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Quaternary refugia of the sweet chestnut (*Castanea sativa* Mill.): an extended palynological approach

Abstract Knowledge about the glacial refugia of the thermophilous European *Castanea sativa* Mill. (sweet chestnut) is still inadequate. Its original range of distribution has been masked by strong human impact. Moreover, under natural conditions the species was probably admixed with other taxa (such as *Quercus*, *Fraxinus*, *Fagus*, *Tilia*) and thus possibly represented by low percentages in pollen records. In this paper we try to overcome the difficulties related to the scarcity and irregularity of chestnut pollen records by considering 1471 sites and extending the palynological approach to develop a *Castanea* refugium probability index (IRP), aimed at detecting possible chestnut refugia where chestnuts survived during the last glaciation. The results are in close agreement with the current literature on the refugia of other thermophilous European trees. The few divergences are most probably due to the large amount of new data integrated in this study, rather than to fundamental disagreements about data and data interpretation. The main chestnut refugia are located in the Transcaucasian region, north-western Anatolia, the hinterland of the Tyrrhenian coast from Liguria to Lazio along the Apennine range, the region around Lago di Monticchio (Monte Vulture) in southern Italy, and the Cantabrian coast on the Iberian peninsula. Despite the high likelihood of *Castanea* refugia in the Balkan Peninsula and north-eastern Italy (Colli Euganei, Monti Berici, Emilia-Romagna) as suggested by the IRP, additional palaeobotanical investigations are needed to assess whether these regions effectively sheltered chestnut during the last glaciation. Other regions, such as the Isère Département in France, the region across north-west Portugal and Galicia, and the hilly region along the Mediterranean coast of Syria and Lebanon were classified as areas of medium refugium probability. Our results reveal an unexpected spatial richness of potential *Castanea* refugia. It is likely that other European trees had similar distribution ranges during the last glaciation. It is thus conceivable that shelter zones with favourable microclimates were probably more numerous and more widely dispersed across Europe than so far assumed. In the future, more attention should be paid to pollen traces of sporadic taxa thought to have disappeared from a given area during the last glacial and post-glacial period.

Keywords Refugium · Palynology · Anthracology · *Castanea sativa*

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Introduction

There is currently a broad consensus in the scientific community that the Quaternary cold periods substantially reduced the woodland diversity, in terms of the number of taxa and the genetic diversity within the taxa, in Europe to a restricted number of shelter zones mostly located in the southern part of the Continent (Comes and Kadereit 1998; Taberlet et al. 1998). A shelter zone is usually called a "refugium" and is defined as an area of any size in which a taxon persisted at any population density during a cold period (Bennett et al. 1991). According to this theory, the forest recolonisation of the European continent during the interglacial and postglacial periods started out from these core sites (refugia) and the definitive disappearance of a

species from Europe implied that it had failed to survive in the refugia (Tzedakis 1993; Brewer et al. 2002). For ecologists, the study of the locations, extent and nature of the Quaternary tree refugia provides opportunities for obtaining insights into the autecology, competitive fitness, survival and immigration potential on different time scales (Newton et al. 1999). These aspects are becoming increasingly important, given the current interest in possible ecological responses to ongoing climatic changes (Walther et al. 2002).

A classic approach to reconstructing changes in the distribution limits and abundance of tree species (and therefore of refugia as well) is to map radiocarbon dated pollen spectra geographically (West 1977; Huntley and Birks 1983; Bennett et al. 1991). Fossil data alone, however, do not always allow a complete and detailed interpretation of the biogeographic history of all trees, as the study sites may not be systematically distributed in the area of interest, and the data tend to be biased in favour of wind-pollinated, wet- and peatland taxa and those with an abundant pollen distribution and dispersion. In addition, the interpretation of the data is complicated by possible contamination with long-distance transported pollen dispersal and by a limited morphological/taxonomic resolution (Jacobson and Bradshaw 1981; Bennett et al. 1991; Comes and Kadereit 1998). Since it is plausible to assume that during the LGM (and later under natural conditions) *Castanea sativa* grew together with other trees, it is likely that very low values and even single pollen grains could reflect its local presence. Therefore, it is impossible to conclusively exclude the presence of a taxon if no pollen is present in stratigraphical records. However, with increasing pollen frequencies, the probability of correctly identifying a refuge area increases. This approach of positive pollen evidence has been used by the so far only attempt at a synthesis on *Castanea sativa* on a continental scale which was compiled by Huntley and Birks (1983).

Macrofossil and charcoal analyses may provide additional information. Macrofossils usually derive from more local vegetation and can often be determined to species level (Birks and Birks 2000). Analysis of macroscopic charcoal particles in soils proved to be very helpful in determining the presence of tree species during the Last Glacial Maximum (LGM) (Willis et al. 2000).

Recently, the development of molecular markers for ecological studies has allowed an improved reconstruction of past distribution, re-colonisation dynamics, genetic variation and possible management and conservation strategies, at or below the species level (Comes and Kadereit 1998; Newton et al. 1999; Hewitt 1999). Petit et al. (2002) used cytoplasmatic, maternally-inherited genomes (chloroplast and mitochondria) of European white oaks to hypothesise the species' post-glacial colonisation routes and to argue for the existence of additional refugia despite the lack of pollen evidence. Unfortunately, Petit et al.'s (2002) work on the European oaks remains unique for the moment. In the case of *Castanea sativa* Mill. (sweet chestnut) with the present state of the art it can be assumed that the molecular phytogeographic approach

will be restricted because of the strong human influence on the reintroduction and distribution of the species in many parts of Europe (Frascaria et al. 1993; Villani et al. 1994; Conedera et al. 2004).

Improved knowledge about Quaternary refugia and the autecology of the sweet chestnut is needed, especially considering the trend in many chestnut regions of Europe towards discontinuing the traditional management of the old chestnut woods. In the absence of cultural inputs, chestnut woods tend to be invaded by other trees, giving way to evolutionary dynamics toward climax forests, as observed in many European regions in recent decades (Arnaud et al. 1997; Conedera et al. 2000; Conedera et al. 2001; Paci et al. 2000; Maltoni and Paci 2001).

In this paper we attempt to find out where the main refuge macroregions were situated, including scattered microenvironments allowing limited chestnut populations to survive in Europe during the LGM and the postglacial period. We integrate the information from a large set of pollen profiles with data from anthracological and macrofossil records. A new synoptic index of refugium probability (IRP) is proposed which combines pollen percentages and other important information such as the reliability of chronology, chronological position, etc.

Material and methods

Definition of the study area

The distribution of the genus *Castanea* has undergone many changes in response to the climatic and geographical modifications of the northern hemisphere during the Tertiary. The genus *Castanea* was in fact already present in there around 80–65 million years ago (Groot and Groot 1962; Drugg 1967; Snead 1969; Rouse et al. 1971; Stone 1973; Jarzen 1978; Kedves and Herngreen 1980). During this period, cool and moderate climates were rather confined to extreme latitudes (Ashraf and Mosbrugger 1996). The genus *Castanea* completed the colonization of the northern hemisphere at the latest about 40 million years ago, that is, before the definitive separation of Europe from North America. Between the Miocene (25–5 million years ago approximately) and the Pliocene (about 5–1.8 million years ago) chestnut was probably at the peak of its spontaneous presence, both in terms of number of individuals, and of number of different species (Mai 1995). Chestnut was an important component of Tertiary hardwood forests, where mean annual temperatures ranged between ca. 10 and 15°C and the mean annual precipitation between 500 and 2500 mm.

During the final phase of the Tertiary, the climate began to exhibit periodic cooling that introduced, over a few million years, the Quaternary phase with the first glaciations (Mannion 1999). Chestnut probably became extinct in the northernmost zones of Europe during the transition between the Tertiary and the Quaternary (Tomskaya 1980), while the position of the Alpine range hindered its withdrawal to the south. During the lower Pleistocene (1.8–0.5 million years ago) glacial phases became more frequent and pronounced, making the survival of chestnut much more difficult in most regions north of the Alps.

Recent pollen studies have been able to place the definitive disappearance of chestnut north of the Alps during the middle Pleistocene, probably starting during the glacial stages preceding the Eemian (see the examples in Welten 1982a; Welten 1988; Sidler 1988; Wegmüller 1992; Burga and Perret 1998). These glacial phases may also have caused the disappearance of the chestnut tree on the southern side of the Alps, at least at the foot of the Alpine chain (Brambilla 1992; Eberhard 1992; Sidler 1992; Felber 1993).

Fig. 1 Distribution of the sites considered in the study area
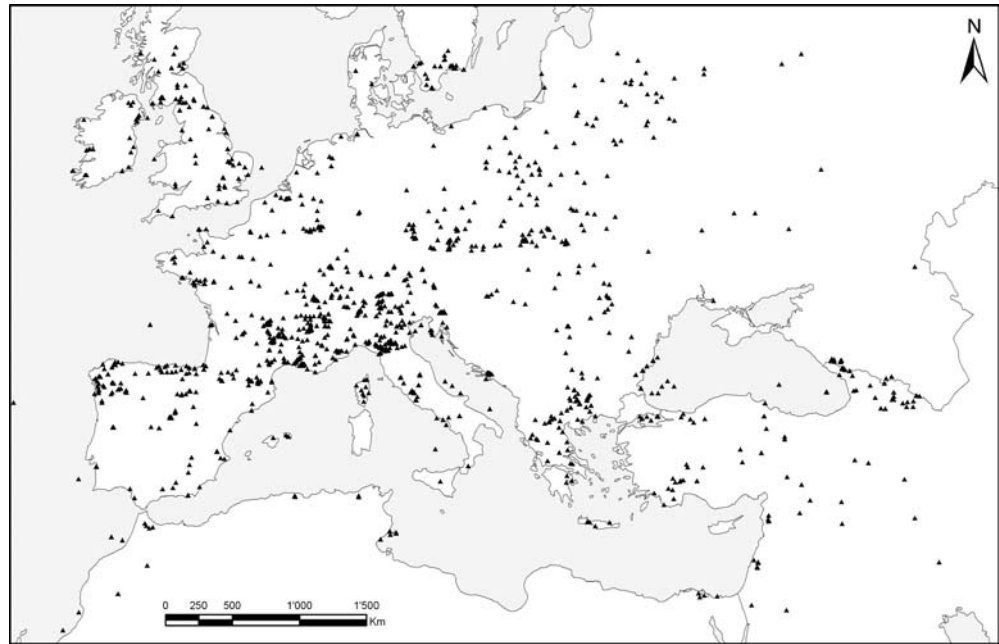
The repeated cold waves of the more severe stages at the end of the last glaciation starting around 70 kyr ago and culminating with the last glacial maximum around 20 kyr ago, had devastating consequences for the distribution area of chestnut. Since then *Castanea sativa* has managed to survive only in particularly favourable areas (Paganelli 1996).

For the definition of the study area we combined this information with that about *Castanea*'s present distribution, and took into account references to the chestnut in the classical literature (Greek, Roman), and its presence in some pollen results. An additional safety margin was added, so that the final area considered covers the greater part of Europe including the mountains of the Caucasus, and ranging in latitude from approximately 60°N to 30°N, including the North African coastal countries of the Mediterranean basin.

Analysed sites

We started our search for pollen sequences data by analysing the existing databases on the web. We focused on the data-bases WDC (2003), EPD (2003), CiMPI (2003) and the Palaeoecological Atlas of Northern and Western Africa (2003), and on pollen diagrams published in scientific journals. According to Brewer et al. (2002), pollen percentages obtained directly from evaluation of pollen diagrams are reliable.

Given our interest in the large-scale distribution of chestnut, we also considered sites at high altitudes and even above the timberline, although these pollen records are likely to have been affected by extra-local to long-distance transport. In total 1471 sites were considered in the study area (Fig. 1). For the full list of the analysed sites see http://dx.doi.org/10.1007/s00334-004-0041-z.

Chronology

The profiles used were classified according to the quality of dating. For profiles providing a time axis or strong and coherent dating we proceeded to a linear interpolation between the dates. Where profiles had mismatched radiocarbon dates or have been dated with an analogous dating approach based on a comparison among sites with similar pollen stratigraphies, we adopted the datings proposed by the authors. We assigned to profiles without any chronology datings extrapolated from representative taxa for which the recolonisation

history is well known (that is, *Fagus*, *Corylus*, *Abies*, *Carpinus*, Lang 1994). If this was not possible, the profile was rejected. The problem of doubtful dating will be taken up again in the discussion.

Pollen records

Pollen records provide very useful information for reconstructing the past vegetation cover during the last 20 kyr. Pollen grains and spores preserve well after sedimentation in anoxic environments, such as in lake sediments or peat bogs (Brewer et al. 2002), enabling us to investigate the environmental conditions of the past.

The reliability of pollen studies varies greatly. Generally it can be said that post-1960 studies are of satisfactory quality as they use core samples obtained with modern drilling techniques that recover undisturbed and continuous sediment cores for subsampling (for example, piston corers, see Wright et al. 1984; Lang 1994). Other qualitative aspects to be considered are the number and reliability of the radiocarbon datings, as well as the number of analysed samples and the average pollen sums estimated. In trying to reconstruct the vegetation outside wetlands, the presence of Cyperaceae pollen and other potentially semi-aquatic plants must also be considered as it is sometimes included in the total pollen sum. These elements may belong to aquatic vegetation or to hydroseres along the margins of or in the marsh and can be excluded from the pollen sum (Wijmstra 1969). In addition, the pollen source area depends on a multitude of variables such as the size of the lake, the morphology of the lake basin, and the presence or absence of inflowing streams (Jacobson and Bradshaw 1981).

Besides the general palynological problems, chestnut pollen presents additional difficulties. Where the pollen percentage of chestnut is less than 1–2%, it is difficult to exclude systematic confusion with the pollen of the genera *Lotus*, *Hypericum* or *Sedum*, which are morphologically very similar to *C. sativa* (Sanchez Goñi 1993). A striking example of this difficulty in identification is the case of the Portuguese profiles of Serra de Estrela, where van der Knaap and van Leeuwen (1995) contest that the pollen grains found in the stratigraphy of 6 kyr B.P. are of *C. sativa* and suggest that they were confused with the very similar pollen of *Sedum arenarium*, on the basis of a re-examination of the original pollen slides of van den Brink and Janssen's (1985) and other pollen profiles of the region. One approach to estimate possible confusion is to check whether pollen of *Lotus*, *Hypericum*, *Sedum*, *Genista*-type and *Ulex*-type are represented or completely absent from the

original pollen diagrams. If all or the majority of these types is missing, then identification of *Castanea* is suspect (van der Knaap, pers. comm.). Most palynologists today, however, should be aware of this problem and pay particular attention when identifying *Castanea* pollen (Mateus 1992). This caution may be absent from earlier publications, even if the question of a possible misclassification of *Castanea* pollen and its false attribution to similar herbaceous species could be a matter of discussion as well. In any case, often the summarised, published pollen profiles report most of the herb taxa only at the family level (for example Fabaceae, Rosaceae, Crassulaceae), providing details at the species or genus level only for the most significant pollen types (such as *Plantago lanceolata, Rumex acetosella, Artemisia*, and *Urtica*).

Another difficult aspect is the determination of the origin of the pollen and therefore of the effective spatial representation of the pollen curves. According to Huntley and Birks (1983) the presence of *Castanea* pollen can be regarded as a fairly reliable indication of the local occurrence of mixed woodland with some chestnut trees, whereas widespread chestnut woodlands near the site are represented by pollen values >5%. Other authors claim that local topography combined with special meteorological conditions may cause long-distance transport (up to more than 100 km) of significant amounts of chestnut pollen (Jochimsen 1986; Peeters and Zoller 1988), also along an altitudinal transect (Brugiapaglia et al. 1998). According to Kvavadze and Efremov (1995), the largest quantity of local pollen is found at the lowest altitudes near the upper treeline. Above 2800–3000 m most pollen derives from long distance transport, due to thinning of the tundra vegetation and the increased strength and duration of the winds. Under certain conditions, up to 80 to 85% of the pollen may be long distance transported (Kvavadze and Efremov 1995). It is important to bear in mind, however, that wind patterns in the past could have been different from those today (Kvavadze and Efremov 1995). In fact, both palaeoclimatological simulations and empirical studies using proxy data such as aeolian sedimentation records indicate that the LGM and today's atmospheric global circulation patterns were similar, though some authors assume a more southern position of the polar front and frequent westerly winds for Europe (Ganopolski et al. 1998; Leger 1990; Cacho et al. 2000). Furthermore, Kvavadze (1993) and Kvavadze and Efremov (1995) note that the pollen spreads better in arid conditions, but the production of *Castanea sativa* pollen is, like *Fagus*, higher in wet climates (Kvavadze 1993). Finally, in the specific case of the chestnut tree, the interpretation of the presence or absence of the species in the pollen diagrams must take into account the fact that the species avoids limestone soils (for example, Gobet et al. 2000) and poor drained soils in the plains.

In this study, we try to estimate the occurrence of chestnut on a wide geographic scale. We consider, therefore, any record of *Castanea* pollen and do not exclude data by setting a cut-off percentage threshold or an elevation limit for the site. Potential misinterpretations of the data are considered in the discussion.

Anthracological and macrofossil records

Information about the chestnut tree during the post-glacial period is nearly exclusively palynological. Reasons for this may include the very low probability of finding any macro-remains of this species in archaeological sites (Behre 1990), bogs and lakes as well as potential confusions between *Castanea* and *Quercus* wood that are anatomically very similar. Nevertheless, any records in the literature, mostly of charcoal macro-remains (for example Uzquiano 1992), were considered and the corresponding data were specially marked on the maps.

Pollen data analysis

In their study of the spread of deciduous oaks since the last glacial period, Brewer et al. (2002) defined two types of refugia: primary refugia for locations where the existence of a population persisted during the entire glacial period, and secondary refugia represented by sites which provided shelter for a population during a shorter cold period and which therefore played an important role in the range expansion. Findings of *Castanea* pollen have so far been too scarce and irregular to make such a distinction.

Nevertheless, we have tried to maximize the information power of our data by using two different approaches. First, we defined three main periods of observation: The Last Glacial Maximum (LGM, in this paper defined as 18±0.5 kyr B.P.); second, the period after the rapid rise of the temperature in the early Holocene starting at about 11.5 kyr cal B.P. (10 kyr B.P., Walker 1995; Lang 1994), when the temperature reached a first Holocene equilibrium at around 10 kyr cal B.P. (9 kyr B.P.), as shown by several studies in Greenland and in the Alps (e.g. Dansgaard et al. 1993; Grootes et al. 1993; Wick and Tinner 1997; Tinner and Theurillat 2003); third, the late phases of climatic change from continental to more oceanic that gave rise to the so-called Atlantic period according to Godwin (1975; see also Lang 1994) that succeeded the Boreal period at about 8.2 kyr cal B.P. (7.5 kyr B.P., Tinner and Lotter 2001). This climatic change could have favoured the natural expansion of *Castanea* because chestnut requires suitably warm conditions and has a rather marked preference for an oceanic climate with sufficient precipitation. For large areas of western and central Europe as well as for Italy, Spain and Portugal, the period 8.2±0.5 kyr cal B.P. marks the last occurrence of quasi-natural conditions before the onset of the Neolithic (Lang 1994). Therefore the considered periods should be early enough to avoid the first strong human influences found later in different areas and at different times throughout the study area (Bottema and Woldring 1990; Bottema 2000; Yasuda et al. 2000; Ermolli and di Pasquale 2002). Long time spans (around 1000 years) were considered to take into account the non-linearity of climatic changes during the post-glacial period in Europe and the problems of precise ^{14}C dating (Walker 1995).

The three time windows, 18±0.5 kyr B.P., 10±0.5 kyr cal B.P. (9 kyr B.P.) and 8.2±0.5 kyr cal B.P. (7.5 kyr B.P.), were analysed to identify possible refugia. It was assumed that during the last two periods the range of the species expanded spontaneously because of changes to more favourable climatic conditions: the climate became warmer from 10 kyr cal B.P. and drought became less frequent from 8.2 kyr cal B.P. In total we classified 89 sites for the 18 kyr B.P. time period, 499 for 10 kyr cal BP (9 kyr B.P.) and 570 for 8.2 kyr cal. BP (7.5 kyr B.P). The pollen percentages reached by *Castanea sativa* at the different sites during these periods are given in the maps (Figs. 2, 3, and 4).

The second step involved estimating a so-called index of *Castanea*-refugium probability (IRP) for each site studied (a total of 1471 sites). For this we used an enlarged set of information based on the pollen profiles. Since it takes into consideration the whole time span reported in the profiles, the problem of detecting underrepresented pollen types, such as chestnut, can be partly overcome. IRP was defined to take into consideration different factors influencing the likelihood of a site being *Castanea* refugium, according to the following formula:

$$IRP = [w\_SUM + w\%\_SUM + FREQ + (n\_GRAIN/3)$$
$$+ (n\_DUMB/60)] * ELEVATION * DATING \qquad (1)$$

where:

w_SUM   is the weighted sum of pre-arboricultural samples (earlier than chestnut cultivation) with *Castanea*;
w%_SUM   is the mean pollen percentage value of the pre-arboricultural samples with Castanea
FREQ   is the frequency of pre-arboricultural samples with Castanea
n_GRAIN   is the mean number of grains in the pre-arboricultural samples with Castanea
n_DUMB   is the number of dumb basal samples
ELEVATION   is the correction factor according to the elevation of the site
DATING   is the correction factor according to the reliability of the chronology

Fig. 2 Site conditions and chestnut pollen percentages for the profiles based on available data for 18 kyr B.P.
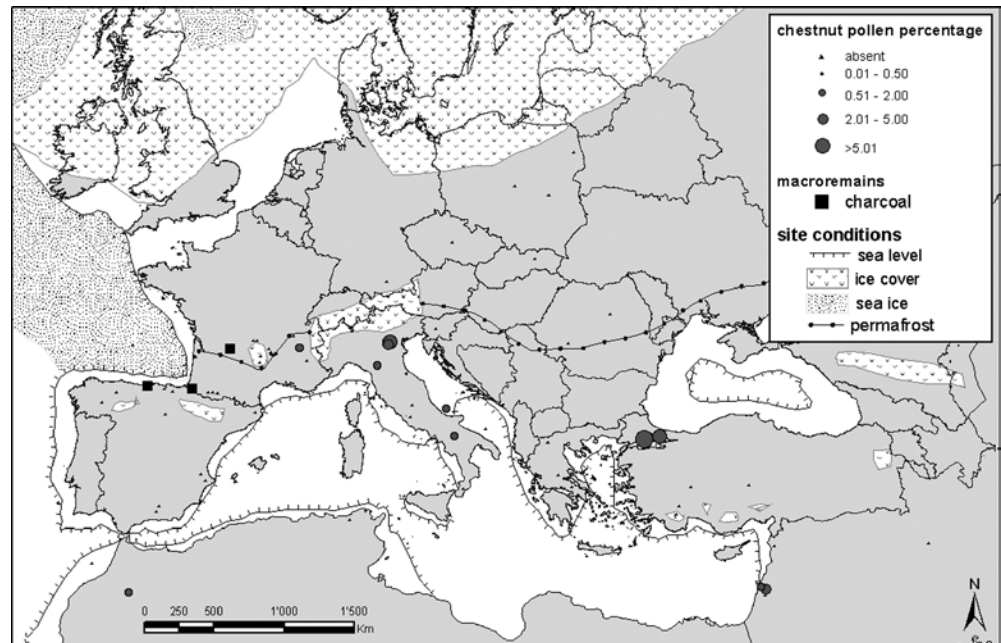
The weight of the different parameters considered is given by the coefficient of the formula and of the multiplication factors for the different categories (for details see Table 1). The weights within the parameters, w_SUM, were attributed empirically, the maximum weight of w_SUM was 2.5 if the species was present between 15,000–28,000 B.P. The absolute values of the coefficients were also empirically determined in order to obtain values between 0.01 and 100 for the pre-arboricultural presence of *Castanea* pollen. Our definition of the date of the change between the arboricultural and the pre-arboricultural period (see parameters w_SUM, w%_SUM, FREQ, n_GRAIN) differs from east to west. It was around 3500 B.P. in Anatolia and Greece, 3000 B.P. in the Italian peninsula, 3000 to 2000 B.P. according to the single profile for France and the Iberian peninsula and 2000 B.P. for central and northern Europe. The IRP equation gives negative values to sites not likely to have been refugia for *Castanea*. A value of 0 indicates that there is no information whether a site was a chestnut refugium or not. The resulting IRP values were grouped into categories and are shown on a map (Fig. 5a,b).

Data representation

All the maps presented were produced using a geo-referred map of Europe drawn up with ArcGis software. For the LGM map (18 kyr B.P.) we added the glaciers, sea ice, permafrost and sea level limits given in Hewitt (1999). For the other maps, the pollen percentages of the sites where *Castanea* occurred are represented by dots whose size is proportional to the percentage class.

Results and discussion

Figure 2 shows the current pollen and charcoal evidence for the occurrence of chestnut during the LGM (18 kyr B.P.) in Europe. Seven sites can be detected: Israel (Horowitz 1971, Hula lake), northwestern Anatolia, corresponding to the present northwest Turkey (Caner and Algan 2002, Marmara sea), central Italy (Lowe et al. 1996, Adriatic sea), northern Italy (Paganelli and Miola 1991), Morocco (Lamb et al. 1989, Tigalmamine), eastern

France in the central French Alps (Nakagawa 1998, Tourbière de Peuil) and the anthracological site in the French Basque Country (Uzquiano 1992, Grotte d'Azkonzilo). However, profiles containing information about the LGM period are scanty and irregular in distribution. The number of profiles from 9 kyr B.P. (10 kyr cal B.P.) is greater, as shown in Fig. 3a,b. In particular, additional profiles indicating a strong chestnut presence are added, such as the sites in the Caucasus, in central and northern Greece and in Sicily. The profiles in southeastern Spain contained chestnut pollen for the first time and its area of occurrence extended to central Italy, northern Italy and northern Spain (Cantabria), but it disappeared from profiles from Israel and Morocco. For the period around 7.5 kyr B.P. new chestnut areas appeared in northern Turkey, southern Greece, Bulgaria and southeastern France and the percentage of the species in the pollen sum increased. Higher pollen percentage values suggest that long-distance transport in the Alps took place (Fig. 4b). The variation in the pollen presence during the analysed period exemplifies the difficulty of detecting refugia in general using pollen analysis (Petit et al. 2002) and for chestnut in particular.

Figure 5a,b gives an overview of IRP values for each site. This additional synoptic approach permits a much more comprehensive overview of the probability of chestnut sites during the last glacial period. The clustering of sites with positive indices is then interpreted in terms of refugium probability as proposed in Fig. 6. Some regions have a particularly high concentration of sites with elevated IRP values. In these areas, it is likely that chestnut trees survived during the LGM.

The most consistent shelter zone is represented by the Trans-Caucasian region (located mostly south of the Caucasian chain, in the territory of today's Georgia, Figs. 5a and 6). Unfortunately, no pollen profiles from

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Fig. 3a,b a) Chestnut pollen percentages for the profiles based on available data for 9 kyr B.P. b) eastern Mediterranean area
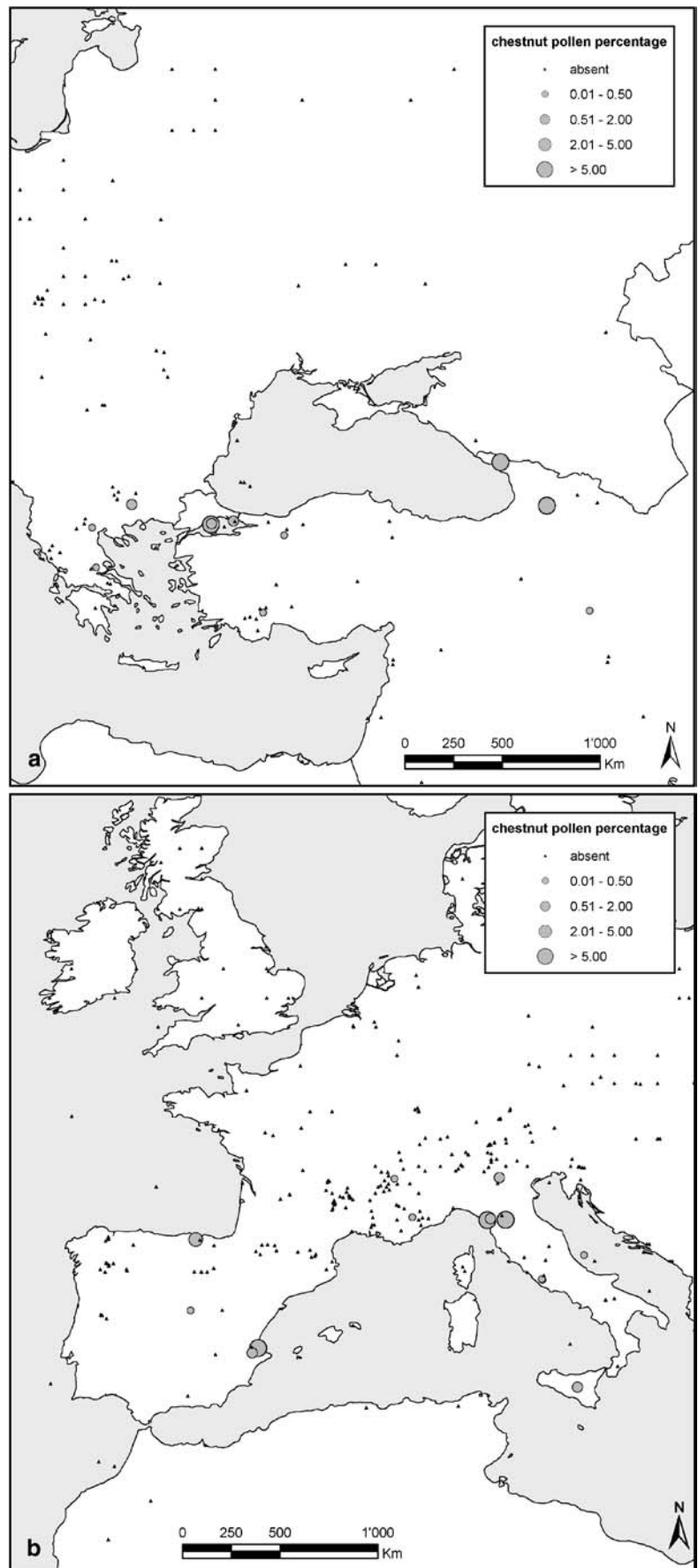
Fig. 4a,b a) Chestnut pollen percentages for the profiles based on available data for 7.5 kyr B.P. b) eastern Mediterranean area
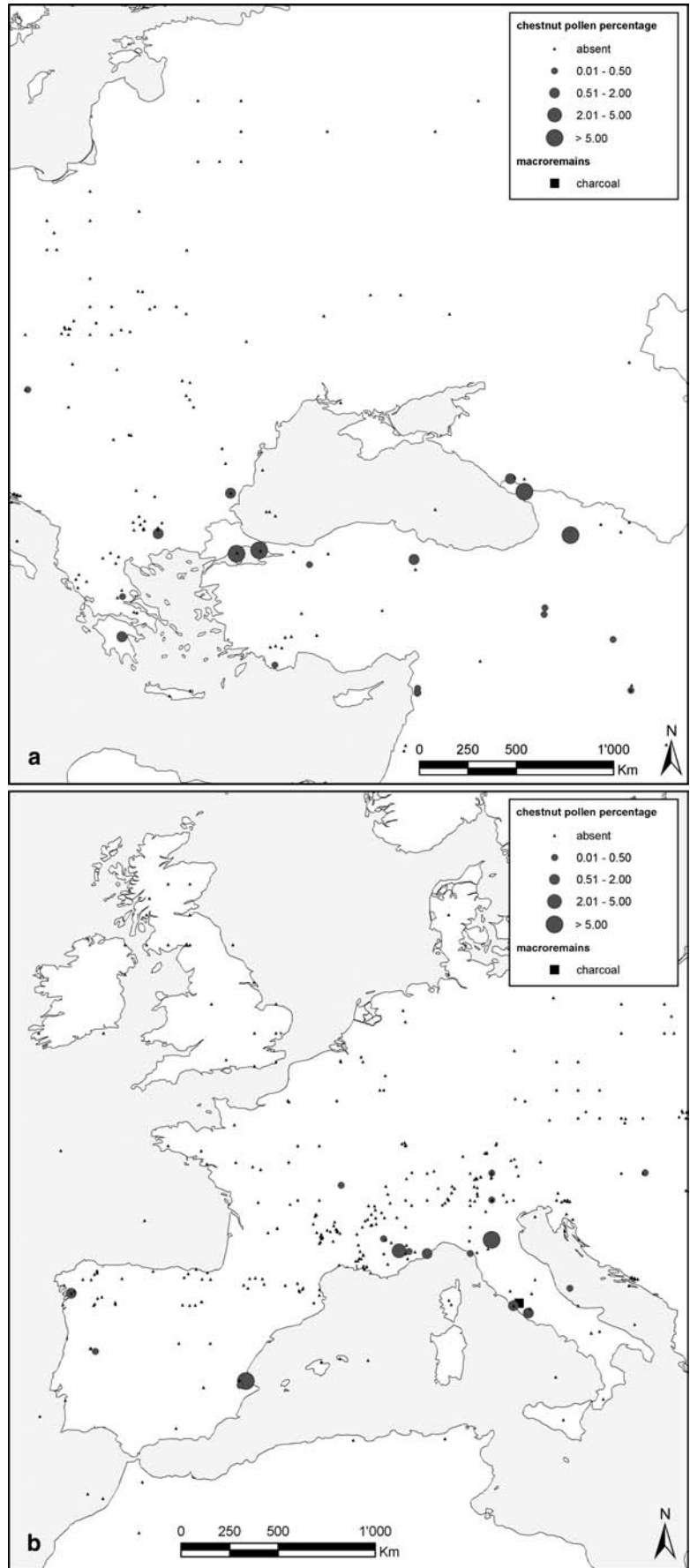
Table 1 Definition of the parameters for calculating the Index of Refugium Probability (IRP)

Parameter	Name	Definition	Formula
w_SUM	Weighted sum of pre-cultural samples with *Castanea*	Sum of product of the number of pre-cultural samples with *Castanea* pollen (PCS) and the weighting factor w_p, defined according to the period of reference as follows: w=0.15, 0–3000 B.P. w=0.50, 3000–5000 B.P. w=1.00, 5000–10000 B.P. w=1.50, 10000–15000 B.P. w=2.50, 15000–28000 B.P. w=1.00, 28000–73000 B.P. w=0.15, 73000–111000 B.P. w=0.03, 111000–186000 B.P.	$\Sigma\,(PCS_p * w_p)$
w%_SUM	Mean pollen percentage of the pre-cultural samples with *Castanea*	Sum of the percent of *Castanea* pollen (C%) in the pre-cultural samples divided by the number of pre-cultural samples with *Castanea* (PCS) and weighted as function of the pollen types considered using the following weighting factor (z): z=1.00, if all the sporomorphs are included z=0.67, if only selected taxa according to the site type are excluded (i.e. aquatic plants) z=0.40, if only the arboreal pollen are included	$\Sigma C\%/PCS * z$
FREQ	Frequency of pre-cultural samples with *Castanea*	Number of pre-cultural samples with *Castanea* (PCS) divided by the number of total samples of the pre-cultural time (S), and corrected by the sum of 3 and the square root of S in order to avoid overestimation due to profiles with few pre-cultural samples	$(PCS/S)*(3+S^{-2})$
n_DUMB	Dumb basal samples	Number of samples without *Castanea* before the first pre-cultural samples with *Castanea*	
n_GRAIN	Mean number of grains in the pre-cultural samples with *Castanea*	Sum of the absolute number of pollen grains (G) divided by the number of pre-cultural samples with *Castanea* (PCS)	$(\Sigma G)/PCS$
ELEVATION	Correction factor according to the elevation of the site	Correction factor based on the elevation above sea level of the site: ELEVATION = 1, lower than 1000 m ELEVATION = 0.9, between 1001 and 1500 m ELEVATION = 0.75, between 1501 and 2000 m ELEVATION = 0.5, above 2001 m	–
DATING	Correction factor according to the reliability of the chronology	Correction factor based on the accuracy of the dating as follows: DATING = 1.3, excellent DATING = 1.1, good DATING = 0.9, sufficient DATING = 0.6, insufficient DATING = 0.2, totally insufficient	–

there for the LGM and the deglaciation period are available in our material. In many studies radiometric datings are completely absent and no ages can be estimated (Schatilova 1973; Sluka 1973; Kvavadze 1993; Kvavadze and Stuchlik 1996). On the other hand, many authors report that chestnut was abundant and persistent from the beginning of the Holocene (Bintliff and van Zeist 1982; Kvavadze 1982). Seventeen percent of all sporomorphs determined in the Gagra profile (Kvavadze 1982) and more than 10% in the Cheliagele lake profile (in the mountainous region of Radja in Georgia) were chestnut (B. Ammann, pers. com.). This constant high level of chestnut pollen allows us to assume the existence of an important refugium during the LGM. This hypothesis is supported by the conclusions of Petit et al. (2002), who postulate the existence of a primary oak refugium in the same region on the basis of chloroplast DNA data. This main refugium centre could even be extended to the northwest (northern slope of the Caucasian range), to the southwest (Anatolian coast of the Black Sea) and to the east (eastern Georgia). However, in Fig. 6 this option is represented with a medium probability because of the general lower class of the refugium probability index.

A second main refugium area is centred in the Bosphorus and in the Dardanelles Strait (Turkey). Regions with lower probability extend to the north to Bulgaria, mostly along the hilly elevations near the coast of the Black Sea and to the east along the western Anatolian coast (Fig. 6). The presence of chestnut in Bulgaria is mainly supported by pollen finds in Arkutino and Poveljanovo 2 dating back before 5000 uncal B.P. (Bozilova and Beug 1992, Bozilova and Beug 1994) and by the timber macroremains found in the Neolithic settlements of Goljamo Delcevo (Bottema 2000) and Gălăbnik (Marinova et al. 2002). During the LGM, the Marmara Sea region was not submerged, as the sea level was about 120 m lower than today (Fairbanks 1989, in Caner and Algan 2002). In this region the percentage of *Castanea* is very high, reaching values of more than 9% during the period of maximum cold (Fig. 2, Caner and Algan 2002), suggesting good survival conditions. Curiously, no evidence has been reported so far that this area was a shelter zone for other trees and shrubs. On the other hand, genetic analyses (Villani et al. 1999, Fineschi et al. 2000) clearly demonstrate the intermediate character of north-west Turkey with respect to the eastern Black Sea

Fig. 5a,b a) Chestnut refugium
probability index for each site
considered. b) eastern Mediter-
ranean area. Chestnut refugium
probability index for each site
considered, western Mediter-
ranean area
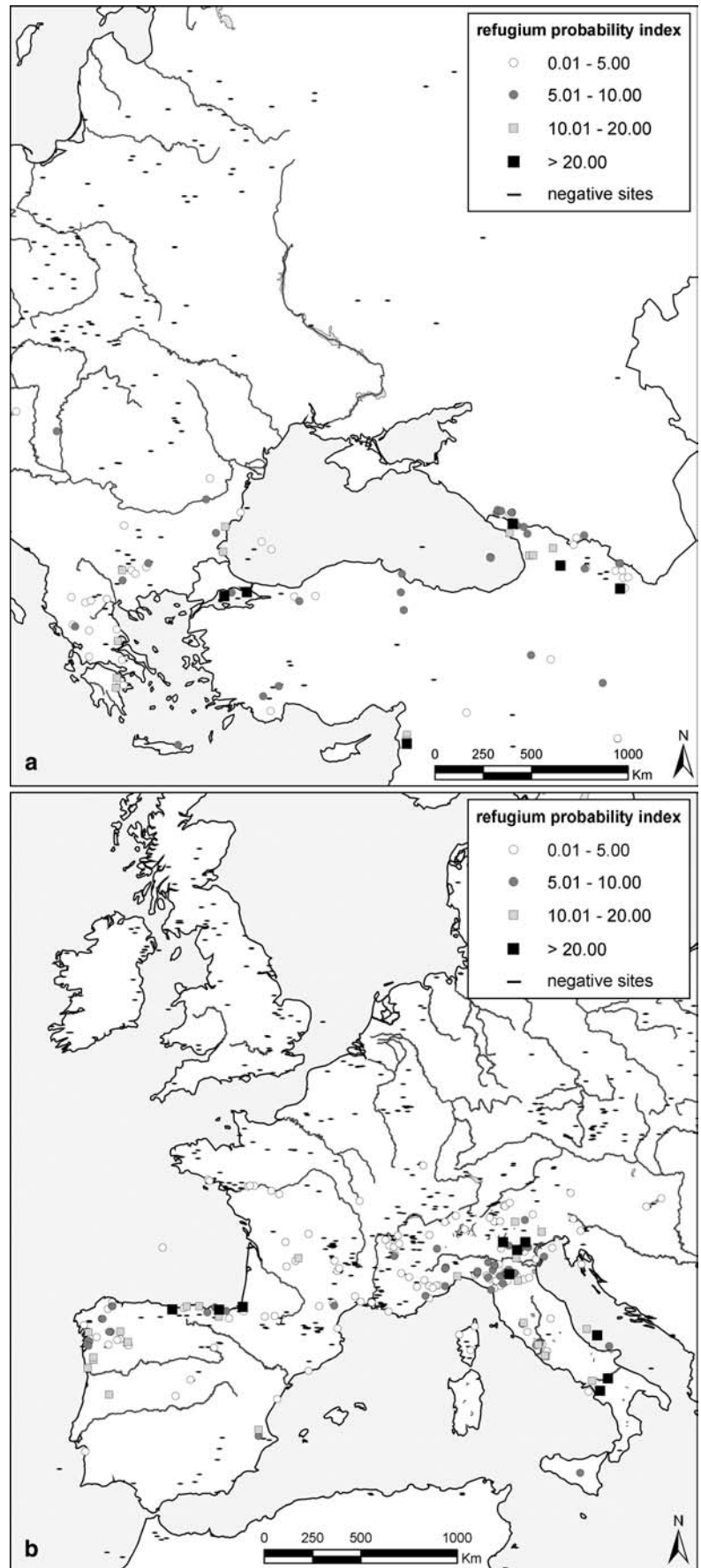
Fig. 6 Main refugium areas of the European chestnut according to their probability level
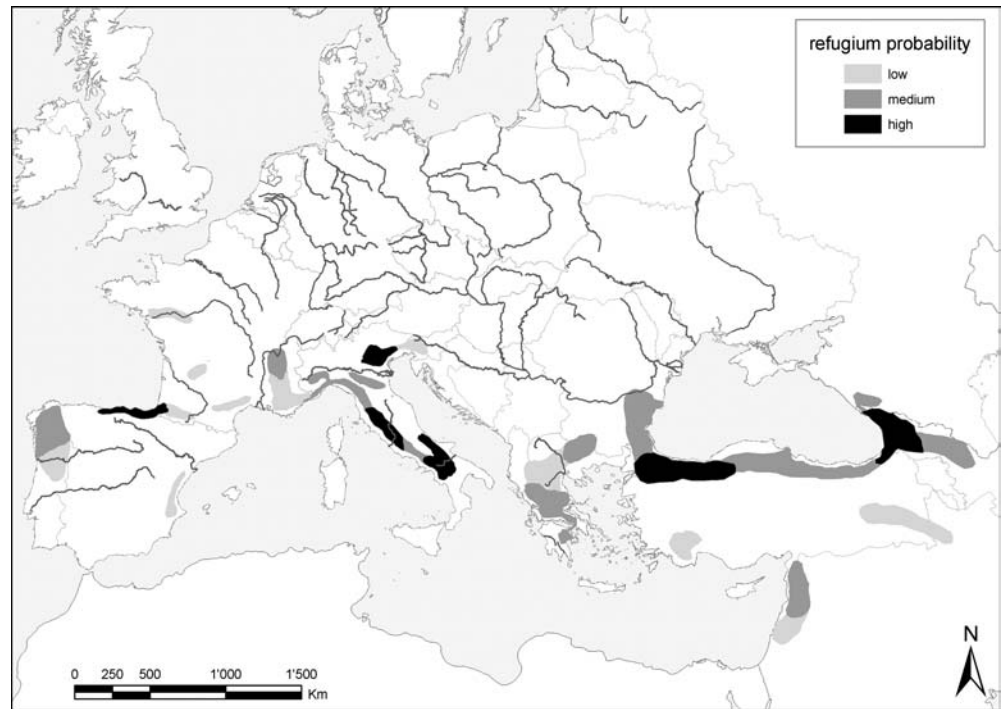
chestnut population and the southern Mediterranean population.

The IRP calculated for the profiles of the Italian peninsula suggest the existence of four main shelter zones. One is located north of the Po plain in the hilly region to the east of the Lago di Garda (Monti Lessini, Monti Berici and Colli Euganei). For this northern region, there is a wealth of palynological evidence for chestnut having survived the last glaciation. In some cases chestnut pollen clearly exceeds 1%, with prehistoric maxima of 2% near Villaga-Barbarano and 2.5% in Carturo on the Brenta (Paganelli and Miola 1991). High IRP values north of the Alps (Fig. 5b) could support the hypothesis of a shelter zone near the southern Alps that provided enough pollen for long-distance transport to central Europe. Our result is in contrast with the conventional assumption that during the LGM climatic conditions in the Po Plain were cold and dry everywhere. This assumption is based on the general palaeogeographic setting, since the region was rain-sheltered to the west by mountain chains and to east the northern coast of the Adriatic Sea was located several hundreds of km south, compared with today's position (at the latitude of the Gargano). Since the species has relatively high temperature and moisture demands, such general climatic conditions are considered not to be suitable for chestnut survival. However, new preliminary results of an investigation at Colli Euganei in the eastern Po plain (Kaltenrieder et al. 2003) confirm an early to mid Holocene presence of *Castanea* in that region and the hypothesis of a shelter zone north of the Apennines (Kaltenrieder, pers. com.). The core sample was recovered with modern drilling techniques. Moreover the pollen record was AMS dated with terrestrial macrofossils and taxonomic resolution is very high, including the de-

termination of *Hypericum*, *Sedum*, *Genista-type*, *Lotus*, and Mediterranean Apiaceae, so that a misidentification seems highly unlikely. Unfortunately no information about determination of *Hypericum*, *Sedum*, *Lotus* and possible misidentifications of *Castanea* pollen are provided in the published data of the earlier studies referring to this region (for example Paganelli 1966, Paganelli and Miola 1991). The presence of limestone soils unsuited for chestnut in the western southern Alps and their foothills could explain the fact that the reconstructed northernmost Italian shelter zone is restricted to the region east of Lago di Garda.

The second Italian shelter zone lies in the hilly region of Emilia-Romagna. Some profiles from this area show a rather strong presence of chestnut starting at 15 kyr B.P. (for example, San Pellegrino moor in Pavullo, Modena Province) and reaching peak percentages of chestnut greater than 5% during the Holocene (5.3% at 9500 B.P. and 12% around 7500 B.P.; Bertolani-Marchetti et al. 1994). Preliminary results of an ongoing research (Tinner and Kaltenrieder, unpubl.) on the same site revealed no chestnut pollen presence before the Roman period so far. This information indicates that the data of Pavullo we used for our maps may overestimate the actual Holocene importance of *Castanea sativa* at that site. However, a definitive judgment of the importance of the species at Pavullo will need additional, more reliable efforts.

A third refugial zone was situated in the hinterland of the Tyrrhenian coast from Monte Amiata (Tuscany) to the Colli Albani (Lazio). Unfortunately, the profiles of the slopes of the volcanic Monte Amiata provide inconsistent information, given that the studies of Bertolani-Marchetti and Jacopi (1962) assign, without any radiometric dating, a constant and, in certain cases, extremely abundant

chestnut presence during the Eemian Period. The study concerning Val Farma (Ferrarini and Marraccini 1978) showing a reappearance of chestnut during the Atlantic period with values up to 30% after a gap during the LGM was not considered because of an insufficient chronology. Nevertheless, similar information is provided by studies in the Lazio Region: on the northern side of the volcanic region of the Colli Albani chestnut was consistently present between 200 and 120 kyr B.P., whereas it disappeared suddenly returning only about 6000 B.P. (Alessio et al. 1986; Follieri et al. 1988; Narcisi et al. 1992). In the profiles located in the outskirts of Rome, chestnut traces disappear around 45 kyr B.P. (Follieri 1979) and reappear around 10,000–8000 B.P. (Kelly and Huntley 1991; Lowe et al. 1996). On the other hand, the profiles of Lago di Martignano (Kelly and Huntley 1991), Albano and Nemi (Lowe et al. 1996) give a coherent picture of the presence of chestnut between 12,000 and 4000 B.P. (about 40 appearances in 100 samples). In conclusion, the high pollen percentages and the high IRP values suggest the presence of a shelter zone in this region.

The fourth presumed refugium is located in the south, where a large number of profiles gives evidence of a possible chestnut shelter zone (Fig. 6). In Lago Grande di Monticchio, in particular, chestnut was present in seven samples in the period between 28 kyr and 15 kry B.P. (11 grains on total with a mean chestnut pollen percentage of 0.4%, Allen et al. 2002). The existence of a chestnut shelter zone in southern Italy is supported by the finds of charred macroremains in the Castelcivita cave (Salerno Province) dated 35 kyr B.P. that Castelletti and Maspero (1992) determined as chestnut.

Unfortunately, is not possible to say on the basis of the available data whether the three mentioned shelter zones south of the Po plain were connected to a huge refugium covering the Italian peninsula moving from the south-easternmost part of France to southern Italy along the Apennine chain (Fig. 5b). Genetic analysis has so far failed to provide further evidence, because there was strong human impact on diffusion and cultivation of chestnut (Pigliucci et al. 1990; Fineschi et al. 2000).

A further possible shelter zone is represented by the hilly region of the Cantabrian coast, from the Picos de Europa in Asturia, Spain, to the French side of the Basque regions (Figs. 5b and 6). It is generally assumed that climatic conditions during the LGM in northern Iberia were quite continental, as they were in northern Italy, and therefore inadequate for thermophilous species such as chestnut. Unfortunately, the published pollen profiles give no detailed information on the pollen of taxa that may be confused with *Castanea*, so that no conclusive consequences can be drawn using pollen evidence alone. Nevertheless, it seems that the evidence of a pre-Roman presence of *Castanea* in northern Iberia continues to increase, especially in recent publications (Martín-Arroyo et al. 1999; Ruiz Zapata et al. 2003; Carrión et al. 2003; Muñoz Sobrino et al. 2004).

Because of the difficulties in determining *Castanea* macro-remains mentioned above, the strong anthraco-logical evidence for the presence of chestnut during the last glaciation given by Uzquiano (1992), who refers to chestnut macrofossils at the sites at Altamira and Azkonzilo, may be inconclusive. It is however striking that Uzquiano's data for LGM and the Late Glacial report other thermophilous species such as *Arbutus unedo*, *Quercus ilex*, *Buxus sempervirens*, *Ulmus* sp., *Juglans regia*, *Prunus amygdalus*, and *Ilex aquifolium*, especially in wind-protected sites. Climatic conditions allowing the survival of such thermophilous taxa (including Mediterranean evergreen species) would certainly be favourable for *Castanea sativa* as well.

For the Greek peninsula, the existing literature gives contradictory views whether chestnut survived there during the LGM or not (Fig. 5a). Some studies report that chestnut was completely absent (Bottema 1974; Bintliff and van Zeist 1982; Willis 1992a–c), but a number of others found traces of chestnut starting from the late Glacial period. The most convincing evidence for the presence of chestnut traces during pre-arboricultural time is available for the western Peloponnese (starting at 7500 B.P., Bottema 1990; Bottema and Woldring 1990; Atherden et al. 1993; Jahns 1993; Atherden and Hall 1994) and in Thessaly (starting at 9500 B.P., as reported for the profile of the former city of Halos, Bottema 1979). However, according to our IRP, the Greek peninsula was classified as a refugium area of only medium probability for chestnut (Fig. 6). This finding is surprising, since the Balkans are considered to be an important refugium area for other thermophilous tree species (Bennett et al. 1991; Petit et al. 2002). A similar pattern was found in northern Portugal and Galicia, Spain (Figs. 5b and 6). Chestnut pollen finds start at 14 kyr B.P. (Muñoz Sobrino et al. 2004, Laguna de las Sanguijuelas and Lleguna; Muñoz Sobrino et al. 2001, Lagoa de Lucenza; Allen et al. 1996, Sierra Cabrera) suggesting that both the Balkans and the north-western Iberian peninsula were at most secondary refugia *sensu* Brewer et al. (2002).

For France, the only coherent sign of a possible chestnut refugium is located in the southern part of the Département of Isère. The findings of Thiébault (1988) in the Grotte des Sarrasins (near Grenoble) could be confirmed by the more recent study of Nakagawa (1998), who reported the first chestnut traces during the LGM. Unfortunately, no further pollen indications for the presence of chestnut in the Dordogne region have been reported since the identification of charcoal macroremains in the cave of Lascaux (Leroi-Gourhan et al. 1979) and pollen findings in the Abri du Facteur (Leroi-Gourhan 1968). In northern and western France, no chestnut pollen before the Roman period has been reported so far (Guinier 1951; Jacquiot 1960; Leroi-Gourhan 1961, Leroi-Gourhan 1968; Beaulieu and Reille 1984; Beaulieu et al. 1985; Jalut et al. 1988; Reille 1991; Sanchez Goñi 1993), but this is not surprising as, during the LGM, most of northern France was probably exposed to permafrost conditions (Fig. 2).

A last area of medium refugium probability is located in the Near East in the hilly region along the Mediter-

ranean coast of Syria and Lebanon. Only a few sites testify to the existence of a chestnut refugium (for example, Niklewski and van Zeist 1970; van Zeist and Woldring 1980; Bottema and Woldring 1990). An indirect indication of the presence of chestnut is the abrupt and probably human-induced reappearance of chestnut around 8500 kyr B.P. in the Ghab Valley (Yasuda et al. 2000).

One common feature links all the presumed refugia: all sites are located in mountainous regions of southern Europe, even if at low to mid altitude and at the margins of mountain chains. This agrees with the conclusions already endorsed by Bennett et al. (1991) who report a similar finding for northern European trees. Other authors confirmed this finding (Carrión et al. 2003, Tribsch and Schönswetter 2003) emphasizing that mountain areas are in general important areas for refuges because of high habitat diversity. Moreover, they may supply enough water for plants during dry periods by collecting orographic precipitation.

Other regions with minor evidence of chestnut presence during the last glaciation are reported with low probability in Fig. 6 and are not further discussed in this paper. Additional data may provide new insights about these areas in the future.

Finally, there are a number of regions where the pollen profiles available are exhaustive and coherent enough to exclude the presence of chestnut refugia. This is the case, for instance, for all the sites north of the Alps and within the Alps (Germany, the Swiss and Austrian inner-Alpine regions), the southern Alps west of Lago di Garda (Burga 1980; Welten 1982b, Welten 1982c; Sidler 1988; Welten 1988; Wegmüller 1992; van der Knaap and Ammann 1997; Richoz 1998; Schwalb et al. 1998), the very southern part of the Iberian peninsula (Pons and Reille 1988; Carrión 2002), central Portugal (van der Knaap and van Leeuwen 1994, 1995, 1997) the northern and western parts of Romania (Björkman 2001), the Czech Republic (Svobodova et al. 2001), Slovakia and the Ukraine (Artjushenko et al. 1982). No conclusive statement can be made for the territory of the former Yugoslavia, given that the few existing palynological sites are concentrated on the coast (Brande 1973; Beug 1977; Willis 1994).

Conclusions

In this paper, possible chestnut refugia during the last glaciation were reconstructed by mapping radiocarbon-dated pollen spectra and anthracological and other macrofossil records. In order to maximize the information of the scarce and irregular chestnut pollen records, we developed an extended palynological approach, drawing up a *Castanea* refugium probability index on the basis of all the information available from the pollen profiles. A large number of new sites have been analysed for pollen since the early 1980s (Huntley and Birks 1983), enabling us to give a much more detailed picture of possible chestnut refugia. Our findings indicate that *Castanea*

sativa most probably survived the cold periods of the last glaciation in Europe, together with other thermophilous European tree taxa such as *Quercus*. This fits in with the assumption that the ice cover on the southern slope of the Alps was narrowed during the LGM (Felber 1993). The few divergences are due more to our selection of sites, especially those described in the local literature that are not listed in internet data bases, than to any fundamental disagreements about the data and data interpretation. For certain areas, however, the reliability of the existing pollen profiles (including questionable identifications of *Castanea*) is too poor to allow conclusive statements about the past existence of chestnut refugia.

Our results show that the European *Castanea sativa* refugia are probably greater in number than so far assumed. In particular spatial distribution patterns may have been much more complex than is depicted in our synthetic map (Fig. 6). In fact, it is conceivable that in marginal positions of mountainous areas, niches with a favourable microclimate may have existed despite a generally dry and cool climate. In these microenvironmental oases, small pockets of thermophilous tree species may have survived (Willis et al. 2000).

The large genetic variability of *Castanea sativa*, as shown by Lauteri et al. (1997, 2002) who analysed present populations growing in Europe in areas with different precipitation and temperature regimes may have resulted from the fragmentation of the refugia during the LGM and previous glaciations. In addition to genetic variability, the outstanding resprouting capacity of *Castanea sativa* may have favoured its survival during unfavourable climatic conditions by providing the opportunity to endure through centuries only by vegetative reproduction.

We emphasize that reconstructions of past situations such as the identification of refugial areas should keep in mind all environmental factors and consider more than just oversimplified model assumptions as for instance the overall cold-dry climatic situation during the LGM or the survival of European thermophilous tree species merely in southernmost Europe. Generally speaking, in reconstructing and describing past scenarios the evidence of a complex reality should be kept in mind when building models that synthesize the results.

In the future more attention should be paid to pollen traces of sporadic taxa that are commonly thought to have disappeared from a given area during the last Glacial and Late-Glacial periods. As already noted by some authors, spurious pollen traces may conceal very interesting information that is too often assumed to have been transported a long distance (Renault-Miskovsky 1972; Leroi-Gourhan 1992). Furthermore, this kind of synthetic work should also be encouraged for other taxa, as a useful basis for studies of the phylogenesis and the autecology of the European trees.

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