

Climate changes and tree phylogeography in the Mediterranean

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The Mediterranean Basin is expected to be more strongly affected by ongoing global climate change than most other regions of the earth. Given the magnitude of forecasted trends, there are great concerns for the particularly rich biodiversity found in the region. Studies of the consequences of past climate shifts on biodiversity represent one of the best sources of data to validate models of the ecological and evolutionary consequences of future changes. Here we review recent findings from palaeoecology, phylogeography and climate change research to (1) explore possible antecedents of the predicted climate warming in the younger geological history of the Mediterranean Basin, (2) assess how tree populations have reacted to them, and (3) evaluate the significance of the evolutionary heritage that is at stake. A major question of our retrospective approach is whether Quaternary tree extinctions took place primarily during glacial or during interglacial episodes. Available data are scanty and somewhat conflicting. In contrast, abundant phylogeographic evidence clearly indicates that the bulk of genetic diversity in European temperate tree species is almost invariably located in the southernmost part of their range. Long-term persistence of isolated populations have been common phenomena in the Mediterranean, to the point that the current genetic structure in this area probably often reflects population divergence that pre-dates the onset of the Mediterranean climate in the Pliocene. In particular, Tertiary migrations into the Mediterranean of tree taxa originating from Asia seem to have left their footprints in the current genetic structure in these slowly evolving organisms. Moreover, phylogeographic studies point to heterogeneous rates of molecular evolution across lineages that are inversely related with their stability. We conclude that relict tree populations in the Mediterranean Basin represent an evolutionary heritage of disproportionate significance for the conservation of European plant biodiversity.

KEYWORDS: forest trees, genetic diversity, glacial refugia, Mediterranean climate, Quaternary climates, relict populations.

INTRODUCTION

Climate change is expected to be more pronounced in the Mediterranean Basin than in most other regions of the world (IPCC, 2001). One way to evaluate its consequences is to look for lessons from the past. The study of palaeoarchives could constitute a basis for understanding the adaptability and vulnerability of the biota to climate change. Woody plants are well represented in the sediments and represent therefore a potentially useful class of organisms for such an approach. Furthermore, phylogeographic surveys of Mediterranean tree taxa and of temperate taxa whose southern distribution includes Mediterranean regions can be used to reconstruct the history of surviving lineages and to evaluate the conservation value of the extant heritage. Biodiversity is not unlike a good investment: it improves over time. Hence, a time frame to evaluate the ancestry of lineages in an

area would be particularly important, but is often missing in available phylogeographic surveys. However, the increase over time of genetic divergence is generally not linear: a growing body of data indicates that evolutionary rates vary among lineages, even closely related ones (e.g., Andreasen & Baldwin, 2001). We need, therefore, not only an accurate time frame but also a better understanding of the consequences of past dynamics of lineages on the accumulation of mutations.

In this paper, we will describe the consequences of past global changes on Mediterranean tree taxa and will present phylogeographic case studies to illustrate how past climate changes and corresponding range dynamics have left their traces in genetic population structure and diversity of the species, with particular attention to heterogeneities in evolutionary rates.

PAST AND PREDICTED CLIMATE CHANGES IN THE MEDITERRANEAN REGION

A way to evaluate the risks of the current anthropogenically-induced climate warming on Mediterranean plant diversity is to examine if there have been climates in the Quaternary that were as warm as or warmer than the present. Pollen records have long been used to infer past climate changes across Europe. More recently, these records have been complemented by a wide range of proxy data involving diverse research disciplines. Such interdisciplinary work is generating a more and more detailed picture of past climates spanning much of the Quaternary (e.g., Allen & al., 1999; EPICA, 2004; North Greenland Ice Core Project, 2004). The amplitude of climate oscillations has increased during the last 740 Ka, as a consequence of an increase of the temperatures during the interglacials, whereas the duration of the interglacial periods has rather decreased (EPICA, 2004). However, the last interglacial (about 125 Ka ago) was at least as warm as the current one (and probably even warmer) due to increased insolation (Kukla & al., 2002; Felis & al., 2004; North Greenland Ice Core Project, 2004). Comparisons between different warm stages require some caution, given that different regions of Europe have sometimes experienced markedly divergent climate trends during the Holocene (and presumably during previous interglacials). For instance, the widely cited mid-Holocene climatic optimum around 6000 years Before Present (BP) is observed only over northern Europe, whereas southern Europe and the Mediterranean have undergone a regular warming from around 10 Ka to ca 6 Ka years BP that has continued until now in southwestern Europe (Cheddadi & al., 1997; Davis & al., 2003). These results are confirmed by other sources of evidence. For instance, Terral & Mengual (1999) used the anatomy of olive charcoal to estimate temperatures during the early and mid-Holocene in southeastern Spain and southern France. They reconstructed annual temperatures between 1.5°C (France) and 3.5°C (Spain) lower than at present, hence confirming a regular warming of the climate in these regions.

Hence, the widespread belief that Europe had experienced higher temperatures than those of today in the relatively recent past is now challenged, at least for parts of the Mediterranean region. The conditions to be faced in these regions as a consequence of the human-induced warming should therefore be the warmest ever experienced during this interglacial and among the warmest experienced during the Quaternary, a worrying prospect. Optimists might still argue that abrupt climate changes at regional scales have always been common, including before the industrial period (e.g., Allen & al., 1999; Alley

& al., 2003). However, the environmental conditions have changed greatly due to human land use (e.g., Hansen & al., 2001). Moreover, where past warm periods existed, they were generally less arid (e.g., Cheddadi & al., 1998).

It is now acknowledged that most of the global warming observed over the last 150 years (pre-industrial period) is attributable to human activities, in particular to the emission of greenhouse gases (Indermühle & al., 1999; IPCC, 2001). The atmospheric CO₂ concentration during the last five interglacials was much lower than today (Petit & al., 1999). Measurements at the global scale between 1900 and 2000 indicate that temperature has already increased by 0.2°C to 0.6°C (IPCC, 2001). Temperatures are expected to continue to increase in the coming decades, with considerable effects on human society and the environment (European Environment Agency, 2004). Mediterranean climate regions are expected to experience disproportionately strong increases of temperature and aridity compared to other regions (IPCC, 2001). Whereas temperatures should increase on average by 1.4 to 5.8°C worldwide, the difference should be at least 3°C in the Mediterranean Basin. In the twentieth century, global precipitation has increased by about 10 to 50% in some areas and decreased by the same magnitude in others. In the Mediterranean region, where rainfall is a major limiting factor for organisms, precipitation has decreased by about 30% during the last century. Climate models (IPCC, 2001) also indicate that the Mediterranean Basin will be one of the areas subject to the most drastic reductions in precipitation. While most of Europe will have a rather positive water balance, precipitation in the countries surrounding the Mediterranean Sea are expected to experience the largest decrease on the globe, more than 20%.

In conclusion, climate in the Mediterranean Basin since the Last Glacial Maximum (LGM; around 20 Ka BP) has been variable but generally colder than today. Moreover, interglacials have become warmer during the Quaternary. Hence, the modern increase in both temperature and water stress, resulting from the increasing atmospheric concentrations of greenhouse gases not recorded during the last 2 Ma appears to be without historical precedents in the Quaternary.

CONSEQUENCES OF CLIMATE CHANGES FOR TREES IN THE MEDITERRANEAN BASIN

Vegetation models and climate scenarios are now routinely used to predict future species distributions. The most comprehensive example for Europe and the Mediterranean is provided by Bakkenes & al. (2002),

who attempted to forecast future ranges of some 1400 plant species. According to these authors, the strongest reshuffling would take place in southern Europe, where 60–80% of the flora present in 1990 in a given grid cell of the map they used would go extinct by 2050 (Bakkenes & al., 2002), compared to “only” 20–40% further north. In view of the expected rapid future climate changes, especially in the Mediterranean Basin, many authors have asked whether species will be able to migrate rapidly enough, given the fragmentation of landscapes and the possible lack of seed dispersers (e.g., Dyer, 1995; Pitelka, 1997). According to the predictions, Mediterranean species would have to quit their current range and establish somewhere further north. This is obviously unlikely (Travis, 2003; Hampe, 2004; Svenning & Skov, 2004; see also Midgley & al., 2002), and the survival of Mediterranean populations, rather than their migration into a new range, is the safest way to preserve these species and their genetic resources. Unfortunately, much more research has focused on plant migration at the “leading edge” of species distribution than on the southern (Mediterranean) “rear edge”, whose conservation value remains largely under-appreciated (Hampe & Petit, 2005).

Woody plants represent an important component of the Mediterranean flora. The number of tree species living in the Mediterranean exceeds greatly those living in central Europe, a region four times as large (100 vs. 30 species, respectively, with the genus *Quercus* alone presenting more than 20 species; Jalas & Suominen, 1976). Trees evolve slowly, probably a consequence of their long generation times (e.g., Sinnott, 1916; Bousquet & al., 1992; Andreason & Baldwin, 2001). In the Mediterranean Basin, most tree genera and species have evolved before the onset of the summer-dry Mediterranean climate around 3.2 Ma ago in the Pliocene (Suc, 1984; Palamarev, 1989; Mai, 1995), whereas many shrub genera have apparently evolved under Mediterranean climate conditions. A series of other ecological differences exist between “Paleo-Mediterranean” taxa, evolved prior to the Pliocene under tropical or subtropical climatic conditions, and “Neo-Mediterranean” taxa, which appeared by speciation after this period (Herrera, 1992; Peñuelas & al., 2001; Verdú & al., 2003).

Besides typical Mediterranean taxa, the flora of the region also includes many tree and shrub species of the cool-temperate Eurasian flora. These species typically have some relict footholds in Mediterranean mountain ranges, where populations persisted during the LGM (Bennett & al., 1991). These so-called refugial areas have long been considered as the starting point of post-glacial recolonisation, given the lack of evidence for fossil remains further north (e.g., Frenzel & Troll, 1952). New fossil and genetic evidence indicate that this con-

clusion was probably premature (e.g., Hampe & al., 2003; Willis & van Andel, 2004; Magri & al., in prep.). For many species, the source of postglacial colonisation would have lied instead north of the Mediterranean region itself, e.g., at $\geq 45^\circ$ latitude, and populations further south expanded little or not at all. These populations should therefore be considered relicts rather than “refugial”, if a refugium is understood as a (comparatively) short-term shelter to extreme environmental conditions. In fact, several species are now only represented by relict Mediterranean populations (e.g., *Zelkova*: Fineschi & al., 2002), whereas many others have completely disappeared from Europe since the end of the Tertiary (Tallis, 1991). For our retrospective approach, an important question is whether these extinctions took place during glacial or interglacial periods. Phylogenetic analyses of several European alpine plant taxa have shown that temperature is positively correlated with extinction rates—in other words, extinctions would occur mostly during interglacial periods (Kadereit & al., 2004). This supports the hypothesis of Bennett & al. (1991) that survival of European tree refugial populations during interglacial rather than glacial periods might have been determinant for species persistence. Such a conclusion would back up pessimistic views of the consequences of future global warming on population and species survival during the current interglacial. However, a recent macroecological analysis of European trees (Svenning, 2003) has arrived at opposite conclusions. The author reconstructed climatic requirements of tree taxa known to have existed in Northwest Europe during the late Tertiary and compared extinct and surviving genera. (For the first group, climatic requirements were inferred from modern populations growing outside Europe.) He observed that currently widespread taxa are more cold-tolerant than taxa restricted to the Mediterranean Basin, and that the latter are more drought-tolerant than extinct ones, suggesting that extinction was a deterministic process triggered by climate (Svenning, 2003). Since climatic reconstructions for the Mediterranean Basin point to both very cold and very arid conditions during the LGM—even drier than at present (e.g., Figueiral & Terral, 2002)—this supports the hypothesis that most extinction events took place during glacial periods. Unfortunately, there are few detailed reports of the timing of tree extinctions during the Quaternary to support either view. One of the rare well-recorded cases is that of *Picea critchfieldii* in North America (Jackson & Weng, 1999). This species, which was abundant during the LGM, disappeared during the last deglaciation, at a time of rapid climate change. Clearly, more work is needed to determine under which conditions most tree extinctions took place.

Results from the retrospective approach are therefore somewhat equivocal with respect to the reactions of

tree taxa to climate change. A related question is how much inertia to global change exists in Mediterranean ecosystems as far as tree species are concerned. Conflicting results have likewise been reported by studies of climate change effects at higher levels of biotic organisation, such as forest communities and ecosystems (Hansen & al., 2001). For instance, a Mediterranean woody plant community submitted over four years to experimental warming experienced a reduction of species diversity resulting from increased seedling mortality (Lloret & al., 2004). On the other hand, vegetation models based on plant physiological parameters indicate that positive effects of increased CO₂ on growth and productivity of Mediterranean sclerophyllous forests could to a certain extent offset detrimental effects of rising temperatures (Osborne & al., 2000). Similarly, several authors have shown that under high CO₂ concentration plant stomata will reduce the evapotranspiration, which could compensate water stress for some species (van de Geijn & al., 1998; Johnson & al., 2002), although it is unclear if this will be sufficient given the magnitude of the expected decrease of precipitation in the Mediterranean. Likewise, individual-based physiological models suggest that at least some species may resist expected increases of water stress relatively well (Martínez-Vilalta & al., 2002), and that biotic interactions such as competition with newly arriving species might be as important as direct climate effects for erosion of species' southern range margins (Loehle, 1998; see also Ackerly, 2003).

In summary, we have several reasons for concern regarding the consequences of climate change on tree biodiversity in the Mediterranean Basin. First, natural climate trends during the Holocene already involve a recent rise of temperature in parts of the Mediterranean Basin; second, human-induced climate change is predicted to be particularly strong in Mediterranean regions worldwide; and third, there has been a steady, deterministic loss of tree taxa during the Quaternary. However, the present-day tree flora of the Mediterranean Basin is made up of very resilient taxa that have already experienced many abrupt and intense climatic changes in the past. Physiological mechanisms could partly buffer the effects of global changes on Mediterranean-type vegetation—at least when the functioning of existing ecosystems is guaranteed (Osborne & al., 2000). The problem cannot therefore be reduced to the question of how to establish tree species somewhere further north. Instead, any efforts should be made to maintain these ecosystems where they are (Hampe & Petit, 2005). To better realise what is at stake, we will now describe the phylogeography of some trees growing partly or completely within the Mediterranean region.

THE THREATENED HERITAGE: TREE PHYLOGEOGRAPHY IN THE MEDITERRANEAN

During the past decade, numerous population genetic and phylogeographic surveys have been conducted on temperate tree and shrub species with southern range margins in the Mediterranean Basin (e.g., Comps & al., 2001; Petit & al., 2002a, b, 2003; Hampe & al., 2003). Except for those tree species that can withstand boreal climate, a very general finding is that the bulk of the genetic diversity is found in the Mediterranean, even though this region hosts only a small fraction of the species' range. This so-called trend from “southern richness” to “northern purity” (Hewitt, 1996) holds only at the regional scale, however, not at the within-population level, because many Mediterranean populations are genetically depauperated. The “southern richness” stems from the fact that Mediterranean populations are often highly divergent from those of the rest of the range; even nearby populations can have strikingly different genetic composition (Petit & al., 2003). This suggests three inferences: (1) Mediterranean populations of temperate tree species have exchanged few genes with other populations during both glacial and interglacial periods of the Quaternary; (2) they have been very stable over time; and (3) most of them have not been the source of post-glacial colonization, as pointed out above. All three conclusions support the idea that dispersal limitations have been particularly strong for these species in the Mediterranean region. Interestingly, a recent comparison of current tree distribution ranges with potential ranges based on species' climatic tolerance point to a particular low range filling in southern Europe (Svenning & Skov, 2004). This observation can be attributed to a large extent to dispersal limitation, in agreement with the previous conclusions based on intraspecific genetic data.

Populations that remain in place for extended time periods in comparatively stable habitats should retain ancestral characters. On the contrary, expanding populations readily accumulate new mutants (i.e., derived characters) (Fig. 1). In the case of the influenza virus, for instance, continuous replacement of circulating strains with new variants results in a particular phylogeny with a slender “trunk” that develops across the years (Ferguson & al., 2003). Such a signal could in principle be present in phylogenetic trees of taxa that have undergone stepwise colonization at any temporal scale. For instance, in the genus *Fraxinus* (Oleaceae), internal transcribed spacer sequences of nuclear ribosomal DNA seem to respond to intercontinental and intracontinental dispersal events by an acceleration of their evolutionary rate (see Fig. 4 in Jeandroz & al., 1997). Similarly, in the genus *Halenia* (Gentianaceae), increases in diversifica-

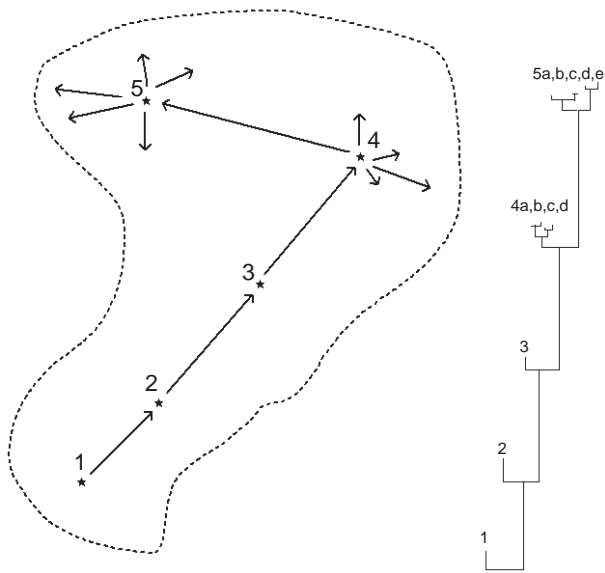


Fig. 1. Expected relationship between phylogeny and expansion of species, assuming that invasions of new territories result in accelerated rates of molecular evolution and haplotype diversification.

tion occurred following the colonization of Central and South America (von Hagen & Kadereit, 2003). These accelerations of diversification rates were interpreted as resulting from the availability of new geographical and ecological opportunities. After an initial rapid increase, a reduction in diversification rate was observed, probably illustrating density-dependence of speciation rates (von Hagen & Kadereit, 2003).

In the Mediterranean Basin, the initial stepwise colonization of their currently fragmented range by many tree species, which resulted in genetically highly divergent populations, could have led to the same pattern observed at the interspecific level: increasingly derived

lineages along the routes of colonization. In contrast, populations close to the source of the first invasion should have mostly ancestral characters. Such a phylogenetic interpretation of range expansion (Thorpe, 1984) has rarely been possible at the intraspecific level in trees, given their slow substitution rates.

Nevertheless, evidence for such a pattern can be found in alder buckthorn (*Frangula alnus* Miller), a shrub with Eurasian distribution (Hampe & al., 2003; see Fig. 2): Chloroplast (cp) DNA haplotypes from one (blue) lineage involved in the expansion across central and northern Europe (haplotypes 15–21) appear to have diversified more quickly than those found further south, which form instead a nearly linear series (haplotypes 1–9 and 10–14). Long-term stability in southern populations (also reflected in the much higher level of genetic fixation in these populations, Hampe & al., 2003) appears to have inhibited diversification. The linear arrangement in the south was interpreted as the result of a much more ancient (probably Tertiary) stepwise expansion of the species across the Mediterranean. In the absence of a suitable outgroup to root the tree, the direction of this more ancient colonization across the Mediterranean cannot definitively be inferred. However, populations from Southern Iberia and Morocco differ remarkably from those growing in other parts of the range, showing a markedly greater plant size and a twofold life span (Hampe & Arroyo, 2002; see Fig. 2). These features resemble the species' probable nearest congener, the Macaronesian tree *F. azorica* V. Grubow, and might indicate the ancient character of SW Mediterranean *F. alnus* populations. The shrub-like growth form found today throughout most of the Eurasian range of the species would then have evolved during an eastward expansion through the Mediterranean Basin.

An exceptionally well-documented example of a

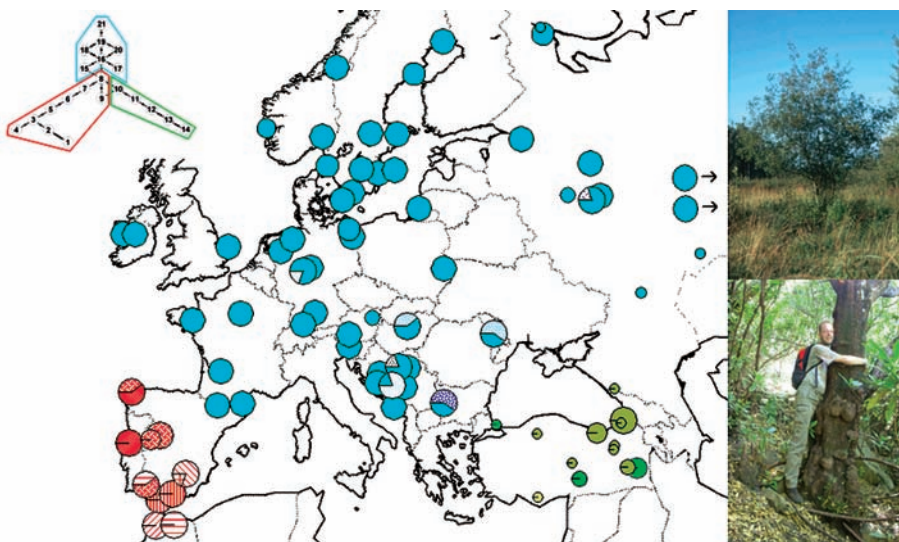


Fig. 2. Phylogeography of *Frangula alnus* Miller according to Hampe & al. (2003). The map shows the geographical distribution of detected haplotypes, whose phylogenetic relationships are presented in the haplotype network (see Hampe & al., 2003, for further details). Different colour tones indicate the three distinct lineages observed. The two photos to the right show a big individual of the shrublike nominate subspecies, which grows over most of the species' range (above), and the trunk of an old individual belonging to the subspecies *F. a. baetica* endemic to South Iberia and North Morocco (below).

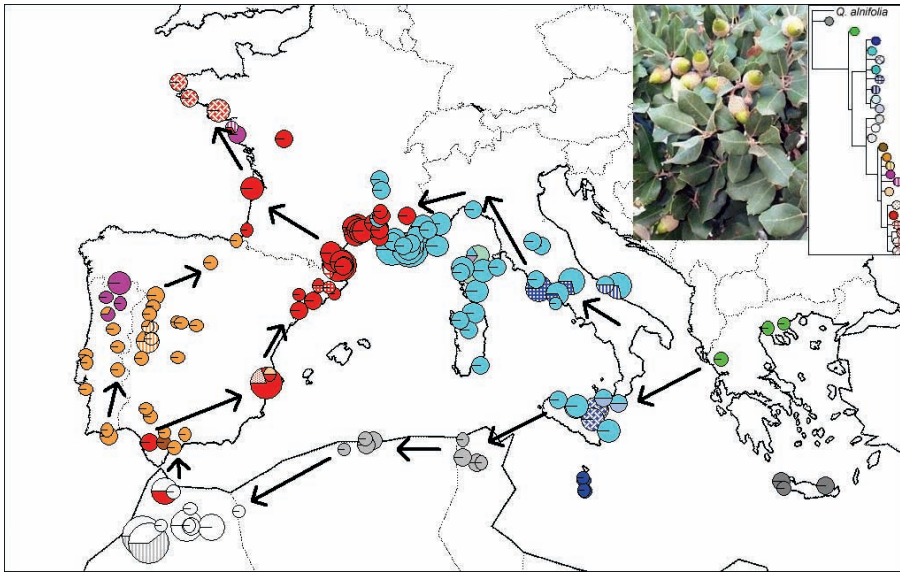


Fig. 3. Phylogeography of *Quercus ilex* L. according to Lumaret & al. (2002). The map shows the geographical distribution of detected haplotypes, whose phylogenetic relationships are presented in the haplotype network on the right. Note that increasingly divergent haplotypes are found westwards, along the inferred route of colonisation.

very old range expansion is provided by a study of cpDNA variation in the holm oak, *Quercus ilex* L., one of the most emblematic Mediterranean trees (Lumaret & al., 2002). Starting from the sister taxon *Q. alnifolia* that grows in the eastern Mediterranean (Cyprus), a progressive differentiation of *Q. ilex* populations into more and more derived cpDNA types is apparent towards the west (Fig. 3). First, the Greek populations can be distinguished, followed by those from Italy and those from North Africa. The latter appear ancestral to those from Iberia and from southwestern and western France. The three crossings of the Mediterranean Sea (from Greece into Italy, from Italy into North Africa and from there into Iberia) could have taken place during the Messinian salinity crisis in the late Miocene (about 5.5–4.5 Ma ago), when Africa and Europe were connected for the last time (Hsü, 1973; Caujapé-Castells & Jansen, 2003), even though the intervening area was not suitable for trees. If true, this would illustrate the deep divides between Mediterranean populations of the same species and the fact that, unless invasion of new areas takes place, the apparition of new cpDNA variants can be highly retarded (Fig. 1).

The westward (rather than eastward) colonisation of the Mediterranean Basin by *Q. ilex* during the Tertiary probably corresponds to the most common situation (e.g., Stebbins, 1974; Caujapé-Castells & Jansen, 2003). Although examples of colonisation in the opposite direction exist as well, as illustrated by the example of *Frangula alnus* (see also Vargas, 2003), a westward invasion should be more likely for most tree genera, given the relatively isolated position of Iberia at the western edge of Eurasia and the Asian origin of many tree genera. In beech, for instance, the hypothesis of westward diffusion is confirmed not only by the presence of another very

similar but more variable species (*F. orientalis* Lipsky) in the Near East and in southeastern Europe but also by the much greater allelic richness at isozyme loci in southeastern Europe (Comps & al., 2001). Another cline of decreasing genetic diversity towards the west has been described in a typically Mediterranean taxon (*Pinus halepensis* Miller); furthermore, conifer species from the western part of the Mediterranean Basin are clearly genetically less diverse than species from the eastern part (Fady-Welterlen, 2005).

The results obtained so far with forest trees confirm that, for temperate species that have persisted in the Mediterranean throughout the Quaternary and part of the Tertiary, most regional diversity is confined to the Mediterranean Basin (see Petit & al., 2003, for a study involving 22 woody taxa). Even if populations experience increased mutation rates during range expansions, the duration of an interglacial (~10–15 Ka) is far too short for acquiring a degree of divergence comparable to that observed among different Mediterranean populations (probably separated since several millions of years). In fact, their long-term stability appears to have preserved the footprints of past expansions dating back from the Tertiary.

CONCLUSIONS

Despite low evolutionary rates in trees, exacerbated in the Mediterranean by the great stability of their populations, they have accumulated much intraspecific biodiversity thanks to the great antiquity of their populations. It is therefore particularly important—more so than in most other organisms—that their biodiversity be appreciated and valued at the intraspecific level. So far, the

slow evolutionary rate of trees has hampered attempts to date divergence times between populations using sequence divergence, although a few exceptions exist (e.g., Dick & al., 2003). Our analyses and interpretations suggest that when studying the phylogeography of plant species, rate heterogeneities are to be expected, so that molecular clock estimates should be used with caution. What is already clear for Europe is that conservation areas should not be shifted to the north to anticipate predicted climatic changes, as this would mean the sacrifice of some of the most ancient and genetically unique populations. It is therefore urgent that studies on the consequences of climate changes start to consider also relict populations at the rear edge of tree species distributions instead of focusing only on the dynamic “leading edge” at high latitudes.

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