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Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: A review

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ABSTRACT

The forests in the Iberian Peninsula have been strongly influenced by past climatic changes, but reconstructing their historical distributions and dynamics is very difficult due to the complex climatic characteristics and relief of the region. Research disciplines such as phylogeography and species distribution modelling can describe the past range dynamics of individual tree species in relatively great detail and help elucidate how these species have reacted to climatic changes. Here we review phylogeographical and modelling studies from species representative of the major Iberian forest types and attempt to extract general trends from the diversity of individual species histories in the Peninsula. To date most studies focus on geographical range dynamics during the Pleistocene, but an increasing body of evidence shows that some species have also retained the genetic imprints of much more ancient processes. Many widespread Iberian species show a deep and often remarkably clear-cut divide between populations from the Mediterranean and from the Atlantic regions of the Iberian Peninsula, suggesting that both areas have independently sustained viable populations over extended periods. In fact, phylogeographical studies commonly find that species had several glacial refugia across the Iberian Peninsula. On the other hand, distribution models help identifying further suitable areas that could have sustained so far undetected refugia. Such studies are of interest for species conservation, because refugium populations are high-priority targets due to their long-term persistence and unique evolutionary trajectory. Overall, we conclude that palaeoecology, phylogeography and species distribution modelling have a great potential to inform each other because of their complementary perspectives and results. A true integration of these approaches is therefore fundamental for further progress in our understanding of past Iberian environments and the organisms they harboured.

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1. Introduction

The vegetation of the Iberian Peninsula is a mosaic of forests except in the most extreme habitats (arid zones in the Southeast or alpine environments where conditions are not suitable for tree growth), putting aside unforested areas due to human disturbance since the Neolithic (Blanco et al., 1998). There has been a wealth of literature dealing with the description of different types and their ecological correlates (e.g. Rey Benayas et al., 2002). More recently, investigations have increasingly focused on their functional traits (e.g. Valladares et al., 2004, Villar et al., 2004), assembly rules (Zavala, 2004; Bascompte and Jordano, 2007) and historical dynamics (Morla et al., 2002; Arroyo et al., 2004). Important insights into the history of the Iberian forests have been gained in recent years through palaeobotanical studies (see this issue). Another informative approach has been to reconstruct the past dynamics of Iberian forest components by using inferential methods, in particular those of phylogeography and of species distribution models.

Phylogeography attempts to identify the historical processes responsible for the contemporary geographical distributions of taxa by analysing the spatial structure of gene genealogies (Avise, 2000). Phylogeography and palaeoecology produce highly complementary perspectives upon historical vegetation dynamics and therefore are ideal candidates for integrated studies (e.g., Cheddadi et al., 2006; Magri et al., 2006). In fact, palaeoecological information from the fossil record is now routinely used to inform the phylogeographical interpretation of genetic data (Hewitt, 2000). Vice versa, genetic data compensate for some of the shortcomings of the palaeoecological approach and therefore are increasingly used to address long-standing questions in palaeoecology (Hu et al., 2009).

Species distribution modelling (also known as 'bioclimatic', 'habitat suitability' or 'niche' modelling) is a young but rapidly developing tool used to infer the geographical distribution of species (or sites suitable for species occurrence) at varying environmental conditions (Guisan and Zimmermann, 2000). Among their many

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applications, these models are frequently used to investigate the impacts of climate changes on species distributions (Pearson and Dawson, 2003). Briefly, such modelling exercises attempt to project the 'bioclimatic envelope' of species—that is, the range of climatic conditions under which they can exist—onto given climatic scenarios to estimate how their geographic range could change in response to a changing climate. Although most current research focuses on predicting the impacts of future climate change on species distributions (forecasting), an increasing number of studies is addressing past range dynamics (hindcasting; e.g., Hugall et al., 2002; Martínez-Meyer and Peterson, 2006; Hilbert et al., 2007; Pearman et al., 2008). Building on a rapidly growing body of spatially explicit palaeoclimatic information, species distribution models can readily provide reconstructions of species range dynamics at spatio-temporal scales rarely attainable by palaeodata alone (Rodríguez-Sánchez and Arroyo, 2008). However, palaeobotanical (or phylogeographical) data remain critical for the validation of model assumptions and results. Therefore, the strongest inferences are obtained through the integration of evidence from diverse sources (e.g., Cheddadi et al., 2006; Waltari et al., 2007; Alsos et al., 2009; Rodríguez-Sánchez and Arroyo, 2010).

This paper describes the historical distributions and dynamics of Iberian forest trees based on evidence from phylogeography and distribution models. Our aim is to provide a complementary perspective to the palaeobotanical information assembled in this Special Issue. We follow a species-by-species approach emphasising those trees and shrubs that we consider representatives of different forest types found in the Iberian Peninsula. On the other hand, we focus largely on relatively recent periods (in geological terms) due to the constraints imposed by the available phylogeographical and distribution models. We first review a number of case studies illustrating phylogeographical research of tree species, highlighting some shared trends among species and the main emerging views. We then overview distribution models and provide a conceptual bridge with phylogeographical studies aimed to understand the past range dynamics of Iberian tree species.

2. Inferences from phylogeographical studies

Past demographic events often have left long-lasting imprints on the genetic structure of extant populations. Phylogeographical studies use molecular markers to infer ancestor–derivative relationships between individuals (typically those belonging to different populations of the same species) and to situate these relationships in a geographical context (Avise, 2000). This allows tracing the genetic 'footprints' of species' historical population and range dynamics, which can then be interpreted considering their life history and ecology as well as the assumed palaeoenvironmental conditions.

The molecular markers most commonly used in plant phylogeographical studies are located on organelle DNA (chloroplasts and mitochondria). This DNA is usually uniparentally inherited, and genetic polymorphisms therefore arise exclusively from mutation, not from recombination (i.e., through sexual reproduction). As a consequence, organelle DNA markers allow tracing purely uniparental (maternal or paternal) lineages, which are much easier to follow than lineages subject to regular recombination (although the exchange of organelles between hybridising and backcrossing species such as *Quercus* spp. may complicate the interpretation of their phylogeographical patterns; e.g. Olalde et al., 2002).

Maternally inherited markers are most commonly used in plant phylogeography, because they are dispersed via seeds and therefore permit detecting past colonisation events (which can only occur through seeds, not through pollen). Markers based on nuclear DNA are sometimes used when genetic variation at organelle markers is too reduced to be informative. Nuclear markers are considerably more polymorphic, yet their biparental inheritance renders the reconstruc-

tion of past population dynamics much more difficult. Hence, the main utility of nuclear markers is to determine geographical patterns of genetic diversity, which can to some extent be used to infer past dynamics, too (e.g. López de Heredia et al., 2005).

Phylogeographical studies have described historical population and geographical range dynamics of numerous tree taxa growing in temperate and Mediterranean Europe (Petit et al., 2002a, 2003, 2005). Much research has focused on the range expansions that took place after the Last Glacial Maximum (LGM, 18–21 kyr BP). The advent of molecular tools has made it possible to test and refine several hypotheses regarding the Pleistocene history of populations, species and communities previously based on coarser (phenotypes, karyotypes: Favarger and Contandriopoulos, 1961; Stebbins and Dawe, 1987) or fragmentary (fossil record: Willis, 1996; Stewart and Lister, 2001) evidences. For instance, phylogeographical studies have clearly corroborated that the responses of species to climate changes were highly idiosyncratic, which helps explain the widespread existence of non-analogue plant communities documented in the fossil record. Genetic surveys also have elucidated the biological processes that were involved in the rapid postglacial range expansion of numerous species (most importantly successive long-distance dispersal events followed by exponential growth of resulting pioneer populations; Hewitt, 2000), thereby contributing to solve a long-standing palaeoecological debate (Reid, 1899; Clark et al., 1998).

Perhaps the most widely known contribution of phylogeography consists in the location of areas where species resided during the Quaternary cold stages (typically called 'glacial refugia'). Early influential works emphasized the role of the three major peninsulas in southern Europe (Iberia, the Balkans and to a lesser extent Italy) for the cold-stage survival of the temperate European forest flora and fauna (Hewitt, 1996, 2000; Taberlet et al., 1998). Subsequent studies have been refining this general picture in several directions. In particular, a rapidly growing body of evidence indicates that numerous species survived also in so-called 'cryptic refugia' (Provan and Bennett, 2008) or 'microrefugia' (Rull, 2009) situated at higher latitudes or altitudes than the major refugial regions. These cryptic refugia typically contained only small populations, whose existence is very difficult to detect by fossils alone but can sometimes be inferred from the genetic population structure of species (Hu et al., 2009). On the other hand, an increasingly extensive sampling of populations across the major refugial areas on the South European peninsulas is revealing an outstanding diversity of populations and species histories that reach much further back in time than those at higher latitudes (Lumaret et al., 2002; Petit et al., 2003; Fady-Welterlen, 2005; Magri et al., 2007). Both developments have contributed to sharpen the phylogeographical profile of the Mediterranean Basin and to help overcome early simplistic views that centred mostly on its function as a source for the postglacial recolonisation of central and northern Europe by biota (Petit et al. 2005; Gómez and Lunt, 2007).

The great environmental heterogeneity of the Mediterranean Basin, including the Iberian Peninsula, and its relative climatic stability compared to higher latitudes can render the interpretation of genetic population structures quite challenging. General patterns are far from being definitely ascertained, although a recent burst of phylogeographical studies on Mediterranean plants is successively improving our understanding of the complex Mediterranean palaeobiogeography (Médail and Diadema, 2009). At present, the Iberian Peninsula counts with the most abundant phylogeographical records of the three major European refugia. Notwithstanding, phylogeographical studies on emblematic Mediterranean species such as *Pistacia lentiscus*, *Myrtus communis*, or *Rhamnus alaternus*, for instance, are still lacking. In consequence, our current picture of the past distributions of forest species and communities is likely to undergo further transformations and precisions as more (and more detailed) case studies will become available.

3. Phylogeography of Iberian forest trees

Here we review phylogeographical records of the past range dynamics of several tree and shrub taxa representative of different Iberian forest types (many in fact being keystone species of their respective communities). We present case studies involving broad-leaved deciduous, sclerophyllous evergreen, broadleaved evergreen, and gymnosperm species, a grouping that roughly corresponds to the main forest types in the Iberian Peninsula. Note, however, that their past dynamics do not necessarily coincide with (or even be representative of) those of other members of their communities (e.g. Jackson and Overpeck, 2000). Nonetheless, the history of the species treated should provide informative insights about the ecological changes that the Iberian Peninsula has experienced through the Neogene.

3.1. Broadleaved deciduous species

Temperate deciduous forests are mostly distributed along the northernmost fringe of the Iberian Peninsula, in mountain ranges that are under the influence of relatively mild Mediterranean–Atlantic climates, or as gallery forest along water courses. The largest deciduous forests are dominated by white oaks (*Quercus* spp., subgen. *Quercus*) and in some regions by beech (*Fagus sylvatica* L.). Both have been intensively studied within the frame of European-wide research programmes (Petit et al., 2002a,b; Magri et al., 2006). These studies outstand for their integration of population genetic and palaeoeco-logical approaches, and their results are based on an empirical evidence of rarely achieved quality.

Seven white oak species occur on the Iberian Peninsula (*Quercus pyrenaica* Willd., *Q. faginea* Lam., *Q. canariensis* Willd., *Q. robur* L., *Q. petraea* (Matt.) Liebl., *Q. pubescens* Willd. and the prostrate *Q. lusitanica* Lam.). Their great propensity to hybridise makes it virtually impossible to infer phylogeographical patterns for individual species, which were therefore mostly described for the white oaks as a whole

(only excluding *Q. lusitanica*; Olalde et al., 2002; Petit et al., 2002a,b). Analyses revealed two major genetic lineages that are remarkably well-separated in space along a line running approximately from the southern tip of the Iberian Peninsula to the western Pyrenees (Fig. 1). Both lineages are well-developed and diverse, a clear indication of the long-term persistence of white oaks on the Iberian Peninsula. The divide between the two lineages suggests that their populations survived the Quaternary cold stages in separate refugia located near the Mediterranean and Atlantic coasts of the Peninsula, respectively, from where they expanded subsequently inland until they met each other. These glacial refugia would be located on the southern Peninsula according to pollen records (Brewer et al., 2002), whereas genetic data suggest that some refugia also existed further north (Olalde et al., 2002). The two lineages underwent very different dynamics after the LGM (see Fig. 1). The western lineage is currently widespread across central, northern and northwestern Europe, and genetic data clearly show that it colonised these areas passing the Pyrenees on their western side. In contrast, the eastern lineage did not arrive to cross the Pyrenees, which are instead occupied by two lineages that expanded into the Iberian Peninsula from Italy and the Balkans, 'blocking' the northward advance of the East Iberian lineage. The two immigrant lineages are unusually closely linked to *Q. petraea* and *Q. pubescens*, which suggests a recent colonisation of the Iberian Peninsula (Petit et al., 2002b). Finally, an interesting finding is the relatively close relationship between the East Iberian lineage and genotypes present in southern France, Corsica, Italy and Algeria (Petit et al., 2002a). Given that these areas were separated during the early Miocene (approx. 20 Myr BP), the authors did not dare to infer any vicariance processes from this resemblance (Petit et al., 2002a). Recent evidence from other species (see below) indicates however that the genetic similarities observed across the western Mediterranean Sea might indeed still reflect some deep Tertiary plate tectonic events (Hampe and Petit, 2007).

The history of beech on the Iberian Peninsula is notably different and markedly less complex (Magri et al., 2006). At present, the species
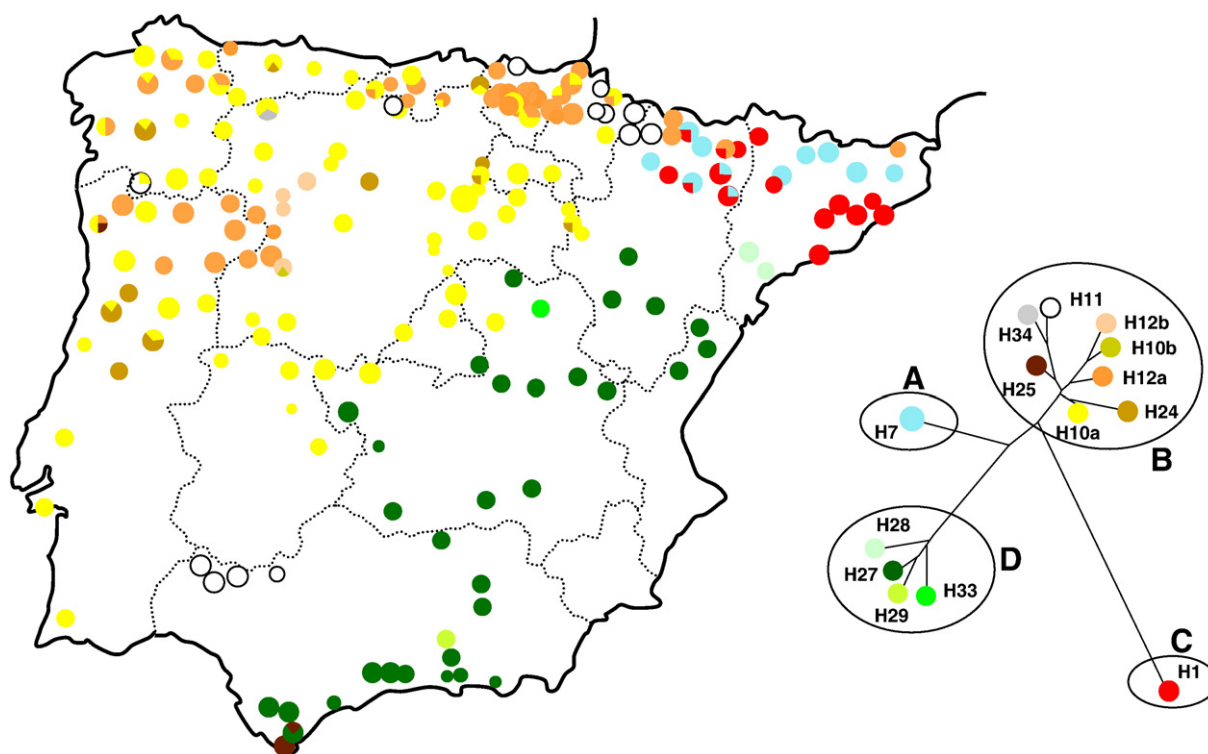

Fig. 1. White oaks (*Quercus* spp.) phylogeography in the Iberian Peninsula (reproduced with permission from Olalde et al., 2002). Note the divide of the major lineages from eastern and western Iberian Peninsula, and the presence of haplotypes of Italian–Balkan origin (H1 and H7, shown in red and light blue colours, respectively) in the northeast. The Gibraltar area harbours haplotypes from both eastern and western lineages, plus one private/endemic haplotype.

is distributed along the northernmost Iberian mountain ranges from the eastern Pyrenees to northwestern Cantabrian range. Combined palaeoecological and genetic data indicate the existence of three glacial refugia located in the eastern and western Pyrenees as well as in northwestern Spain. This proximity between the location of LGM refugia and the current distribution range suggests that postglacial range dynamics were very limited and probably occurred mostly in altitudinal direction. Contrary to the white oaks, Iberian beech populations did not participate in the postglacial colonisation of Europe by the species.

Other deciduous broadleaved species for which phylogeographical studies exist are *Fraxinus excelsior* L. (Heuertz et al., 2004) and *Corylus avellana* L. (Palmé and Vendramin, 2002). Unfortunately, sparse population sampling in the Iberian Peninsula and lack of genetic polymorphism limit possible inferences to the fact that both species probably recolonised western and central Europe in a fashion similar to that of the West Iberian white oak lineage (i.e., surrounding the Pyrenees in their western end). On the contrary, Iberian populations of *Fraxinus angustifolia* Vahl did apparently not expand north of the Peninsula (Heuertz et al., 2006). This result appears striking given that *F. angustifolia* is closely related with *F. excelsior* and both species hybridise (although *F. excelsior* appears to be more cold-tolerant). Further phylogeographical studies have been conducted on *Alnus glutinosa* (King and Ferris, 1998), *Betula* spp. (Palmé et al., 2003a,b; Maliouchenko et al., 2007), and *Salix* spp. (Palmé et al., 2003), yet the lack of a limited sampling in the Iberian Peninsula precludes detailed inferences upon their phylogeographical structure and range dynamics in the area.

A more complete and informative account exists for *Frangula alnus* Mill., a shrub or small tree that is widely distributed across central and northern Europe but restricted to humid areas in the mountain ranges of the Mediterranean Basin (Hampe et al., 2003). The study revealed past population dynamics at two different temporal scales. First, the postglacial range expansion of the species could be traced back to glacial refugia located in the Balkans, while Iberian populations did not participate in this process. Second, the authors found clear signs for a range expansion spanning the Mediterranean Basin in longitudinal direction. Levels of genetic divergence between populations indicated that this expansion must be of ancient origin, and the authors speculate that it could in fact have occurred before the onset of the mediterranean summer-dry climate in the Pliocene. As a result, *F. alnus* populations growing in the mountain ranges of Mediterranean Spain are characterized by an outstanding genetic and micro-evolutionary uniqueness, which renders them high-priority targets for conservation (Hampe and Petit, 2005).

Similarly, most Iberian populations of *Populus nigra* L. display a high genetic distinctiveness, presumably as a result of their long-term presence in the Iberian Peninsula and relative isolation from other European populations (Cottrell et al., 2005). Forty-five out of a total of 81 non-hybrid haplotypes identified across its range were present in the Iberian Peninsula. From these, only 7 haplotypes were found outside the Iberian Peninsula, pointing to limited migration across the Pyrenees. Genetic structure was much higher in the northeast (Ebro valley) than in central Iberian populations, suggesting that this area would have been an important refugium for the species.

Finally, chestnut (*Castanea sativa* Mill.) represents the strongly contrasting case of a species whose historical population dynamics in the Iberian Peninsula have been profoundly affected by man (Fineschi et al., 2000). Palaeoecological records indicate that the species was present before the last glaciation and went extinct (or largely extinct, as some recent evidence points to the possible existence of LGM populations in northern Spain; Krebs et al., 2004). Then it appeared again in many parts of the Peninsula in historical times, presumably re-introduced by man. As a consequence, the populations included in the study of Fineschi et al. (2000) only show genetic signs of this latest, anthropogenic 'colonisation', while the genetic heritage enclosed in the extinct autochthonous populations is lost. Another striking example of human-mediated colonisation and range expansion of a tree species within the Iberian Peninsula is that of elm (*Ulmus minor* L.). Two major lineages are currently found in the Iberian Peninsula, and one of them was apparently introduced in historical times from Italian source populations (Gil et al., 2004). Both the native and the introduced lineages are today similarly widespread across the Peninsula, demonstrating that human translocations can have severe impacts on the genetic structure and distribution patterns of Iberian tree species.

3.2. Sclerophyllous evergreen species

This group includes many emblematic trees of Mediterranean origin, which represent the most widespread component of Iberian forests (partly due to intentional planting or historical land management practices). There has been a recent burst of interest in the phylogeography of sclerophyllous tree species, particularly on the two most widespread Iberian evergreen oaks (holm oak *Quercus ilex* L./*Q. rotundifolia* Lam. and cork oak *Q. suber* L.) and the olive tree (*Olea europaea* L.). All have been thoroughly studied and their phylogeography is reasonably well understood, although the time frame of their most significant range changes is still debated (Petit et al., 2005; Magri et al., 2007).

The study by Lumaret et al. (2002) on *Quercus ilex* is the single most comprehensive and informative phylogeographical study performed on a genuinely Mediterranean tree species. A sample of 174 populations covering the entire distribution range enabled the authors to situate the most ancient holm oak populations in the Aegean Sea, from where the species expanded along both sides of the Mediterranean Sea (Fig. 2). Interestingly, every long-distance colonisation event across a sea barrier (from Greece to Italy, from Sicily to Tunisia, and from Morocco to Spain) was followed by the rapid formation of a new lineage that diversified during its further advance. Overall, the genetic divergence of populations clearly indicates that the processes involved are of ancient origin, very probably reaching back well into the Tertiary (Petit et al., 2005).

Quercus ilex reached the Iberian Peninsula from the south via the Strait of Gibraltar (Fig. 2). The distribution of haplotypes across the Peninsula itself resembles that of the white oaks. Two well-developed and clearly separated lineages occupy the western and the eastern sectors of the Iberian Peninsula, indicating that the two coasts have sustained populations for an extended period with negligible interchange between them (at least via seeds; the markers used do not reflect gene flow through pollen). In contrast to the white oaks, *Q. ilex* passed the Pyrenees in their eastern side, and the East Iberian lineage arrived to colonise southwestern France till reaching areas that it encountered already occupied by populations of Italian origin. Finally, combined genetic and palaeoecological analyses (reviewed in López de Heredia et al., 2007) suggest the existence of numerous LGM refugia of *Q. ilex* in several regions (both coastal and inland) across the Peninsula.

The range-wide population genetic structure of *Quercus suber* provides another spectacular insight into the deep phytogeographic history of the western Mediterranean Basin (Magri et al., 2007; Lumaret et al., 2009). It consists of five distinct groups of populations, two of them distributed in Iberia and Morocco and two more in Italy. The fifth group shows a disjunct distribution along a narrow belt that spans southern France, Corsica, Sardinia and Tunisia. Magri et al. (2007) argued that such a pattern is very unlikely to arise from multiple long-distance dispersal events but is instead geographically consistent with the Oligocene and Miocene break-up events of the European–Iberian continental margin. They suggested consequently that *Q. suber* populations "have persisted in a number of separate microplates, currently found in Tunisia, Sardinia, Corsica, and
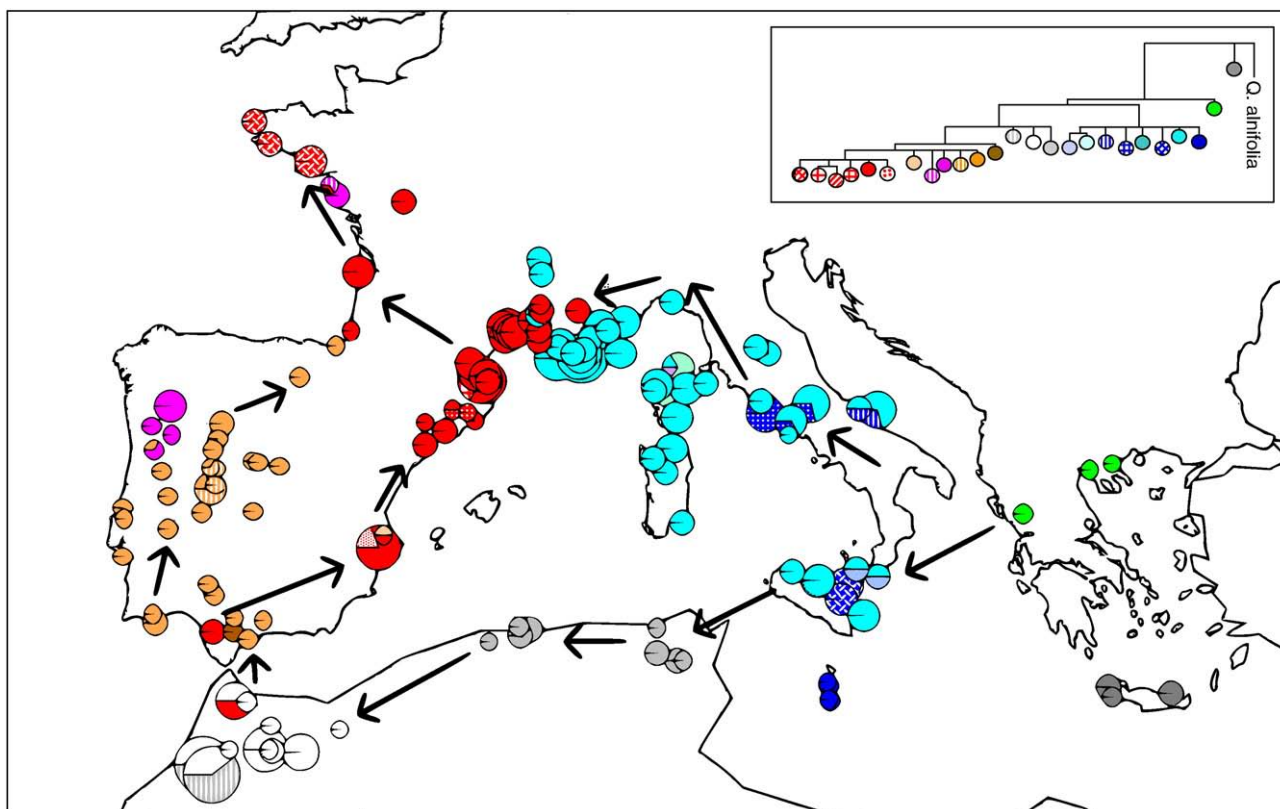
Fig. 2. Holm oak (*Quercus ilex*) phylogeography in the Mediterranean Basin (reproduced with permission from Petit et al. (2005); original data from Lumaret et al. (2002)). This species exemplifies the phylogeographical pattern of many ancient tree species that colonised the Mediterranean Basin from east to west. A higher differentiation of haplotypes is found westwards. The east–west divide within the Iberian Peninsula is also clearly shown. *Q. ilex* apparently entered the Iberian Peninsula from the south and expanded along both Atlantic and Mediterranean sides of the Peninsula. Only the eastern lineage crossed the Pyrenees.

Provence, without detectable chloroplast DNA modifications for a time span of over 15 million years" (Magri et al., 2007, p. 5259).

Unfortunately, the low polymorphism encountered in *Quercus suber* limits inferences concerning the Iberian Peninsula. An east–west divide is again apparent, although it is somewhat less clear-cut than in the previously described cases. Interestingly, the divide is not limited to the Peninsula but continues through the Moroccan distribution range. Remarkable introgression by *Q. ilex* in eastern populations, together with palaeobotanical evidence, suggest that several *Q. suber* populations may have survived glacial periods in the eastern Iberian Peninsula in addition to the main refugium in the Southwest (López de Heredia et al., 2007). In much younger times, populations apparently passed the Pyrenees on both sides to colonise the southwest of France (Magri et al., 2007).

A different type of evergreen forest is that of oleaster (or wild olive, *Olea europaea*) communities that prevail in the warmer and drier parts of the Iberian Peninsula. Several studies have traced the phylogenetic and phylogeographical history of oleaster, olive and their relatives across the Mediterranean. In common with other tree species with whole-Mediterranean distribution (e.g. Lumaret et al., 2002; Hampe et al., 2003; Rodríguez-Sánchez et al., 2009), a marked genetic differentiation between the eastern and western ends of the Mediterranean Basin points to an ancient occupation of the area with limited (seed-mediated) exchange between different regions. The eastern Mediterranean harbours the most ancient forms, both for wild and domesticated lineages (reflecting natural colonisation processes and the expansion of olive cultivation, respectively; Zohary and Spiegel-Roy, 1975; Besnard et al., 2002; Lumaret et al., 2004).

Today, populations of wild, cultivated and naturalized *Olea europaea* often grow in close proximity and it sometimes is very difficult to distinguish them in the field. However, their organelle DNA shows clear differences, since cultivated and naturalized plants belong to genetic lineages originating in the eastern Mediterranean (Lumaret and Ouazzani, 2001; Besnard et al., 2002; Lumaret et al., 2004; Rubio de Casas et al., 2006). This particularity has been used to document the autochthonous status of *O. europaea* populations growing in the Eurosiberian north of the Iberian Peninsula (Vargas and Kadereit, 2001). On the other hand, studies based on nuclear DNA have shown that wild olive populations throughout the Mediterranean Basin are heavily swamped by pollen-mediated gene flow from cultivars (Lumaret and Ouazzani, 2001). This observation raises specials concerns for the genetic conservation of autochthonous *O. europaea* populations because naturalized cultivars usually contain markedly lower levels of genetic diversity than 'real' wild populations as a consequence of the domestication process (Lumaret et al., 2004).

3.3. Gymnosperms

Forests dominated by gymnosperm species represent another vegetation type of wide distribution in the Iberian Peninsula. They are usually dominated by single species of pine (*Pinus*), and in some regions fir (*Abies*) or juniper (*Juniperus*), which sometimes co-occur with deciduous or sclerophyllous broadleaved species (e.g., *Quercus* and *Fagus*). All three gymnosperms genera count with phylogeographical surveys in the Iberian Peninsula, although levels of knowledge vary considerably among species.

There are currently six wild pine species in the Iberian Peninsula, four with a mostly Mediterranean range and two distributed farther north. Of the latter, Scots pine (*Pinus sylvestris* L.) is common throughout central and northern Europe. Its range-wide population dynamics were subject to one of the first studies that combined palaeoecological and phylogeographical records with palaeodistribution modelling (Cheddadi et al., 2006). Based on a thorough database, the authors concluded that Iberian populations did not contribute to

the postglacial recolonisation of Europe by the species and suggested at least three areas in Catalonia, northwestern and southeastern Spain, respectively, that would have sustained populations during the LGM. Today, natural *P. sylvestris* stands are restricted to areas above 1000 m in northern Spain and to a few sites above 2000 m in the Southeast Spanish Sierra Nevada and adjacent ranges. The particular genetic composition of the Sierra Nevada populations was early recognized and assigned to a long-term isolation that would date back to the Tertiary (Sinclair et al., 1999). Genetic differences are also strong and geographically structured across other Iberian mountain ranges (Soranzo et al., 2000), which would likewise point to a long-term isolation (concerning seed-mediated gene flow) of populations from different mountain ranges that has not been blurred by Pleistocene glaciations.

The Iberian pine with the most complete phylogeographical account is maritime or cluster pine (*Pinus pinaster* Ait.), a species distributed across mountain ranges of the western Mediterranean Basin and in lowlands of southern and western France. Within this range, there are three well-separated main maternal lineages corresponding to northern Morocco, to western France and Iberia, and to southern France, Italy and Tunisia, respectively (Burban and Petit, 2003; Bucci et al., 2007). The distribution of the latter lineage resembles that of cork oak and has been suggested to result likewise from mid Tertiary plate tectonics (Magri et al., 2007; Hampe and Petit, 2007). Analyses of paternally inherited DNA markers show that pollen-mediated gene flow has been significantly more extensive than gene flow through seeds (Burban and Petit, 2003).

Abundant fossil records document that *Pinus pinaster* was present in several regions of the Iberian Peninsula during the LGM (Carrión et al., 2000, 2003). A detailed genetic analysis involving 22 Iberian populations (Bucci et al., 2007) revealed a significant divide between southeastern and western stands. Southeastern populations are markedly more diverse than those from the western Peninsula, which suggests (in line with the fossil record) that Southeast Spain harboured larger maritime pine populations during the LGM than the Atlantic coast regions (Bucci et al., 2007). However, the postglacial recolonisation of northern Spain occurred from refugia near the Atlantic.

European black pine (*Pinus nigra* J.F. Reynold) is perhaps the most representative circum-Mediterranean mountain pine. Although a range-wide phylogeography of the species is lacking, Afzal-Rafii and Dodd (2007) compared a number of populations from Southeast Spain, the Pyrenees, southern France, and Italy and found that their respective genetic differentiation was too strong to be of postglacial origin. The authors applied coalescent modelling to estimate divergence times between these population nuclei and concluded that their mutual isolation probably occurred in fact much before the LGM.

The whole-Mediterranean Aleppo pine (*Pinus halepensis* Mill.) shows a notably different phylogeographical structure. The species appears to have its origins in the eastern Mediterranean and genetic surveys have documented a continuous westward decline of population genetic diversity, which is thought to result from the species' colonisation history (e.g. Fady-Welterlen, 2005; Grivet et al., 2009). *P. halepensis* appears to be a relatively recent member of Iberian forests that entered the Peninsula from the northeast and spread until the extreme south along the coastal areas (Gómez et al., 2005).

Finally, stone pine (*Pinus pinea* L.) represents a very particular case. The species grows scattered across the entire Mediterranean Basin, and a recent range-wide study revealed that its populations contain the lowest levels of genetic diversity that have to date been reported for a widely distributed tree species (Vendramin et al., 2008). Only four genetic variants were detected using numerous chloroplast DNA microsatellites, a marker type that usually is quite polymorphic in conifers. One variant occupies virtually the entire species range, while two others were found in three Lebanese populations and one further in two central Spanish stands. The authors of the study suggest that *P. pinea* suffered a severe and prolonged genetic bottleneck in a past of undetermined age, followed by a recolonisation (aided by man) that was too rapid to go along with a genetic differentiation. The resulting genetic structure does not allow to infer where stone pine persisted the LGM in the Iberian Peninsula. However, at least two glacial refugia located near Málaga and Gibraltar have been documented by charcoal remains (Badal, 1998; Finlayson et al., 2006).

Fir (*Abies*) forests are much less common in the Iberian Peninsula than pine forests, with only two native species. European silver fir (*A. alba* Mill.) is widespread in mountain ranges of central and Southern Europe, reaching the Pyrenees in the southwest. These mountains harboured one of the species' glacial refugia, although populations probably suffered a severe bottleneck as indicated by the low genetic diversity of the extant stands (Vendramin et al., 1999; see also Alba-Sánchez et al., 2010). Notwithstanding, the Pyrenean refugium played an important role during the postglacial recolonisation of Europe by the species, and *A. alba* populations of Pyrenean origin can be found as far northeast as in Poland (Liepelt et al., 2002). Spanish fir (*A. pinsapo* Boiss.) is endemic to three Andalusian mountain ranges. Low levels of nuclear DNA differentiation among these ranges indicate that they are, or have been until recently, connected to some extent by (probably pollen-mediated) gene flow. On the contrary, *A. pinsapo* stands are clearly distinct from populations of the closely related North Moroccan endemic *A. maroccana* Trab. This distinctness is thought to have its origins in a separation that pre-dates the opening of the Strait of Gibraltar in the Pliocene (Terrab et al., 2007).

Forests dominated by junipers (*Juniperus* spp.) are very distinct from other Iberian gymnosperm forests, being characterized by low tree cover and density and extreme environmental conditions (e.g. sandy soils in coastal areas, cold-dry mountains; Blanco et al., 1998). Most juniper species have a wide distribution across the Mediterranean and are reasonably frequent in the fossil record, which renders them suitable organisms for phylogeographical studies. However, only a few studies are available and even fewer adopt a proper phylogeographical approach beyond quantifying geographical patterns of genetic diversity. The most detailed work is that of Terrab et al. (2008) on Spanish juniper (*Juniperus thurifera* L.), a species distributed across mountain ranges of the western Mediterranean Basin. Once again, the authors observe a strong differentiation between European and Moroccan populations whose origin is thought to be older than the separation of the African and the Iberian plates in the Pliocene. The phylogeographical relationships of populations from continental Europe, Corsica and Algeria remain less clear and may have been shaped by vicariance as well as long-distance colonisation events (Terrab et al., 2008). It is noteworthy that all three European lineages of *J. thurifera* are currently present in the Iberian Peninsula, which was apparently an important refugium for the species.

3.4. Broadleaved evergreen species

Forests dominated by broadleaved evergreen (lauroid) species represented the dominant vegetation of the Tethyan region, and the Iberian Peninsula in particular, until the mid-late Miocene (Utescher et al., 2007; Postigo Mijarra et al., 2009). Today remnants of this vegetation in the Iberian Peninsula are rare and restricted to small and isolated areas of particularly mild and humid climate. The number of species is limited but includes emblematic taxa such as bay laurel (*Laurus nobilis* L.), common rhododendron (*Rhododendron ponticum* L.) or Portuguese laurel (*Prunus lusitanica* L.). Many species have scattered geographical distributions ranging from the Macaronesian Islands in the west to the Black Sea area and the Caucasus in the east,

which presumably constitute relics of their former, more continuous ranges (Sunding, 1979; Denk et al., 2001; Rodríguez-Sánchez and Arroyo, 2008).

The single most comprehensive phylogeographical study of a Mediterranean lauroid species is that of Rodríguez-Sánchez et al. (2009) on *Laurus nobilis*. Despite low levels of chloroplast DNA diversity, the authors detected a clear phylogeographical structure. Like many other species, *L. nobilis* shows a clear divide between populations from the eastern and the western end of the Mediterranean Basin. In fact, western Mediterranean populations are genetically more related to those growing on the Macaronesian Islands (traditionally considered as a different species, *L. azorica* (Seub.) Franco) than to eastern Mediterranean populations. The eastern lineage seems to be more ancient and no signs of past movements are detectable, whereas the western lineage shows clear signs of intense past range dynamics. The genetic markers used by Rodríguez-Sánchez et al. (2009) did not allow to elucidate migration patterns at finer scales, nor the period of the major movements. However, niche-based distribution models based on the fossil record and the species' present distribution indicate a marked effect of the Pleistocene climate oscillations on the range dynamics of *L. nobilis* (Rodríguez-Sánchez and Arroyo, 2008). In addition, an earlier genetic study based on AFLP markers (Arroyo-García et al., 2001) distinguished groups of populations which could correspond to some Pleistocene refugia scattered along coastal areas of the Iberian Peninsula.

European holly (*Ilex aquifolium* L.) and ivy (*Hedera* spp. L.) are other members of the Iberian broadleaved evergreen forests that have been subject to phylogeographical surveys (Grivet and Petit, 2002; Rendell and Ennos, 2003). Both studies underpin the long-term presence of these species in the Iberian Peninsula but their sampling does not provide specific insights into their past population dynamics in this region. Iberian *I. aquifolium* populations contributed to the postglacial recolonisation of western Europe, while no clear inferences are possible for the role of Iberian *Hedera* populations in this process.

3.5. Synthesis

The slow pace of evolution of trees and their abundance in the fossil record render them ideal organisms to throw light on the 'shallow' and 'deep' phytogeographic history of the Mediterranean Basin (Petit et al., 2005). The case studies reviewed here illustrate that different species, and populations within species, have responded in a very idiosyncratic manner to past climatic changes. Their population dynamics have been governed by a still poorly understood mixture of manifold causes including the life history, dispersal ability and ecological requirements of species as well as the particular geographical context in which populations perform (Pitelka et al., 1997; Petit et al., 2004). Some common 'themes' can however be extracted from the diversity of patterns observed across the Iberian Peninsula.

The most salient feature is the strong and remarkably clear-cut divide between lineages from the Atlantic and the Mediterranean regions of the Peninsula, which is a consistent pattern across species in different genera. This widespread divide is traditionally assigned to the existence of mutually isolated glacial refugia located near each of the two coasts, from which populations would have expanded inland after the LGM until encountering terrains occupied by populations originating in the other refugium. Such a scenario is probably valid for many (or even most) tree species that are currently distributed across the Iberian Peninsula. However, this only explains the maintenance of the east–west divide but not its origin itself. Edaphic preferences of species might be relevant in this regard (Alvarez et al., 2009), as the eastern and the western Iberian Peninsula are characterised by siliceous (acidic) and calcareous (more basic) soils, respectively, that might act as selective filters promoting isolation and differentiation of species and lineages (Blanco et al., 1998). Notwithstanding, the evidence reviewed in this paper allows two more interesting

inferences concerning this origin. First, the geographical distribution of genetic lineages and their different genetic variants indicates that the divide probably arose when species entered the Iberian Peninsula from the south and then expanded independently along both coastlines. In contrast, few species entered Iberia apparently from the northeast, and these remained mostly restricted to its Mediterranean sector. The notion of a predominantly southern provenance of currently widespread species is further backed by the fact that several taxa show peculiar and relatively original genetic variants of narrow distribution in populations located in southwestern Spain (e.g. Lumaret et al., 2002; Olalde et al., 2002; see also Fig. 1). Second, the well-developed genetic lineages found within each region indicate that the original formation of the divide probably often antedates the LGM, although not necessarily occurred during the Tertiary.

Most phylogeographical studies that were based on an appropriate population sampling have found evidence suggesting that species persisted through the LGM at various places of the Peninsula, usually near the coasts but sometimes also inland (e.g. *Quercus ilex* and *Juniperus thurifera*). These different populations contributed very differently to the postglacial recolonisation of Iberia and Europe. Such a result may appear relatively commonplace, yet the complex internal population structure of the Mediterranean Peninsulas has only very recently been fully appreciated and still remains poorly understood (López de Heredia et al., 2005; Petit et al., 2005; Gómez and Lunt, 2007). Moreover, genetic surveys demonstrate that those populations that have persisted roughly *in situ* over extended periods have accumulated outstanding levels of genetic differentiation and represent unique stores of species' evolutionary history (Hampe and Petit, 2005).

On a European scale, the Iberian Peninsula appears as one of the most significant sources for postglacial range expansions of forest trees. Our review also highlights the role of the Pyrenees as a very effective barrier to postglacial northward range expansions, with expanding populations bypassing them by the west or east. The resulting delay in expansions and range dynamics facilitated in some cases the advance of competing populations from Italy or even the Balkans, thereby restricting the space available for Iberian lineages. This problem concerned mostly East Iberian lineages, whereas West Iberian populations usually expanded rapidly enough to fill large parts of western and northwestern Europe with their descent.

Perhaps the most fascinating aspect of Iberian tree phylogeography is related with its more genuinely Mediterranean context. Only a few years ago phylogeographical studies hardly considered timescales beyond the LGM, yet rapidly increasing evidences leave no doubt that tree populations can sometimes conserve traces of past dynamics spanning timescales that have been long enough to allow the diversification of entire plant and animal genera (Hampe and Petit, 2007). This provides a great opportunity to further elucidate the 'deep' phytogeographic history of the Mediterranean Basin, to date mostly accessible through a fragmentary fossil record and interspecific phylogenetic studies.

Finally, phylogeographical studies have also served to document the influence of human management on several Mediterranean tree species. Deliberate cultivation (e.g. *Castanea sativa*, *Ficus carica*, *Ulmus minor*, *Olea europaea*, and *Pinus pinea*) or accidental introductions (e.g. *Ulmus pumila*) have sometimes left long-lasting traces in the genetic structure of populations (e.g., Fineschi et al, 2000; Gil et al., 2004; Vendramin et al., 2008). Tree species have been managed and sometimes even domesticated since early times (Zohary and Spiegel-Roy, 1975). It therefore is important to keep in mind that anthropogenic activities may sometimes pervasively confound phylogeographical patterns.

4. An introduction to species distribution models

In addition to palaeobotanical and phylogeographical data, a new source of information about past distributions of species has recently

been added to the biogeographer's toolbox. Species distribution models comprise a broad array of statistical approaches (including generalised additive and linear models, neural networks, regression trees or maximum-entropy algorithms) that relate species distributions to particular environmental variables—predominantly, although not exclusively, related with climate (Guisan and Zimmermann, 2000). The principal aims of such modelling exercises are to gain a better understanding of the factors that shape the geographical distribution of species, and to infer their geographical ranges for different time periods or regions (Pearson and Dawson, 2003; Morin et al., 2007).

There are currently two main approaches to model species distributions (see Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Guisan and Thuiller, 2005; Kearney and Porter, 2009 for reviews). Mechanistic or process-based models are based on a sound knowledge of the ecology of species and their physiological tolerance to environmental conditions, whereas correlative models seek statistical associations between the current distribution of species and selected environmental variables of potential relevance that can be considered as predictors. Mechanistic models usually require a species-specific collection of long-term field and/or laboratory data, which are often costly and hard to obtain (Kearney and Porter, 2009). In contrast, correlative models are relatively easy to implement due to their phenomenological nature, and their implementation is favoured by the rapidly increasing availability of environmental data with appropriate large-scale geographical coverage and resolution (Graham et al., 2004). Although species distribution models are generally built for particular species or subspecies, they may also be applied to plant functional types (e.g. Hilbert et al., 2007) or other *ad hoc* groups of organisms. Correlative models have proved to be useful for predicting species distributions across geographical regions and time periods (Araújo et al., 2005; Thuiller

et al., 2005; Hijmans and Graham, 2006), even though they are based on some wide-ranging and partly unrealistic biological assumptions (see below). Recent studies have attempted to overcome some of these limitations, e.g. by combining them with spatially explicit population models (Keith et al., 2008) or introducing dispersal processes during range expansion (De Marco et al., 2008). Concomitantly, niche-based species distribution models are increasingly applied in an evolutionary context, to address questions such as niche evolution across phylogenies (Yesson and Culham, 2006; Evans et al., 2009) or the ecological delimitation of lineages (Kozak et al., 2008).

Two kinds of data are required to build a correlative species distribution model (Fig. 3): (1) a list of geo-referenced occurrences of the species (which may be complemented by known absences); and (2) a corresponding dataset of environmental variables (e.g. climate, soil types, and topography). By combining these two data layers one can extract the environmental conditions at localities where the species is present versus those where it is absent (Guisan and Zimmermann, 2000). Once the statistical relationship between species distributions and the environment has been fitted and the predictive ability of the model been verified, it can be used (with due caution) to infer the distribution of species across time and space by projecting its 'bioclimate envelope' onto past or future climate scenarios. This extrapolation onto different spatial or temporal realms relies upon a series of assumptions, which have been subject to debate and critiques of the approach (Davis et al., 1998; Hampe, 2004; Dormann, 2007). For instance, the environmental requirements of species are assumed to remain stable over time, and their current geographical distribution is assumed to be environmentally-driven and in equilibrium. The latter may be difficult to justify for some Mediterranean species whose distribution has been largely influenced by human activity, though there are ways to circumvent this limitation (e.g. Latimer et al., 2006).
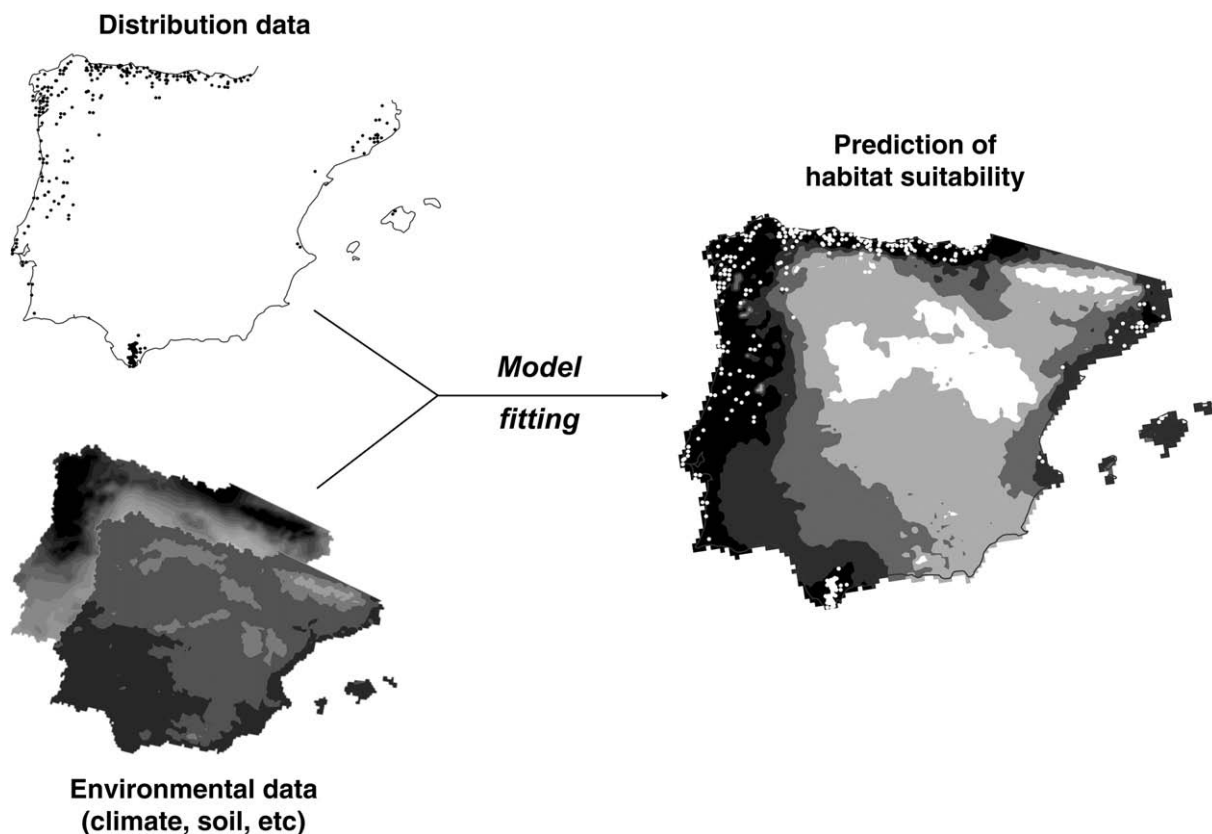

Fig. 3. Outline of the workflow to predict species ranges by means of species distribution models. These models relate distribution data with the environmental conditions at sites where species are present in order to predict suitable areas for the species in past, present or future environmental conditions. Sometimes, data on known absences of the species at particular sites are also used (see Guisan and Zimmermann, 2000).

The implications of these assumptions are exacerbated by the fact that the realism and predictive value of model outputs are very difficult to evaluate, because appropriate tests require independent data. Attempts have been made using fossil evidence (Pearman et al., 2008; Rodríguez-Sánchez and Arroyo, 2008), new locations of invasive species in their recently colonised range (e.g., Thuiller et al., 2005), or phylogeographical records (Hugall et al., 2002).

Until recently, most studies using species distribution models have focused on the impacts of modern climate change on future geographic ranges (Guisan and Thuiller, 2005). However, an increasing number of studies is attempting to reconstruct past species distributions (Cheddadi et al., 2006; Martínez-Meyer and Peterson, 2006; Hilbert et al., 2007; Pearman et al., 2008; Rodríguez-Sánchez and Arroyo, 2008; see Nogués-Bravo, 2009 for a review). Most works have focused on the LGM or the mid-Holocene climatic optimum (c. 6 kyr BP), because these periods count with relatively precise and well-established palaeoclimatic reconstructions (Cane et al., 2006). In contrast, the lack of suitable data has until very recently limited analyses of species range dynamics farther back in the past. This is however changing with the advent of palaeoclimate reconstructions for earlier periods, and first modelling exercises (e.g., Rodríguez-Sánchez and Arroyo, 2008) have extended their projections to periods earlier than the Pleistocene (see also Yesson and Culham, 2006 for a combined phylogenetic approach).

Nonetheless, the reliability of palaeodistributions inferred from models fitted to present data is likely to decrease as one moves further back in time, because other confounding processes (e.g. biological interactions or niche evolution) may become increasingly relevant (Pearman et al., 2008). Furthermore, model outputs ought to be understood as estimates of environmental suitability rather than a 'portrait' of the actual distributions of species, which may well be shaped by other factors such as interspecific competition or dispersal limitation beyond the fulfilment of climatic or environmental requirements (Davis et al., 1998; Hampe, 2004). In other words, species may have been actually absent from areas inferred to be suitable according to the model. Thus, the hypothetical role of these areas as actual refugia needs to be confirmed by palaeobotanical or phylogeographical data. Additionally, several modelling strategies and palaeoclimatic reconstructions should ideally be used in order to quantify and reduce the uncertainty of the projected palaeodistributions (Nogués-Bravo, 2009). Furthermore, estimates of the uncertainty surrounding the reconstructed palaeodistributions should also be provided, in order to assess the robustness of the inferred distribution scenarios.

How can palaeoecology and distribution modelling inform each other? For instance, palaeoecological data can help test model predictions as well as provide independent evidence to reject or refine proposed palaeodistributions. In turn, species distribution models may be successfully used to identify unknown refugia (e.g. Hilbert et al., 2007; Leroy and Arpe, 2007), particularly of taxa with scant or absent palaeobotanical remains.

5. Palaeodistribution models of Iberian tree species

There are yet only a few studies that used species distribution models to reconstruct past ranges of Iberian tree species, and all but one deal with LGM or mid-Holocene distributions. Unfortunately, palaeoclimatic reconstructions generated by global-scale general circulation models did until recently hardly provide sufficient spatial resolution to assess regional-scale climatic patterns across the Iberian Peninsula, although some novel high-resolution estimates (e.g. Jost et al., 2005) should help to this end (see Fig. 4). Meanwhile, model projections of past species distributions remain relatively coarse-grained, and it is likely that some smaller potential refugia are missed.

Regardless of these limitations, studies clearly indicate that the Iberian Peninsula provided suitable climatic conditions for numerous European tree species during the LGM. Thus, Leroy and Arpe (2007) used current knowledge on climatic limitations to tree growth to infer the distribution of European temperate deciduous trees during the LGM, distinguishing between 'cool' and 'warm' summer-green trees. For both guilds, several regions located in the northwestern, southwestern and southeastern Iberian Peninsula appeared suitable for tree persistence (as well as several other, more or less restricted areas in the Mediterranean and Black Sea Basins). Similarly, Svenning et al. (2008) confirmed the suitability of the Mediterranean Peninsulas as glacial refugia for numerous boreal and nemoral European trees. All 22 species included in this study counted with areas of variable size in the Iberian Peninsula that would have allowed population persistence through the LGM.

Interestingly, Svenning et al. (2008) also identified areas with suitable LGM conditions for some species that do not have extant natural populations in the Iberian Peninsula (*Alnus incana* (L.) Moench, *Picea abies* (L.) H. Karst, *Ulmus laevis* Pall.), or are very locally distributed (*Carpinus betulus* L.) but count with late-Pleistocene palynological or macrofossil records (Ramil-Rego et al., 1998; Postigo Mijarra et al., 2008, this issue). These results are complemented by the study of Pearman et al. (2008), which estimated mid-Holocene distributions of several European tree taxa and found that *C. betulus* and *P. abies* have been experiencing a process of range retreat since the LGM that continues up to the present. This case study nicely illustrates how the combination of fossil data and modelling approaches can help elucidate long-term trends of species that would not be detectable by either approach on its own.

The most exhaustive and detailed reconstruction of the range dynamics of Iberian tree species was performed by Benito Garzón et al. (2007). These authors modelled potential distributions during the LGM and the mid-Holocene for up to 19 tree species or subspecies, including several gymnosperms and broadleaved species (e.g., *Abies alba*, *Pinus pinea*, *P. sylvestris*, *P. pinaster*, *Fagus sylvatica*, *Quercus suber*, *Q. ilex*, *Q. robur*, and *Castanea sativa*). A summary map of predicted species richness at the LGM (Fig. 5) suggests that climatic conditions in northwestern Iberian Peninsula and the foothills of the Pyrenees at the LGM may have enabled the persistence of a number of species, particularly beech (*F. sylvatica*), sweet chestnut (*C. sativa*), temperate *Quercus* and montane gymnosperms (*A. alba* and *P. uncinata*). In contrast, the relevance of southern Iberian refugia, confirmed by multiple palaeobotanical and phylogeographical data (Carrión et al., 2003, 2008; Rodríguez-Sánchez et al., 2008), appears somewhat undervalued in this study due to the particular ecogeography of the species included. As previously suggested by palaeobotanical evidence (Carrión, 2002, Carrión et al., 2003), pines appeared to be a widespread and dominant component of full-glacial forests in the Iberian Peninsula, whereas the distribution of more thermophilous species (e.g., *Quercus ilex*, *Q. suber*, and *Q. faginea*) was markedly more restricted than at present. Most species survived in mountain areas that allowed them to perform altitudinal shifts following climate changes. The milder climate of the mid-Holocene would have enabled the range expansion of most species (Fig. 5), thus increasing the extension of Iberian forests in detriment of shrublands and steppe landscapes, as previously suggested by palaeobotanical data (Muñoz-Sobrino et al., 1997; Carrión, 2002).

Whilst Benito Garzón et al. (2007) focused on tree species that are currently widespread members of Iberian forests, two other recent studies explored the past range dynamics of *Prunus lusitanica* and *Laurus nobilis*, two characteristic elements of the formerly widespread Tethyan lauroid tree flora that is currently restricted to small areas with particularly benign microclimates. Calleja et al. (2009) assessed the potential distribution of *P. lusitanica* in the Iberian Peninsula since the LGM. Results indicate that this warm and moist-loving species found suitable growing conditions during the LGM only at a few sites scattered along the Atlantic coast. Today *P. lusitanica* is absent from large areas that would in principle provide suitable climatic
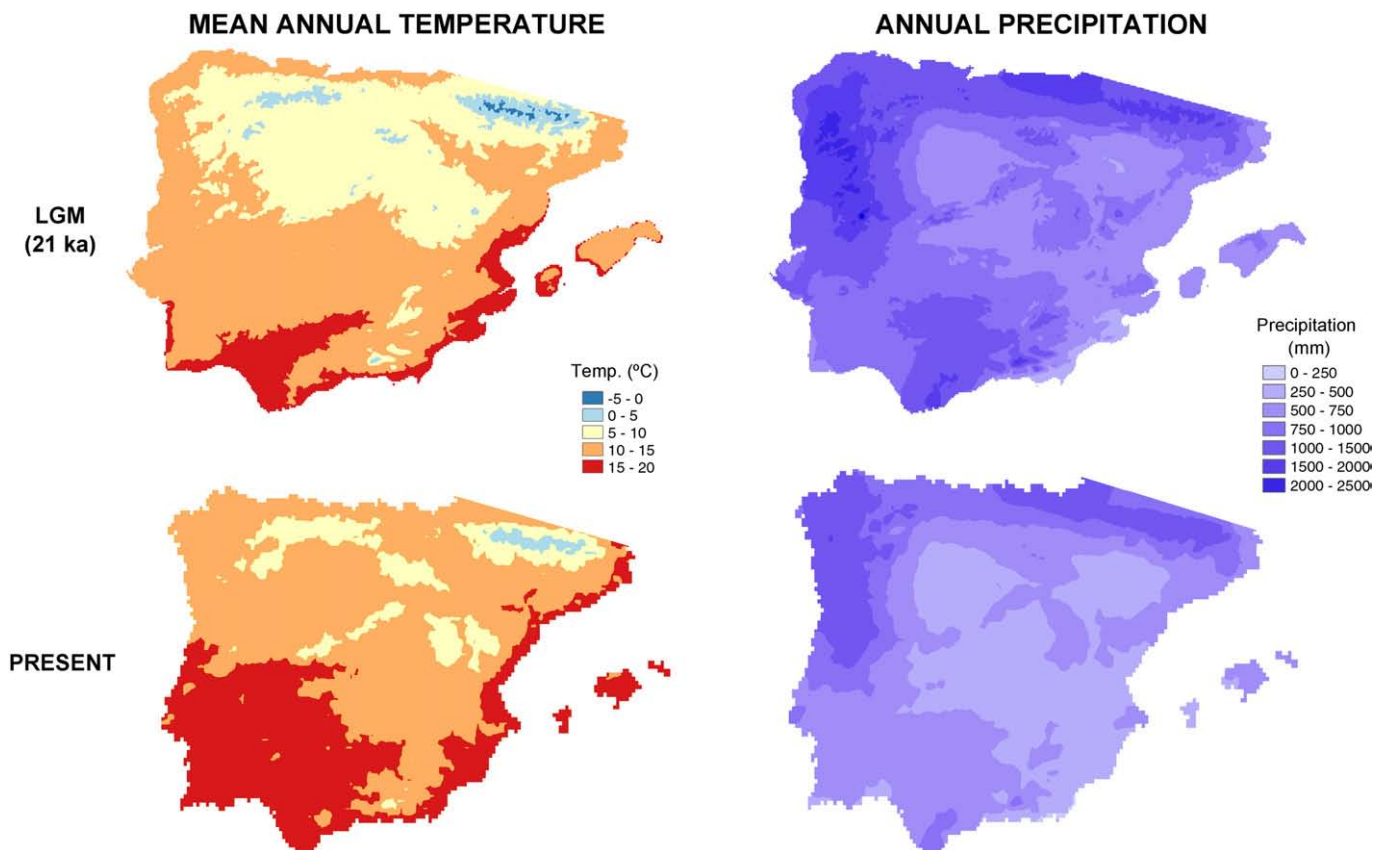
Fig. 4. Map of the Iberian climate during the Last Glacial Maximum (21 kyr BP) according to the most recent reconstructions based on general circulation models (PMIP2; Braconnot et al., 2007). Palaeoclimatic estimates from the CCSM and MIROC models were averaged, and the result statistically downscaled to attain higher spatial resolution. Current climate maps are shown for comparison. Data provided by PMIP2 and Worldclim (Hijmans et al., 2005; htpp://www.worldclim.org).

conditions. The authors suggest that this mismatch is likely to result from the species' limitation to recolonise these areas after the LGM, more recently exacerbated by human impacts from forestry, over-grazing and agricultural uses (Calleja et al., 2009). The study of Rodríguez-Sánchez and Arroyo (2008) on *L. nobilis* indicates that this species experienced a similar restriction of potential growing sites during the LGM as *P. lusitanica*. In contrast to other studies, these authors did not limit their scope to the LGM but also attempted to reconstruct the Pliocene distribution of *L. nobilis* (Fig. 6). Interestingly, the species range dynamics were relatively predictable even over this long time scale, as shown by the fact that the current distribution of *L. nobilis* could be fairly well derived from a relatively simple climatic characterization of its fossil occurrences from the middle Pliocene (Rodríguez-Sánchez and Arroyo, 2008). This suggests that niche conservatism—the evolutionary conservation of the ancestral ecological requirements of species (Wiens and Graham, 2005)—has driven largely deterministic range dynamics in *L. nobilis* under the changing climates since the late Tertiary.

5.1. Synthesis

The long-term availability of favourable climatic conditions in the Iberian Peninsula, promoted by its latitudinal situation, large oceanic-maritime influence and environmental heterogeneity, favoured the persistence of a complex and rich mixture of tree taxa of diverse biogeographical origins and environmental affinities, including ancient subtropical taxa, temperate deciduous species, and montane gymnosperms, among others. All studies agree in hindcasting heavily reduced and fragmented ranges for most species during the LGM (pines being the most notable exception), followed by a rapid recovery of potential ranges at the earlier Holocene. Mid-Holocene

distributions of some species might have been more extensive than today, shrinking later due to increasing aridity and to the more recent human influence on Iberian landscapes (Carrión, 2002).

Although more modelling studies of species palaeodistributions are clearly needed, the available evidence confirms that the Iberian Peninsula has continuously provided suitable growing conditions for many Palaearctic tree species in the northwestern, southwestern, southeastern and, to a lesser extent, northeastern Iberian sectors (Benito Garzón et al., 2007; Carrión et al., 2008). For most species, these suitable areas remained relatively isolated over long periods, thereby generating a geographical pattern of 'refugia within refugia', previously suggested by phylogeographical analyses (Gómez and Lunt, 2007). An increasingly accurate identification and evaluation of these potential LGM refugia by means of species distribution modelling should soon become possible with the advent of high-resolution palaeoclimate reconstructions (Jost et al., 2005). Further-more, the recent development of palaeoclimate simulations for periods earlier than the LGM should allow a better assessment of the temporal component of species' range dynamics in the future. As recently stressed by phylogeographical studies (Hampe and Petit, 2007), there is a need to extend our reconstructions of the past range dynamics of Mediterranean species over time scales more relevant for ancient, slow-evolving species such as trees in the relatively complex geological and climatic history of the Mediterranean Basin.

Finally, the evidence presented here underpins that tree range dynamics are constrained by both deterministic and stochastic processes acting on different spatial and temporal scales. On one hand, the remarkable evolutionary conservatism of species' climatic requirements translates into largely deterministic extinction process-es and range dynamics at continental scales and over extended time periods, that are primarily driven by secular climate changes
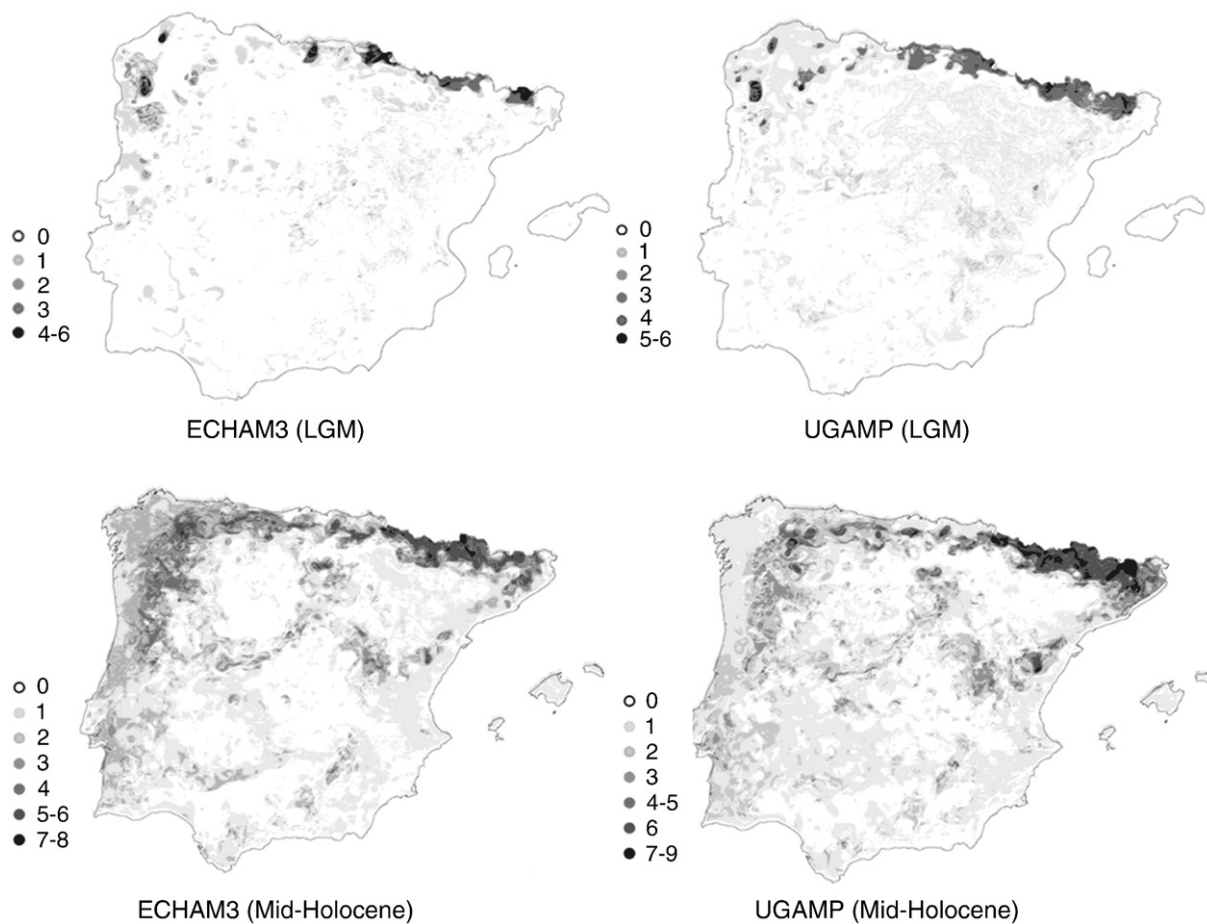
Fig. 5. Number of tree species predicted to be present in the Last Glacial Maximum (LGM) and mid-Holocene, according to palaeodistribution models using two palaeoclimatic simulations (ECHAM3 and UGAMP) (reproduced with permission from Benito Garzón et al., 2007; see text for details).

(Svenning, 2003; Martínez-Meyer and Peterson, 2006). Therefore, when faced with a rapidly changing climate, long-lived species such as trees usually track suitable habitats by migration (as opposed to adaptation *in situ*), and persist at places that satisfy their environmental requirements (Huntley and Webb, 1989; Jackson and Overpeck, 2000). On the other hand, stochastic processes such as historical contingencies and metacommunity assembly dynamics (Hubbell, 2001; Holyoak et al., 2005) seem to play a more relevant role at regional or more local scales (see Carrión et al., this issue). The latter could explain the idiosyncratic population dynamics of species found in most phylogeographical studies. Thus, the integration of evidence from diverse scientific disciplines enables a better understanding of species range dynamics at different scales and the factors driving them.

6. Concluding remarks

Climatic changes have strongly influenced the historical distributions and dynamics of Iberian forests. Research disciplines such as phylogeography and species distribution modelling help elucidate how tree species have reacted to these changes. New evidence allows increasingly precise descriptions of species' past range dynamics in a region like the Iberian Peninsula whose climatic characteristics and heterogeneous orography render reconstructions of forest history a particularly challenging puzzle.

Most studies to date have investigated how geographical distributions evolved during the Pleistocene, yet examples are now accumulating of woody species that have retained the genetic imprints of much more ancient range dynamics. This development

goes along with the advent of distribution modelling exercises that draw on pre-Pleistocene climate scenarios.

Although individual species responded idiosyncratically to past climatic changes, some major, shared, trends are evident. The most prominent phenomenon is a deep and often remarkably clear-cut divide between populations from the Mediterranean and the Atlantic regions of the Iberian Peninsula, which indicates that both areas have independently sustained viable populations over extended periods (that is, probably over multiple glacial cycles).

Many species had several glacial refugia across the Iberian Peninsula, whose geographical situation can be identified with relative precision by phylogeographical surveys. In addition, distribution models help detecting further suitable areas that could have sustained so far undetected refugia. Populations in these areas are often high-priority targets for conservation due to their long-term persistence and unique evolutionary trajectory.

Palaeoecology, phylogeography and species distribution modelling have a great potential to inform each other because of their complementary perspectives and results. Therefore, a true integration of these approaches is fundamental for further progress in our understanding of past environments and the organisms they harboured.
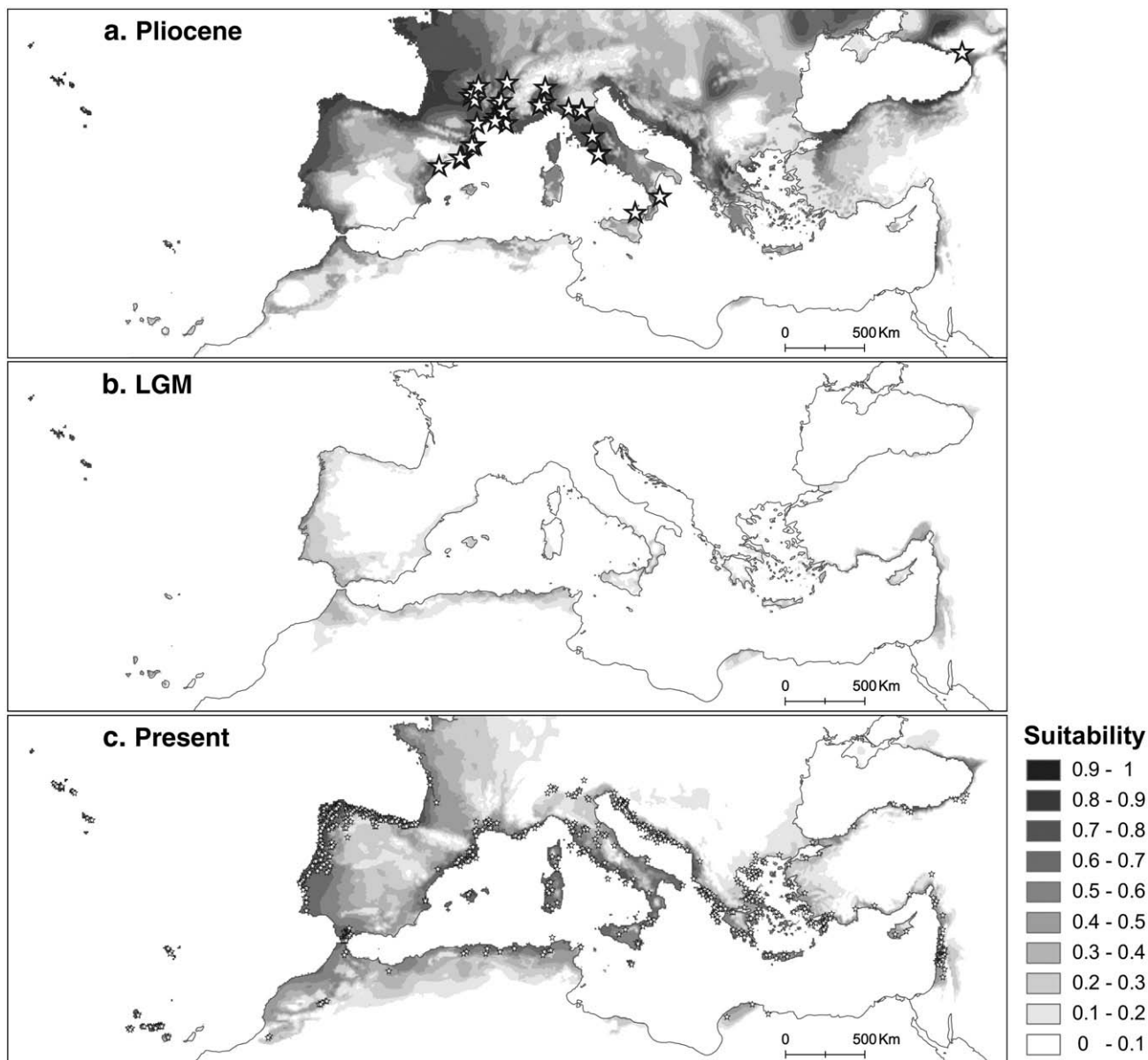
Acknowledgements

Fig. 6. Map of climatically suitable areas for *Laurus* at the middle Pliocene (3 Myr BP), Last Glacial Maximum (LGM, 21 kyr BP) and at present, as inferred by models of *Laurus*' climatic niche projected onto palaeoclimatic data (reproduced with permission from Rodríguez-Sánchez and Arroyo, 2010). Actual occurrences of *Laurus* for the Pliocene and present are shown by white stars.

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