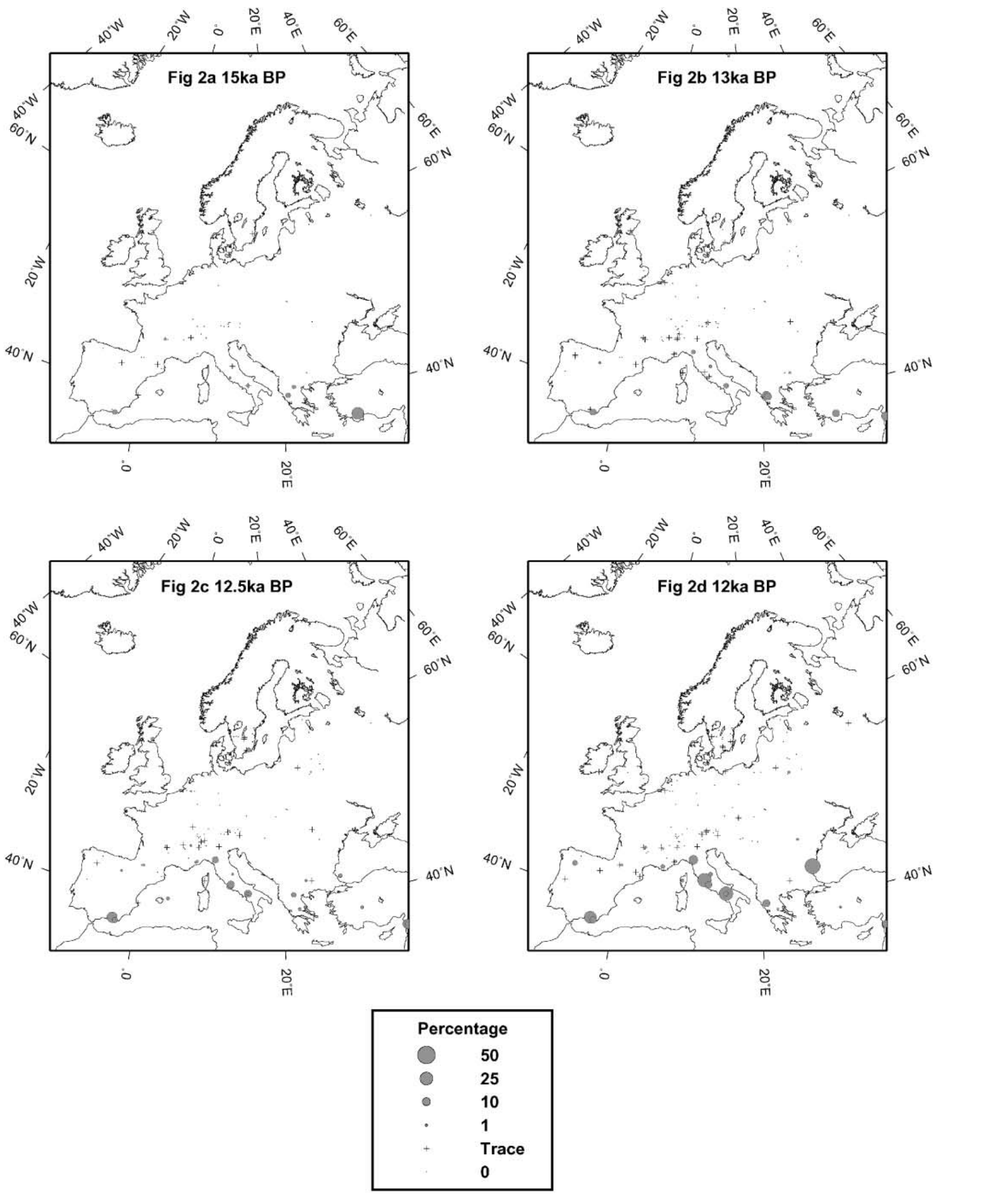

Fig. 2. (a–n) Maps showing the variation in pollen percentages at sites across Europe between 15 and 6 ka BP. The points represent sites where no oak pollen was found at that period, and the cross where traces (<0.5%) were found.

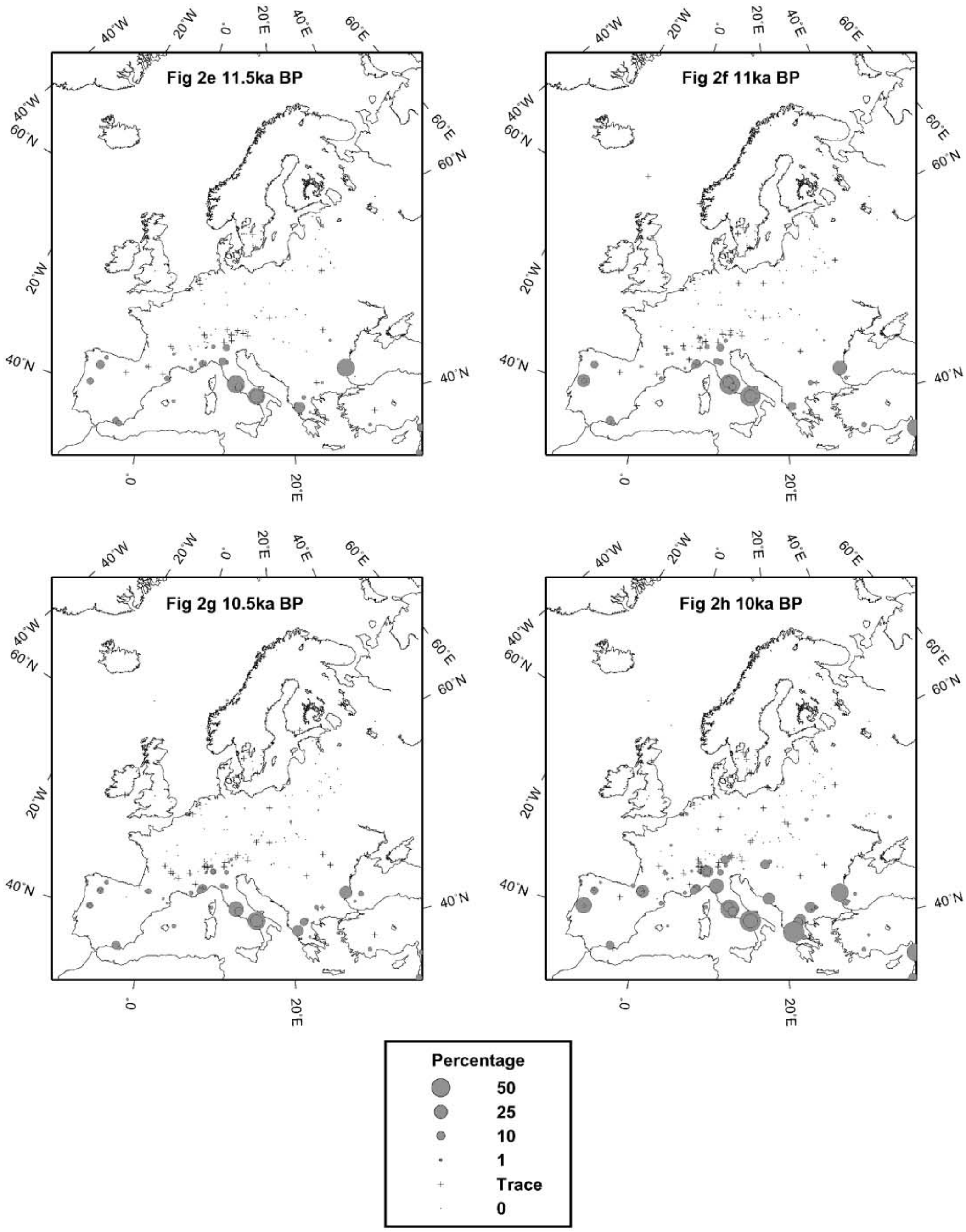

Fig. 2. (*Continued*).

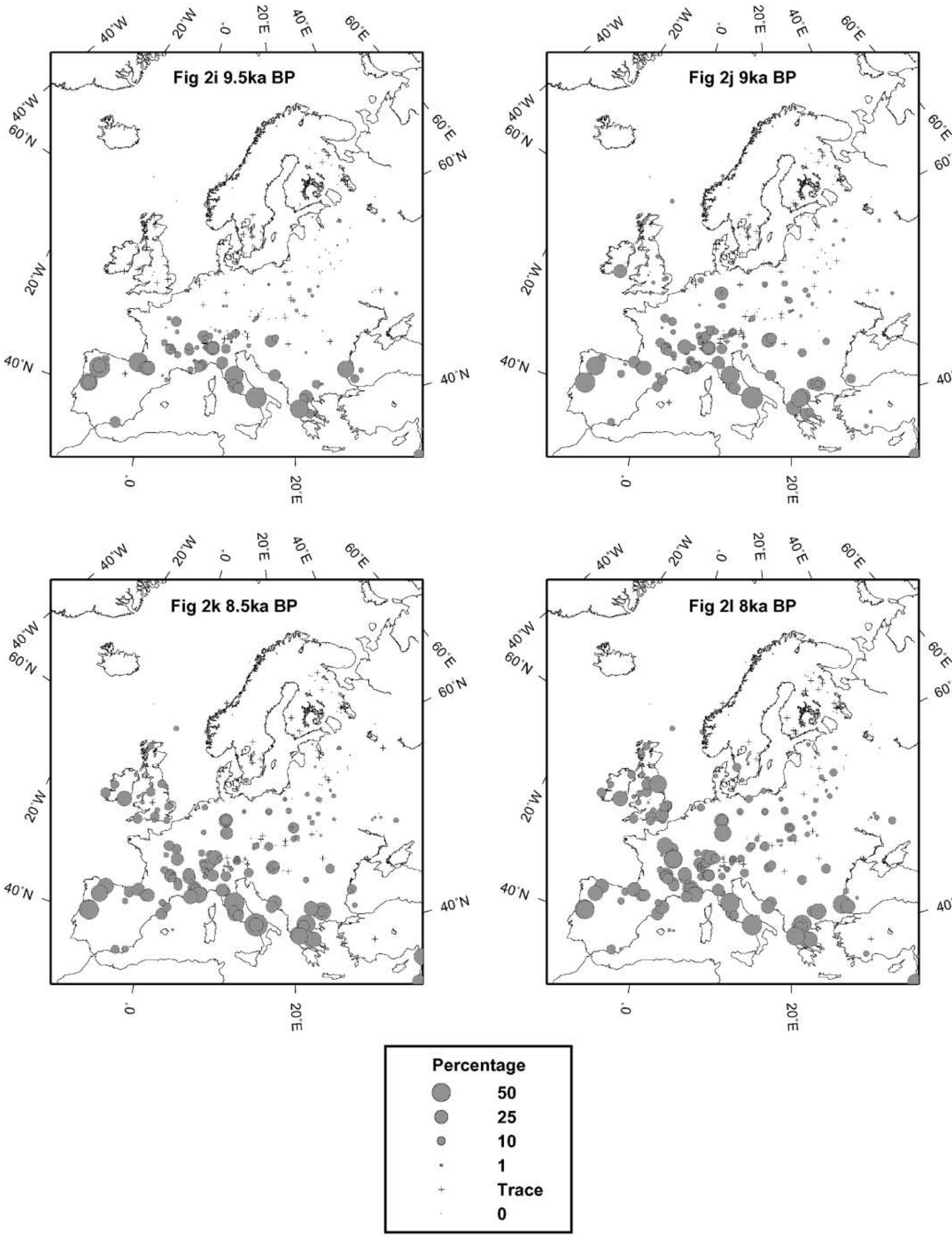

Fig. 2. (*Continued*).

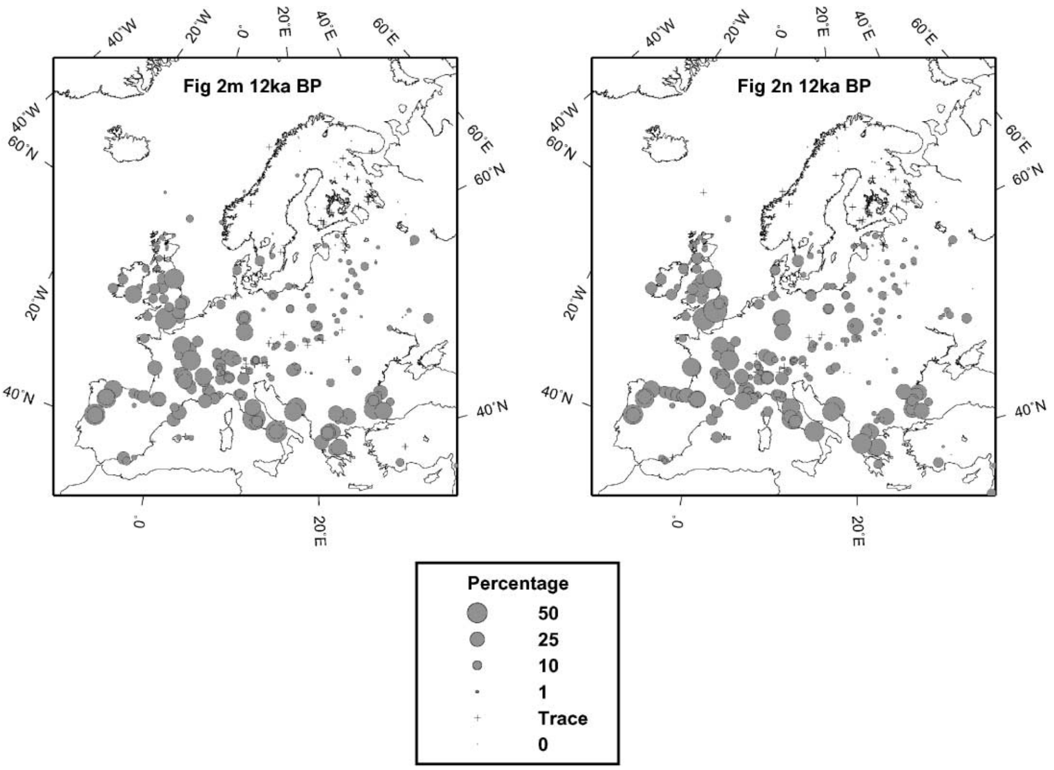

Fig. 2. (*Continued*).

counts are available and the accuracy is greater than 99% (Brewer, unpubl.).

In all, approximately 600 sequences were used to build the time slice maps. Fig. 1d shows the distribution across Europe of the pollen sequences used. (Details of the sites used are listed in Appendix A.)

2.4. Data extraction and mapping

Oak pollen percentages were calculated for every dated sample based on a pollen sum of trees, shrubs and herbaceous plants. At each site, percentages were taken from the sample with an age closest to that of the required time period. If the difference in ages was greater than 250 years, the sample was dropped from the set. Where two samples had the same age difference, the average was taken. The set of sample percentages obtained have been plotted as a series of maps showing the distribution of the oak pollen percentages for a series of time-slices between 15 and 6 ka BP (Fig. 2a–n).

In order to summarise the data, two maps (Fig. 1a and b) have been produced showing isochrones for the spread of *Quercus* across the European continent (see Birks (1989) for a review of the method). The range increase has been split into two periods, the late-glacial interstadial and the Holocene. Arrival times were estimated using the rational limit, the age at which the pollen curve begins to rise to high percentages (Smith and Pilcher, 1973). In some areas, these were supplemented using diagrams available in the literature. The resulting set of times was interpolated onto a 15 arc-min grid using ordinary kriging with a trend model (Deutsch and Journel, 1998) to show the progressive spread of the deciduous oak across the European continent, and contoured to produce the isochrone map (Fig. 1a and b). The trend model is included to take into account the natural north–south trend in the data-set. Fig. 1c shows the standard deviation of the interpolated ages, which allows a check of the reliability of the interpolation. The deviation increases greatly in areas where no sample data was available, but for the majority of Europe it is relatively low. It should be noted that the number of sites is limited in southern Europe, and the interpolation should be treated with greater caution in this area.

3. Discussion

In interpreting the distributions presented on these maps, it is important to take into account the problems described above: erroneous chronologies can indicate the presence of oak pollen earlier than or later than the actual time of arrival and long-distance transport of pollen may produce a signal at a site some kilometres away from the real limit of the oak at a certain period. Regional studies were used to help avoid misinterpretations resulting from these problems.

In order to explain the late and post-glacial change in distribution of the oak, it is necessary to take into account both the rapidity and the non-linearity of climatic changes during the late-glacial period. We have therefore defined two types of refugia. The first, called primary refugia, are those locations which allowed the existence of populations during the entirety of the glacial period. The second type represents those sites which provided shelter for oak populations during the shorter cold periods, therefore, playing an important role in the range expansion (see discussion below).

3.1. Location of glacial refugia

The restrictions on the distribution of the oak by the climatic conditions of the LGM has been described above. In order to locate the refugia from which modern populations originated, it is necessary to reconstruct this distribution as closely as possible. The primary refugia for deciduous *Quercus* are therefore most easily identified from the single map dated to the end of the glacial period at 15 ka BP (Fig. 2a). The isochrone map (Fig. 1a) further indicates that the source populations for the modern day forest were restricted to these sites where local favourable conditions prevailed. These maps identify three possible regions of Europe that acted as primary refugia for the oak during the last glacial period:

1. Southern Iberian peninsula (refugia type site Padul, Pons and Reille (1988));
2. Southern Italy (refugia type site Laghi di Monticchio, Watts et al. (1996));
3. The southern Balkan peninsula (refugia type sites Ioannina (Tzedakis, 1994) and the Black Sea (Shopov et al., 1992)).

Further, the diagrams at these sites show continuous deposition of oak pollen further back into the glacial period. The Balkan refugium contains two refugial areas, Greece and the western coast of the Black Sea. This second refugium is not shown on the map at 15 ka BP, but is represented on the isochrone map. At the site in south–west Turkey which shows a presence of approximately 20% oak pollen in the sediments at this time, the pollen has been identified as that of *Quercus cerris* (Bottema and Van Zeist, 1991), and may be considered as a refugium for this species. All refugia type sites are located in or near mountainous areas: the Sierra Nevada in southern Spain, the southern Apennine chain in Italy and the Pindos mountains in Greece. This supports the idea that the refugia for the deciduous trees would have been located at mid-altitude sites, where the precipitation would have been higher than on the plains during the arid glacial period (Van der Hammen et al., 1971; Beug, 1975).

Previous work on the location of glacial refugia of the deciduous oak has indicated eight possible refugia (Huntley and Birks, 1983, p. 628; Bennett et al., 1991). Our results enabled us to confirm half of these locations, and more clearly define the position of these refugia. No evidence was found in this study for the refugia proposed in northern Spain, southern France, or in the Alps and northern Balkans (Huntley and Birks, 1983). The change in the delimitation of the refugial zones is a result of two factors. Firstly, the improvements in the data-set on which these maps are based. The new data-set includes sites that has not been studied in 1983, and is predominantly based on sequences with independent chronological information. Secondly, the extension back in time to 15 ka BP. Since the work of Huntley and Birks (1983) which began at 13 ka BP, studies have shown that improvements in the climate occurred from 15 ka BP onwards (Walker, 1995). Therefore, by 13 ka BP, changes in the oak distribution may have already taken place. Our set of maps begin at 15 ka BP, which should provide a closer representation of the glacial distribution of oaks.

Our interpretation of the location is limited by the relative scarcity of pollen sequences covering the glacial period. In addition, proof cannot be offered for the absence of a taxon at a site, only for its presence. Therefore, it is possible, indeed probable, that refugia existed elsewhere within the European continent. Some possibilities are discussed below and in other articles within this project (e.g. Petit et al., 2002; Olalde et al., 2001). However, taking into account the climatic data discussed above and the evidence observed on the maps, we conclude that the primary European refugial zone is constrained to the extreme south of the continent.

It is notable that the location of the proposed refugia follow a line that is not entirely horizontal. The latitude of the refugia increases with distance away from the Atlantic coast, and runs parallel, if somewhat lower than, the proposed distribution of permafrost on the European continent during the glacial period (Bell and Walker, 1992, p. 87). The oceanic impact on the distribution of the oak can be clearly seen here. During the glacial period, cold arctic waters limited the distribution of oaks below 40°N, the level of the NAPF. The impact of these waters diminished with distance from the coast and so refugia may be expected at higher latitudes in the interior mountains than along the coast. In contrast, the warmth and moisture from the Gulf Stream allows the current survival of the oak at higher latitudes along the Atlantic coast than in the interior of the continent (Hultén and Fries, 1986).

As discussed above, no direct evidence can therefore be taken from the pollen maps about the possible location of each oak species during the glacial period. For certain species with a currently restricted distribution, a glacial period refugium may be postulated in the refugial zone defined above, that is closest to the actual distribution. However, this does not take into account the possibility of the disappearance of the species in other parts of Europe. For the more widespread species (e.g. *Q. petraea*, *Q. pubescens* and *Q. robur*), such a distinction is harder to make.

3.2. Range expansion during the late-glacial interstadial

The series of maps (Fig. 2a and b) show in a detailed manner the change in the distribution of the fossil oak pollen deposits. This series suggest that the colonisation took place in two stages, the first during the late-glacial interstadial, and a second step from temporary refugia located further north during the climatic optimum of the early Holocene.

This first step was a spread from the glacial refugia (see above) northwards across southern Europe. During the period between 13 and 11 ka BP, the NAPF retreated northwards as far as Iceland (Ruddiman and McIntyre, 1981), with increased temperatures and moisture availability across the European continent. At the same time, there is an increase in the percentages recorded of oak pollen in sites south of the main European mountain ranges, concurrent with new occurrences in these regions. Notably, there is a strong increase throughout Italy from 12.5 ka BP, and on the western Iberian coast from 11.5 ka BP. However, any corresponding expansion on the eastern Adriatic coast is obscured due to a lack of sites.

In Italy, oak spread rapidly northwards along the Apennine chain, reaching the north–west between 12.5 and 12 ka BP (Lowe et al., 1996). From here, oak spread west beyond the Alps along the Mediterranean coast by the middle of the late-glacial interstadial (Nicol-Pichard, 1987). The dispersal into the north–east was slower, reaching the southern Alps by the end of the late-glacial interstadial (Schneider and Tobolski, 1985). Dispersal appears to have been more rapid in Italy than from the other refugia, possibly suggesting a refugia in the central Italy. However, whilst oak pollen has been recorded at sites in this area during the glacial periods, the low quantities and discontinuous nature of the records suggest long-distance transport (e.g. Lowe et al., 1996). If mountainous regions offered ideal conditions for the oak, as for many deciduous tree species (Huntley and Birks, 1983), the observed rapidity of spread may simply result from the ideal north–south alignment of the Apennine chain. The high percentages of deciduous oak pollen, particularly after 12 ka BP, suggest that it formed a dominant part of the vegetation assemblage during the late-glacial period. Oak pollen is present at a site on Corsica from between 12.5 and 12 ka BP (Reille et al., 1997). There are two possible sources for this presence: either transport across the sea from Italy, or an endemic refugium on either Corsica or Sardinia. In the absence of pollen data from Sardinia, or from the glacial period on Corsica (Reille et al., 1997), neither hypothesis can be confirmed.

In the Iberian peninsula, this spread was less rapid, reaching the region of Galicia in the north–west by 12 ka BP. By 11.5 ka BP, there is a significant presence along the west coast, and south of the Pyrenees, and by the end of the late-glacial interstadial, oak pollen is recorded in sites in both the west and east Pyrenees. It is, however, difficult to discern the pattern of spread, due to the lack of sites in the centre and south–west of the Iberian peninsula. The dispersal may have been fan-shaped, spreading out across the peninsula from the south–east, or may have followed a south–north path along the coasts. This second hypothesis gives rise to the possibility of a second glacial refugium in the south–west. The site of El Asperillo in the south–west of Spain (Stevenson, 1984), indicates a possible regional presence of *Quercus* at the start of the late-glacial interstadial period (ca. 13 ka BP). However, the date attributed to this pollen deposit is too imprecise to confirm or reject this hypothesis. At a site on the east coast of Spain, there is no evidence for the establishment of the oak during the late-glacial period (Navarrés, Carrion and Van Geel, 1999). The first establishment of oak forests come at approximately 6 ka BP, with the decline of the dominant pine forest. Whilst the authors state that the regional development of *Quercus* cannot be extrapolated from this record, this nevertheless suggests that the spread of oak was delayed on the Spanish Mediterranean coast. The distributional changes in the east of the Iberian peninsula would therefore have taken place inland.

In contrast to the expansion of oak seen at sites on the Iberian and Italian peninsulas, there is little observed increase in the distribution range at the Greek sites. Bottema (1979) suggests that the expansion in this area was limited by the lack of available precipitation. As stated above, the interpretation of the vegetation history of the Balkans is made more difficult by the lack of sites in the central region, which cover the late-glacial interstadial. Two sites on the Adriatic coast, the island of Mljet (Beug, 1960) and Vid (Brande, 1973) both show a strong presence of oak from the early Holocene onwards, but no inference can be made from these about a potential occurrence in the late-glacial. However, a new dated diagram from Taul Zanogotti (Farcas et al., 1999) in the west of the Carpathian chain indicates a low but regular occurrence of deciduous *Quercus* pollen in the late-glacial interstadial. There are also several sites that give evidence from the late-glacial in the north of the Balkan peninsula. The extensively studied Ljublana moor in Slovenia indicates an arrival of *Quercus* towards the end of the late-glacial interstadial (Culiberg, 1991). In the absence of any direct evidence from the central Balkans, our interpretation is based on this evidence and a latitudinal comparison across Europe, between 13 and 11 ka BP, the oak spread northwards from its southern glacial refugia, to reach the Carpathian chain, and the south-eastern Alps. There is no evidence from the maps of an expansion north of these mountain chains. This may result from the physical barrier imposed by the mountains, or from climatic conditions that remained unfavourable to in the north.

3.3. Location of secondary refugia

Little change in distribution is seen between 11 and 10 ka BP; there is no significant outward spread, and the values in southern Europe decline. This period corresponds to the cold Younger Dryas period, and an re-advance of the NAPF to the level of north–west Spain (approx. 43°N, Ruddiman and McIntyre, 1981). Available precipitation declined across Europe (Walker, 1995; Isarin and Renssen, 1999). In pollen records across Europe, the impact of this period can be seen as a decline in the mesophilous taxa, and an increase in steppic elements (e.g. *Artemisia*). The reaction of *Quercus* to this climatic change appears to vary between sites. At some sites, *Quercus* pollen is no longer deposited during this period, whilst at other sites there is a continuous but reduced deposition of pollen. This reduction is more pronounced in the northern parts of the range. However, it is possible that the impact of the YD is not fully represented on the map at 10.5 ka BP. The 500-year time interval may therefore represent the limit, imposed by the problems described above, of the temporal resolution possible for mapping pollen data at this scale.

The sites with a continued presence of *Quercus* pollen appear to act as temporary refugia, enabling *Quercus* to remain further north during this relatively short cold period, than in the full glacial period. We retain the term refugia as the climatic conditions of the Younger Dryas stadial had an adverse effect on thermophilous vegetation that has been well-documented (e.g. Berglund et al., 1996; Hoek, 1997). We propose an area for these secondary refugia that is south of a line running from the Pyrenees in the east to the Carpathian chain in the west. Higher precipitation due to the orographic effect of the mountain chains of central Europe (Pyrenees, Alps, Carpathians) would have allowed the survival of small populations of trees.

3.4. Range expansion during the Holocene period

After approximately 10 ka BP, there was a shift in the climate from the cold, dry conditions to warmer conditions (Huntley and Prentice, 1993). This warming coincided with a shift northwards of the NAPF to a position north of Iceland (approx. 65°N, Ruddiman and McIntyre, 1981), and a resulting increase in moisture availability across Europe.

Coupled with the increased summer insolation, the period 10–9 ka BP was an optimal period for the expansion of mesophilous tree species. The late-glacial expansion and resulting secondary refugia had left populations of the oak in ideal positions to spread into the northern European continent. From the beginning of the Holocene, *Quercus* spread rapidly north and west into France, reaching the south of Ireland and England between 9.5 and 9 ka BP. However, the Alps played a major role in slowing the spread of oak northward into central Europe. The Vosges mountains may have also prevented the effects of the Gulf Stream from reaching southern Germany. These geological barriers may explain the much later appearance of oak to the north of the Alps. The maps indicate the presence of oak south of the Alps as early as 11.5 ka BP while the presence on the northern slopes is dated around 9 ka BP. Once oak has reached the southern part of the central Europe, around 9 ka BP, its spread was much faster, reaching southern Scandinavia in less than 1000 years. To the east of the Alps, oak had reached northern Belorussia by 8 ka BP. However, to the east the dispersal was patchy, in contrast to the relatively smooth spread in the west, indicating that the expansion may have been limited by a secondary factor, possibly competition. By approximately 6 ka BP, however, oak had filled the majority of its modern-day range.

The rapidity of the dispersal into northern Europe makes it hard to define the dynamics of the spread during the Holocene. Three possible colonisation pathways may be identified from the isochrone map: western, central and eastern. The west path follows the French Atlantic coast from the Pyrenees to the British Isles. In the east, a path can be discerned spreading north from the Carpathian mountains into the region east of the Baltic sea. In central Europe, the situation is unclear: the dispersal into Germany, and ultimately Scandinavia may have come from the Pyrenees, the central or south-eastern Alps, or from a combination of all three.

The complete late- and post-glacial range expansion of deciduous *Quercus* can be seen more clearly on the summary map (Fig. 1a), which shows the spread from the southern refugia to the northern mountains. From this position, populations of oak spread rapidly into north-western Europe at the start of the current warm period, but slower in north-eastern Europe. It is important to note that the area bounded by the contours on this map (Fig. 1a) do not indicate the presence of oak forest. They should be interpreted as the areas indicated as suitable by the interpolation to have contained small populations of oak.

4. Conclusions

The present study has allowed a better definition of the position of glacial refugia, timing of spread of oak and its colonisation pathways throughout Europe since the last glacial period than previous studies. We propose that two types of refugia may be identified from the study of the range expansion of oaks.

- Primary refugia, which we have identified only in the extreme south of the continent for *Quercus*, are situated in areas able to sustain the species even during the glacial maximum (18 ka BP) provide the full glacial or primary refugia for these mesophilous tree species.
- Secondary or temporary refugia have been identified during the climatic variations of the glacial–interglacial transition period (13–11 ka BP). These are found in areas that were unable to sustain viable populations in the prevailing conditions of the glacial maximum, but able to provide temporary refugia during the shorter climatically adverse periods within this transition period, e.g. the Younger Dryas.

From this, we can explain the pattern of spread of *Quercus* in the following manner. The deciduous oak taxa survived the last glacial period in three principal southern refugial areas (southern Spain, southern Italy and the southern Balkans).

The climatic change to warmer/moister conditions at 13 ka BP offered suitable conditions for the northward spread of *Quercus* from the glacial refugia. By the end of this period, at about 11 ka BP, they had reached the main central mountain ranges (Alps, Pyrenees and Carpathian mountains) and possibly beyond.

The return to colder/dryer conditions during the Younger Dryas cold period (11–10 ka BP) halted this spread, and led to the extinction of any populations north of these mountain ranges, and the reduction of other populations. However, certain locations within these mountain ranges provided refugia for the oak during this short-lived but cold period.

The warming at the start of the Holocene (10 ka BP) allowed a rapid dispersal of oak along the Atlantic coast, but in central Europe the northward spread was delayed by the physical barrier of the Alps. Once the Alps were passed, the distribution increased relatively rapid across central and eastern Europe, but the reduced pollen percentages indicate that expansion of populations in the east was limited by a secondary factor. The rapidity of the spread in the early Holocene presents problems in clearly defining the colonisation pathways in northern Europe.

The climate of the late-glacial and early Holocene acted as the strongest controlling factor on the spread of the deciduous oak. There is a notable correlation between the movements of the NAPF and the spread of the trees. Whilst the apparent refugial zone has been precisely defined in this study, the actual locations of the refugial sites remain unclear. Further studies, notably of long, well-dated sequences in the area described may help to resolve this problem.

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Appendix A. List of sites used in this project (full details of the sites, including references can be obtained from the authors)

Site name	Latitude	Longitude
Abernethy Forest	56.23	−3.72
Aegelsee	46.65	7.54
Ageröds Mosse	55.83	13.42
Ahlenmoor	53.70	8.73
Aholami	61.88	25.22
Akuvaara	69.12	27.68
Albufera Alcudia	39.79	3.12
Aletschwald	46.38	8.02
Algendar	39.94	3.96
Allt na Feithe Sheilich	57.32	−3.90
Alp Lüsga, Belalp	46.38	7.98
Alpi di Robièi, Val Bavona	46.43	8.52
Alsa	43.12	−4.02
Altenweiher	48.01	6.99
Ampoix	48.17	2.93
Amsoldingersee	46.72	7.58
Amtkel	43.27	41.31
Antas	37.21	−1.82
Arkutino lake	42.37	27.73

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Arsenala-Varna lake	43.20	27.83
Arts Lough	52.95	−6.43
Atxuri	43.25	−1.55
Ballinloghig Lake	52.20	−10.31
Ballybetagh	53.17	−6.25
Banyoles [Girona]	42.13	2.75
Bebrukas lake	54.09	24.12
Belle Lake	52.18	−7.03
Bergakyllen	57.17	16.15
Besbog-2	41.75	23.67
Beysehir Gölü I	37.54	31.50
Bezdonnoe	62.03	32.77
Bezymiannoe	54.22	30.00
Biot	43.80	7.10
Biscaye	43.03	−0.08
Björkedöds Mosse	56.28	12.50
Black Sea South	42.07	28.48
Black Sea South–west	42.18	28.92
Black Sea SW	42.07	28.89
Blato (Zispachy)	49.04	15.19
Blavasstjonn	64.92	11.67
Bledowo lake	52.55	20.67
Blomoy	60.53	4.88
Blusovie	43.68	41.16
Bobrov	49.45	19.57
Boehnigsee Goldmoos	46.26	7.84
Bol'shoe Eravnoe Lake	52.58	111.67
Bonnecombe	44.57	3.12
Borkovicka Blata	49.22	14.90
Bosscherheide	51.58	6.09
Breitnau	47.97	8.21
Brugiroux	45.15	2.85
Bruvatnet	70.18	28.42
Cala Galdana	39.94	3.96
Cala'n Porter	39.87	4.13
Cam Loch	58.08	−5.00
Chabada (central Yakutia)	61.98	129.37
Charco da Candieira	40.34	−7.58
Chernikhovo	53.42	26.43
Chernoe lake	50.95	106.63
Clapeyret	44.15	7.24
Clatteringshaws Loch	55.07	−4.28
Coire Bog	57.85	−4.42
Col des Lauzes	45.77	6.53

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Colfiorito	43.02	12.92
Coolteen	52.35	−6.60
Cooran Lane	55.12	−4.40
Creich Castle	56.38	−3.08
Crovani	42.47	8.68
Cueto de la Avellanosa	43.12	−4.36
Dallican water	60.39	−1.10
Danyagiin-Hara-Nur	48.62	88.95
Darzlubie Forest	54.70	18.17
Derput, Yakutia	57.03	124.12
Dlinnoe	62.32	33.85
Dolgoe	55.23	28.18
Domsjön	58.30	12.45
Domsvatnet	70.32	31.03
Donvold	68.13	13.58
Dood-Nur	51.33	99.38
Dossaccio, Bormio	46.47	10.33
Drassanes	41.38	2.18
Dry Lake II [Rila mountain]	42.05	23.53
Durchenbergried	47.73	8.98
Dürrenecksee-Moor	47.17	13.87
Dvur Ansov	48.79	16.39
Edessa	40.82	21.95
Egelsee	47.60	12.17
Eggen ob Blatten	46.37	7.98
Etang de Cheylade	45.09	2.90
Etang d'y Cor, Montana	46.30	7.47
Ezerisch	55.85	30.00
Fjällnas	62.55	12.17
Fjallsjön 1	57.75	12.86
Flaatevatn	59.70	6.17
Flögeln	53.67	8.76
Fougères	48.52	0.83
Frasne (Doubs)	46.83	6.16
Frengstadsetra	62.57	10.13
Freychinède	42.47	1.44
Fuchsschwanzmoos	47.12	13.90
Galtsjön	56.22	15.22
Gänsemoos, Schwarzenburg	46.83	7.35
Garaselet-Lappviken (Byskeälven)	65.33	19.93
Gerlos	47.23	12.13
Ghab	35.68	36.30
Giannitsa	40.67	22.32

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Giering	47.47	12.35
Gioux	45.27	2.64
Glubokoe	61.07	36.05
Gondo-Alpjen	46.20	8.10
Gotnavolok	62.20	33.80
Gourg Nègre	42.63	2.22
Grächen-See	46.20	7.83
Grande Brière	47.37	−2.25
Grasvatn	63.70	8.70
Greicheralp, Riederalp	46.37	8.02
Gretskoe	55.63	27.77
Grosses Überling Schattseit-Moor	47.17	13.90
Hakulls Mosse A5	56.28	12.52
Halos I	39.17	22.83
Hälsegyl	56.55	14.61
Halsjön II	56.23	15.32
Haslacher See	47.75	10.78
Hawks Tor	50.53	−4.60
Hières sur Amby	45.79	5.28
Hirvilampi	60.62	24.25
Hochmoos	47.42	13.20
Hockham Mere	52.5	0.83
Hort Timoner	39.88	4.13
Hovi	61.52	−6.75
Hozelec SK-5-A	49.05	18.30
Huleh	33.20	35.32
Iezeru Calimani	47.38	25.27
Imatu mire	59.13	27.43
Ioannina	39.65	20.92
Iosipovo	51.20	28.00
Isokärret	60.22	22.13
Jasiel	49.37	21.89
Jaslo	49.78	21.47
Jestrebske blato	50.60	14.59
Kaarkotinlampi	61.42	25.87
Kaartlamminsuo	60.73	24.22
Kalsa mire	58.17	27.45
Kalven	56.53	14.56
Kamenicky	49.73	15.97
Kanjerjoki [Kuusamo]	66.12	29.00
Kansjon	57.63	14.53
Kararmik Batakligi	38.42	30.80
Karas'e Lake	53.03	70.22

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Karasieozerskoe	56.77	60.75
Kastoria	40.55	21.32
Kepskoe	65.08	32.17
Khimaditis I	40.62	21.59
Khodzal	42.95	41.91
Khomin Mokh	51.20	28.00
King's Pool	52.81	−2.11
Kirikumae	57.67	27.25
Kirkkosaari	60.87	24.50
Kluki	54.71	17.28
Kolczewo	53.92	14.67
Koldychevo	53.27	26.07
Kolmiloukkonen	66.23	28.48
Koppalosuo	62.28	33.65
Kotyrkol' Peat Bog	52.97	70.42
Kroksjön	56.27	15.02
Kubenskoe Lake	59.70	39.50
Kuivajarvi	60.78	23.83
Kupena (Western Rhodopes Mts.)	41.98	24.33
L. Albano	41.75	12.60
La Grande Pile	47.73	6.50
La Taphanel	45.27	2.68
Lac de Creno	42.20	8.95
Lac de Villa	45.68	7.76
Lac du Mont d'Orge, Sion	46.23	7.33
Lac Long Inférieur	44.06	7.45
Lac Mouton	44.06	7.44
Lac Noir	45.45	2.63
Lac Saint Léger	44.42	6.34
Ladoga Lake	61.56	31.34
Lago de Ajo	43.05	−6.15
Lago de Arreo	42.78	−2.98
Lago di Castiglione	41.89	12.76
Lago di Ganna	45.90	8.80
Lago di Ledro	45.87	10.75
Lago di Martignano	42.12	12.33
Lago di Trasimeno	43.20	12.10
Lago di Vico	42.35	12.10
Lago Grande di Monticchio	40.94	15.60
Lago Padule	44.30	10.21
Lagoa Comprida 2	40.36	−7.64
Lagodekhi	41.93	46.42
Laguna de la Roya	42.22	−6.77

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Lake Balaton	46.74	17.40
Lake Beloslav-Poveljanovo	43.20	27.83
Lake Boguda	63.67	123.25
Lake Duranunlak	43.67	28.55
Lake Ermistu	58.37	23.97
Lake Glubelka	54.95	26.42
Lake Karujarv	58.38	22.20
Lake Khomustakh	63.82	121.62
Lake Kolmilaträsk	60.28	20.15
Lake Kvarnträsk	60.35	19.98
Lake Lednica	52.56	17.39
Lake Lerna	37.58	22.75
Lake Maardu	59.43	25.00
Lake Madjagara (central Yakutia)	64.83	120.97
Lake Mirabad	33.08	47.72
Lake Nero	57.18	39.45
Lake Nuochaga	61.30	129.55
Lake Racze	53.92	14.67
Lake Sambösjön	57.13	12.42
Lake Shabla-Ezeretz	43.83	28.85
Lake Skvzetuszewskie	52.55	17.36
Lake Solso	56.13	8.63
Lake Srebarna	44.08	27.12
Lake Urmia	37.58	45.47
Lake Van	38.50	43.00
Lake Xinias	39.05	22.27
Lake Zeribar	35.53	46.12
Landos	44.85	3.82
Landruchie Mire	61.00	39.00
Landshaftnoe	64.57	30.53
Lanegegger Filz	47.70	10.77
Lanser Moor	47.23	11.42
Le Beillard	48.07	6.80
Le Fango	42.42	8.66
Le Grand Lemps	45.47	5.42
Le Jolan	45.14	2.86
Le Marais de la Perge	45.38	−1.12
Le Monge	43.05	−0.02
Le Moura	43.45	−1.55
Le Suc	44.72	3.10
Ledine	46.28	14.12
Les Enfers	47.25	7.17
Les Veaux	47.25	7.17

Appendix A. (*Continued*)

Site name	Latitude	Longitude
L'Estivalet	44.86	3.39
Leveäniemi	67.63	21.02
Liivjarve Bog	59.22	27.58
Lilla Gloppsjön	59.80	14.63
Lillsjön	57.08	12.53
Linden	46.85	7.68
Lindenmoos	47.50	12.03
Liptovsky Jan	49.04	19.68
Little Loch Roag	58.13	−6.88
Ljubljana Moor	45.98	14.53
Ljungsjön	57.73	13.33
Llyn Gwernan	52.68	−4.87
Lobsigensee	47.03	7.30
Loch a'Chroisg	57.57	−5.33
Loch Ashik	57.25	−5.83
Loch Clair	57.56	−5.34
Loch Cleat	57.07	−6.33
Loch Dungeon	55.12	−4.32
Loch Einich	57.08	−3.80
Loch Fada	57.45	−6.20
Loch Lomond Ross Dubh	56.09	−4.58
Loch Maree	57.08	−5.48
Loch Mealt	57.60	−6.13
Loch of Winless	58.47	−3.20
Loch Sionascaig	58.06	−5.18
Loch Tarff	57.15	−4.60
Lochan an Druim	58.47	−4.70
Lochan coir a'Ghobhainn	57.18	−6.30
Lochinskoe	53.55	28.60
Logylet	56.30	14.98
Loucky	49.32	15.50
Lourdes	43.03	−0.08
Luderholz	51.67	10.33
Luganskoe	43.73	40.69
Luttersee	51.58	10.17
Maanselänsuo	65.62	29.60
Mabo Moss	58.02	16.07
Maj	50.05	17.22
Maksimkin Yar	58.33	88.17
Maleshevska Mts.	41.70	23.03
Malhaire	48.50	1.00
Malo Jezero	42.78	17.35
Maloe	54.18	28.20
Malschätscher Hotter	46.67	11.45

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Marais de la Perge	45.40	−1.01
Mariahout	51.52	5.54
Masehjavri	69.05	20.98
Mayralampi	62.33	26.23
Meerfelder Maar	50.20	6.80
Mekelermeer	52.77	6.62
Menez-Cam	48.25	−3.50
Mezhgornoe	66.37	30.70
Mieminger See	47.28	10.97
Mikolajki lake	53.77	21.42
Mire Garvan	44.12	26.95
Mire Johvika	58.50	22.33
Mire Pelisoo	58.47	22.38
Mire Petrolivo	56.00	31.98
Mire Saviku	58.40	27.23
Mire Sosvyatskoe	56.20	32.00
Miroshy	51.20	28.00
Mittlere Hellelen	46.28	7.83
Mobeche Forest	48.52	1.00
Moerzeke	51.05	4.18
Mohos	46.20	26.15
Mokre Louky (south)	48.83	14.83
Moossalmmoor	47.75	13.52
Morrone Birkwoods	57.00	−3.43
Moselotte	48.03	7.00
Mosfell [Grimsnes]	64.13	−20.61
Moshkarnoe	62.25	34.05
Mossen	60.12	21.60
Motta Naluns	46.80	10.27
Moulin de Prugnolas	45.85	1.65
Mukkavaara	68.92	21.00
Mullsjön	58.28	14.23
Mur de Sologne	47.40	1.50
Mustusuo	61.81	33.50
Mutorog-Southern Pirin Mts.	43.52	23.62
Naroch	54.82	26.75
Navarrés	39.10	0.68
Nemino	62.75	34.58
Nenazvannoe	61.81	33.48
Niechorze	54.00	15.05
Nigula	58.00	24.67
Nizhnevartovsk	76.67	62.00
Nosuo	64.57	30.83
Notsel	51.55	4.77

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Novolsky	56.77	26.18
Novo-Uspenka	56.62	84.17
Nowiny	53.94	19.33
Nulsaveito	67.53	70.17
Oltush Lake	51.70	23.96
Onego Lake	61.72	34.92
Ospitale	44.16	10.78
Osvea	56.05	28.08
Ovrazhnoe	56.25	85.17
Ozerki	50.42	80.47
Padul	37.00	−3.07
Paidre	58.27	25.63
Pannel Bridge, East Sussex	50.90	0.68
Pashennoe	49.37	75.40
Pechsee	52.48	13.22
Pelléautier	44.52	6.18
Pervoe Maya	56.37	37.18
Peschanoe	51.98	25.48
Peschanoe bog	56.90	60.32
Petropavlovka	58.33	82.50
Peyrelevade	45.71	2.38
Pickletillem SSSI	56.40	−2.90
Pico del Sertal	43.22	−4.44
Pillon, Gsteig-Diablerets	46.35	7.20
Popovo Ezero	41.72	23.67
Pratignano	44.18	10.82
Prato Spilla	44.45	10.30
Prémery	47.15	3.30
Prémery	47.15	3.30
Ptichje	66.35	30.57
Puerto de Belate	43.03	−2.05
Puerto de las Estaces de Trueba	43.12	−3.70
Puerto de Los Tornos	43.15	−3.43
Punozerka	62.82	33.58
Punso	57.68	27.25
Puscizna Rekowianska	49.48	19.82
Puy de Pailleret	45.52	2.82
Quintanar de la Sierra	42.03	−3.02
Rapperhausen Moor	50.30	10.50
Rasna pond	49.23	15.37
Rattuvarri	69.35	20.32
Redmere	52.43	0.43
Regetovka	49.42	21.28
Rezabinec	49.25	14.12

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Ribnoe	43.71	41.21
Rinderplatz	46.63	11.48
Rödschitzmoor	47.55	13.90
Roquetas de Mar	36.79	−2.59
Rotsee	47.08	8.33
Rottenbach Moor	50.35	10.90
Roztoki	49.72	21.58
Rudushskoe Lake	56.50	27.55
Rugozero	64.08	32.63
Rukatunturi	66.17	29.15
Ryönänsuo	60.43	24.17
Sabbion	44.13	7.47
Saint Julien de Ratz	45.35	5.62
Saint Michel de Braspart	48.42	−3.67
Saint Sixte	45.42	5.62
Saksunarvatn	62.25	−7.18
Saldropo	43.05	−2.72
Saleccia	42.72	9.20
San Rafael	36.77	−2.60
Sanabria Marsh	42.10	−6.73
Sandsjön	56.75	13.42
Sandvikvatn	59.28	5.50
Schleinsee	47.62	9.65
Schwarzes Moor	50.27	10.00
Schwarzsee, Reschenscheideck	46.87	10.47
Schwemm	47.65	12.30
Selle di Carnino	44.15	7.69
Semmeldalen	76.67	15.33
Serni	43.67	40.48
Shombashuo	65.12	32.63
Sibista	43.23	41.43
Silberhohl	51.92	10.25
Simplon, Hopschensee	46.25	8.02
Simplon/Gampisch-Alter Spittel	46.23	8.00
Skvarran	57.20	16.15
Sluggan Moss	54.93	−6.30
Sögüt Gölü	37.05	29.88
Solnechnoe	65.83	34.33
Sommersüss	46.75	11.67
Son Bou	39.92	4.03
Spisska Bela	49.18	20.45
Spjällsjön	56.69	14.59
Spoli JC-13-A	48.97	14.90
Sredna Gora mountains	42.83	24.83

Appendix A. (*Continued*)

Site name	Latitude	Longitude
St. Antonio	44.37	10.84
Suollakh, Yakutia	57.03	124.10
Suovalampi	69.58	28.83
Svatoborice-Mistrin	48.83	17.17
Svencele bog	55.50	21.29
Sverdrup	74.50	79.50
Svitjaz	53.43	25.92
Swienskuhle DAH III	53.67	8.72
Syrjälänsuo	61.22	28.12
Szymbark	49.63	21.10
Tarnawa Wyzna	49.10	22.83
Tarnowiec	49.70	21.62
Taul Zanogutii	45.33	22.47
Tegler See	52.58	13.22
Tenaghi Philippon	40.98	24.78
The Bog [Roos]	53.73	−0.07
Thorpe Bulmer	54.72	−1.30
Tondi	59.47	24.92
Tontelange Heideknapp	49.72	5.82
Toubière des Nassettes	44.47	3.64
Tourbière de Champlong	45.82	7.81
Tourbière de la Borde	42.53	2.08
Tourbière de Pilaz	45.82	7.83
Tourbière de Santa Anna	45.86	7.65
Tourves	43.50	5.90
Trollvatnet	69.88	23.47
Tschokljovo marsh	42.37	22.83
Tullerinsuo	61.33	21.95
Uddelermeer	52.24	5.76
Uitbergen	51.02	3.94
Ust'Mashevskoe	56.32	57.88
Vallée de la Voise	48.42	1.75
Vallon de Provence	44.39	6.40
Vasikkasuo	64.67	27.87
Velky Ded	50.08	17.22
Vernerovice	50.10	16.25
Vid	43.20	17.80
Vishnevskoe Lake	60.50	29.52
Voros-mocsar	46.48	19.19
Vracov	48.98	17.20
Wachseldorn Untermoos	46.82	7.73
Wallbach, Lenk	46.42	7.40
Westrhauderfehn	53.12	7.55
Wildmoos	46.95	11.02

Appendix A. (*Continued*)

Site name	Latitude	Longitude
Wolin II	53.83	14.67
Woryty (near Gietrzwald)	53.75	20.20
Ylimysneva	62.13	22.87
Zaboinoe Lake	55.53	62.37
Zamedvejca	45.98	14.42
Zapovednoe	65.12	32.63
Zarnowiec peat bog	54.72	18.12
Zaruckoe	63.90	36.25
Zavidkovice	49.65	15.41
Zbudovska Blata	49.83	14.33
Zirbenwaldmoor	46.86	11.02
Zlatnicka dolina	49.52	19.28
Zsombo-swamp	46.36	19.99
Zuratkul'	54.90	59.27
Zurawiec	54.42	16.50
Zyrardow	52.05	20.44

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