



Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene

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ABSTRACT

Aim Climate changes are thought to be responsible for the retreat and eventual extinction of subtropical lauroid species that covered much of Europe and North Africa during the Palaeogene and early Neogene; little is known, however, of the spatial and temporal patterns of this demise. Herein we calibrate ecological niche models to assess the climatic requirements of *Laurus* L. (Lauraceae), an emblematic relic from the Tethyan subtropical flora, subsequently using these models to infer how the range dynamics of *Laurus* were affected by Plio-Pleistocene climate changes. We also provide predictions of likely range changes resulting from future climatic scenarios.

Location The Mediterranean Basin and Macaronesian islands (Canaries, Madeira, Azores).

Methods We used a maximum-entropy algorithm (Maxent) to model the relationship between climate and *Laurus* distribution over time. The models were fitted both to the present and to the middle Pliocene, based on fossil records. We employed climatic reconstructions for the mid-Pliocene (3 Ma), the Last Glacial Maximum (21 ka) and a CO₂-doubling future scenario to project putative species distribution in each period. We validated the model projections with *Laurus* fossil and present occurrences.

Results *Laurus* preferentially occupied warm and moist areas with low seasonality, showing a marked stasis of its climatic niche. Models fitted to Pliocene conditions successfully predicted the current species distribution. Large suitable areas existed during the Pliocene, which were strongly reduced during the Pleistocene, but humid refugia within the Mediterranean Basin and Macaronesian islands enabled long-term persistence. Future climate conditions are likely to re-open areas suitable for colonization north of the current range.

Main conclusions The climatic requirements of *Laurus* remained virtually unchanged over the last 3 Myr. This marked niche conservatism imposed largely deterministic range dynamics driven by climate conditions. This species's relatively high drought tolerance might account for the survival of *Laurus* in continental Europe throughout the Quaternary whilst other Lauraceae became extinct. Climatic scenarios for the end of this century would favour an expansion of the species's range towards northern latitudes, while severely limiting southern populations due to increased water stress.

Keywords

Bioclimatic envelope, climate change, ecological niche modelling, glacial refugia, Lauraceae, Macaronesian islands, niche conservatism, Pleistocene, range limits, Tertiary.

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INTRODUCTION

Climate has long been recognized as the main determinant of plant range limits and dynamics on a continental scale (Woodward, 1987). Although other factors (e.g. soil types, biotic interactions, dispersal limitation) progressively gain importance at smaller scales (Pearson & Dawson, 2003), large areas in which a plant species can grow and reproduce appear to be primarily determined by the latter's climatic requirements (Huntley *et al.*, 1995; Morin *et al.*, 2007). Furthermore, there is solid evidence of climate-driven range expansion, retreat or even extinction of species (Davis & Shaw, 2001; Parmesan, 2006). Bioclimatic envelope and ecological niche modelling have proved to constitute successful tools for inferring plant distribution as a function of climate or other environmental factors (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003). Under certain assumptions, models can be fitted by relating species presence (and absence) in certain sites with local environmental conditions, and then used to predict distribution shifts resulting from changing environments (Pearson & Dawson, 2003).

Potential threats posed by modern climate change (IPCC, 2007) have reinforced interest in the relationship between climate and the distribution of organisms, and in recent years many modelling studies have attempted to anticipate the consequences of future climate changes (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005). An increasing number of studies are also employing these tools to infer range changes associated with past climate dynamics (e.g. Martínez-Meyer & Peterson, 2006; Pearman *et al.*, 2008b). Establishing how past climates have shaped distributions and brought about extinctions is of great relevance for both historical and applied conservation biogeography, because a better understanding of the biological consequences of past climate dynamics could provide useful insights for anticipating future changes.

During most of the Palaeogene and early Neogene, broadleaved evergreen sclerophyllous vegetation (the 'Madrean–Tethyan' flora; Axelrod, 1975) covered low and middle latitudes of the Northern Hemisphere. These lauroid subtropical forests were dominated by thermo-hygrophilous woody plants, with tropical families such as Lauraceae, Myrtaceae, Palmae etc. being well represented (Mai, 1989). A sustained trend towards cooler and drier climates since the Upper Miocene led to the decline of this unique vegetation. However, during the 'mid-Pliocene climatic optimum' (c. 3 Ma), the climate was still substantially warmer and moister than at present (Haywood & Valdes, 2004). At that time, relict genera of the Tethyan flora (e.g. *Myrica*, *Ocotea*, *Cinnamomum*, *Persea*) still coexisted in southern Europe with ancestors of extant Mediterranean taxa (*Olea*, *Quercus*, *Pistacia*, *Nerium*; Kovar-Eder *et al.*, 2006). The onset of the Mediterranean climate in the Pliocene, with hot and dry seasons, and the glacial–interglacial cycles of the Quaternary, with recurrent periods of cold and arid conditions, ultimately caused the extinction of many members of the Tethyan Palaeogene flora in Europe and North Africa (Mai, 1989; Svenning, 2003). Today, many of the surviving taxa are restricted to the Macaronesian Islands and Transcaucasia, while a small number still persist in the Mediterranean Basin.

Whilst the Quaternary range shifts of many temperate European plant species are now relatively well understood (Hewitt, 2004), the actual range dynamics of the ancient Tethyan flora remain obscure. This is in part due to the scarcity of fossil data (Kovar-Eder *et al.*, 2006). Predictive distribution models, however, can be used to detect probable refugia and biogeographical connections at a spatio-temporal resolution that cannot be attained with the use of palaeodata alone. Fossil records, as well as results from phylogeographical analyses, can in turn be used to support or reject model predictions. Here, we use predictive models to reconstruct the range dynamics of *Laurus*, one of the most emblematic relics of the Tethyan flora, as determined by climate changes since the Pliocene. Fossil data are subsequently used to validate our model-based scenario.

The specific objectives of this paper are the following: (1) to determine the range of the climatic conditions required for the long-term persistence of *Laurus*; (2) to evaluate the extent to which *Laurus* is subject to niche conservatism (evolutionary maintenance of ancestral ecological characteristics; Wiens & Graham, 2005): to this end, we compared niche models fitted to *Laurus*' current and Pliocene distributions; (3) to perform a reconstruction of *Laurus* range dynamics as driven by climate over the past 3 Ma: three climatic stages were considered including the middle Pliocene (3 Ma), as the last documented 'climatic optimum' period, the Last Glacial Maximum (LGM, c. 21 ka), as an extremely unfavourable period characteristic of Pleistocene glaciations, and present climatic conditions as surrogate for interglacial periods; (4) to address the prediction of distribution changes caused by ongoing climate change. According to IPCC (2007), the climate of the Mediterranean Basin has already started to become warmer and drier and is predicted to follow the same trend in the future. Relict long-lived plants of former mild climates, such as *Laurus*, might be particularly vulnerable to predicted increases in water stress (Hampe & Petit, 2005).

METHODS

Study species

Laurus (the laurel tree) is the only Lauraceae genus that has persisted in Europe and North Africa from the early Neogene to the present. Although it reached temperate latitudes (i.e. Germany, Hungary) during the Miocene, its current distribution is limited to the Mediterranean Basin, occupied by *Laurus nobilis*, and to most of the Macaronesian Islands (Canaries, Azores, Madeira), inhabited by *Laurus azorica*. Herein we treat both described species jointly, as their independent status is questioned by ecological, morphological and genetic evidence (Ferguson, 1974; Arroyo-García *et al.*, 2001; Rodríguez-Sánchez *et al.*, unpublished data).

Data on historical and current species distribution

We obtained data on present and historical *Laurus* occurrences by means of an extensive review of diverse sources, including national and regional floras, atlases, bibliographic references and

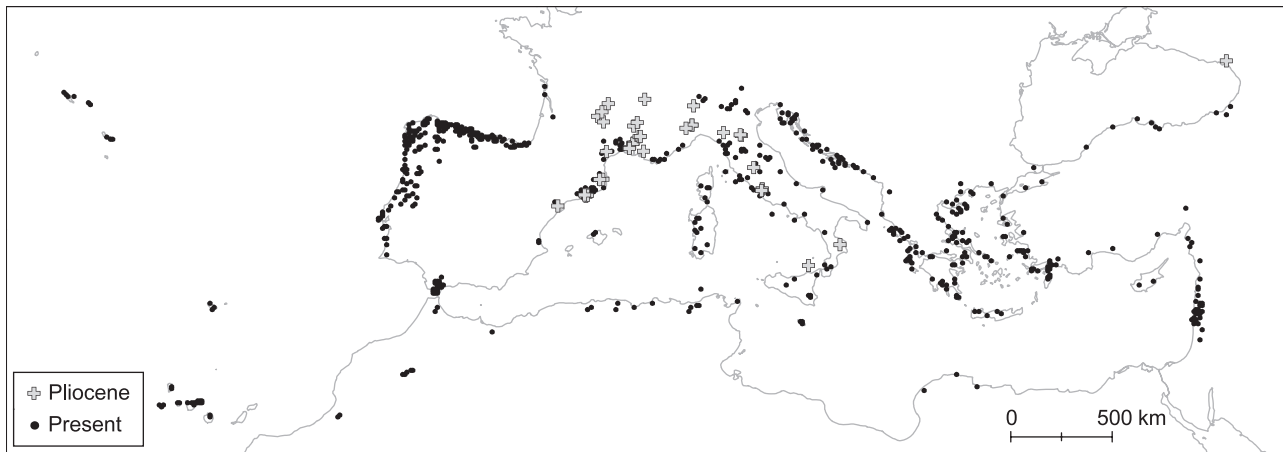


Figure 1 Map of current and Pliocene fossil locations of *Laurus* (see Appendix S1 for sources).

online data bases (see Appendix S1 in Supplementary Material for a complete list of sources), and from our own field surveys. All records of presumably cultivated individuals or sites that could not be properly georeferenced were excluded from our analyses. We obtained 36 Pliocene fossil records and 925 sites of current presence, which translated to 589 10×10 km occupied cells (Fig. 1). We removed duplicate presence records from grid cells to avoid pseudoreplication and to lessen the effect of variation in sampling effort. We consider our data set to be very comprehensive, thereby accurately representing the actual distribution of the species and covering the whole range of climatic conditions it may experience. Moreover, the large sample size of the distribution data set enabled us to incorporate interactions between predictor variables in the model, along with a robust estimation of complex responses (Phillips & Dudík, 2008).

A minimal model of plant distribution and climate

As we were interested in the role of climate as the main factor establishing range size and limits on a geological time-scale, we needed a generalized model transferable in time and based upon environmental variables directly linked to the physiology of the species (as opposed to indirect predictors or surrogates of habitat conditions such as elevation or aspect). Temperature, light and water availability are fundamental environmental factors for plants. Light availability was discarded for this study because *Laurus* is shade-tolerant, readily growing in forest understoreys and shady gorges, and light should therefore not constitute a limiting factor in Mediterranean woodlands. In addition to climate, soil type can sometimes act as an important ecological filter for plants. As *Laurus* grows in a variety of soil types, however (Villar, 1998), we did not consider this factor to be an important constraint for species' distribution.

Thus, we formulated a bioclimatic model including only variables related to temperature and water availability, namely mean temperatures of the coldest (January) and warmest (July) months, and water deficit estimated as the annual mean of the ratio of actual to potential evapotranspiration (AET/PET). The AET/PET ratio takes values from 0 to 1, with higher values

representing reduced water deficiency. This model – or modified versions with related variables – has been widely used in previous studies of plant distribution and climate, and is rooted in sound physiological knowledge (Prentice *et al.*, 1992; Stephenson, 1998). In addition, we included the altitudinal range (maximum – minimum elevation) of each 100 km^2 grid cell as a surrogate of within-cell microclimatic heterogeneity, as the resilience of plant populations to climate changes is often linked to the environmental diversity provided by topographic relief (e.g. Tzedakis, 1993).

Climate data

For Pliocene climate, we made use of an improved simulation based on Haywood & Valdes (2004). For the LGM we used the output from the Palaeoclimate Modelling Intercomparison Project (Joussaume & Taylor, 2000; <http://pmip.lsce.ipsl.fr/>). Simulation results from two different general circulation models (ECHAM3 and UGAMP; DKRZ, 1992; Dong & Valdes, 1998) were used to account for the uncertainty resulting from significant variability in model projections throughout the study area (Kageyama *et al.*, 2001). Data for present climate and future scenarios (end of the 21st century) were obtained from Worldclim 1.4 (Hijmans *et al.*, 2005; <http://www.worldclim.org/>). For future conditions we used a high-resolution simulation of the CCM3 general circulation model (GCM) with a CO_2 -doubling scenario (Govindasamy *et al.*, 2003). We adopted the following protocol for climatic data preparation from GCM outputs in order to guarantee that: (1) climatic values were consistent across time stages and regions; (2) fine-scale patterns in present climate observations (of higher resolution) were retained for the other time stages and (3) any global or regional biases of the different GCMs were minimized. For each GCM and time stage, we first calculated the relative change or anomaly (additive for temperature, multiplicative for precipitation) between the climate of each period and the present climate, as simulated by the GCM. We then downscaled these anomalies to 100-km^2 grid cells through spline interpolation. Finally, we calculated the projected climate for each time period from current climate data and interpolated anomalies.

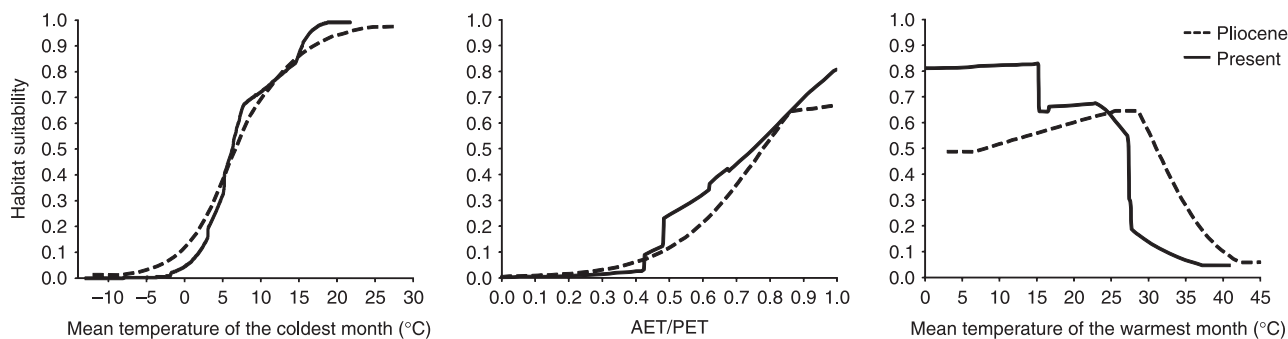


Figure 2 Fitted response curves to climatic variables [mean temperature of the coldest month, actual/potential evapotranspiration ratio (AET/PET) and mean temperature of the warmest month, in decreasing order of importance] for the Pliocene (dashed lines) and the present (solid line).

Statistical modelling

The relationship between species distribution and climate was modelled using Maxent (Phillips *et al.*, 2006; Phillips & Dudík, 2008), a machine learning algorithm based upon the maximum entropy principle. According to this principle, in order to estimate an unknown probability distribution (in this case related to the probability of presence), we should find the probability distribution of maximum entropy constrained only by our incomplete information about the distribution. Thus, Maxent estimates species distributions by finding the distribution of maximum entropy (i.e. closest to uniform) subject to the constraint that the expected value of each environmental variable (or functions thereof) under this estimated distribution matches its empirical average (Phillips *et al.*, 2006).

We used Maxent for the following reasons: (1) It functions with 'presence-only' data (Guisan & Zimmermann, 2000), and we could therefore avail ourselves of the information on species occurrence contained in natural history collections and bibliographic references. (2) Maxent offers several theoretical, statistical and computational advantages (Austin, 2007): it does not assume a priori just any (unjustified) form for the relationship between climatic variables and species presence; it gradually accommodates complex response curves and interactions between variables; the additivity of the model allows for clear interpretation of how each environmental variable relates to suitability; and the efficient algorithm implemented always converges to the optimal maximum entropy distribution while controlling over-fitting. Due to these and other advantages (see Phillips *et al.*, 2006; Phillips & Dudík, 2008), Maxent has outperformed other common techniques in recent comparative studies (Elith *et al.*, 2006; Hijmans & Graham, 2006).

We used the latest available version (Maxent 3.2.1, downloadable from <http://www.cs.princeton.edu/~schapire/maxent/>). In an initial step, we fitted the niche model to present climate and occurrences, which was then used to predict the potential distribution of *Laurus* in the mid-Pliocene, the LGM (according to both GCMs, ECHAM3 and UGAMP) and the end of the 21st century. In a second stage, we calibrated the climatic niche model for Pliocene climate and *Laurus* fossil sites, and projected it onto current climatic conditions. Model predictive performance was evaluated by means of a threshold-independent measure, the area

under the curve (AUC) of the receiver operator characteristic (ROC) function (Fielding & Bell, 1997). An AUC value of 0.5 indicates a random prediction (useless model), whereas the closer the value to 1, the better the predictive ability of the model. Note, however, that the maximum achievable AUC in Maxent is less than 1 (Phillips *et al.*, 2006). We ran each model 20 times, always keeping a random partition of 30% of the occurrences data set for model testing. We used a jackknife procedure to assess the contribution of each environmental variable and to optimize model complexity: we compared model performance (AUC value) for repeated runs, first omitting each environmental variable and subsequently using it in isolation.

RESULTS

The predictive performance of our bioclimatic model, based on mean temperatures of the coldest and warmest months and on an estimate of water deficiency (AET/PET), was fairly high (mean AUC = 0.905). Topographical heterogeneity, estimated as within-cell altitudinal range, was finally excluded from the model as it did not significantly improve performance and, more importantly, showed inconsistent relationships across time stages. Mean temperature of the coldest month was the most relevant factor (contributing 50% of the model fit), followed by water deficit and mean temperature of the warmest month (38% and 12%, respectively). Neither inclusion of a spatial trend surface polynomial nor a reanalysis with coarser grain size (50 × 50 km) affected model fit or structure, a fact that supports the robustness of the bioclimatic model with respect to spatial autocorrelation.

Across geological time, *Laurus* consistently occupied warm and relatively moist climates with low seasonality. Response curves to climate were virtually identical for both present and Pliocene conditions (Fig. 2), despite the small sample size and resulting higher risk of bias in the latter case. Probability of presence increased sharply with warmer temperatures in the coldest month, but declined with summer temperatures higher than 28–30 °C. Thus, the range of optimal temperatures spanned c. 15–30 °C. Regarding water availability, values of the AET/PET ratio below 0.4 clearly limited the presence of *Laurus*. Above this threshold, climatic suitability was always favoured by increased moisture levels (i.e. reduced drought stress).

The projection of the niche model fitted to present climate onto geographical space accurately reproduced the species' current distribution (Fig. 3a). According to the model, the most suitable regions were the Atlantic side of the Iberian Peninsula and the Macaronesian islands, in particular the Azores and Madeira. Within the Canary archipelago, the model successfully discriminated between the arid eastern islands (Lanzarote, Fuerteventura) and the moister western islands, which still harbour sizeable laurel forests. Within the Mediterranean Basin, only some islands and relatively moist coastal regions located in the Balkan countries, the Italian Peninsula, the North African Tell Mountains (Algeria, Tunisia), the Strait of Gibraltar area, south-eastern France and the eastern Iberian Peninsula had suitability values greater than 0.6 (on a scale of 0–1). Likewise, a fringe along the south-eastern Black Sea (Turkey, Georgia) presented a suitable climate. On the contrary, inland mountain ranges were less suitable due to their more extreme temperatures, despite frequent higher precipitation.

The strong niche conservatism shown by climatic response curves for the Pliocene and present conditions (Fig. 2) was confirmed by the congruency of the model projections through different periods. Thus, the projection of the Pliocene-fitted model onto current climate (Fig. 4b) tallied well with present *Laurus* distribution (AUC = 0.89), although suitability values were generally lower than those predicted by the model fitted to the present (Fig. 3a). Similarly, the prediction of *Laurus* Pliocene distribution by the model fitted to present conditions (Fig. 3b) was generally well supported (AUC = 0.81) by the limited number of fossil occurrences.

In general, model projections across the different time stages showed that climate changes that have occurred since the Pliocene drastically reduced mean environmental suitability for *Laurus* (Table 1, Figs 3, 4). Suitable areas in the mid-Pliocene were much more extensive than at present (Figs 3b & 4a),

especially in central and south-eastern Europe, due to a warmer climate (4–5 °C higher; Table 1; Appendix S2). More favourable temperatures would thus have permitted the presence of *Laurus* in northern latitudes up to the Pleistocene transition. Likewise, northern Mediterranean *Laurus* populations appeared less fragmented than today. At lower latitudes, in contrast, suitable areas were smaller as a result of the GCM predicting higher water deficit and summer temperatures than today.

Both GCM (ECHAM3 and UGAMP) simulations of the LGM climate coincided with regard to global patterns (Table 1), although regional discrepancies translated into slight variations in predicted suitability (see Appendix S2). Compared to UGAMP, the ECHAM3 model generally predicted warmer winters but lower summer temperatures, as well as higher water availability in the western Mediterranean. Not surprisingly, LGM climate was markedly colder (mean decrease of 5 °C) and drier (35% mean reduction of annual precipitation) than at present. As a result, mean suitability at the LGM dropped eight-fold compared with the mid-Pliocene period (Table 1), forcing the extinction of laurel populations located north of the Mediterranean Basin. Few regions apparently remained appropriate for the persistence of *Laurus* during the LGM (Fig. 3c,d): the Macaronesian Islands, the Iberian Peninsula, North Africa, southern Italy, the Aegean region, Transcaucasia and the Near East appear as the main glacial refugia for *Laurus*.

Climatic scenarios for the end of this century predicted higher temperatures and reduced water availability across the current *Laurus* distribution (Table 1, Appendix S2). Accordingly, the niche model predicted for the end of 21st century a slight northward expansion of the potential distribution of *Laurus*, with a simultaneous and notable reduction of climatic suitability in the Mediterranean Basin, more remarkable in North Africa, the southern Iberian Peninsula and the Aegean region (Fig. 3e; see also Appendix S3). In general, suitability was lower than at

Table 1 Climatic features and predicted suitability for *Laurus* at each time stage. Modal values, 10th and 90th percentiles (in parentheses) and overall range (in square brackets) are given. Results from both General Circulation Models (ECHAM3 and UGAMP) are shown for the Last Glacial Maximum (LGM).

	Pliocene	LGM (ECHAM3)	LGM (UGAMP)	Present	End of 21st century
Mean temperature of the coldest month (°C)	16.2 (3.4, 16.4) [−13.2, 25.5]	7.4 (−11.4, 8.8) [−21.4, 16.5]	5.1 (−16.3, 8.0) [−26.2, 16.0]	10.6 (−3.2, 11.6) [−15.3, 18.4]	12.2 (−1.6, 13.4) [−13.3, 20.1]
Mean temperature of the warmest month (°C)	26.9 (20.5, 36.6) [3.2, 42.6]	21.6 (11.7, 26.1) [−2.2, 33.3]	23.9 (10.9, 26.5) [−3.4, 33.0]	21.1 (17.3, 30.7) [2.2, 37.6]	25.7 (19.8, 33.7) [4.6, 40.5]
Water availability (AET/PET)	1 (0.03, 1) [0, 1]	1 (0.08, 1) [0, 1]	1 (0.10, 1) [0, 1]	1 (0.10, 1) [0, 1]	1 (0.09, 1) [0, 1]
Environmental suitability	0 (0, 0.67) [0, 0.99]	0 (0, 0.10) [0, 0.92]	0 (0, 0.07) [0, 0.92]	0 (0, 0.50) [0, 0.95]	0 (0, 0.48) [0, 0.97]
Suitable area* (10 ⁶ km ²)	2.33	0.13	0.11	1.40	1.13

*We used a threshold probability value of 0.31 for estimation of the suitable area, based on the maximization of sensitivity plus specificity (Liu *et al.*, 2005). Total terrestrial study area (as in Fig. 1): 6.60 × 10⁶ km².

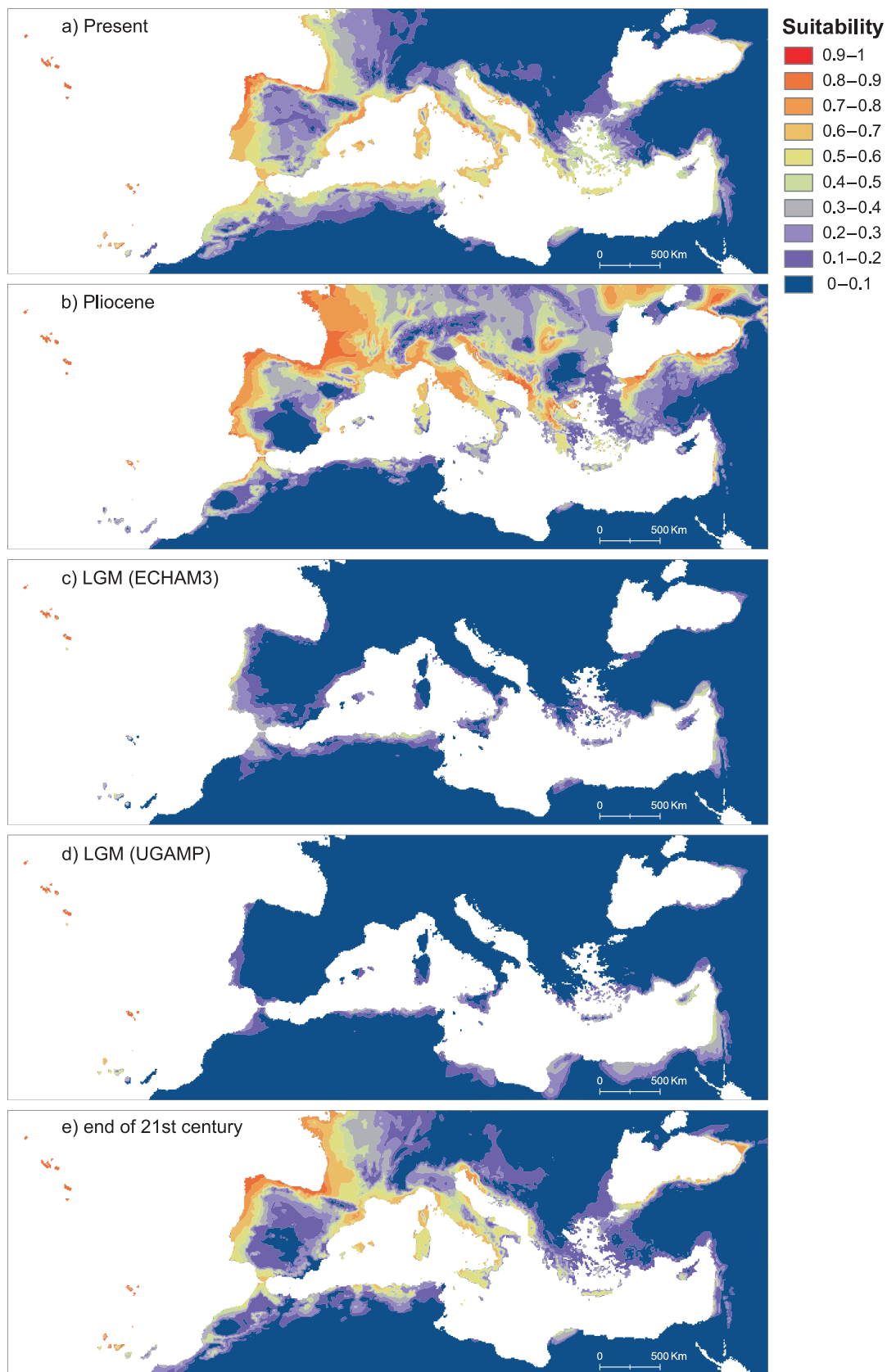


Figure 3 Maps of predicted environmental suitability for *Laurus* across time stages, according to the niche model fitted to present locations and climate: (a) present, (b) mid-Pliocene, (c) Last Glacial Maximum (ECHAM3 model), (d) Last Glacial Maximum (UGAMP model), (e) end of the 21st century.

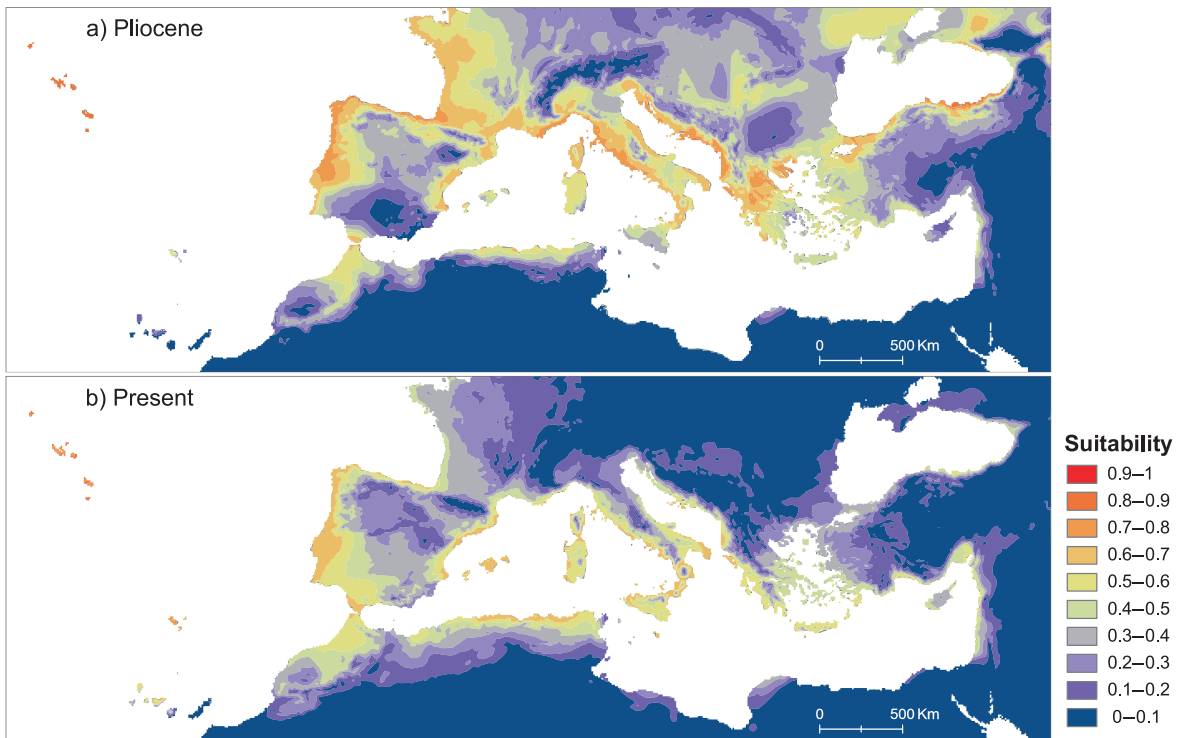


Figure 4 Maps of the predicted environmental suitability for *Laurus*, according to the model fitted to Pliocene fossil locations and climate, for (a) mid-Pliocene and (b) current conditions.

present for most coastal environments where current populations occur, but increased in nearby inner regions, favoured by warmer temperatures. As a result, projected climate change may promote an upward altitudinal migration concomitant with the northward extension of current geographical range.

DISCUSSION

Ecological niche models have proved successful for predicting plant distribution in a diverse array of regions and climatic zones around the world (e.g. Huntley *et al.*, 1995). In the present paper, we successfully predicted the distribution of *Laurus* with a simple bioclimatic model, based on mean temperature of the coldest and warmest months and the annual mean of the AET/PET. The former variables capture the role of extreme – particularly cold – temperature events that may constrain plant physiology and performance (Woodward, 1987; Prentice *et al.*, 1992, Morin *et al.*, 2007). The latter variable estimates the water deficiency or drought stress experienced by the plants as evaporative demand that cannot be satisfied due to limited water supply (Stephenson, 1998). Consistently with most Lauraceae species, which mainly inhabit tropical regions, *Laurus* showed a marked preference for warm climates with low seasonality and reduced water deficit. Furthermore, these climatic requirements have remained virtually unchanged for the last 3 Myr, as seen in the close match between climatic response curves for the Pliocene and the present (Fig. 2). Although some adaptive changes cannot be discarded, the differences observed between fitted responses might in fact be due to sampling artefacts, given the limited availability of fossil records.

Evidence for strong niche conservatism has been reported for a number of plant groups (Prinzing *et al.*, 2001; Svenning, 2003; Wiens & Graham, 2005; Martínez-Meyer & Peterson, 2006), but rarely has it been documented at the intraspecific level through different geological periods. Niche conservatism constitutes an important requirement of successful projections of species distribution over time (Pearman *et al.*, 2008a), thereby supporting the reliability of the reconstruction of past *Laurus* ranges presented here.

Evidence of the role played by climate in *Laurus* ecology and distribution

The importance of warm and moist climates for the Tethyan Tertiary flora, including *Laurus*, has long been recognized (Giacobbe, 1939; Axelrod, 1975). Experimental studies in both *L. azorica* and *L. nobilis* have reported adult leaf damage after brief exposure to temperatures of between -6 and -10 °C (Larcher, 2000; González-Rodríguez *et al.*, 2005). Likewise, frost and desiccation reduce the viability of their recalcitrant seeds (Takos, 2001), thus preventing *Laurus* species from establishing in areas with recurrent cold winters or dry climates. Indeed, cold spells have been responsible for mass mortalities in northern populations (Giacobbe, 1939). Moreover, water stress accounts for limited regeneration and reduced adult growth in Mediterranean populations (Rodríguez-Sánchez *et al.*, unpublished data). In short, water deficit is probably the main climatic factor constraining the southern range limits of *Laurus*, while cold temperatures may limit its range expansion towards northern

latitudes, continental regions of central and eastern Europe and higher elevations.

Some authors have argued that factors other than climate might influence range limits, such as biotic interactions or dispersal limitation (e.g. Hampe, 2004; Svenning & Skov, 2004). Notwithstanding this, water availability and low temperatures have been found to predict reasonably well the range limits of many Northern Hemisphere plants (e.g. Huntley *et al.*, 1995; Thuiller *et al.*, 2005; Morin *et al.*, 2007). Furthermore, several ecological characteristics of *Laurus*, such as its shade tolerance and its interaction with generalist mutualists and herbivores, suggest a limited role of biotic interactions in regulating its geographical range (Soberón & Peterson, 2005). Dispersal limitation also seems unlikely at this scale as *Laurus* is an ancient species with a widespread former distribution. Indeed, no suitable regions are currently devoid of laurel populations. In other words, *Laurus*' range filling (the ratio of realized versus potential range; Svenning & Skov, 2004) appears to be high, supporting the role of climate rather than dispersal limitation at the geographical and time scales considered here. Moreover, other factors not accounted for in our bioclimatic model, such as varying CO₂ concentrations, may influence plant–climate relationships over extended time periods. However, the long-term effects of different CO₂ concentrations on plant performance are just starting to be understood (Körner, 2006).

Climate changes and *Laurus* range dynamics over time

Former *Laurus* range dynamics appear to be severely constrained by the marked decrease in climatic suitability of Eurasia and North Africa since the Pliocene. Under changing climates, *Laurus* niche conservatism would have forced strongly predictable range changes. In fact, current *Laurus* distribution could be reasonably well predicted by means of simple climatic characterization of its Pliocene occurrences.

Our results show that although the demise of *Laurus*, together with other broadleaved evergreen thermophilous species, probably started before the end of the Miocene (Mai, 1989), environmental conditions during the middle Pliocene still allowed its persistence in large portions of central and eastern Europe. However, Pleistocene glaciations reduced suitable climatic zones to narrow coastal strips in the Mediterranean Basin and probably caused the definitive extinction of the most thermo-hygrophilous Tethyan–Madrean taxa in Europe (Svenning, 2003). The locations of glacial refugia predicted by our model are supported by Pleistocene fossil records and coincide with the known major refugia of many European thermophilous trees (Bennett *et al.*, 1991; Finlayson & Carrión, 2007): the eastern Mediterranean and Aegean regions, southern Italy, the Iberian Peninsula and North Africa. The Macaronesian archipelagos appear to be little affected by Plio–Pleistocene climate changes, thereby probably acting as long-term refugia for *Laurus*, although higher-resolution climate data are required for improved predictions in this region.

Throughout the Pleistocene, *Laurus* appears to have undergone recurrent cycles of range dynamics, with widespread regional-scale extinctions followed by partial recolonization

during suitable interglacial periods. It seems likely that the glacial refugia of *Laurus* were strongly reduced in area and became well isolated, exacerbating the risks of stochastic extinction and decreasing adaptability to new conditions (Hampe & Petit, 2005; Willis *et al.*, 2007). In fact, genetic data suggest that Macaronesian and western Mediterranean populations have been completely isolated from eastern Mediterranean populations throughout most of the Pleistocene (Arroyo-García *et al.*, 2001; Rodríguez-Sánchez *et al.*, unpublished data).

Towards a better understanding of the demise of the Tethyan flora

Under large climatic changes, plants have two mutually non-exclusive alternatives to extinction: migration to suitable regions or adaptation to the novel climatic features (e.g. Davis & Shaw, 2001). In contrast to Asia and North America, available refuges for the Madrean–Tethyan flora in Europe seem to have been narrowly distributed and highly isolated, thus exacerbating the extinction of most species of this biome (Huntley, 1993). Furthermore, the long generation cycles and limited sexual reproduction of most relict trees reduce their adaptive potential (Davis *et al.*, 2005; Jump & Peñuelas, 2005).

What specific features enabled *Laurus* to survive in Europe while all other Lauraceae became extinct? Modern fast-paced global change underpins the relevance of this biogeographical question. *Laurus azorica* seems to be less sensitive to low temperatures and to have lower moisture requirements than other Lauraceae species of the Canary Islands laurel forest (Santos, 1990; Fernández-Palacios, 1992; González-Rodríguez *et al.*, 2005). Moreover, it seems that *Laurus* is capable of recovering easily from drought-induced xylem cavitation (Salleo *et al.*, 2004). Hence, it seems likely that *Laurus* (contrary to many other Tethyan taxa) survived the climatic fluctuations that have been occurring since the Pliocene due to its relatively greater resistance to climatic stress. This conclusion receives further support from Svenning (2003), who showed that the extinction of temperate European trees at the Plio–Pleistocene boundary was a largely deterministic process, surviving taxa being more tolerant to drought and low temperatures than extinct species.

Perspectives for the future

Range changes predicted for *Laurus* in the near future coincide with those already forecast for most European plant species (Thuiller *et al.*, 2005). As low temperatures cease to be a limiting factor, more suitable habitats will become available towards north-eastern locations and at higher elevations (see Sperling *et al.*, 2004 for detailed predictions for the Canary Islands). Indeed, range expansions of thermophilous species are already being observed in montane areas of southern and central Europe (Walther, 2003), and northern *Laurus* populations might be experiencing a similar process (eventually helped by the species' widespread use as an ornamental plant). In contrast, *Laurus* populations at the southern limit of the species' current range will experience increasingly adverse climatic conditions due to

higher water stress. In fact, reproductive failures in Moroccan and southern Spanish populations seem to be widespread during dry years (Rodríguez-Sánchez *et al.*, unpublished data). If increased water deficit reduces fecundity and thus sexual regeneration, the potential for adaptation and selection of genotypes more resistant to novel climates would be further compromised (Jump & Peñuelas, 2005). In contrast to past periods, the pace of current climatic change could be too fast to enable tree adaptation (Davis *et al.*, 2005; Jump & Peñuelas, 2005). Impaired fecundity also reduces the potential of marginal *Laurus* populations to track climate change by means of migration. However, given that these populations usually occur in mountain regions and could track suitable climatic conditions by means of relatively minor altitudinal shifts, such constraints might be of relatively minor importance. In fact, such altitudinal shifts in response to past climate changes have probably been a major factor enabling *Laurus* to withstand historical climate changes (cf. Tzedakis, 1993). Furthermore, some life-history features of *Laurus* (i.e. long lifespan and a good sprouting ability), though adverse to processes of evolutionary adaptation, might further promote the resilience of southern marginal populations to adverse climatic conditions (Rodríguez-Sánchez *et al.*, in press).

Conservation of these remnant populations is of great relevance as they share a long history and usually harbour a disproportionately large fraction of the species' genetic diversity (Hampe & Petit, 2005; Rodríguez-Sánchez *et al.*, unpublished data). Given that these populations are living close to the Mediterranean-desert interface, an area of extreme climatic sensitivity (IPCC, 2007), robust monitoring of population dynamics would actually provide much needed insight into the effects of global changes at species range limits and, ultimately, into the implementation of appropriate conservation planning.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of source references for *Laurus* distribution data.

Appendix S2 Maps of climatic variables for each time stage.

Appendix S3 Map of relative suitability changes for the end of the 21st century.

This material is available as part of the online article from:

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