Quercus suber range dynamics by ecological niche modelling: from the Last Interglacial to present time

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A R T I C L E I N F O

A B S T R A C T

Ecological Niche Modelling (ENM) is widely used to depict species potential occurrence according to environmental variables under different climatic scenarios. We tested the ENM approach to infer past range dynamics of cork oak, a keystone species of the Mediterranean Biome, from 130 ka to the present time. Hindcasting implications would deal with a better species risk assessment and conservation management for the future.

We modelled present and past occurrence of cork oak using seven ENM algorithms, starting from 63,733 spatially unique presence points at 30 arc-second resolution. Fourteen environmental variables were used and four time slices were considered (Last Interglacial, Last Glacial Maximum, mid-Holocene and present time). A threshold-independent evaluation of the goodness-of-fit of the models was evaluated by means of ROC curve and fossil or historical evidences were used to validate the results.

Four weighted average maps depicted the dynamics of area suitability for cork oak in the last 130 ka. The derived species autoecology allowed its long-term occurrence in the Mediterranean without striking range reduction or shifting. Fossil and historical post-processing validation support the modelled past spatial extension and a neglected species presence at Levantine until the recent time.

Despite the severe climatic oscillation since the Last Glacial Maximum, cork oak potential distribution area experienced limited range changes, confirming its strong link with the Mediterranean Basin. The ecological amplitude of Quercus suber could be therefore adopted as a reference to trace the Mediterranean bioclimate area. A better knowledge of the past events of Mediterranean vegetation, a wider range of study species and environmental determinants are essential to inform us about its current state, its sensitivity to human impact and the potential responses to future changes.

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1. Introduction

The factors shaping the distribution patterns of living organisms on Earth are the key issues of a recent multidisciplinary perspective that includes ecology, ecophysiology, population biology, biogeography, evolutionary studies, genetics, phylogeography, and history as well (Novicic et al., 2012). The main challenge is to understand how species interact with biotic and abiotic factors, and react to changes in the ecosystem where they live (González-Salazar et al., 2013). This is worthy of interest especially for the over implications of climate change on biodiversity under future scenarios (Lepetz et al., 2009).

It is widely accepted that the present geographic distribution of a species is the result of environmental driving forces which acted in the Quaternary period, i.e. the last 2.6 Ma (Hampe and Jump, 2011), and cyclically produced range contraction, especially of warm-adapted taxa, during glaciations and expansion in the warm-interglacial periods (Hewitt, 2003; Stewart et al., 2010; Beatty and Provan, 2013), together with human influence as a landscape modeller especially in species with commercial relevance (Valbuena-Carabaña et al., 2010). Such range fluctuations mostly reflect the behaviour of a species to track its favourite conditions by shifting the geographic range (niche conservatism), or to respond to environmental changes by adjusting the niche through an adaptive process (niche evolution). Stability of realized niche, in particular, played a key role in recent biogeographic and ecological modelling studies to forecast distribution under several climate change scenarios in tree species, which have dominated terrestrial ecosystems for over 370 Ma (Ruiz-Labourdette et al., 2013).

Palaeoecology, palynology, macrofossil analyses and phylogeography pointed out migrational lags or plant community shifting in the Northern Hemisphere, supporting distribution prediction modelling of many taxa from the Last Glacial Maximum (LGM ~ 21 ka BP) to recent times (Harrison and Sanchez Goñi, 2010; Normand et al., 2011). In Europe, the occurrence of southern refugial areas, mainly located in the Iberian, Italian and Balkan peninsulas, was confirmed. Here, a wide variety of species were restricted at the LGM and hereafter dispersed in various directions, although evidences of northerly refugia beyond these peninsulas have been recently provided (Bhagwat and Willis, 2008; Petit et al., 2008; Svenning et al., 2008; Rull, 2009; Keppel et al., 2012; Tzedakis et al., 2013).

It is therefore widely acknowledged that southern Europe, and especially the Mediterranean Basin, played an important role as main refugial areas for almost the whole European flora; today it still hosts such a considerable richness of plant lineages to be recognised as a prominent biodiversity hotspot of global importance (Médail and Diadema, 2009; CEPF, 2010). However, the ongoing rapid and wide-ranging climate change around the Mediterranean is threatening such a heritage, and forecasting large-scale species distribution is becoming a crucial component to face future scenarios. In view of this, the evolutionary processes and the ecological behaviour of plant species and communities will be fundamental topics, to be possibly explored by investigating species distribution to different periods in the past. Presently, novel multivariate techniques such as climate envelope models (CEMs), also known as ecological niche modelling (ENM), have promising development as an approach to estimate niche changes by exploring the climatic conditions that allow a species to persist through time (Martinez-Meyer and Peterson, 2006; Nogues-Bravo, 2009).

The Mediterranean flora has been the recent subject of many investigations focused on hindcasting and forecasting approaches, and it is still increasing rapidly (e.g. Garzon et al., 2007; Pearman et al., 2008; Calleja et al., 2009; Beatty and Provan, 2013).

Among several study cases, attention has been dedicated to cork oak (Quercus suber L., Fagaceae), a Mediterranean palaeo-endemic, sclerophyllous tree growing along the Atlantic and Mediterranean coastlines of west European and North African countries, with scattered enclaves in Southeastern Italy and Croatia (Simeone et al., 2009).

Studies on present cork oak distribution modelling have been carried out at local scale with high resolution to predict suitable areas for reforestation or conservation concerns (Vogiatzakis and Careddu, 2003; Hidalgo et al., 2008; Vessella and Schirone, 2013). On the other hand, many predictions at wider range used a species distribution with a reduced sample size together with environmental data at a coarse resolution, thus generally leading to an overestimation of the habitat suitability (Song et al., 2013).

These works pointed out the substantial need to join a fine-scale species distribution and the investigation at full-range level. In addition, the hindcasting of climate envelope models to past distribution of cork oak could lead to a more reliable understanding of the species ecological behaviour, at least in terms of response to climatic variables. Soil nutritional factors, dispersal capacity, species competition or regeneration performance would be very informative but hard to implement in a spatial analysis mainly due to lack of data (Pearson and Dawson, 2003).

This study makes a tentative approach to perform a niche modelling of Q. suber on its whole range and through time, using a detailed stand distribution and the most popular algorithms for CEMs. Four temporal frameworks have been considered: Last Interglacial (LIG ~ 130 ka BP), Last Glacial Maximum (LGM ~ 21 ka BP), mid-Holocene (~6 ka BP) and present time. The

final goals are (i) to depict the most probable species range dynamics by means of thermo-pluviometric variables through the latest major climatic transitions, (ii) to contribute to increasing our knowledge in Mediterranean refugial areas patterning, (iii) to test the applicability of niche modelling as a complementary tool for future conservation/restoration strategies of Mediterranean forest habitats.

2. Material and methods

2.1. Data collection

The most updated national forest inventories and databases were used to obtain a detailed cork oak distribution, namely: SuberItalia National Project (Italy, data 2010), Inventaire Forestier National (France, http://inventaire-forestier.ign.fr, data 2012), Mapa Forestal de España 1:200000 (Spain, www.anthos.es, data 2010), Inventario Florestal Nacional (Portugal, www.icnf.pt, data 2005), Inventaire Forestier National (Morocco, www.eauxforests.gov.ma, data 2005), EUFORGEN (Algeria, courtesy of Prof. Fazia Krouchi and Dr Michele Bozzano, data 2009), Institut National de Recherche en Génie Rural Eaux et Forêts (Tunisia, www.iresa.agrinet.tn, and www.euforgen.org, data 2009). For North African countries, data were refined using AVHRR satellite images of the University of Maryland Department of Geography, Global Land Cover Classification (http://glcf.umd.edu/; Hansen et al., 2000). Overall 109,019 points represent the actual distribution of cork oak. Since the accuracy of the prediction modelling is constrained by the quality of occurrence data and by the resolution of environmental data sets, multiple points falling within a cell were considered as a single presence point in order to avoid pseudo-replications and to lessen the effect of variation in sampling effort. 63,733 spatially unique points were retrieved under a resolution of 30 arc-seconds according to the requirements of the ENM adopted methods.

2.2. Past and present environmental layers

The climatic niche of Q. suber was modelled from the current species distribution and the predictive data selected as main determinants for the species range. Ten climatic raster data were chosen from WorldClim 1.4 at 30 arc-seconds resolution to represent the actual climatic envelope for cork oak (Hijmans et al., 2005).

Elevation was achieved from ASTER Global Digital Elevation Model (http://gdem.ersdac.jspacesystems.or.jp) and re-scaled to 30 arc-seconds resolution to match with WorldClim data; aspect and slope were handled from elevation using ArcGis 9.3.1. The Emberger Index was additionally included to indirectly summarize evapotranspiration and draughtiness in a single parameter, and preferred to other similar indexes (e.g. Mitrakos, or Rivas-Martinez) because easily achievable from past and present WorldClim data sources. A list of variables employed is summarized in Table 1.

The palaeoclimate simulations of the bioclimatic layers were achieved from a coupled, global general circulation model: the Community Climate System Model 3 (CCSM3; last access December 2013) (Otto-Bliesner et al., 2006; Braconnot et al., 2007).

Concerning LIG and LGM reconstructions, the bioclimatic rasters based on Palaeoclimate Modelling Intercomparison Project 3 (PMIP3; http://pmip3.lsce.ipsl.fr/) were achieved directly from WorldClim; coastlines and elevations during LGM were retrieved from ETOPO1 Global Relief Model (www.ngdc.noaa.gov/). For the mid-Holocene climatic pattern, temperature and precipitation raw monthly data were obtained from PMIP3 at a 2.5 arc-minutes spatial resolution and interpolated to surfaces using thin-plane smoothing splines with the tension option. Anomaly maps were

Table 1
List of environmental layers used in this study. All variables are raster data at 30 arc-second resolution.

Variable type	Source
Annual Mean Temperature (°C)	WorldClim
Mean Diurnal Range (°C)	WorldClim
Temperature Seasonality (SD × 100) (°C)	WorldClim
Max Temperature of Warmest Month (°C)	WorldClim
Min Temperature of Coldest Month (°C)	WorldClim
Temperature Annual Range (°C)	WorldClim
Annual Precipitation (mm)	WorldClim
Precipitation of Wettest Month (mm)	WorldClim
Precipitation of Driest Month (mm)	WorldClim
Precipitation Seasonality (Coeff. of Variation)	WorldClim
Digital Elevation Model (m)	ASTER GDEM
Slope (degrees)	Derived from DEM
Aspect (degrees)	Derived from DEM
Emberger Q Index	This work

retrieved calculating the differences between mid-Holocene climatic surfaces and pre-industrial conditions also obtained from PMIP3, then added to WorldClim current climate data to get a downscaled 30 arc-seconds rasters as the other temporal frameworks considered in this work (Mitasova and Mitas, 1993).

2.3. Ecological niche modelling

Cork oak potential distribution was modelled starting from the spatially unique points dataset (Fig. 1f) and the environmental layers as set of georeferenced rasters. The software openModeller 1.1 was employed to run within the same framework the most used algorithms set up based on the correlative approach (Muñoz et al., 2011). Seven algorithms were chosen to calculate the species present potential distribution starting from real occurrence: Bioclim, Climate Space Model (CSM), Envelope Score, Environmental Distance, Genetic Algorithm for Rule-set Prediction (GARP), Maximum Entropy (MaxEnt) and Support Vector Machine (SVM) (Muñoz et al., 2011 and reference therein).
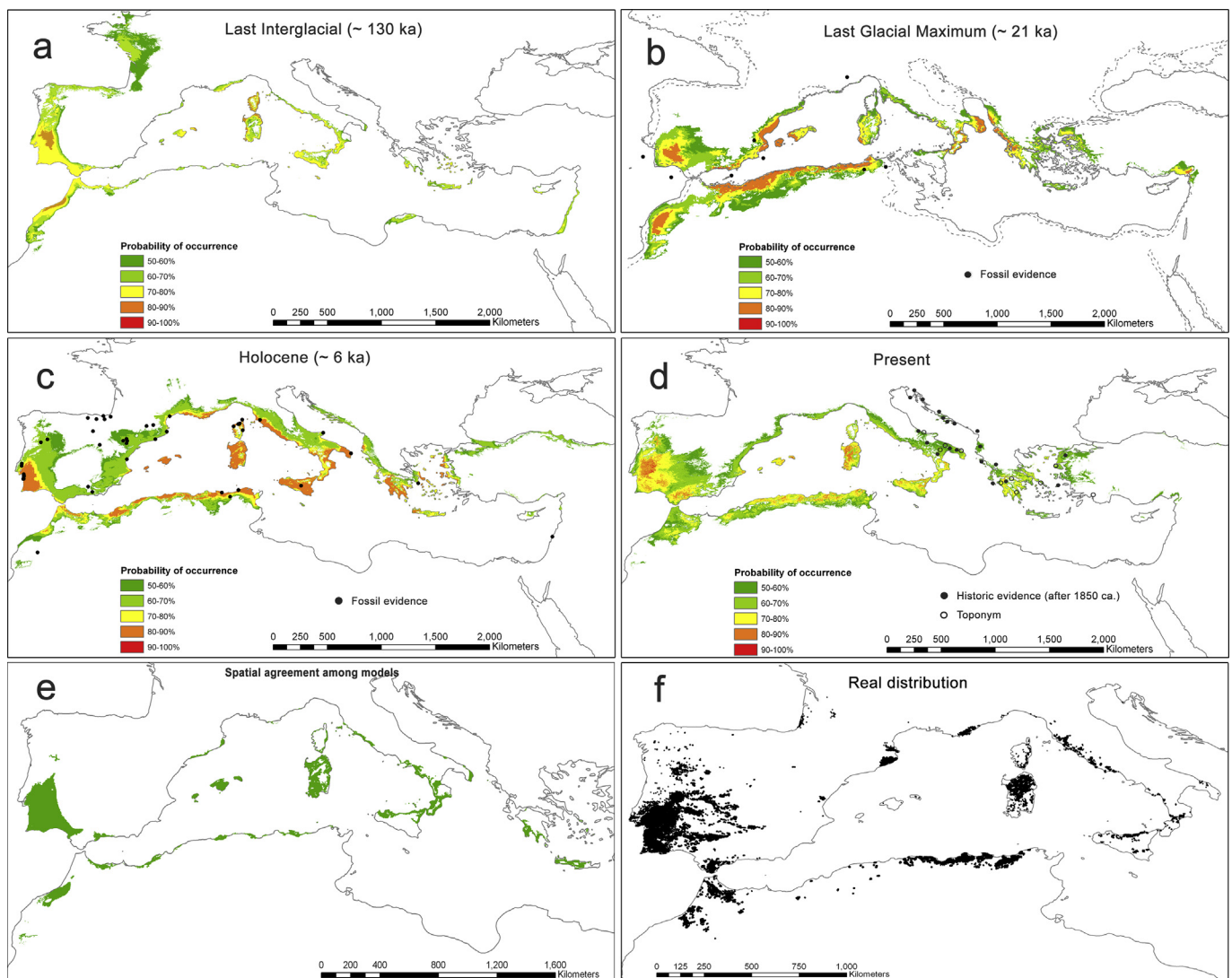

Fig. 1. Potential distribution of *Quercus suber* during the Last Interglacial (**a**), Last Glacial Maximum (**b**), Holocene (**c**), present time (**d**) spatial agreement (**e**), i.e. areas identically predicted through time, in estimates of cork oak potential range for the temporal framework considered in this study. Real species distribution made by spatially unique points dataset is also given (**f**). Black circles show fossil evidences (pollen, charcoal or wood) or historic references (only for East Mediterranean), dated approximately to the considered time windows, and used to evaluate models performance. Open circles on the present prediction map indicate toponyms of Latin or Greek origin.

Table 2
Accuracy (1 minus error rate on testing data), AUC, sensitivity and omission error of internal and external tests for each algorithm used to predict present potential distribution of cork oak. Short vertical bars in each column separate internal and external test values respectively.

Algorithm	Accuracy	AUC	Sensitivity	Commission error
Bioclim	100 | 99.94	0.96 | 0.96	1 | 0.99	4.47×10^{-4} | 5.74×10^{-4}
CSM	59.58 | 54.74	0.94 | 0.93	0.59 | 0.55	0.02 | 0.03
Envelope Score	100 | 100	0.96 | 0.96	1 | 1	0 | 0
Environmental Distance	100 | 99.95	0.99 | 0.99	1 | 0.99	0 | 6.68×10^{-6}
GARP	94.8 | 93.9	0.98 | 0.98	0.95 | 0.94	5.65×10^{-3} |5.81×10^{-3}
MaxEnt	83.5 | 82.7	0.83 | 0.84	0.77 | 0.78	4.55×10^{-6} | 6.83×10^{-6}
SVM	99.4 | 99.2	0.99 | 0.99	0.99 | 0.99	1.20×10^{-5} | 1.67×10^{-5}

The models returned potential distributions as 30-seconds resolution rasters with suitability value for each grid cell, later reclassified in ArcGis using ten classes.

For a threshold-independent evaluation of the goodness-of-fit of the models, the receiver operating characteristic curve (ROC curve) approach was used by calculating the area under the curve (AUC). Models quality was further evaluated by fossils and pollen records retrieved from literature, and toward a bibliographic investigation of two-centuries of botanical surveys especially in the central-east Mediterranean.

Since every algorithm implies a specific statistical approach and may lead to a peculiar prediction map, at least in terms of suitability value or geographical extent, the level of agreement among the models was estimated by calculating the weighted average of the raster value per grid cell, taking into account the AUC value of each model. This computation produced a "consensus map" with cell values ranging from 0 to 100%. To focus on the higher probability classes, we decided to display and analyse cells with values higher than 50%. This output represented the source for calculating the variables ranges at the present climate conditions, and for hindcasting species niche to past temporal frameworks.

Finally, the spatial agreement through time was assessed by overlapping the prediction maps; the result is expected to represent the geographical location of suitable areas for the persistence of cork oak from the Last Interglacial to present time.

3. Results

3.1. Models performances and present potential distribution

The performances of the seven tested algorithms are fairly high showing AUC values from 0.84 (MaxEnt) to 0.99 (SVM and

Environmental Distance). Accuracy shows that the discriminatory power of the models is far from random results (Table 2). Geographical extents of prediction maps differ among models, especially for areas in Central Europe, which are larger in Bioclim, Envelope Score and Environmental Distance outputs. However, a core area located around the Mediterranean coasts can be detected in each computation (see Appendix A). The consensus map points out a present potential distribution of cork oak niche encompassing the Mediterranean, but extending more eastward than the actual occurrence. In particular, suitable areas are detected along the Dalmatian coast, Greece, Crete, Aegean Islands, Cyprus, and Asia Minor with scattered occurrence on the Turkish Black Sea coasts and around the Gulf of Iskenderun (Fig. 1d; Appendix B). On the other side, the restrictions imposed to the consensus map omitted some areas currently occupied by scattered populations, i.e. the Atlantic area of Aquitania and the peninsula of Istria. As a result, 2.2% of the actual points which are spatially unique is excluded, equal to 1426 records in 63,733. Cells with the highest suitability values (more than 80%) are geographically located in southern Portugal, Andalusia, Balearic Islands, Algerian coasts, Sardinia, southern Italy, and Peloponnesus. The spatial extent of the predicted present distribution has a surface of 687,561 km² out of which 45,954 km² currently represent the real species occurrence.

3.2. Cork oak occurrence from Last Interglacial to mid-Holocene

Hindcasting the ecological distribution of cork oak, retrieved from present climatic and topographic variables (Table 3), it was possible to suggest that the potential species occurring surface did not change remarkably through time, at least from the Last Glacial Maximum, while a striking change is pointed out during the Last Interglacial (Fig. 1a−c; Appendix B). The potential ecological suitability for cork oak chronologically occupied a surface of

Table 3
Real and predicted ranges of the environmental layers used in this study within the zones defined as the most suitable for cork oak, i.e. those cells related to the consensus maps with weighted suitability value over 50%. Mean values (bold = highest; underlined = lowest) with standard deviation (in brackets) have been reported for real, present and past climatic scenarios. All values in a row are statistically significant under the Fisher's least Significant Difference tests at α < 0.05 probability level. About aspect, prevalent orientation instead of mean value in degrees is reported. Units are omitted (see Table 1).

| Variable | Min−Max | | Mean values (st. dev.) | | | | |
	Real occurrence	Prediction models	Real	Present	Holocene	LGM	LIG
Annual Mean Temperature	8−19.9	10.9−20.1	**16.0** (1.3)	15.7 (1.6)	15.2 (2)	<u>14.4</u> (2.2)	14.7 (2.4)
Mean Diurnal Range	5.4−15.3	4.9−15.9	9.9 (1.5)	10 (1.9)	9.3 (1.5)	**11.3** (2.4)	<u>9.2</u> (1.4)
Temperature Seasonality	2997−7230	3039−7304	<u>5405</u> (721)	5826 (684)	**6480** (583)	5594 (972)	6419 (758)
Max Temp. Warmest Month	21.9−31.8	23−36.9	30.7 (2.2)	30.8 (2.5)	**31.5** (2.3)	<u>29.5</u> (4.1)	30.6 (3.2)
Min Temp. Coldest Month	−4.2 to 9	−1.5 to 9.9	**5.1** (2)	4.2 (2.1)	3.5 (2.5)	<u>2.3</u> (2.9)	3.4 (2.4)
Temp. Annual Range	15.1−36.2	16.3−35.2	<u>25.5</u> (3.3)	26.7 (3.5)	**28** (2.9)	27.4 (4.9)	27.2 (2.9)
Annual Precipitation	293−1512	309−1430	696 (157)	<u>621</u> (165)	705 (209)	719 (281)	**776** (226)
Prec. Wettest Month	41−264	40−264	107 (32)	<u>94</u> (31)	106 (37)	112 (45)	**122** (36)
Prec. Driest Month	0−69	0−47	7 (5)	8 (7)	**17** (12)	<u>6</u> (5)	16 (13)
Prec. Seasonality	13−88	18−88	**58** (11)	54 (13)	<u>48</u> (16)	57 (13)	53 (17)
Elevation	0−1984	−24 to 1470	332 (250)	387 (281)	391 (308)	**553** (369)	<u>236</u> (235)
Slope	0−22.4	0−22.8	2.8 (1.1)	2.7 (2.6)	**3** (2.8)	<u>1.6</u> (1.3)	2.7 (2.1)
Aspect	0−360	0−360	S	S	N/S	S	S
Emberger Q Index	39−293	38−198	96 (25)	<u>82</u> (27)	95 (31)	92 (36)	**100** (33)

413,756 km² during the LIG, where 788,678 km² in the LGM and 757,955 km² in the mid-Holocene. It is worth noting that, 179,646 km² (23% ca) of the species potential range during the LGM persisted in areas presently submerged. On the other hand, the percentage of overlapped surface through time gives evidence of a species geographical stability ranging from 41% (LIG to LGM) to 66% (mid-Holocene to Present). The predicted potential surface constantly occupied by cork oak from LIG to present time results in 122,334 km², and spatially splits into six major areas (SW-Iberia, W-Morocco, Balearic Islands, Sardinia, S-Tyrrhenian Italy, S-Greece and Crete) plus several micro-sites (e.g. N-African coast, Catalonia, Apulia, Corse, Central-Tyrrhenian coast) (Table 4 and Fig. 1e).

3.3. Climatic and topographic statements of present and past distributions

According to the range of suitability for each environmental layer, the cork oak potential area deals with different mean values through time (Table 3). Climatic conditions were more severe during the LGM as expected, so the species would have mainly occupied colder areas. LGM prediction model also resulted in having the highest number of minimum or maximum mean values among the study variables.

On the other hand, mid-Holocene and LIG seem to have been more favourable periods, in which cork oak might have occurred on areas characterized by similar mean values of temperature seasonality, minimum temperature of the coldest month and precipitation of the driest month.

Besides the mean values, frequency distributions of the environmental layers ranges, related to the zones mainly suitable for the species, point out a general constriction of the real distribution around narrow intervals, as shown by high peaks of the smoothing curves in almost all the graphs, especially with respect to LGM (Fig. 2). A detailed list of concerns can be inferred about the climatic and topographic features of the suitable areas for cork oak, by means of comparison among the frequency curves.

Regarding topographic features, elevation is worthy of mention. Low values characterized LIG, while a more homogeneous distribution is observed in the LGM (Fig. 2a). Thermal regimes also show notable variations. For example, the lowest mean annual temperature and diurnal range during the LGM (Fig. 2d, e), right-skewed curves of seasonality at LIG and mid-Holocene (Fig. 2f), different modalities of maximum temperature (Fig. 2g), symmetry of minimum temperature (especially between the present occurrence and LGM scenario; Fig. 2h) and temperature annual range (real presence versus mid-Holocene, LGM and LIG; Fig. 2i).

Concerning the precipitation, some discordances are pointed out among models and the real cork oak occurrence. However, it must be generally considered that most of the area presently occupied by the species is characterized by narrow ranges, for instance, of annual precipitation or seasonality; this pattern is

confirmed by smaller standard deviations if compared with the models' values. For example, real mean annual precipitation (Fig. 2j) resulted to be lower than predicted models, present prediction excepted, similarly to the precipitation of the wettest month with the present potential to be the driest scenario (Fig. 2k). Noteworthy are the precipitation values of the driest month observed during LGM, which could perhaps be ascribed to the exclusion of solid precipitation from the variable calculation (Fig. 2l).

The precipitation seasonality (Fig. 2m) seems to state as real occurrence and LGM would be interested by a more heterogeneous precipitation regime, while mid-Holocene the opposite. The Emberger Index (Fig. 2n) confirms LIG as the wettest period, present prediction as the driest, and mid-Holocene with LGM very close to real conditions.

3.4. Validation of model accuracies

Predictions provided by the intersection of the seven algorithms in each time slice underwent a further test of consistency. Fossil data (pollen and charcoal) were collected from literature and assigned to a study period according to their estimated age. These data were limited and mostly restricted to the Iberian peninsula, since the species co-occurs in the rest of the Mediterranean Basin with closely related oaks having undistinguishable pollen structure (Magri et al., 2007). Fifty-three records dated from 41 ka to 2.5 ka and described as "*Q. suber*", "*Q. suber type*", "*Q. suber/Quercus cerris group*" or "*Q. cerris type*" were considered and overlapped to the resulting models (Fig. 1b, c and Appendix C). Nowadays, no fossils strictly related to cork oak date back to Last Interglacial, thus we have no evidences to validate our model. Eight out of 53 records dated to Last Ice Age, and they are consistent with predictions except in the case of the inland pollen found in the south-western Alps. Four records were found in front of the Iberian coasts, but closely connected with the suitable surface of the model and near to the LGM coastline reconstruction, so to be included as validating records as well. The remaining 45 proofs date back to the end of the Last Glacial period to ca 2500 BP: thirty are inside the mid-Holocene predicted area, six are outside but within a radius of 30 km, and nine are excluded from the model, but mainly located on the eastern Cantabrian mountain and in front of the Gulf of Biscay.

Concerning the present model validation, we focused on the last 150 years of cork oak evidences, and its presumed hybrids, from the Adriatic coast to the Eastern Mediterranean, in addition to Greek and Latin toponyms from the same area (Fig. 1d and Appendix D). Fifteen observations directly refer to *Q. suber*, five of them outside the present prediction model; 22 are the toponyms, 2 of them did not validate the model (located in Lycia, Turkey). Finally, the evidences of presumed cork oak hybrids pointed out 51 additional records, 31 of them related to localities outside the suitable area of the model, mainly grouped along the northern Dalmatian coast and Istria.

4. Conclusions

Species distributions can be hindcasted with high accuracy, even after notable climate change events, but focussing on a temporal framework for which robust data and validation proofs are available. The investigation of *Q. suber* climatic niche provides new insights on its suitability area changes during the last 130 ka.

On a global scale, the species ecological amplitude always encompassed those areas characterized by the Mediterranean climate *sensu* Rivas-Martínez et al. (2004), especially after the LIG-LGM transition, when a severe species range retreat was observed

Table 4
The first column shows cork oak total predicted surfaces related to the displayed suitability classes of consensus maps in Fig. 1. The second column indicates the overlapped surface in km² and percentage between two consecutive time periods.

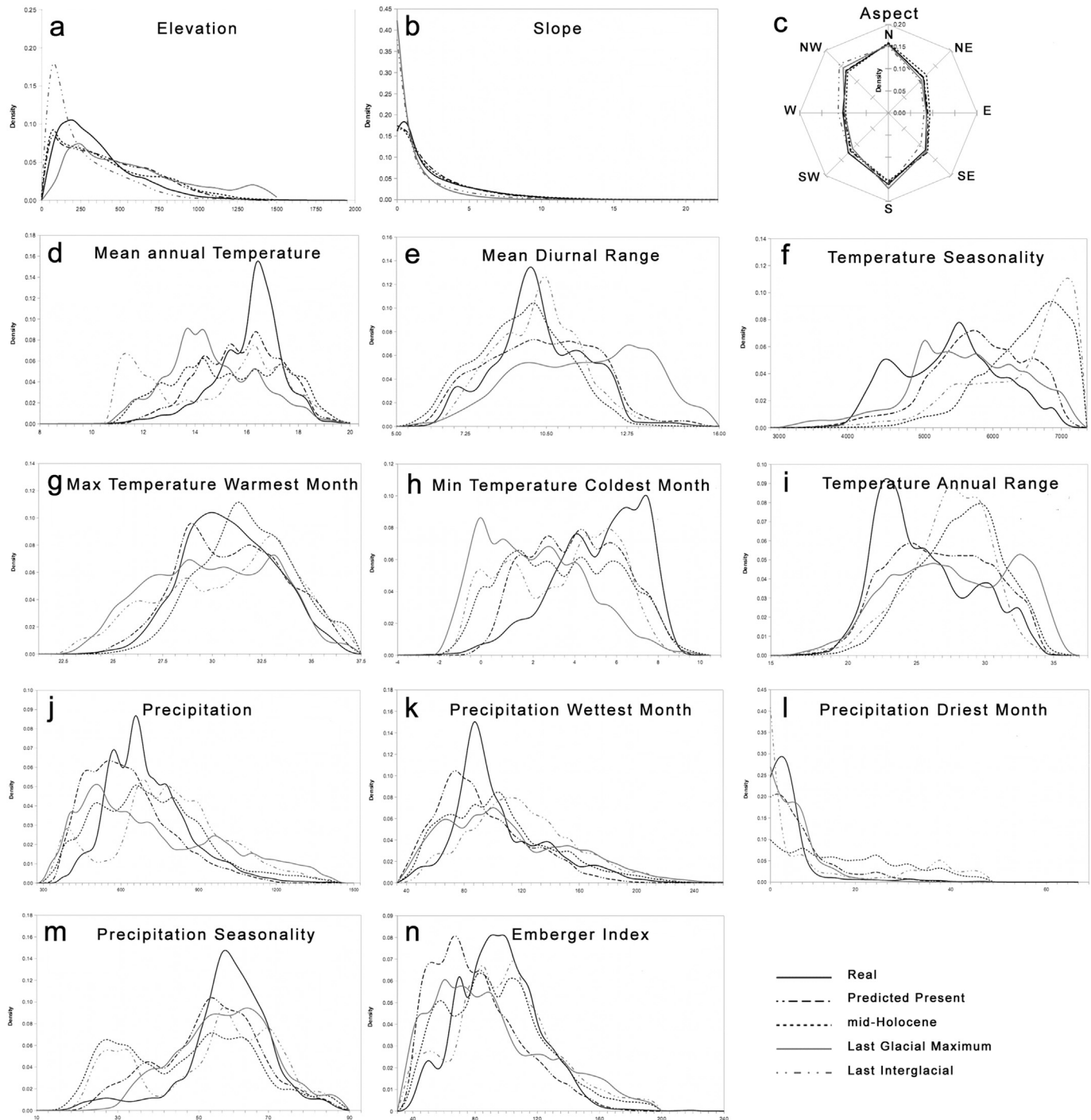|	Area (km²)	Spatial agreement (km²)	
LIG	413,756	LIG	
		↓	171,159 (41%)
LGM	788,678	LGM	
		↓	340,822 (43%)
Holocene	757,955	Holocene	
		↓	501,238 (66%)
Present	687,561	Present	
		Overall agreement	**122,334**

Fig. 2. Frequency curves showing the range of suitability of cork oak for the environmental variables used in this study related to the real occurrence and to the four prediction models. Different line patterns are used for each scenario; y-axis indicates the relative frequency of the variable values, thus the total area under the curve represents the probability density normalized to 1. Variables units are reported in Table 1.

in the north-western side (W-France and N-Spain). This is in line with the dynamics already described for other taxa and despite the existence of northerly areas acting as cryptic refugia for temperate and boreal species (Hampe et al., 2013). In fact, the ongoing colder climate produced a general contraction and shifting of species occurrence in Central and Northern Europe to lower-latitudes also on a local scale (Hughes and Woodward, 2008; Médail and Diadema, 2009; Normand et al., 2011). The resulted potential cork oak suitability area during LGM was constrained around the Mediterranean coasts by a colder and drought climate; this is consistent with the distribution of Mediterranean species of intermediate range size, which were restricted to the Iberian peninsula, Italy and the western Balkan coasts (Svenning and Skov, 2007; Magri, 2010). We found evidences of local expansions in those areas with respect to the LIG distribution, for example in the eastern and southern Iberian coasts, in North Africa, and with less magnitude in Italy. These results are reinforced by palaeoecological data (Ben Tiba and

Reille, 1982; Carrión et al., 2000 and reference therein) and seem to match with the climatic reconstructions and vegetation types, which included Mediterranean and steppe-like associations with oak woodland elements including *Q. suber* (e.g. Kuechler et al., 2013). At the same time our findings exclude areas like the Baetic Range and the Rif, supposed to host mostly temperate species belonging to genus Pinus and Abies (López-Tirado and Hidalgo, 2014). Overall, the predicted suitable surface for cork oak increased until LGM, especially in North Africa and Iberia, mainly benefitting from the favourable conditions of several interstadials which permitted some expansion of the Mediterranean vegetation zone southward (Hooghiemstra et al., 1992); in this view, cork oak might have taken advantage of its successional behaviour to be one of the first tree species to colonize new areas.

Many studies pointed out fluctuations of the vegetation development and composition at decadal-to-centennial time-scales the Pleniglacial to mid-Holocene in the Central-Western Mediterranean Basin (e.g. Desprat et al., 2013), although divergent information and chronological uncertainties still need to be clarified to understand the magnitude of their effects to the biomes shifts (Prentice et al., 2000).

Regrettably, we were able to model the suitable niche for cork oak only at the outer limits of this great climatic disruption phase, i.e. the species range assessment after several instabilities. Among the driving forces leading to a northward shift of a cork oak suitability area, a key role was probably played by the African Humid Period, and the following desiccation of the Sahara (e.g. Kropelin et al., 2008). Nevertheless, the resulted Mediterranean environmental assessment about 6 ka lead to more suitable conditions than the present time, as inferred by the comparison between the modelled surfaces.

In addition, there are intrinsic features affecting species ability to track areas with a suitable climate from the postglacial migration until recent time. Our models point out a theoretical cork oak niche distribution through time, but they are not able to locate exactly the real past species occurrence within those areas. From the results synthesized in Fig. 2, the species ecological plasticity might seem wider than what is presently assessed. This could be partially explained by range restriction and anthropic impacts (e.g. cultivation, seed transfer or local spread) which may have affected the original species genepool and the related adaptiveness to the Mediterranean environment.

However, it might be possible to infer a long-term persistence around the Mediterranean Basin *sensu stricto* characterized by limited latitudinal and more remarkable longitudinal oscillations. The modelled niche mostly overlapped through time, the limited long-distance dispersal of oaks and the consequential importance of accessibility to sites and species resilience, echoes the geographical heterogeneity of the region with the presence of many physical barriers (Austerlitz and Garnier-Géré, 2003; Svenning et al., 2010; Normand et al., 2011; Acácio and Holmgren, 2014). When the present predicted distribution and real occurrence are compared, two areas are missed by the model computation: the temperate areas of the Gulf of Biscay and Istria. These extrazonal occurrences might reinforce the idea of cork oak as a Mediterranean species *sensu stricto*, long-term occurring around the Basin, and we could suggest it as keystone species to state the Mediterranean bioclimatic limits *sensu* Rivas-Martínez et al. (2004).

Worthy of mention is also the location of those areas constantly predicted through time (Fig. 1e), notably their inherent agreement with putative refugia retrieved from phylogeographical models of a large set of Mediterranean tree species and from previous specific studies on cork oak (Lumaret et al., 2005; López de Heredia et al., 2007; Médail and Diadema, 2009).

At the same time, attention should be paid to the Eastern Mediterranean, reconsidering the potential species distribution hub.

The role of Levantine as a suitable area for cork oak through time gives a questionable result in contrast with many previous researches considering the species as the only oak belonging to subgenus *Cerris* always gravitating around Western Mediterranean and there differentiated (Magri et al., 2007). Alternatively, fossil records from oak species of subgenus *Cerris*, notably *Quercus sosnowski* (Palamarev, 1989), together with evidences of past occurrence of cork oak until last century and phylogenetic investigations, already planted a seed of doubt concerning at least its natural presence in the South Eastern Mediterranean (Lumaret et al., 2005; Simeone et al., 2013; Schirone et al., 2015 and references therein).

Theoretically, our results are consistent with Thuiller et al. (2003) and further clues from different research fields, which already pointed out the probability for a cork oak potential occurrence eastward until recent times. We also found predicted areas for cork oak since LIG in Crete and south Peloponnesus, very similar to the two putative refugia defined by Médail and Diadema (2009).

If confirmed, the steady rarefaction of the species might be due to natural factors, namely the climatic events of the last millennia aggravated by a poor competition, especially with respect to *Quercus ilex*, on carbonate and alkaline soils very common in the Eastern Mediterranean, and by a striking long-term anthropic impact which shapes the landscapes from millennia (Böhner et al., 2008; Petroselli et al., 2013).

The species apparently was eroded and relegated westward, but reconstructing a clear framework of the events leading to the present distribution could be still premature, and further evidences need to be gathered. For example, other species with a markedly polar gravitation, e.g. *Pinus pinaster* Aiton at West might be investigated and compared with cork oak.

In this view, ENM approaches might provide statistical quantitative hindcasting of the species, increasing our understanding on vegetation dynamics. Further past climatic reconstructions would enrich even the models results, in order to evaluate the range of projected distributions by means of comparison and estimation of the uncertainties among them. This information could also be useful for knowledge about the potential responses to future changes in climate and/or land use patterns (Collins et al., 2012; Gavin et al., 2014). Soil nutritional factors could improve estimation of the potential geographical range of tree species, in particular of cork oak, toward the exclusion of climatic but not pedological suitable areas (Coudun et al., 2006). Unfortunately, the implementation of such variables in ENMs is related with the data availability along the species range, and researchers often have to deal with this lack of information. In addition, a modelization of distant past pedological features would be very hard to assess.

In fact, the dramatic climatic oscillations of the last 130 ka in Europe produced a wide variety of species extinctions, migrations and range shifts (e.g. Langgut et al., 2011; Aranbarri et al., 2014). Local glacial refugia played a fundamental role in keeping the present vegetation safe; however, our results suggest their function could have been of minor effect for cork oak, as an element of the Mediterranean vegetation having a remarkable ecological amplitude. Overall, Southern European physical heterogeneity always provided a large number of suitable habitats to prevent the extinction of *Q. suber* (and associated species) (Médail and Diadema, 2009). Nevertheless, the Mediterranean landscape and the cork oak stock populations have sensitively changed in the last millennia (Acácio and Holmgren, 2014). Human perturbations and threats such as over-grazing, cork over-exploitation, wrong silvicultural practices, recurrent fires, genepool erosion (due to domestication, reduction of gene flow and natural regeneration),

the growing occurrence of invasive species and exotic plantations, habitat degradation and fragmentation due to agriculture and the increasing growth of human infrastructures, are likely to negatively affect the ability of both the Mediterranean territory and the species itself to cope with climatic change. Urgent strategies of risk assessment and conservation management are therefore required to allow the species (and the whole Mediterranean biome) to extricate their inner plasticity and buffering attitude that permitted them to overcome the dramatic crisis of the past.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2015.04.018.

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