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Cenozoic climate changes and the demise of Tethyan laurel forests: lessons for the future from an integrative reconstruction of the past

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Abstract

Climate on earth has always been changing. Despite decades of investigation, our limited knowledge of the ecological and evolutionary effects of climate changes often translates into uncertain predictions about the impact of future climates on biodiversity. Integrative biogeographical approaches using palaeobotanical, phylogenetic and niche-based species distribution models, when permitted by data availability, may provide valuable insights to address these key questions. Here we combine palaeobotanical and phylogeographical information with hindcast modelling of species distribution changes to reconstruct past range dynamics and differentiation in the bay laurel (*Laurus* spp., Lauraceae), an emblematic relict tree from the subtropical laurel forests that

thrived in Tethyan realms during most of the Tertiary period. We provide plausible examples of climate-driven migration, extinction and persistence of populations and taxa, and discuss the factors that influence niche conservatism or adaptation to changing environments. Finally, we discuss the likely impacts of the predicted climate change on laurophyllous taxa in the Mediterranean and Macaronesia.

13.1 Introduction

The reconstruction of the evolutionary history and distribution of plants has been based primarily on the information supplied by two relatively independent research fields: palaeobotany and phylogenetics. More recently, it has also relied on statistical modelling approaches to hindcast species distributions on geological timescales. Palaeobotany has long relied on the description of fossils, the resolution power of microscopes and fossil sampling in cores. Isotope dating, and other approaches for absolute timing of events, then led to a methodological revolution in this field (Stewart and Rothwell, 1993). Concurrently, the field of phylogenetics has developed quickly, particularly in the past two decades, because of its strong conceptual framework, the generation of huge amounts of new data and new methods to analyse these data (Felsenstein, 2004). Despite both fields sharing a number of aims, there has been little contact between them, and their research agendas have remained mostly separated. There is now recognition that a better understanding of the history of living organisms and their ecological and evolutionary processes can be accomplished through the integration of independent evidence. This has fuelled a number of studies combining both palaeobotanical and molecular data (e.g. Petit et al., 2002; Magri et al., 2006; López de Heredia et al., 2007 – see also Posadas et al., 2006, for a review of past and current approaches in historical biogeography). Furthermore, the use of habitat suitability or species distribution models (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005) to hindcast the palaeodistributions of species has become a new source of biogeographical inference. This new tool is especially powerful when combined with fossil data (Martínez-Meyer and Peterson, 2006; Pearman et al., 2008a), phylogenetic information (Hugall et al., 2002) or both (Cheddadi et al., 2006); the integrative approach appears particularly useful for solving long-standing questions for biogeographers (Donoghue and Moore, 2003; Posadas et al., 2006). In general, the reliability of biogeographical reconstructions increases when supported by different types of data (Cleland, 2001); disagreement between data types may uncover neglected processes or sources of error, and may also highlight new conceptual advances and research questions (Givnish and Renner, 2004; Pulquerio and Nichols, 2007).

Currently, one of the most active research topics in biogeography deals with the ecological and evolutionary effects of climate change. A range of studies has examined the role of climate change in shaping the evolutionary differentiation, extinction and distribution of taxa (see Jansson and Dynesius, 2002, and Parmesan, 2006, for reviews). Despite the existence of some clear-cut patterns (e.g. Svenning, 2003), there are still wide gaps in our knowledge of the actual processes by which climate change affects the ecology and evolution of species, and how different species and/ or populations may react to them. This limited understanding translates into considerable uncertainty when trying to predict species' persistence, migration and/ or extinction under future climate change (Thuiller, 2004; Araújo et al., 2005). The analysis of past events can certainly provide solid evidence for or against hypotheses on the response of taxa to future scenarios of climate change. However, the enormous potential of historical approaches for assessing such hypotheses has not yet been achieved, perhaps because of the scarcity of systematic data for most taxa and regions, but also because of the traditional bias towards experimental hypothesis testing (Cleland, 2001).

The origin and diversification of Mediterranean flora has long interested botanists and biogeographers (Quézel, 1985; Thompson, 2005). Despite the diversity of methodological approaches (analyses of floristic diversity, palaeobotanical, phylogenetic and/or phylogeographical reconstructions) and the range of studied taxa, our knowledge of Mediterranean biogeography is biased towards recently evolved taxa and recent processes, while the history of ancient taxa and the processes that moulded such patterns remain largely unknown (Petit et al., 2005). Among these ancient plants, laurophyllous taxa (e.g. *Laurus nobilis* L., *Prunus lusitanica* L., *P. laurocerasus* L. and *Rhododendron ponticum* L.) are particularly interesting, as they represent members of one of the ancestral vegetation types prior to the establishment of the current Mediterranean vegetation, now dominated by sclerophyllous trees and shrubs, malacophyllous shrubs and annual plants (Thompson, 2005). They are the few survivors of the once extensive laurel forests that covered southern Eurasia and North Africa from the early Cenozoic until the Miocene (Mai, 1989). Profound long-term climate change (Fig 13.1) provoked the gradual southward retreat of these laurel forests, and finally the extinction of most of their constituent species (Kovar-Eder et al., 2006; Utescher et al., 2007). The few extant laurophyllous taxa in the Mediterranean basin are currently restricted to particular regions of mild climate, while some species become more frequent in the adjacent Macaronesian region (Azores, Canary Islands, Cape Verde Islands and Madeira). Only one species, the bay laurel (*Laurus nobilis*, Lauraceae), has an extensive range throughout the Mediterranean, whereas the congeneric and closely related *L. azorica* (Seub.) Franco is present mostly in Macaronesia. Furthermore, *Laurus* appears relatively frequently in the fossil record since the late Oligocene to early Miocene. Therefore, *Laurus* represents an unparalleled case study to explore the
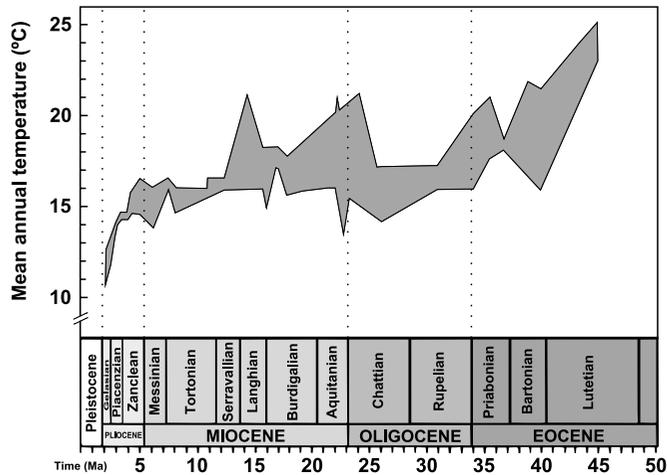
Figure 13.1 Variation of mean annual temperatures in central Europe during the last 45 million years, as inferred from the composition of palaeofloras. The marked trend towards cooler conditions was mainly driven by lower winter temperatures, while summer temperatures remained relatively constant (i.e. increased seasonality). Modified from Mosbrugger et al. (2005).

effects of past climate change and other palaeogeographical events on the range dynamics of plant species and their diversification throughout the Mediterranean over an extended (geological) timescale.

Here we integrate the analysis of the fossil record with palaeodistribution models and phylogeographical analyses of *Laurus* to reconstruct the climate-driven demise of Tethyan laurel forests, and of *Laurus* in particular. The specific aims of this integrative approach are: (1) to infer the processes of climate-driven migration and extinction of Tethyan laurel species; (2) to understand how some species managed to persist and even thrive in largely unsuitable environments; and (3) to investigate the ecological and genetic differentiation patterns within *Laurus* populations and species in the context of Mediterranean–Macaronesian biogeography. Finally, we apply the knowledge gained from these analyses of past events to predict the likely impacts of climate change on the fate of these Mediterranean relict taxa.

13.2 Palaeobotanical evidence of the rise and demise of the Eurasian–Tethyan laurel forests

The widespread discoveries of plant fossil material whose morphological features closely resemble extant tropical–subtropical species impelled early biogeographers to postulate the presence of extensive evergreen laurophyllous forests

in Eurasia during most of the Palaeogene and early Neogene (Mai, 1989, 1995). These forests were dominated by taxa of tropical affinities, such as Lauraceae (e.g. *Lindera*, *Litsea*, *Ocotea*), evergreen Fagaceae (e.g. *Trigonobanalopsis*), Myrtaceae (e.g. *Rhodomyrtophyllum*), Vitaceae and Arecaceae, all requiring warm and humid climates (Mai, 1989, 1995; Collinson and Hooker, 2003). Although the earliest fossils of these subtropical or 'paratropical' taxa go back to the Cretaceous (Coiffard et al., 2007), Eurasian laurel forests apparently reached their maximum diversity and distribution during the early Eocene, a period of warm and humid global climate (Fig 13.1 – Zachos et al., 2001; Mosbrugger et al., 2005). At that time, laurel forests occupied a wide latitudinal belt from North Africa to northern Europe, although the richest assemblages occurred around the Tethys Sea (Utescher and Mosbrugger, 2007).

From the late Eocene, laurel forests experienced a gradual retreat from northern latitudes and a southward migration that is linked to a long-term global cooling (Fig 13.1). Concomitantly, deciduous Arcto-Tertiary vegetation expanded its range southward in northern Europe, while sclerophyllous taxa became locally dominant at more arid sites in southwestern Europe and the easternmost Mediterranean (Axelrod, 1975; Collinson and Hooker, 2003). Nonetheless, laurel forests were still relatively widespread in central Europe and the Mediterranean basin until the middle Miocene (Fig 13.2 – Mai, 1989; Erdei et al., 2007; Utescher et al., 2007). Northernmost satellite populations of laurophyllous taxa such as *Rhododendron*, *Laurophyllum* and *Sassafras* have even been recovered recently from Miocene deposits in Iceland (Denk et al., 2005).

The harsh climatic cooling (Fig 13.1) that occurred since the late Miocene, simultaneously with regional increases in aridity, triggered the southward retreat and the eventual extinction of most laurophyllous taxa. Several Lauraceae were still present in scattered, relict populations at the Pannonian (Erdei et al., 2007),
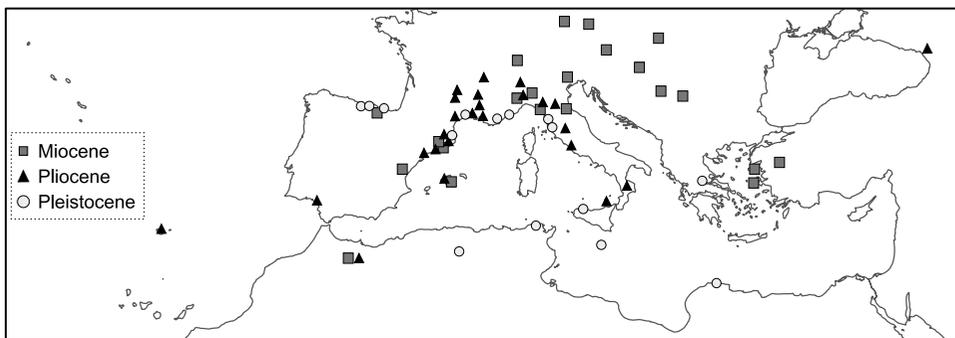

Figure 13.2 Location of Neogene fossil records attributed to *Laurus*. The figure depicts the southward range retreat experienced by Eurasian laurel forests since the mid-Miocene. Redrawn from Rodríguez-Sánchez et al. (2009).

Mediterranean and Black Sea basins (Kovar-Eder et al., 2006) during the lower Pliocene, but only *Laurus* was able to overcome this climatic deterioration and the subsequent Pleistocene glaciations, and thereby persist to the present in relatively moist locations of the Mediterranean and Black Sea basins. *Laurus* and some other Lauraceae species were able to survive in Macaronesian archipelagos (Santos, 1990), where they arrived probably between the Miocene and Pliocene (Axelrod, 1975). The strong regional extinction of laurophyllous taxa that occurred in continental Europe did not occur in eastern Asia or in North America; these regions represented suitable long-term refugia for a significant number of species (Latham and Ricklefs, 1993). Today, excluding a few temperate species, all extant Lauraceae have a tropical–subtropical distribution (Rohwer et al., 1993), and *Laurus* is the only one present in western Eurasia and northern Africa.

Although the fossil record enables a rough reconstruction of the Neogene demise of Tethyan laurel forests, the spatiotemporal patterns of range retreat and extinction are still largely unknown for most taxa. Uncertainty stems mainly from the scarcity of palaeobotanical data for most areas (particularly Macaronesia and the southern Mediterranean) and time periods (e.g. Quaternary). Given the poor pollen preservation of the Lauraceae (Ferguson, 1974), palaeobotanical data are mostly restricted to macrofossils. Furthermore, the limited sampling effort, and particularly its spatial heterogeneity, prevent robust inferences on colonisation dates, local extinctions and other aspects of the range dynamics of species. Other sources of uncertainty are inherent to palaeobotanical data, such as the likely misidentification of poorly conserved fossils, their limited usefulness to infer the distribution and abundance of low-density species, or the difficulty of detecting local extinctions of taxa followed by recolonisations from fragmentary records. Despite these limitations, palaeobotanical data are a fundamental source of information for reconstructing the past. Moreover, inferences provided by palaeobotanical data are likely to broaden when integrated with other tools for biogeographical reconstructions, namely molecular phylogeographies and species distribution models (Cheddadi et al., 2006; Magri et al., 2006). More thorough sampling should therefore be undertaken.

13.3 Reconstructing Plio–Pleistocene *Laurus* distribution shifts through niche-based species distribution models

Species distribution models comprise a diverse group of statistical techniques that relate the geographical distribution of organisms to particular features of the environment, such as climate and soil type, usually with the aim of predicting species distributions at different places or time stages (Guisan and Zimmermann,
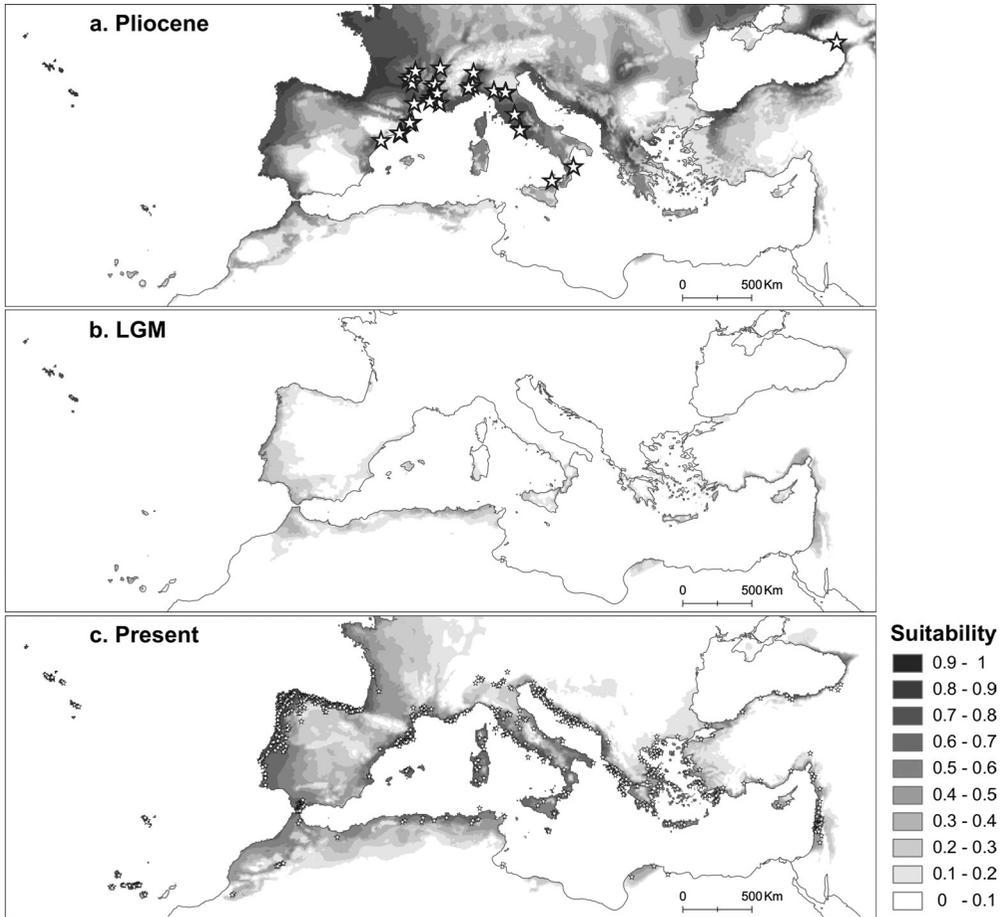
Figure 13.3 Climatically suitable areas for *Laurus* at the mid-Pliocene (3 million years ago), Last Glacial Maximum (LGM; *c.* 21 000 years ago) and present. Habitat suitability inferred from models of *Laurus*' climatic niche projected onto palaeoclimatic data (Rodríguez-Sánchez and Arroyo, 2008). Actual occurrences of *Laurus* for the Pliocene and present are shown by white stars.

2000; Pearson and Dawson, 2003). When successfully fitted to data for a particular time period, these models can be used to predict future (forecasting) or past (hindcasting) species distributions as a function of changing climates or environments (e.g. Pearman et al., 2008a). Rodríguez-Sánchez and Arroyo (2008) employed such an approach to reconstruct the range dynamics of *Laurus* for the last three million years. The scarcity of palaeobotanical data for this period limits the assessment of hypotheses about distribution shifts or location of glacial refugia. Their fossil-validated model predictions (Fig 13.3) documented a process of severe *Laurus* range retreat driven by the overall cooling and, secondarily, by the increase of

thermal and rainfall (drought) seasonality since the end of the Tertiary. At the mid-Pliocene climatic optimum, the potential distribution of *Laurus* was much wider than in later periods, favoured by a warm and relatively humid climate (Haywood et al., 2000). The onset of the Pleistocene glaciations drastically reduced the areas suitable for the persistence of *Laurus*, particularly at northern latitudes (central and southeastern Europe), causing the extinction of temperate relict populations. During the largely unsuitable glacial periods, *Laurus* may have persisted at multiple but small and scattered refugia distributed across the Macaronesian archipelagos, Transcaucasia and the Mediterranean basin (Fig 13.3b), with the Iberian peninsula, North Africa, southern Italy, the Balkan–Aegean region and the Near East as the main glacial refugia. At present (interglacial conditions), *Laurus* inhabits coastal and relatively moist areas in the Mediterranean and Macaronesia. On a coarse geographical scale, the current geographical range of *Laurus* seems to be constrained mostly by climate: cold temperatures impede range expansion towards northern latitudes and inland ranges, while drought stress sets its southern range limits (Rodríguez-Sánchez and Arroyo, 2008). Therefore, climate change seems to have exerted a strong influence on the range dynamics of *Laurus* over geological time.

As an alternative approach to these geographical projections, more mechanistic insights into the fate of *Laurus* species confronted with climate change can be obtained by mapping the climatic requirements of *Laurus*, as estimated by species niche models, onto an environmental space chart, together with the 'realised climates' or range of climatic conditions available at each time stage (Fig 13.4). For a species to persist, there must exist at least some overlap between the climatic requirements of the species and the range of available environmental conditions over time (Jackson and Overpeck, 2000). When there is no overlap, the species must either adapt to the new environment or else migrate to areas conserving suitable climates in order to avoid extinction. In this framework, species niche modelling analyses using two relevant climatic variables and data on the current distribution of *Laurus* showed that its climatic requirements are skewed towards warmer and moister conditions in relation to the available environment (Fig 13.4). Independent experimental evidence confirms the sensitivity of *Laurus* to cold temperatures (Larcher, 2000; González-Rodríguez et al., 2005), which can damage photosynthetic organs and kill seeds or even adult individuals (Giacobbe, 1939; Takos, 2001). Water availability throughout the year also plays a relevant role in limiting distribution, excluding *Laurus* plants from dry sites (those with actual to potential evapotranspiration ratios below 0.5 – Fig 13.5). These climatic requirements are consistent with the subtropical affiliation of *Laurus* (Larcher, 2005). Although here we can only depict part of its climatic niche (that constrained within the range of present climates), both palaeobotanical and experimental data confirm that *Laurus* can inhabit areas with climates warmer than present, as long
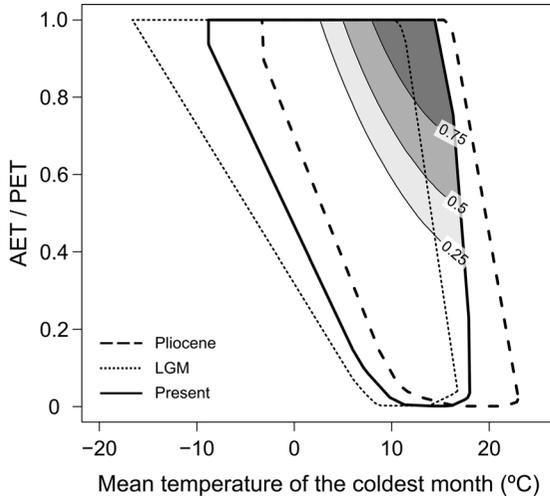
Figure 13.4 Convex hulls enclosing the range of climatic conditions available at the mid-Pliocene, LGM and present for the two climatic variables mostly determining the distribution of *Laurus*. Variables are mean temperature of the coldest month and the actual to potential evapotranspiration ratio (AET/PET). Shaded areas represent relative suitability of climatic conditions for *Laurus* (on a 0–1 scale). The latter was estimated using maximum entropy niche modelling (Phillips et al., 2006) and data on present *Laurus* occurrences and climate (see Rodríguez-Sánchez and Arroyo, 2008). Averaged predictions after 100 random model replicates are shown. Note that *Laurus* requires warm and moist climates (even more than that currently available), and that glacial conditions are largely unsuitable for the species, as shown by the small overlap between the available climatic conditions at the LGM and relative suitability for *Laurus*.

as they also offer high water availability (Konis, 1949; Utescher et al., 2007). Thus, the warm and moist mid-Pliocene climate appeared more suitable for *Laurus* than any other period in the last three million years, as shown by the higher overlap between *Laurus* requirements and the available climate. By contrast, this overlap became minimal during maximum glacial conditions (Fig 13.4). The cold and relatively dry climates of Pleistocene glaciations provoked regional extinction of populations (mainly at northern latitudes) but not the (complete) extinction of the species, as there was still some overlap between the requirements of *Laurus* and the available climatic conditions at some geographical areas (those depicted as glacial refugia in Fig 13.3b).

It is worth noting the close match between the climatic response curves of *Laurus* at the mid-Pliocene and at present (Fig 13.5), which suggests that the climatic requirements of *Laurus* have remained virtually unchanged over millions of years. This marked niche conservatism (evolutionary maintenance of ancestral
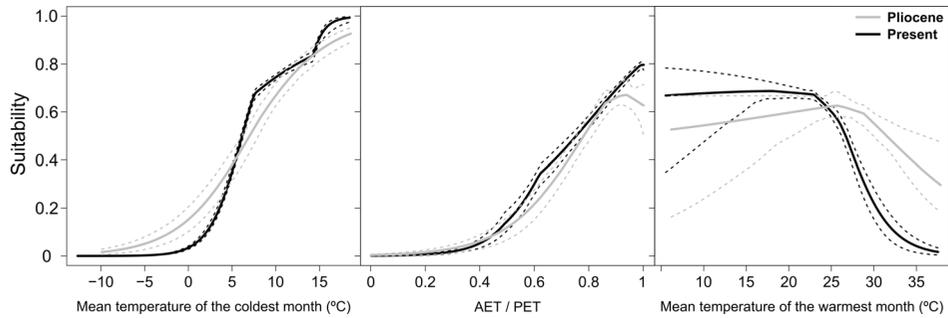
Figure 13.5 Fitted relationships between climatic variables and suitability for *Laurus*, as estimated for the mid-Pliocene and the present. Variables are mean temperature of the coldest month, actual to potential evapotranspiration ratio, and mean temperatures of the warmest month, in decreasing order of importance. The large overlap between the response curves for the two periods points to a high conservatism of *Laurus*' climatic requirements for several million years. Dotted lines enclose the 95% confidence intervals obtained through replicating model fitting 100 times after randomly partitioning the occurrences data set into training and test locations (Rodríguez-Sánchez and Arroyo, 2008). Note that other sources of uncertainty, such as likely biases in palaeoclimatic data, are not accounted for.

ecological characteristics – Wiens and Graham, 2005) has forced largely deterministic (hence predictable) range dynamics of *Laurus* over time in relation to changing climate (see also Svenning, 2003). In fact, the current distribution of *Laurus* could be successfully predicted from a rough estimate of the environments occupied by the species in the mid-Pliocene (Rodríguez-Sánchez and Arroyo, 2008). Although rarely assessed in this kind of study, confirmation of niche stasis over time provides support to palaeodistributions reconstructed through niche-based models (Pearman et al., 2008b).

13.4 Molecular footprints of past range dynamics in *Laurus*

One of the most frequently used approaches for reconstructing the biogeographical history of lineages is molecular phylogeography (Avise, 2000). There has been a proliferation of phylogeographical studies in both animal and plant groups, often aimed at locating refugia and reconstructing species distribution shifts in response to Pleistocene glaciations (Hewitt, 2004). In angiosperms, phylogeographical studies are often based on the analysis of chloroplast DNA (cpDNA) polymorphisms, as they offer advantages compared with those from nuclear DNA markers, such as moderate variation, non-recombination and smaller effective

population size. They also generally show maternal inheritance, which means that patterns of cpDNA variation are not directly influenced by pollen flow among populations (Comes and Kadereit, 1998). Thus, patterns of genetic relatedness of populations based on cpDNA markers should arise exclusively from successful seed dispersal events and hence reflect the history of colonisations and range retreats experienced by the species (Avise, 2000). Alternatively, a number of studies have used nuclear DNA markers, usually to compensate for the low variability of cpDNA, or have worked at the level of whole genomes using markers such as those generated by amplified fragment length polymorphism (AFLP – Vos et al., 1995; Mueller and Wolfenbarger, 1999). The existence of contrasting phylogeographical patterns obtained by both plastid and nuclear markers has sometimes revealed interesting evolutionary events and has thus contributed to a broader picture of the history of taxa (e.g. Arnold et al., 1991).

To date, two studies have attempted a phylogeographical analysis of *Laurus* over most of its distribution range. Firstly, Arroyo-García et al. (2001) used AFLP analyses to assess the genetic relatedness between populations from the western and central Mediterranean (*L. nobilis*) and part of Macaronesia (*L. azorica*). Although their analysis did not consider phylogenetic relationships of the species and populations, they found a clear geographical structure of genetic similarity. Somewhat surprisingly, they found a close similarity between western and southern Iberian populations and those in Macaronesia (even though they are geographically separated and even considered as different species), whereas there was a strong divergence between this western (Iberian and Macaronesian) group and the central Mediterranean (French and Italian) *L. nobilis* populations. Therefore, the Pyrenees seem to have acted as a significant (bio)geographical barrier for *Laurus* over recent historical periods, while some genetic connection, through either pollen or seed, must have occurred among distant western Mediterranean populations. Nevertheless, sampling was limited to the western half of the *Laurus* range and excluded some areas such as northern Africa, which are crucial in order to explain the colonisation of Macaronesia by *Laurus* and, more generally, the historical range dynamics of *Laurus* throughout the western Mediterranean.

A second study (Rodríguez-Sánchez et al., 2009) attempted a historical reconstruction of the past range dynamics of *Laurus* over the whole Mediterranean basin and Macaronesia. This time, *Laurus* populations were sampled throughout the complete geographical range of the genus (from the Azores to the Caucasus, and from the northern Mediterranean basin to the Moroccan Anti-Atlas and the Canary Islands). Overall cpDNA variation was low, but two cpDNA regions (*trnK-matK*, *trnT-trnD*) were sufficiently informative and unambiguous. The use of both phylogeographical and phylogenetic analyses (maximum parsimony
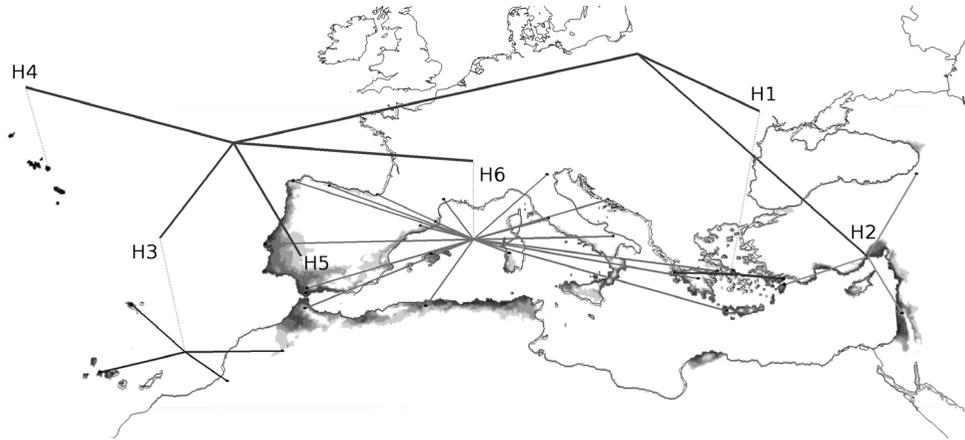
Figure 13.6 Geophylogeny showing the phylogenetic tree (red) and the geographical distribution of the six distinct *Laurus* haplotypes (H1 to H6). After Rodríguez-Sánchez et al. (2009). Shaded areas represent likely glacial refugia for *Laurus*, as predicted by niche-based distribution models (Rodríguez-Sánchez and Arroyo, 2008). See Kidd and Liu (2008) for further details on geophylogenies. *See colour plate section*.

and Bayesian inference) allowed the assessment of relationships among populations, which gave several insights into the differentiation and colonisation patterns of the species. Firstly, *Laurus* was found to be a monophyletic group, an important prerequisite for subsequent analyses of its past migration history. Secondly, six distinct haplotypes were found across its geographical range (Fig 13.6), but, in general, variation was low. This low genetic variability may stem from a number of different causes, but the most likely explanations are the long lifespan of *Laurus* and the subsequent slow generation turnover of its populations, and a historically low mutation rate in the whole lineage of Lauraceae (Chanderbali et al., 2001; Willis and Niklas, 2004; Petit and Hampe, 2006; Smith and Donoghue, 2008). On the other hand, the dioecious breeding system of the species might have promoted haplotype sorting, as separate sexes diminish the effective population size of cpDNA (Cruzan and Templeton, 2000). Thirdly, the six haplotypes were grouped into three lineages, two of which (consisting of one haplotype each) were distributed along the eastern Mediterranean (Fig 13.6). The third clade contained four haplotypes, three of them being exclusive of the westernmost part of the range (Macaronesia, Morocco and southwestern Iberia). Therefore, *Laurus* follows an east-to-west diversification pattern that seems to be common in other ancient Mediterranean lineages, and is consistent with Tethyan–Mediterranean palaeogeographical dynamics (Oosterbroek and Arntzen, 1992; Petit et al., 2005).

13.5 Integrating the fossil record with palaeodistribution models and molecular phylogeography to reconstruct the Neogene history of *Laurus*

Although an absolute time framework could not be provided, Rodríguez-Sánchez et al. (2009) exploited the relatively abundant fossil record of *Laurus* (Fig 13.2) and a previous reconstruction of *Laurus* palaeodistributions based on bioclimatic models (Rodríguez-Sánchez and Arroyo, 2008) in order to provide an integrative interpretation of its past range dynamics. An ancient lineage splitting in the eastern Mediterranean was proposed, followed by a westward migration and a secondary diversification in the western Mediterranean and Macaronesia (four out of six haplotypes). This westerly diversification is probably ancient too, as supported by the relatively abundant Miocene and Pliocene fossils of *Laurus* in Iberia, France and Italy (Fig 13.2), suggesting an early arrival in these areas. Despite the range restrictions imposed by Pleistocene glaciations (Fig 13.3), most populations were able to persist at scattered locations along the Mediterranean and in Macaronesia, as shown by the presence of singular haplotypes at several putative refugia (Fig 13.6). The hypothesis of multiple glacial refugia receives further support from the geographical genetic structure determined by Arroyo-García et al. (2001). However, we cannot exclude the extinction of additional lineages during the Pleistocene. The expansion of one of the derived haplotypes (H6) throughout most of the Mediterranean might be a consequence of relatively recent dispersal processes, probably linked to interglacial periods and even to human-assisted migrations.

Unfortunately, the scarcity of fossils in North Africa and Macaronesia and the low overall genetic variability of the populations preclude further inferences on the dates and migration routes towards and within Macaronesian archipelagos. Nonetheless, the recent finding of a further new haplotype in the Atlas region of North Africa (Rodríguez-Sánchez, unpublished data) supports the hypothesis that this area was an important long-term refugium for *Laurus*. This region has also probably acted as a stepping stone in the migration of *Laurus* to Macaronesia, as has been shown for many other taxa (Vargas, 2007).

13.6 Taxonomic differentiation in *Laurus* and other pre-Mediterranean lineages

The low rate of molecular differentiation and high morphological stasis shown by *Laurus* over geological time are also features in other Tertiary relict taxa from the Mediterranean and elsewhere (Milne and Abbott, 2002). Two species have been

considered traditionally within the genus *Laurus* (*L. nobilis* in the Black Sea and Mediterranean basins and *L. azorica* in Macaronesia), but it may be better to treat them as a single monophyletic group in light of previous morphological reassessments (Ferguson, 1974; Marques and Sales, 1999) and recent molecular studies (Arroyo-García et al., 2001; Rodríguez-Sánchez et al., 2009). Thus, our former sketch of *Laurus'* historical biogeography, as a monophyletic lineage, is valid for the whole genus. The formal taxonomic description of both species is based mostly on continuous, overlapping traits, such as leaf shape and tomentum, and many specimens collected within the alleged disjunct range of the species cannot be unequivocally ascribed to one of the two species (Arroyo-García et al., 2001). Macaronesian *Laurus* was originally described in the mid-nineteenth century as two separate species: *Persea azorica* Seub. from the Azores and *Laurus canariensis* Webb and Berthelot from Madeira and the Canary Islands (see Franco, 1960, who combined both taxa into a single species, *L. azorica*). Later, some *L. azorica* populations were reported from the Middle Atlas and the Anti-Atlas on the African continent (Barbero et al., 1981). *Laurus nobilis* is found hundreds of kilometres from here, and spreads across the rest of the Mediterranean and Black Sea basins. *Laurus nobilis* and *L. azorica* present higher morphological variability within their geographical ranges than amongst them, as shown by a morphometric study based on herbarium specimens in which intrapopulation variability was not considered (Marques and Sales, 1999; see also Giacomini and Zaniboni, 1946). A study across the full range of *Laurus*, incorporating morphological variability within and amongst populations, is thus desirable to ascertain the precise differences, if any, amongst populations and species.

Several hypotheses can be posed regarding this enormous morphological variability. Firstly, the isolated location of most populations, certainly more pronounced in the Macaronesian archipelagos, may have favoured some stochastic morphological differentiation among populations. In particular, founder events may have been more important than genetic drift, given the apparent long generation times of *Laurus*. Hence, a wide range of ancestral phenotypic variation may have existed among populations throughout the Mediterranean and these may have undergone subsequent random local extinction and colonisation events to generate a pattern similar to what is currently observed. Nevertheless, we cannot discard the role of phenotypic plasticity or the possible adaptive significance of population modal values. These should be specifically tested, at least through classical reciprocal transplant experiments. Additional insight may come from ecological niche models. Although there is significant niche overlap (Warren et al., 2008) between both species (actual overlap of 0.75, on a 0–1 scale, while values of niche overlap according to a proper null model span from 0.68 to 0.70), some ecological segregation between the two species also appears to exist (Fig 13.7). In particular, *L. nobilis* is found in colder (i.e. more continental) habitats than *L. azorica*,
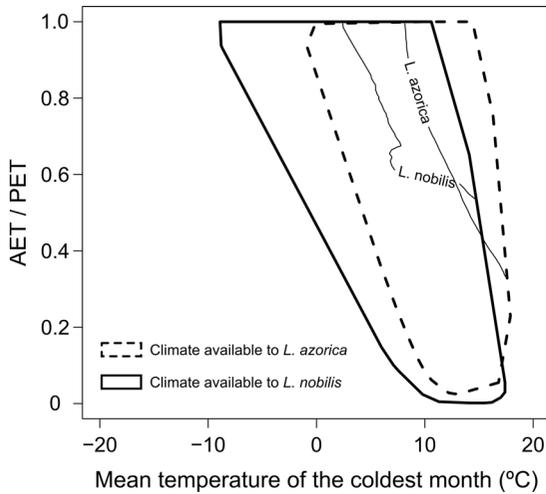
Figure 13.7 Range of current climatic conditions available to *L. nobilis* and *L. azorica*, and the portion of their climatic space occupied by each species. *L. nobilis* is found in colder habitats, but these are also much more common within its distribution area. Warm and moist habitats are optimal for both species. Climatic niches were estimated by maximum entropy niche modelling (see Fig 13.4). For better visibility, environmental suitability values have been thresholded for each species using the maximisation of sensitivity plus specificity criteria (Liu et al., 2005).

which may reflect a better adaptive performance of the former to Pleistocene glaciations that were more intense in continental ranges. In fact, ecophysiological studies have shown higher tolerance to cold stress in continental (*L. nobilis*) populations (Larcher, 2000) than in Macaronesian (*L. azorica*) ones (González-Rodríguez et al., 2005). Nevertheless, this apparent habitat segregation might also result from processes of competitive exclusion in cold habitats or from intense historical land-use change in Macaronesian islands (Parsons, 1981). Thus, further work is needed to explore these hypotheses and ultimately understand the ecological attributes of the two *Laurus* 'species'.

Caryological studies (Ehrendorfer et al., 1968) have found variable ploidy levels within *Laurus* that may help explain its infrageneric morphological differentiation. However, so far the weight of available evidence suggests that *Laurus* should be considered a monospecific genus as proposed by Marques and Sales (1999), and any attempt to split it into new species, such as the recent proposal of *L. novocanariensis* (Rivas-Martínez et al., 2002), should be based on rigorous and comprehensive research.

Most Mediterranean woody taxa (e.g. families Cistaceae, Fabaceae and Lamiaceae) show high phylogenetic diversification and endemism levels as a consequence of adaptive radiation, hybridisation and/or polyploidy processes. Recent

work on rockroses (*Cistus*) has shown strong molecular and taxonomic divergence across the Mediterranean, which probably occurred during the Plio–Pleistocene (Guzmán and Vargas, 2005). An even stronger diversification has been found in Mediterranean *Ulex* spp. (De Castro et al., 2002; Pardo et al., 2004; Cubas et al., 2005). In contrast, there is low taxonomic diversification in *Laurus* and other pre-Mediterranean lineages of subtropical origin, irrespective of their current status as relicts (e.g. *L. nobilis*, *Prunus lusitanica*, *Rhododendron ponticum*) or as widespread species in typical Mediterranean forests and shrublands (e.g. *Myrtus*, *Olea*, *Phillyrea*, *Pistacia* – Herrera, 1992; Milne and Abbott, 2002). The wide phylogenetic span of this pre-Mediterranean guild, with several families represented, does not support phylogenetic relatedness as a possible explanation for their shared low diversification. Instead, their longevities and strong survival capacity against severe disturbance and their subsequent slow generation turnover, together with their frequent vegetative reproduction, emerge as more likely factors (Willis and Niklas, 2004; Smith and Donoghue, 2008). Additionally, genetic constraints, long-term habitat stability and/or historical gene flow among populations may also have precluded differentiation or even adaptation to changing environments (Milne and Abbott, 2002; Ackerly, 2003). This low differentiation and diversification capacity could partly explain the relatively high extinction rates of subtropical taxa at the Plio–Pleistocene boundary (Svenning, 2003). Clearly, more combined molecular, palaeobotanical and ecological evidence is needed to ascertain the causes of the morphological stasis and low speciation rates of Tertiary lineages.

13.7 A cautionary tale for the future of laurel forests in the Mediterranean and Macaronesia

The insights obtained from our integrative reconstruction of the past range dynamics of *Laurus* in relation to historical climate change can tentatively be used to predict the likely effects of future climate changes on *Laurus* and other laurophyllous taxa with similar climatic requirements. All current climatic models coincide in predicting warmer temperatures and an overall reduction in rainfall (i.e. higher drought stress) in the Mediterranean basin (Christensen et al., 2007), with similar predictions for the Canary Islands (Sperling et al., 2004). Although laurophyllous taxa could initially benefit from a warmer climate, a marked increase in water deficit would be detrimental (Rodríguez-Sánchez and Arroyo, 2008). This impact would be stronger in southern Mediterranean *Laurus* populations, which currently harbour most of the genetic diversity of the species. In contrast, the milder climate predicted for western and central Europe would favour the spread of *Laurus* to those regions because predicted warmer minimum temperatures would no longer be limiting. Field observations indicate an ongoing northward range expansion of thermophilous taxa to this area (Walther, 2003), consistent

with previous predictions (Parmesan, 2006). In the particular case of *Laurus*, this northward expansion might be hastened by humans (van der Veken et al., 2008) because *Laurus* is widely used as a cultivated and ornamental plant. Similarly, the authors have detected reduced growth and have recorded reproductive failures caused by dry years in Mediterranean populations from southern Iberia and North Africa (unpublished data). Although long lifespan and resprouting ability confer strong demographic resilience, a sustained trend towards more arid climates would certainly increase the risk of local extinction.

13.8 Conclusions: adaptation, niche conservatism and the evolutionary effects of climate changes

There has been an increase in theoretical and empirical studies trying to foresee the ecological and evolutionary consequences of future climate change, and historical approaches are central to these efforts. They allow researchers to assess competing hypotheses on the effects of varying past climate regimes with actual data obtained from the past. Within this framework, the climate-driven apogee and demise of Tethyan laurel forests during the Cenozoic represents an invaluable case study to explore timely topics of paramount biogeographical relevance. Firstly, it is important to know what ecological factors and/or intrinsic species features determine different resiliences to extinction in different taxa confronted with the same process of climate change. In this regard, it is particularly important to know why *Laurus* was able to endure the Plio–Pleistocene climate changes while all other European Lauraceae went extinct. In a landmark paper, Svenning (2003) showed that the final fate of European tree species (extinction, relictual persistence or wide distribution) after the Plio–Pleistocene transition was mostly determined by their previous climatic requirements. Comparative data from extant Lauraceae in the Canary Islands indeed suggest that *Laurus* is more freeze-tolerant and less drought-sensitive than confamilial taxa (Gandullo et al., 1992; González-Rodríguez et al., 2005), which could help explain its successful persistence in the Mediterranean basin. Secondly, the history of *Laurus* provides an illustrative case of how some plant species manage to persist despite largely unsuitable and changing climates. Although climatic cooling since the late Tertiary provoked the extinction of its once thriving northernmost populations, the existence of several climatically suitable areas through the Quaternary, albeit small and isolated, enabled the long-term persistence of the species.

   A large number of studies have shown that the maintenance of ancestral ecological features of taxa may play a determinant role in the responses of species to climate change. If niche conservatism occurs, rather than adaptation to the new environment, then species must track suitable climates by migration or go

extinct (Huntley and Webb, 1989; Jackson and Overpeck, 2000). Several causes have been proposed to explain the lack of adaptation in natural ecological scenarios, including: (1) lack of sufficient genetic variation; (2) genetic constraints such as pleiotropy; (3) presence of gene flow, which hinders possible local adaptive processes; and (4) the existence of stabilising selection on the climatic niches of species (Wiens and Graham, 2005). The last of these could be promoted by community assembly processes or the ability of species to track suitable habitats (Ackerly, 2003; de Mazancourt et al., 2008). Furthermore, while rapid evolution or adaptation in short-lived plant populations seems likely (Willis and Niklas, 2004; Franks et al., 2007), such processes might be more limited in tree populations, due to the longevity of most tree species and their long generation cycles (Petit and Hampe, 2006). This would reduce their opportunities to adapt to changing climates at a suitable pace (Jump and Peñuelas, 2005). On the other hand, the typically high survival rates of adult trees and their long lifespan (of up to several thousand years) makes them, in principle, more resilient to extinction in transient periods of unsuitable climate (Brubaker, 1986; Bond and Midgley, 2001).

Future studies should focus on the role of the many factors and processes that determine either niche conservatism or adaptive responses of species, as these will ultimately decide the fate of taxa under changing climates. In this sense, historical approaches that integrate information from phylogenetic and phylogeographical analyses, detailed studies of the fossil record, and palaeodistribution statistical models will provide fruitful insights. Furthermore, when combined with experimental, theoretical and contemporary ecological approaches, they will certainly improve our knowledge of the ecological and evolutionary effects of climate change.

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