Biological Journal of the Linnean Society, 2018, **123**, 338–347. With 2 figures.

Ecological niche modelling of pedunculate oak (*Quercus robur*) supports the ‘expansion–contraction’ model of Pleistocene biogeography

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Received 4 October 2017; revised 12 November 2017; accepted for publication 13 November 2017

During the Pleistocene glacial periods, the ranges of many temperate species in Europe contracted southwards to refugia near the Mediterranean Basin. This study tested the ‘expansion–contraction’ model by applying the ecological niche modelling approach to one widespread temperate tree species, pedunculate oak, *Quercus robur* L., distributed across Europe and Anatolia. We projected the distribution of *Q. robur* under climatic conditions of the Present, the mid-Holocene [HOL, *c.* 6000 years before present (YBP)], the Last Glacial Maximum (LGM, *c.* 22 000 YBP) and the Last Interglacial (LIG, *c.* 130 000 YBP). *Quercus robur* was at equilibrium with the climate as the model prediction was highly compatible with the its known distribution range under present bioclimatic conditions. The LIG and the HOL predictions gave a much broader distribution range than that during the LGM, suggesting its range contracted towards favourable areas in southern Europe and Anatolia. The results indicate that the glacial refugia hypothesis, based mainly on the ‘expansion–contraction’ model, applies to *Q. robur*, although possible extra-Mediterranean refugia in northern, western and southern France are also identified. This study therefore supports claims that European biogeography is significantly more complex than previously thought.

ADDITIONAL KEYWORDS: Anatolia – climate change – deciduous tree – extra-Mediterranean refugia – glacial refugia – Iberia – Pleistocene glacial periods – species range – Mediterranean Basin

INTRODUCTION

Species distribution patterns are among the most prominent issues in biogeography. More specifically, investigating these patterns for Late Pleistocene glacial and interglacial periods helps us to understand the evolutionary and ecological processes shaping modern-day populations and communities (Hewitt, 1996; Habel, Junker & Schmitt, 2010). Among these periods, the Last Interglacial [LIG; *c.* 130 000 years before the present (YBP)] and the Last Glacial Maximum (LGM; *c.* 22 000 YBP) greatly impacted Northern Hemisphere ecosystems by fragmenting temperate species’ habitats at both small and large scales (for the LIG: Gür, 2013; Wang *et al.*, 2013; Perktaş *et al.*, 2015a; for the LGM: Hewitt, 1996; Vörös *et al.*, 2016), creating interspecific and/or intraspecific genetic variation (Petit *et al.*, 2003), and altering the distribution and abundance of species by changing vegetation–climate relationships (Svenning & Skov, 2004).

Species responded to climate changes in the Pleistocene in various ways due to different geographical structures across the Palearctic region (Taberlet *et al.*, 1998). For example, the distributions of most temperate species shrank during the LGM into more favourable areas, known as glacial refugia, in southern Europe (Bennett, Tzedakis & Willis, 1991; Hewitt, 1996; Bennett & Provan, 2008; Médail & Diadema, 2009) before re-expanding their ranges northwards

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as the climate warmed. Provan & Bennett (2008) term this pattern the 'expansion–contraction' model. The current greater genetic variation found in lower latitudes in species of the Northern Hemisphere temperate zone is therefore a legacy of Pleistocene glacial periods (Hewitt, 2000). Three glacial refugia are widely accepted for temperate species in Europe: the Iberian, Italian and Balkan peninsulas (Hewitt, 1996; Taberlet *et al.*, 1998; Provan & Bennett, 2008). Besides these, the role of Anatolia, another peninsula in the Mediterranean Basin, has recently been acknowledged as a refugium for various taxa (Rokas *et al.*, 2003; Krebs *et al.*, 2004; Perktas, Barrowclough & Groth, 2011; Gür, 2013; Korkmaz *et al.*, 2014; Perktaş *et al.*, 2015a; Perktaş, Gür & Ada, 2015b; Bagnoli *et al.*, 2016). In comparison with other refugia of the Mediterranean Basin, Anatolia has the most diverse geography, being located at the intersection of Europe, the Middle East, Central Asia and Africa (e.g. Gür, 2016). High endemism among plant species in Anatolia (Médail & Quezel, 1999; Şekercioğlu *et al.*, 2011) reflect this geographical location and its unique biogeographical patterns. However, although there is good evidence that deciduous oak taxa persisted in southern Europe, especially in mid-elevation mountain regions during the LGM (Brewer, Cheddadi & Beaulieu, 2002; Petit *et al.*, 2002), Anatolia's biogeographical role as a refugium has not yet been fully determined.

In this study, we tested the expansion–contraction model for one widespread temperate tree species, pedunculate oak, *Quercus robur* L., distributed across Europe and Anatolia. We used the ecological niche modelling approach to predict the distribution of *Q. robur* under the climatic conditions of the Present, the mid-Holocene (HOL, *c.* 6000 YBP), the LGM and the LIG. Because *Q. robur* is a temperate deciduous tree, we hypothesized that its distribution should have expanded during warmer (interglacial) climatic conditions and contracted during cooler (glacial) conditions. We also tested the role of Anatolia as an additional significant temperate plant species LGM refugium for the Palearctic region.

MATERIALS AND METHODS

STUDY SPECIES

Quercus robur is a long-lived deciduous tree species covering a wide altitudinal range from sea level up to 1200 m in Europe, Russia, the Caucasus and the Near East (Fig. 1). The species shows geographical variation, with four subspecies defined mainly based on morphological features (The Plant List, 2013). Seed dispersal mainly occurs by bird predation, especially by the European jay *Garrulus glandarius* (Bossema, 1979). *Quercus robur* forms hybrids with *Q. petraea* (sessile oak) throughout its range, which has enabled *Q. petraea* to invade the current distribution range of *Q. robur* through hybridization using its greater seed dispersal ability (Petit *et al.*, 2004). *Quercus robur* is highly tolerant of different abiotic factors, including various soil and climate types (Bacilieri, Roussel & Ducousso, 1993), although the distribution of its subspecies is limited by climatic factors (Yılmaz & Yılmaz, 2016).

INPUT DATA

In total, 305 104 occurrence records of *Q. robur* from Europe, Russia, the Caucasus and the Near East were collected from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org). Because GBIF has no records from Anatolia, 106 occurrence records from herbarium samples (Hacettepe University Herbarium and Istanbul University Faculty of Forestry Herbarium) and field observations in Anatolia were added to the GBIF data set to fill this gap. Hence, this study considered a total of 305 210 occurrence records. We omitted GBIF records of hybrid forms and possible hybrid samples that we examined in the herbarium and field data. The occurrence records revealed a more intense distribution in Western Europe. To remove duplicates to prevent sampling bias and to reduce spatial autocorrelation, the records were checked by eye and then rarefied at 100-km intervals using SDMtoolbox (Brown, 2014) in ArcGIS version 10.2. This process provided 171 occurrence records for Europe, Russia, the Caucasus and the Near East for ecological niche modelling. Although this reduced geographical aggregation in the occurrence records, it could not correct for the lack of occurrence records in Russia.

Climate data were obtained from the WorldClim database, version 1.4 (Hijmans *et al.*, 2005; http://www.worldclim.org), at a spatial resolution of 2.5′ (~4.63 km at the equator). For past projections, climate data for the HOL, the LGM and the LIG were obtained from the same source (the WorldClim database, version 1.4). Nine different models for the HOL (BCC-CSM1-1, CCSM4, CNRM-CM5, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM, MPI-ESM-P, MRI-CGCM3) and three different models for the LGM (CCSM4, MIROC-ESM, MPI-ESM-P) were considered. The LIG climate data were based on the Community Climate System Model, version 3 (CCSM; Otto-Bliesner *et al.*, 2006). The resolution of the LIG climatic data was 30″, and we resampled these data at a resolution of 2.5′ to make them compatible with the Present, the HOL and the LGM. In contrast to the multiple models of the HOL and the LGM, there was only one model available for the LIG. Therefore, the prediction was weaker for the LIG than for the HOL and LGM.

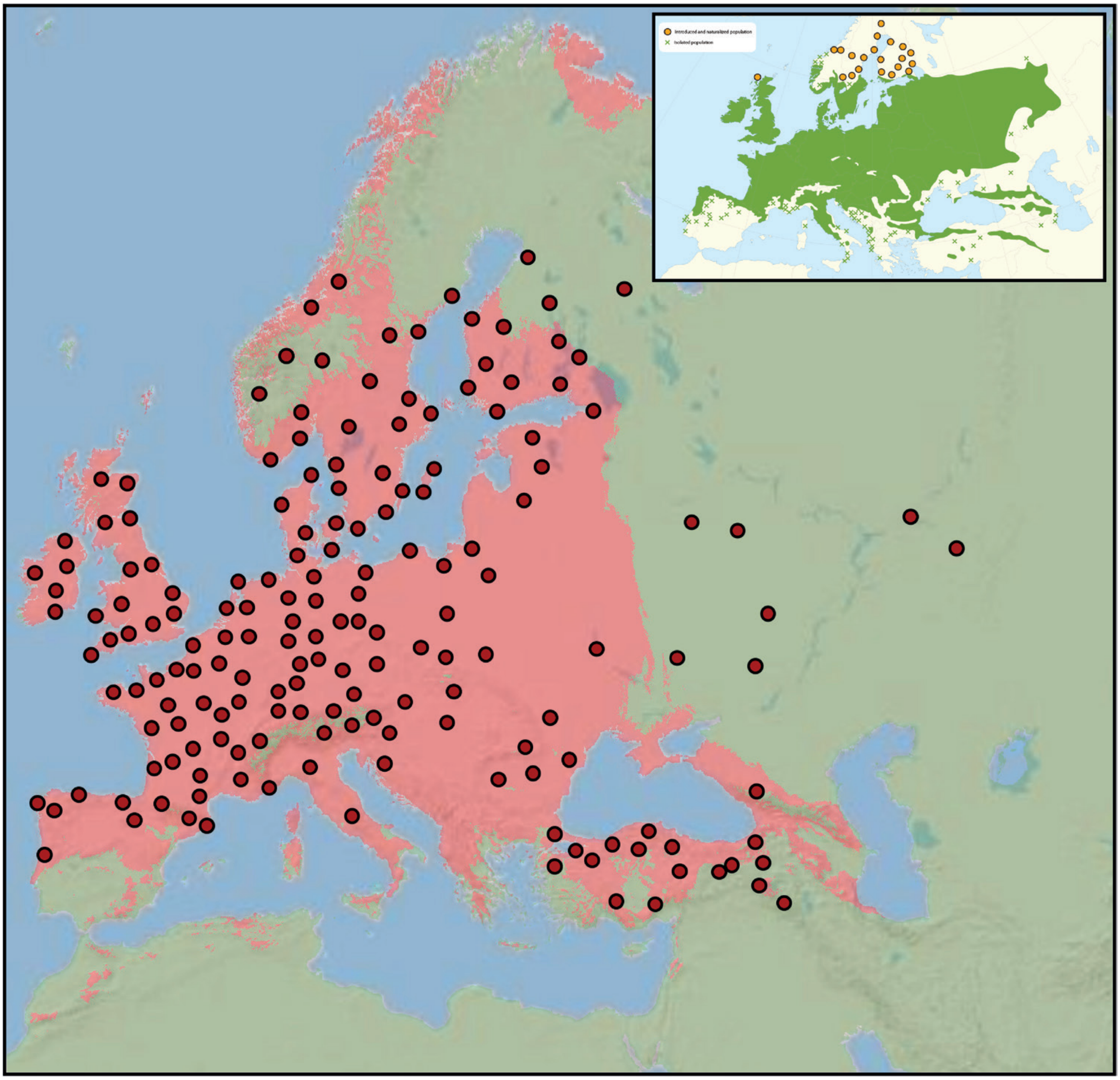

Figure 1. Distribution map of *Quercus robur* (adopted from Eaton *et al.*, 2016) (inset) and predicted present distribution with occurrence points of *Q. robur*. The two maps were largely concordant with each other.

ECOLOGICAL NICHE MODELS

We followed Barve *et al.* (2011) in specifying the study area. The M area (M is the area that the species has been potentially able to reach in a given time) was therefore determined according to the natural history of *Q. robur* (Ducousso & Bordacs, 2003; Den Ouden, Jansen & Smit, 2005; Scharnweber *et al.*, 2011; Moracho *et al.*, 2016) (see Supporting Information S1). We then considered the sufficiently sampled area (S). This approach is important because any ecological niches (e.g. fundamental niche) can be estimated using both real-world landscape and species occurrences in this landscape (Jiménez-Valverde, Lobo & Hortal, 2008; Peterson & Soberon, 2012). Therefore, we hypothesized the M area showed almost all available geographies for *Q. robur* while the S area showed the known distribution of *Q. robur* based on available occurrence points. Finally, the models were calibrated across unique M ∩ S for *Q. robur*. All projections in the ecological niche models were performed with the mask set between 12° and 66°E and 27.5° and 72°N.

Before constructing the models, we first inspected the layers for spatial artefacts: Bio 8–9 and Bio 18–19 showed some anomalies across the study area (e.g. Perktaş, Peterson, Dyer, 2017) so these four bioclimatic variables were removed from the analysis. Secondly, we removed several highly correlated bioclimatic variables ($r > 0.85$ or < -0.85) to reduce multicollinearity, which left six variables: Bio 1 (annual mean temperature), Bio 2 (mean diurnal range), Bio 3 (isothermality) Bio 4 (temperature seasonality), Bio 12 (annual precipitation) and Bio 15 (precipitation seasonality).

We used MAXENT (maximum entropy machine learning algorithm), version 3.3.3k (Phillips, Anderson & Schapire, 2006; Phillips & Dudík, 2008; http://www.cs.princeton.edu/~schapire/maxent), to construct the models under the Present conditions before projecting to those of the HOL, the LGM and the LIG. Because MAXENT uses presence-only records to provide high-performance model prediction even with low occurrence data, it is accepted as the most efficient method of ecological niche modelling (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Phillips *et al.*, 2006; Wisz *et al.*, 2008; Baldwin, 2009; Merow, Smith & Silander, 2013). We used a jackknife procedure using receiver operating characteristic (ROC) analyses in MAXENT, version 3.3.3k, and followed the process suggested by Peterson & Cohoon (1999).

Initially, 35 models were developed using a set of feature types (L, LQ, LQP, LQPH, LQPHT) and seven regularization multiplier values (0.1, 0.2, 0.5, 1, 2, 5, 10) for the calibration area. These models were compared based on the corrected Akaike Information Criterion (AICc), which was produced by ENMTools, version 1.3 (Warren, Glor & Turelli, 2008, 2010). The best model was chosen according to the lowest AICc value. Eventually, based on the best model of the calibration area, 14 different models were developed across the projection region for the Present (one model), the HOL (nine models), the LGM (three models) and the LIG (one model). MAXENT settings for the models were default and bootstrap was the replicated run type. Each model was run ten times with 500 maximum iterations and a 0.00001 convergence threshold. The 10-percentile training presence thresholding approach was used to convert model outputs to binary predictions (Radosavljevic & Anderson, 2014). To assess the statistical robustness of model predictions, we used partial ROC statistics (Peterson, Papes & Soberon, 2008; for methodological details see Perktaş *et al.*, 2017). For the best predictions, in addition to the other metrics (i.e. AICc and partial ROC), we also took into consideration low omission rate. Finally, raster calculation implemented in ArcGIS version 10.2 was used to compute overlap of the nine different HOL models and of the three different LGM models.

RESULTS

Model calibration results based on AICc values showed that the best model included a regularization multiplier of 5 for *Q. robur* and four feature types: linear, quadratic, product and hinge (see Supporting Information S2). The ecological niche modelling results based on the model calibration results provided high area under the curve (AUC) values for the training data, indicating that all models had strong predictive ability (Table 1). Partial ROC statistics showed that all of the models provided predictions of the geographical range of *Q. robur* that were statistically significantly better than random expectations (for all, $P < 0.05$). The response curves showed that bioclimatic variables affected the MAXENT predictions: *Q. robur* was better adapted to an environment characterized by particularly low temperature and precipitation seasonality. Among these variables, Bio 4 (temperature seasonality) and Bio 1 (annual mean temperature) made the greatest combined contribution to the model predictions (for all models, > 80%).

Under present bioclimatic conditions, the model prediction was highly compatible with the known distribution range of *Q. robur* (Fig. 1), suggesting that *Q. robur* is almost at equilibrium with the climate ('almost at equilibrium' because there was no prediction in the eastern part of its distribution range). Under past bioclimatic conditions (the LIG, the LGM and the HOL), *Q. robur* showed instability during the transitions between these periods (specifically, LIG–LGM and LGM–HOL). The LIG and the HOL predictions gave much broader distribution ranges than the LGM predictions, suggesting a contraction towards climatically favourable areas in southern Europe (including France) (Fig. 2; see Supporting Information S3 for individual models of the HOL and LGM).

Table 1. Mean training area under the curve (AUC) values and standard deviations based on ten replicates of each model (see Bagley *et al.*, 2013 for a similar approach).

Model	Mean AUC	SD
Present	0.791	0.014
HOL - BCC-CSM1-1	0.797	0.011
HOL - CCSM4	0.797	0.018
HOL - CNRM-CM5	0.794	0.009
HOL - HadGEM2-CC	0.797	0.016
HOL - HadGEM2-ES	0.789	0.015
HOL - IPSL-CM5A-LR	0.795	0.018
HOL - MIROC-ESM	0.789	0.015
HOL - MPI-ESM-P	0.799	0.018
HOL - MRI-CGCM3	0.798	0.015
LGM - CCSM4	0.789	0.012
LGM - MIROC-ESM	0.788	0.018
LGM - MPI-ESM-P	0.800	0.013
LIG	0.800	0.017

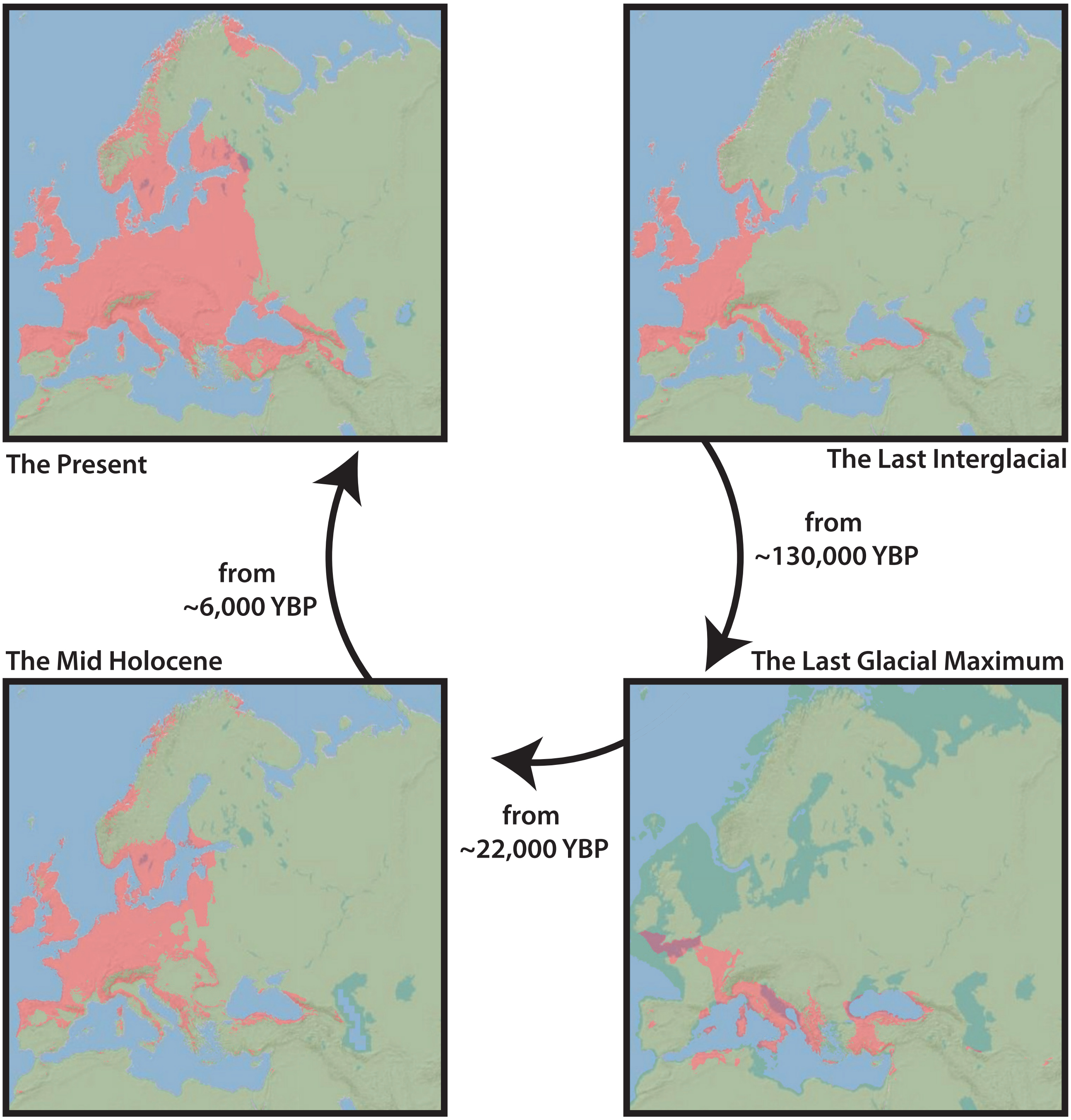

Figure 2. Ecological niche model showing the geographical distribution of *Quercus robur* under the Present (Pre., 1950–2000) and the reconstructed past (the HOL, 6000 YBP; the LGM, 22 000 YBP; and the LIG, 130 000 YBP) bioclimatic conditions.

DISCUSSION

This study tested the glacial refugia hypothesis (e.g. Brito, 2005) in one widespread tree species, *Q. robur*, using ecological niche modelling. According to our results, there is clear evidence of refugia in southern Europe during the LGM for *Q. robur*. According to this hypothesis, many temperate zone species survived in climatically favourable locations in southern Europe during the LGM (e.g. Ferris *et al.*, 1998; Bensch & Hasselquist, 1999; Hampe *et al.*, 2003). Our results show that *Q. robur* also responded to climate changes through Late Pleistocene glacial–interglacial cycles, with its distribution range shrinking towards favourable areas in southern Europe during the LGM. This pattern has also been found for many other European temperate deciduous tree species (e.g. Hampe *et al.*, 2003; Krebs *et al.*, 2004). Our findings are also consistent with those of Ferris *et al.* (1998) and Petit *et al.* (2002), who showed late- and post-glacial expansion of oaks from separate refugia in southern Europe. However, although our ecological niche modelling results support the glacial refugia hypothesis, they also reveal possible extra-Mediterranean refugia for deciduous oak species in northern, western and southern France. These extra-Mediterranean refugia located in France for *Q. robur* are characterized more by temperature than by precipitation according to our model predictions. In contrast to the results of Petit *et al.* (2002), this suggests that precipitation is not an essential element acting as a significant bioclimatic factor for *Q. robur*.

Our ecological niche modelling prediction for the present distribution of *Q. robur* was largely concordant with its known distribution. This demonstrates the species–climate equilibrium of the ecological niche of *Q. robur* based on bioclimatic data (Nogués-Bravo, 2009), which could indicate confidence in the model. Because we used the M ∩ S area for calibration, the model output did not include the eastern part of the distribution range of *Q. robur*. This might have affected the result slightly, as we lacked several occurrence points in the region, and it is uncertain whether the known range of *Q. robur* reaches to the far eastern part of Europe and to Russia. The variables that most strongly affected the predictions were temperature seasonality and annual mean temperature, which suggests that temperature is the most important climatic determinant of the distribution of *Q. robur*, as for many plant species of the temperate region (Huntley, Bartlein & Prentice, 1989; Fang & Lechowicz, 2006; Hamann & Wang, 2006). Our results regarding predictive variables contradict those of Svenning, Normand & Kageyama (2008), who argued that absolute minimum temperature together with water balance and growing degree-days were the most critical predictors of the distribution of Europe temperate trees. Our results may be more realistic, at least for *Q. robur*, because we tried to eliminate highly correlated variables and obtain simpler model predictions using a relatively small climatic data set. We found that temperature-related variables were the most critical variables in projecting the distribution of *Q. robur*.

Quercus robur has four geographically structured cytotypes (Ferris *et al.*, 1998): eastern, central, western and East Anglian. The highly localized East Anglian type (from a region in eastern England) has been considered to be the product of recent diversification as a result of post-glacial colonization of Britain by *Q. robur* (see also Ferris *et al.*, 1995). Alternatively, such genetic variation might indicate the presence of an extra-Mediterranean refugium in France (e.g. Schmitt & Varga, 2012). In possible support of this latter hypothesis, the greatest genetic differentiation has been reported in Iberia (G_{ST} = 0.889, Petit *et al.*, 2002). Inferences from phylogeography are largely consistent with our ecological niche modelling results, which indicate that northwards re-expansion started after the LGM from cryptic refugia (i.e. extra-Mediterranean refugia) located in northern, western and southern France, as well as from the well-known southern European refugia, including Anatolia (Hewitt, 2000). A palaeovegetation modelling study based on pollen data also suggests such a pattern of refugia during the LGM for temperate deciduous trees, including *Q. robur* (Allen *et al.*, 2010). Although a lack of genetic data for Anatolian *Q. robur* populations weakened previous inferences regarding Anatolia's potential role as a refugium, recent evidence indicates that Anatolia and the Balkans remained connected during the Pleistocene, allowing historical gene flow from Anatolia to central and northern Europe for various species (Bilgin *et al.*, 2009; Ansell *et al.*, 2011; Perktas *et al.*, 2015a, b; Korkmaz *et al.*, 2014). By indicating that Anatolia was a plausible refugium for *Q. robur* during the Pleistocene glacial periods, our work supports previous studies suggesting an Anatolian refugium in the western Palearctic biogeographical region for various taxa (Rokas *et al.*, 2003; Krebs *et al.*, 2004; Perktaş, Barrowclough & Groth, 2011, 2015a, b; Korkmaz *et al.*, 2014; Perktaş *et al.*). In addition, Anatolia hosts two pedunculate oak subspecies that can be distinguished based on morphology and geographical distribution (Hedge & Yaltırık, 1982). The subspecies in the eastern part of Anatolia (i.e. subsp. *pedunculiflora*) is separated from the widespread intra-species taxon (i.e. subsp. *robur*) by a definite geographical barrier, the Anatolian Diagonal (for details, see Gür, 2016). This makes the situation more interesting in Anatolia because it is not only a refugium for this species, but may also be a diversification centre. In support of this, Anatolia is the possible origin area of *Q. cerris* and a glacial refugium for this species (Bagnoli *et al.*, 2016). Therefore, further detailed molecular studies are required to understand the natural history of *Q. robur*. The model predictions of CCSM4 and MPI-ESM-P for the LGM show that the central/southern Iberian Peninsula was a suitable refugium for *Q. robur*. On the other hand, the low occurrence of deciduous oak pollen during the LGM in southern Iberia (Pons & Reille, 1988; Naughton *et al.*, 2007) and genetic evidence suggesting an LGM refugium for white oaks (including *Q. robur*) in northern Iberia (Olalde *et al.*, 2002) conflict with our model predictions. This mismatch may indicate that the range of *Q. robur* was restricted during the LGM due to competition with pines and Mediterranean evergreen oaks in southern and central Iberia. Parapatric distributions of Mediterranean oaks (such as *Q. coccifera*, *Q. suber* and *Q. ilex*) with *Q. robur* in the Present (San-Miguel-Ayanz *et al.*, 2016) and the predominant status of pines in the vegetation during the LGM in the Iberian Peninsula (Pons & Reille, 1988; Benito-Garzón, Sánchez de Dios & Sáinz Ollero, 2007) also suggest that biotic interactions (i.e. competition) may have played a role in restricting the distribution of *Q. robur* in Iberia during the LGM, besides climatic factors. This pattern is also consistent with results for some forest-dependent bird species in the region (Perktaş *et al.*, 2015b), and may have occurred in Anatolia, which has more *Quercus* species (18; Hedge & Yaltırık, 1982) than Iberia (12; Do Amaral Franco, 1991). The role of such competition is worth studying in more detail with regard to interglacial–glacial range shifts in deciduous oak species during the Pleistocene.

Interpretation of the predicted LIG distribution of *Q. robur* was not straightforward. The effect of the LIG on the geographical distributions of species has not been discussed in depth, with only a few papers focusing on this period (Petit, Hampe & Cheddadi, 2005; Gür, 2013; Wang *et al.*, 2013; Perktaş *et al.*, 2015a). We expected that the LIG and the Present distributions of *Q. robur* should be almost the same because climatic conditions in the LIG were similar to those in the Present (Qu *et al.*, 2011), with the only differences between them being temperature seasonality and annual mean temperature. During the LIG, these two climatic variables were higher than those of the Present (Cowie, 2007). Our study showed that these two variables had a greater impact on the distribution of *Q. robur* in that, as temperature seasonality increased, the distribution of *Q. robur* contracted. This inference is consistent with the LIG prediction for *Q. robur*.

This study has described the Pleistocene history of *Q. robur* based on the ecological niche modelling approach. The results need further, more detailed investigation, especially by including molecular data, to provide a better understanding of the effects of climate changes on temperate oak species. Nevertheless, it supports conclusions from other studies (e.g. Perktaş *et al.*, 2015b) that European biogeography is significantly more complex than previously thought.

ACKNOWLEDGEMENTS

We thank Barış Özüdoğru for his helpful comments and suggestions. We extend our sincere thanks to Town Peterson, Hakan Gür and one anonymous reviewer for their valuable comments. The fieldwork of this study was financially supported by the Scientific Research Projects Coordination Unit of Hacettepe University (project no.: 014 D06 601 003-619). The study formed part of the requirements for the MSc thesis of E.D.Ü. submitted to Hacettepe University.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

S1. Borders of the M area.
S2. Model comparison based on the corrected Akaike Information Criterion (AICc). The best model is indicated in bold in the first row.
S3. Model outputs for the HOL (BCC-CSM1-1, CCSM4, CNRM-CM5, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM, MPI-ESM-P, MRI-CGCM3) and the LGM (CCSM4, MIROC-ESM, MPI-ESM-P).