Check for updates

Received: 15 May 2023 | Revised: 19 August 2023 | Accepted: 27 September 2023

DOI: 10.1002/ece3.10606

Ecology and Evolution Open Access WILEY

RESEARCH ARTICLE

Distribution patterns of *Quercus ilex* from the last interglacial period to the future by ecological niche modeling

Burak Suicmez[1] | **Meral Avci**[2]

[1]Istanbul University, Institute of Social Sciences, Istanbul, Türkiye

[2]Department of Geography, Faculty of Letters, Istanbul University, Istanbul, Türkiye

Correspondence
Meral Avci, Department of Geography, Faculty of Letters, Istanbul University, Istanbul, Türkiye.
Email: mavci@istanbul.edu.tr

Abstract

The plants' geographic distribution is affected by natural or human-induced climate change. Numerous studies at both the global and regional levels currently focus on the potential changes in plant distribution areas. Ecological niche modeling can help predict the likely distribution of species according to environmental variables under different climate scenarios. In this study, we predicted the potential geographic distributions of *Quercus ilex* L. (holm oak), a keystone species of the Mediterranean ecosystem, for the Last Interglacial period (LIG: ~130 Ka), the Last Glacial Maximum (LGM: ~22 Ka), mid-Holocene (MH: ~6 Ka), and future climate scenarios (Representative Concentration Pathway (RCP) 4.5 and 8.5 scenarios) for 2050–2070 obtained from CCSM4 and MIROC-ESM global climate scenarios respectively. The models were produced with algorithms from the R-package "biomod2" and assessed by AUC of the receiver operating characteristic plot and true skill statistics. Aside from BIOCLIM (SRE), all model algorithms performed similarly and produced projections that are supported by good evaluation scores, although random forest (RF) slightly outperformed all the others. Additionally, distribution maps generated for the past period were validated through a comparison with pollen data acquired from the Neotoma Pollen Database. The results revealed that southern areas of the Mediterranean Basin, particularly coastal regions, served as long-term refugia for *Q. ilex*, which was supported by fossil pollen data. Furthermore, the models suggest long-term refugia role for Anatolia and we argue that Anatolia may have served as a founding population for the species. Future climate scenarios indicated that *Q. ilex* distribution varied by region, with some areas experiencing range contractions and others range expands. This study provides significant insights into the vulnerability of the *Q. ilex* to future climate change in the Mediterranean ecosystem and highlights the crucial role of Anatolia in the species' historical distribution.

KEYWORDS
Anatolia, climate change, keystone species, Mediterranean Basin, paleovegetation, Quaternary

TAXONOMY CLASSIFICATION
Biodiversity ecology, Biogeography, Conservation ecology, Global change ecology, Paleoecology

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2023 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

The climate of the world has been in perpetual change, throughout the geological ages as a result of various internal and external dynamics. In particular, the Quaternary is characterized as a period in which the effects of climate changes were highly pronounced (Rull, 2020). The Pleistocene epoch was marked by recurring cycles of climatic oscillations between glacial and interglacial periods (Lisiecki & Raymo, 2007). Notably, the Last Interglacial period (LIG) is widely recognized as a period of relative warmth in comparison with the present day (Kukla et al., 2002). Conversely, the Last Glacial Maximum (LGM: 22 Ka) is marked by the widespread advance of large ice sheets across North America, northern Europe, and Asia, leading to significant drops in temperature and the emergence of arid environments (Hughes et al., 2013). Climate is widely recognized as one of the most significant environmental variables influencing the geographic distribution of species, including plants, leading to changes in habitat suitability, biotic interactions, and species physiology (Araújo & Rahbek, 2006; Bennett & Provan, 2008; Hewitt, 2000; Svenning & Skov, 2007). The glacial and interglacial periods of the Pleistocene resulted in significant shifts in the distribution of plant communities (Hampe & Jump, 2011), with the most influential changes occurring during the LGM. The LGM caused the range contraction of many temperate species toward suitable areas where the climate was favorable for tree survival, known as glacial refugia in southern Europe, the Iberian, Italian, and Balkan peninsulas (Bennett et al., 1991; Bhagwat & Willis, 2008; Hewitt, 1996, 1999; Svenning et al., 2008), areas forming the Mediterranean Basin, our research area. The Holocene period is characterized by the warming of the climate and the retreat of glaciers following the ice ages, leading to the reappearance of favorable conditions for animal and plant species adapted to temperate conditions. These species exhibited a tendency to expand their ranges northward from refuge areas and have recolonized (Hewitt, 1999). Due to climatic oscillations, refuge areas where the species persist during unfavorable conditions and recolonize stand out as rich genetic diversity areas (Badgley et al., 2017; Davis & Shaw, 2001; Hewitt, 2004). Anatolia's diverse topographical and geomorphological structure has contributed to its rich flora and the high rate of endemism among plant species (Avci, 2005; Médail & Diadema, 2009; Şekercioğlu et al., 2011). It encompasses three biodiversity hotspots (Mittermeier et al., 2004), including the Mediterranean (Caucasus, Iran-Anatolia, and the Mediterranean), and is considered one of the possible origins of the European lineage of certain species (Rokas et al., 2003). In addition, numerous studies suggest the role of Anatolia, another peninsula in the Mediterranean Basin, as a refugia during the LGM (Bagnoli et al., 2016; Bilgin, 2011; Médail & Diadema, 2009; Schmitt, 2007; Tekpinar et al., 2021). The ecological processes observed during the LGM led to the rich and diverse plant diversity of the Mediterranean Basin, which plays the role of refugia for European flora. This heritage of plant diversity is still preserved in the Mediterranean Basin today (Médail & Diadema, 2009).

In recent times, the global climate has undergone substantial changes, primarily due to human influence, contrasting with the natural causes of climate change observed during the Pleistocene (IPCC, 2021). These changes have had a wide-ranging impact on ecosystems, including the loss of biodiversity, alteration of ecosystem functions, and shifts in species distributions (Bellard et al., 2012; Parmesan & Yohe, 2003; Walther et al., 2002). The scale and the intensity of climate change are expected to increase in the near future, with potentially catastrophic consequences for numerous species and ecosystems (IPCC, 2021). Species must adapt in the face of climate change or move toward climate conditions suitable for them (Parmesan & Yohe, 2003). Species persist in their habitat via phenotypic plasticity and genetic adaptations which allow them to survive under new environmental conditions (Hoffmann & Sgrò, 2011; Waldvogel et al., 2020). Species that are unable to adjust to the changing climatic conditions and cannot migrate to areas with suitable climatic conditions are at high risk of extinction (Pacifici et al., 2015; Parmesan, 2006; Thomas et al., 2004; Walther et al., 2002). Due to the rapid pace of climate change, many species may be unable to adapt to the changing environmental conditions, which may ultimately lead to significant consequences for global biodiversity (Corlett & Westcott, 2013). The Mediterranean Basin is recognized as one of the regions that is most sensitive to climate change due to the substantial decrease in average precipitation and increase in precipitation variability during the dry season (Giorgi, 2006; Tramblay et al., 2020; Turkes et al., 2020). Projections indicate that by the end of the 21st century, there could be a 50% reduction in precipitation in some parts of Northwest Africa and a negative precipitation change of up to 20%–25% in the Iberian Peninsula, Balkan Peninsula, and a significant portion of Anatolia. Conversely, some regions in the northern flank of the Mediterranean Basin, such as northern Italy, Slovenia, and the Black Sea region, may experience a transition to "humid-wet" conditions that are more prevalent in mid-latitudes (Barcikowska et al., 2018). In addition to the impact of climate change observed around the Mediterranean Basin, human influence also threatens the richness of the Mediterranean Basin's flora (Guo et al., 2022), therefore the Mediterranean Basin is considered a biodiversity hotspot (Médail & Myers, 2004).

Ecological niche modeling can help predict the likely distribution of species based on occurrence data and environmental variables under different climate scenarios in the past, present, and future times (Elith & Leathwick, 2009; Guisan et al., 2013; Guisan & Zimmermann, 2000; Pearson & Dawson, 2003). Currently, numerous studies are conducted both globally and regionally focusing on predicting changes in the distribution of plant species across different time periods, including past and future scenarios. Knowledge of species range shifts as a result of climate change provides valuable information to make more accurate risk assessments and conservation management for the future, and ecological niche models are increasingly being used to support conservation decision making (Guisan & Thuiller, 2005). As a result, the Mediterranean flora has been extensively studied using ecological niche modeling approaches for predicting past and future distributions, with an increasing number of studies being conducted (Almeida et al., 2022; Benito Garzón et al., 2007; Fyllas et al., 2019; Salvà-Catarineu et al., 2021).

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Quercus ilex is a broad-leaved evergreen tree or shrub that can grow well in a wide variety of soils in different Mediterranean climates, from semi-arid to very humid and from hot to very cold, native to the central and western parts of the Mediterranean Basin, the Balkan regions, the Aegean Islands and North Africa and limited areas in the Aegean and Black Sea coastal areas in Turkey (Barbero et al., 1992; Browicz & Zieliński, 1982; de Rigo & Caudullo, 2016; Günal, 2003; Zohary, 1973). The ecological significance of *Q. ilex* forests is highlighted by the current endangered or critically endangered status of many arthropod species that rely on this tree for sustenance but have not yet undergone conservation status assessments (Hernández-Agüero et al., 2022). It serves as a habitat and breeding ground for various vertebrates in the Iberian Peninsula and provide valuable resources, such as carpentry tools, firewood, and acorns, which are used to feed pigs. Furthermore, it is also utilized for recreational activities in parks and gardens (de Rigo & Caudullo, 2016). Due to these significant ecological and economic roles, *Q. ilex* is considered as a keystone tree species in the midwestern Mediterranean Basin (Hernández-Agüero et al., 2022) and has been the subject of numerous ecological niche studies in the region. These studies were carried out at local scale in high resolution to predict suitable areas for reforestation or the response of species to future climate change scenarios and conservation concerns (López-Tirado et al., 2018; López-Tirado & Hidalgo, 2018; Quinto et al., 2021; Tabet et al., 2018). Consequently, these studies pointed to the need for an ecological niche modeling approach that covers the entire distribution areas of *Q. ilex*. Furthermore, the prediction of ecological niche models to past distribution of *Q. ilex* could lead to a more reliable understanding of the species ecological behavior, at least in terms of response to climatic variables (Nogués-Bravo, 2009; Vessella et al., 2015).

In this study, potential geographic distributions of *Quercus ilex* L. (holm oak), a keystone species of the Mediterranean ecosystem, were predicted by using ecological niche modeling approach with ten algorithms located in the R-package "biomod2" for the LIG: ~130 Ka, the LGM: ~22 Ka, mid-Holocene (MH: ~6 Ka) and future climate scenarios (Representative Concentration Pathway (RCP) 4.5 and 8.5 scenarios for years 2050–2070) obtained from CCSM4 and MIROC-ESM climate models. For this context, we pursue the following objectives: (i) to model the present distribution of *Q. ilex*, (ii) to investigate Quaternary range dynamics by predicting potential distributions of *Q. ilex*, (iii) to project the future distribution of *Q. ilex* under different climate change scenarios. (iv) to identify potential *Q. ilex* climate refugia for Anatolia under past and future climate change.

2 | MATERIALS AND METHODS

2.1 | Occurrence data

We obtained the occurrence records of *Q. ilex* from the Global Biodiversity Information Facility (GBIF) for the Mediterranean Basin (Global Biodiversity Information Facility (GBIF), 2022). Turkey was excluded in the first query because GBIF's data from Anatolia were incomplete and partly incorrect. Thus, 102 occurrence records for Anatolia from the scientific literature and herbaria were added to the GBIF dataset (Akkemik et al., 2021; Browicz & Zieliński, 1982; Hedge & Yaltırık, 1982) As a result, a total of 90,653 occurrence records were considered for the beginning. Then we cleaned the occurrence records step by step. First, we excluded all duplicate records. Since *Q. ilex* does not naturally occur (introduced) in northern Europe and particularly in southern England (Fisher et al., 1994; Southwood et al., 2004), and as GBIF also collects data with citizen science, and not all data refer to natural populations, we removed occurrence records that do not refer to natural populations of the *Q. ilex* according to the limits in the EUFORGEN database (Caudullo et al., 2017). While doing that, we notice that there were some occurrence records in Africa and the Balkans outside of the EUFORGEN limits, we checked those occurrences one by one and included them in our study without removing them because they refer to natural populations. After that, to reduce the effects of sample bias and spatial autocorrelation and improve the prediction performance of the models (Beck et al., 2013; Boria et al., 2014), the records were thinned at 15 km using SDMtoolbox v2.4 (Brown et al., 2017) in ArcGIS version 10.8 (ESRI, 2020). This filter was chosen taking into account the natural distribution of *Q. ilex*, the fact that clusters can occur for ecological reasons, and therefore, removing records from highly clustered areas may obscure true patterns (Barber et al., 2022). This process resulted in 1606 occurrence records for use in ecological niche modeling (Figure 1, Table S1).

2.2 | Bioclimatic variables and study area

To use in the modeling process, the historical (the LIG: ~130 Ka, the LGM: ~22 Ka, and the MH: ~6 Ka), current (1960–1990), and future (2050–2070) climate projections under intermediate and pessimistic Representative Concentration Pathways (RCP4.5 and RCP8.5), 19 bioclimatic variables with 2.5′ (~4.5 km at the equator) were downloaded from the WorldClim (version 1.4) database (Table S2, Hijmans et al., 2005). The potential equilibrium between species distributions and climate in model predictions contributes to a relatively increased reliability of climate predictions over time (Nogués-Bravo, 2009). However, model predictions may fail to accurately predict the paleo distribution of a species; this failure indicates that the current distribution data may not fully represent the entire climate range within which the modeled species could exist, and it demonstrates that the reliability of niche models' transferability over time cannot be solely achieved based on current climate equilibrium (Varela et al., 2009). Therefore, in this study, model predictions have been utilized from the LIG to the future. We are aware that various options are available, such as WorldClim v.2.1 (representing the 1971–2000 climate) containing 23 different global climate models (Fick & Hijmans, 2017) or CHELSA (encompassing the 1981–2010 climate; Karger et al., 2017). However, the WorldClim 2.1 version still does not contain data for

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

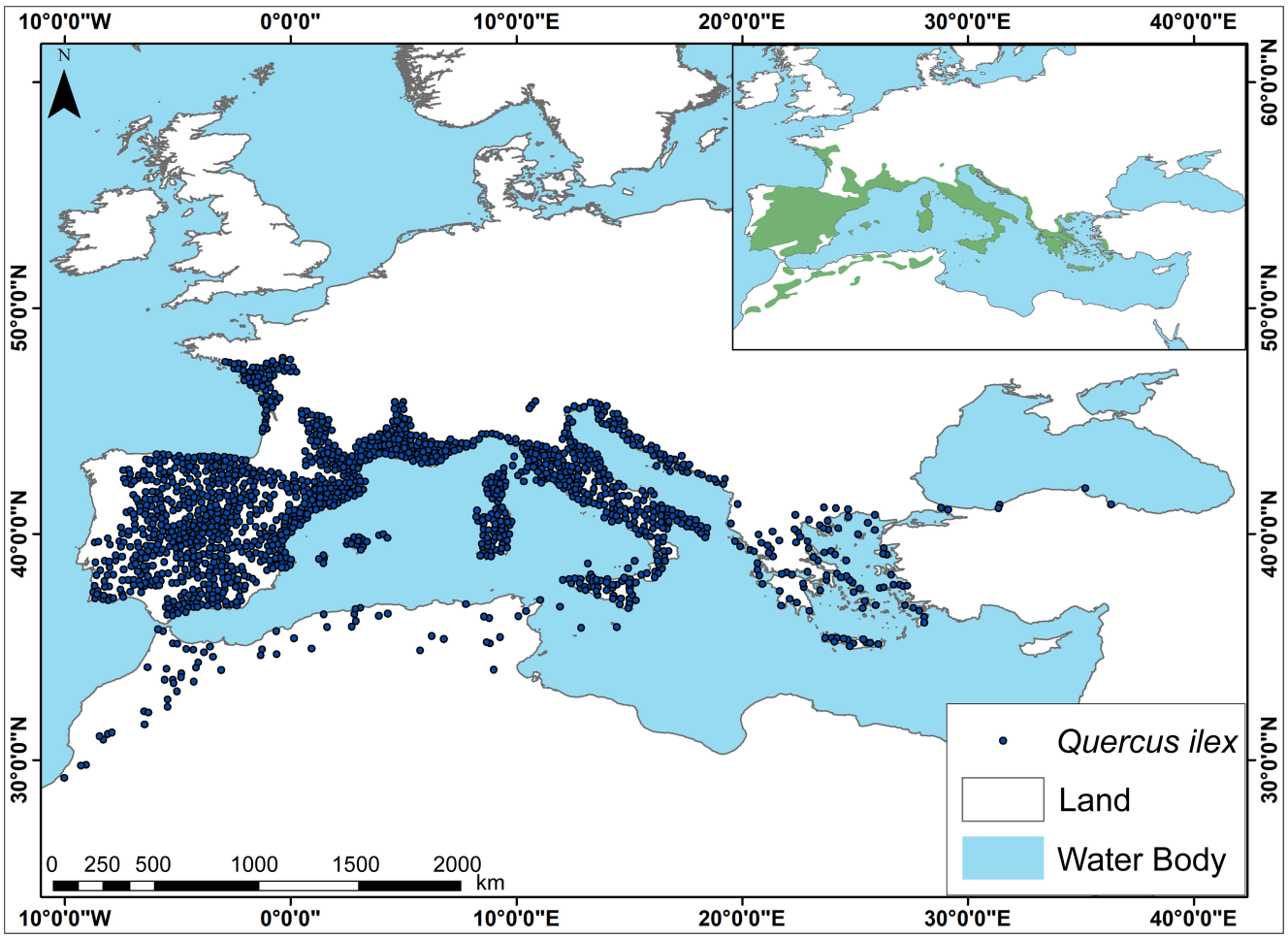


FIGURE 1 All occurrence records (1606) used in the modeling process representing the geographic distribution of *Quercus ilex* L. (Akkemik et al., 2021; Browicz & Zieliński, 1982; Global Biodiversity Information Facility (GBIF), 2022; Hedge & Yaltırık, 1982; including herbarium specimens) with distribution map representing natural populations of *Q. ilex* form EUFORGEN adapted from Caudullo et al. (2017). The area visible on the maps represents the study area.

the past periods and the CHELSA dataset does not provide data for the LIG. Furthermore, due to differences arising from computer limitations, inadequate understanding of physical processes, and climate sensitivity among global climate simulations (Randall et al., 2007), we chose not to use WorldClim v.2.1 for the present and future climate scenarios and WorldClim v.1.4 for the past periods within the same study. In conclusion, despite being an older data version, we utilized WorldClim v.1.4 for all periods included in the study. The present study utilized the Community Climate System Model Version 4 (CCSM4) and Model for Interdisciplinary Research on Climate-Earth System Model (MIROC-ESM) global climate models for ecological niche modeling, as they were the only models providing data for all time periods except for the LIG, which was not available for MIROC-ESM. Therefore, the results for the LIG period were conducted using the CCSM4 exclusively. Initially, we cropped all climate data to the boundaries of our study area (11° W to 45° E; 28°–60° N), which was determined by the known distribution range of *Q. ilex* and possible extensions for past or future range expansions (Figure 1). LIG climate data used in this study were obtained from Otto-Bliesner et al. (2006). The original resolution of the LIG climate data was 30″ (~1 km), which we resampled to 2.5′ resolution to match the other time periods used in our analysis. Pearson's correlation coefficient was then used to eliminate highly correlated bioclimatic variables, retaining only those with a correlation coefficient below .75 (Table S3, Dormann et al., 2013), which left us seven variables (Table S4): Bio 5 (Max Temperature of Warmest Month), Bio 7 (Annual Temperature Range), Bio 8 (Mean Temperature of Wettest Quarter), Bio 11 (Mean Temperature of Coldest Quarter), Bio 15 (Precipitation Seasonality), Bio 16 (Precipitation of Wettest Quarter), and Bio 17 (Precipitation of Driest Quarter). While selecting bioclimatic variables, the ecological demands of *Q. ilex* were taken into account while reducing collinearity within environmental parameters. Previous studies have shown that both temperature and precipitation play a key role in the distribution of *Q. ilex*. We specifically chose to use seasonal climate variables—the hottest, coldest, wettest, and driest seasonal values—in our study as they have been found to have a stronger influence on *Q. ilex* distribution than annual values (Campelo et al., 2009; Gea-Izquierdo et al., 2009; Terradas & Savé, 1992). All process and analyses on climate data were performed in R statistics software (version 4.2.2, R Core Team, 2022) with the "terra" package (Hijmans, 2023).

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2.3 | Ecological niche modeling

To generate potential distribution maps of *Q. ilex*, we utilized 10 different algorithms available in the "biomod2" package (version 3.5.1, Thuiller et al., 2009) in R software (version 4.2.2, R Core Team, 2022). The algorithms used were artificial neural network (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS), maximum entropy (MAXENT), random forest (RF), and surface range envelope (SRE). We built individual models using default settings provided by biomod2. Most of the utilized algorithms require both presence and absence data. In contrast, MAXENT uses presence-only data, and BIOCLIM uses pseudo-absence data (Thuiller et al., 2009), thus, using the biomod2, we generated 10 sets of an equal number of randomly distributed background points (1606) within the study area to increase precision and avoid random bias (Barbet-Massin et al., 2012). To generate the MAXENT distribution model, we chose the more common approach and selected 10,000 background points within the study area, again using biomod2, for modeling purposes, which has been recommended in previous literature (Phillips et al., 2006). The models were created with training sets of 80% and 20% data for the validation set. In total, 1000 model runs were conducted, consisting of 10 algorithms, 10 pseudo-absence selections, and 10 evaluation runs (Figure S1). The relevant code is provided in the Supporting Information (File S1). In order to evaluate the prediction accuracy of the models, the area under the receiver operating characteristic curve (AUC) and true skill statistics (TSS) values are considered together (Guisan et al., 2017). In general, predictive capabilities of AUC values greater than 0.7 indicate good performance, while greater than 0.9 indicate excellent performance (Elith, 2000; Phillips & Dudík, 2008); values above 0.6 and 0.8 for TSS indicate good and excellent performance (Allouche et al., 2006), respectively. Model outputs were presented as means of individual algorithms and were converted into binary predictions (presence/absence) with a given cut-off value (Table 1) in which the TSS having the highest value was defined as the threshold (Liu et al., 2013). To assess the uncertainty of the results of the individual models, the clamping mask was created, which defines the positions when extrapolation is involved (Figure S2, Elith et al., 2010; Yates et al., 2018).

3 | RESULTS

3.1 | Model evaluation and variable contribution

The results indicate that models demonstrated a high predictive capacity, with true skill statistics (TSS) ranging from 0.659 to 0.834, and ROC curve (AUC) values ranging from 0.829 to 0.946 (Table 1). According to the results, RF (mean TSS = 0.834 ± 0.02 and AUC = 0.946 ± 0.01) was the best-fitting algorithm and SREs (mean TSS = 0.659 ± 0.03 and AUC = 0.829 ± 0.02) were the worst-fitting algorithm. Therefore, we will focus on the "biomod2"-generated RF algorithm, which is observed to be the most suitable for *Q. ilex*. Although the environmental variables made different contributions to different models, in general, "Mean Temperature of Coldest Quarter" (bio 11) had the largest contribution of the majority of the models, except ANN and MAXENT. In the case of RF, bio 11 (34%), bio 5, bio 16, and bio 17 (8%) had the largest contribution (Figure S4).

Based on variable importance and response curves (Figures S3,S4), *Q. ilex* prefers locations where the mean temperature of the coldest quarter is near or above the freezing point, and the probability of distribution is optimum at 5°C in the same quarter. Response curves indicate that the species prefers locations where precipitation is concentrated in the winter months. Considering the response curves representing the driest quarter's rainfall, the species can tolerate locations with less than 50 mm of summer rainfall, while more than 100 mm of rainfall in the summer season is optimal. All these findings indicate that the species prefers mild and rainy winter months, adapting to the Mediterranean climate. As these results align with the literature information, it is concluded that the model's results can successfully describe the ecological requirements of the species.

3.2 | Present prediction

Based on models we produced, suitable habitat for *Q. ilex* was predicted to be widespread across the Mediterranean Basin, from the Iberian Peninsula, the Balearic Islands, to the north African coast, the Atlantic region of France (west coast of France), southern France, Corsica, southern Italy, Sardinia, the Dalmatian coast, Greece, the

TABLE 1 Table of model performance (AUC, TSS, Sensitivity, Specificity, and Threshold) for 100 repetitions of each algorithm, including artificial neural network (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS), maximum entropy (MAXENT), random forest (RF), and surface range envelope (SRE).

	AUC		TSS				
Models	Mean	SD	Mean	SD	Sensitivity	Specificity	Threshold
ANN	0.932	0.01	0.797	0.03	96.525	83.168	0.371
CTA	0.915	0.01	0.802	0.03	96.037	84.125	0.348
FDA	0.934	0.01	0.791	0.03	95.463	83.593	0.435
GAM	0.938	0.01	0.813	0.02	96.268	85.011	0.500
GBM	0.943	0.01	0.819	0.02	96.428	85.489	0.515
GLM	0.931	0.01	0.794	0.03	95.277	84.065	0.518
MARS	0.936	0.01	0.802	0.02	95.500	84.704	0.483
MAXENT	0.940	0.01	0.808	0.02	95.410	85.413	0.166
RF	0.946	0.01	0.834	0.02	97.232	86.145	0.424
SRE	0.829	0.02	0.659	0.03	75.919	89.950	0.498

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Aegean Islands, Crete, and Asia Minor which is throughout the Black Sea of Turkey and the Turkish Aegean Sea coast. Under current conditions, the model prediction was highly compatible with the known distribution range of *Q. ilex*, which covers the Mediterranean Basin, but extending further east from the true formation (Figure 2d). In contrast to the scattered occurrence of *Q. ilex* in Turkey along the Black Sea, the model predicted suitable habitats further east of the current known distribution, forming a continuous range. However, although not represented with high probability (brighter colors in Figure 2d), distributions were detected in the Black Sea coast of Georgia, around the Iskenderun Bay from the South-West Mediterranean coast of Turkey, in southern Cyprus and in the Levant region.

3.3 | Historical prediction

Prediction for the past periods, obtained from two different global climate models and 10 different algorithms, gave consistent results despite regional differences, pointing to similar patterns of contractions and expansions for past periods (Figures S5–S24). The predictions generated by the RF algorithm for past periods are presented alongside fossil pollen records spanning the LIG, LGM, and MH periods (Figure 2). During the LIG period, our model predicted that *Q. ilex* was potentially present along the Mediterranean Basin but was more narrowly scattered along the coasts of Europe, North Africa, and Asia Minor. In the western Mediterranean, a slight northward shift of suitable areas was also observed. A high level of suitability was predicted along the Atlantic coast (Portugal, Gibraltar, the south-western Iberian Peninsula, Cantabrian Mountains, western France, and western Morocco), Corsica, south Italy, Sicily, Sardinia, Aegean Islands, Crete, and a small part of Turkey in the eastern Black Sea coast (Figure 2a). Transitions between LIG and LGM have been toward climatically favorable areas on the coasts of the Mediterranean Basin (especially North Africa, Balearic Islands, southern France, southern Italy, Adriatic Sea, Aegean Islands, Crete, and Peloponnese), with contraction in distribution in northwestern France and north of the Iberian Peninsula predicted. It is worth noting that the majority of the species' potential range in all of the Mediterranean Basin coasts during the LGM persisted in areas currently submerged. A high level of suitability was predicted along the Aegean and Black Sea coasts of Turkey, around Iskenderun Bay, Levant region, south Iberian Peninsula, Balearic Islands, southern France, southern Italy, and the Adriatic Sea (Figure 2b). During the MH, the potential distribution was similar to the present-day

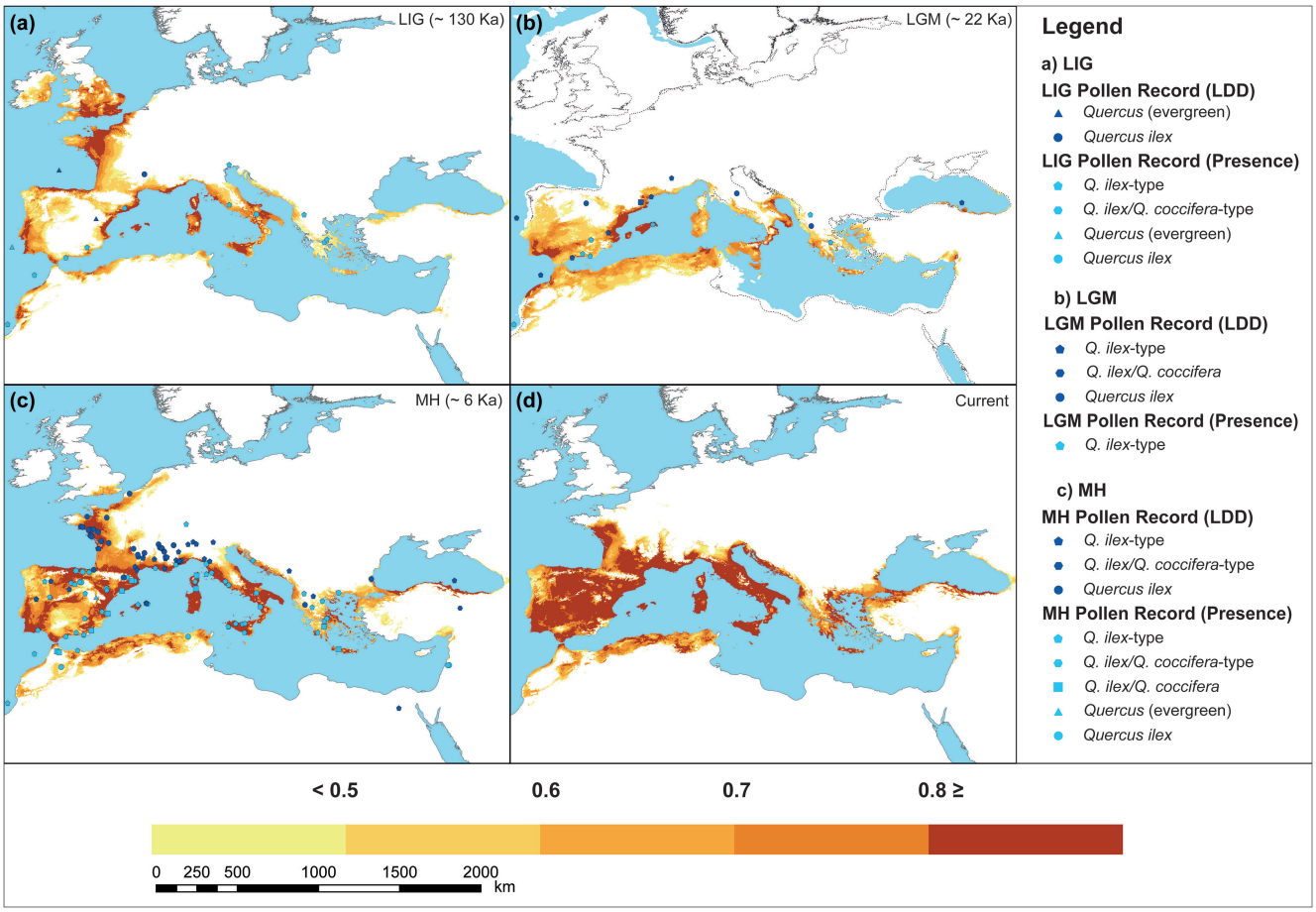


FIGURE 2 Past and current potential distribution of *Quercus ilex* from the mean of all repetition for random forest algorithm, here only CCSM4 is displayed (for MIROC-ESM see Figures S15–S24). Darker colors indicate a higher probability of occurrence. Both light and dark blue figures refer to fossil pollen records (Table S5).

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

distribution, as the model prediction indicates. Differences are observed in the central part of the Iberian Peninsula, such as a narrowing of the distribution compared to the current prediction, and a northward shift in suitable areas in western France (Figure 2c).

3.4 | Fossil pollen data

To compare and validate our model predictions for past periods, we compiled 177 records from the Neotoma Paleoecology Database and the literature, covering the LIG, LGM, and MH periods. These records were described as "*Q. ilex*", "*Q. ilex*-type", "*Q. ilex/Q. coccifera*", "*Quercus* (evergreen)", or "*Q. ilex/Q. coccifera*-type" (Table S5). Some pollen fields contained both continuous and discontinuous low numbers of fossil pollen records. We considered these data to represent long-distance distribution (LDD) and included them in the analysis, as it can contribute to the validation of our model. Thirteen out of sixteen pollen records for the LIG period are consistent with our model prediction. Three pollen records show low values (indicating LDD) and are 50 km away from our model prediction which indicate nearby presence. The majority of pollen records for the LGM period are generally low values and show LDD. Seven of the pollen records in the south of the Iberian Peninsula and in the Balearic Islands are profiles that record abundant *Q. ilex* and overlap our model prediction. Thirteen pollen records for the LGM period contained low values of *Q. ilex*, five of them overlap our prediction and others were nearby our prediction so that they indicate nearby refugia. Unlike LIG and LGM periods, 81 of the 150 records for the MH period were abundant and continuous throughout the current distribution range and northwest France. There were 69 records

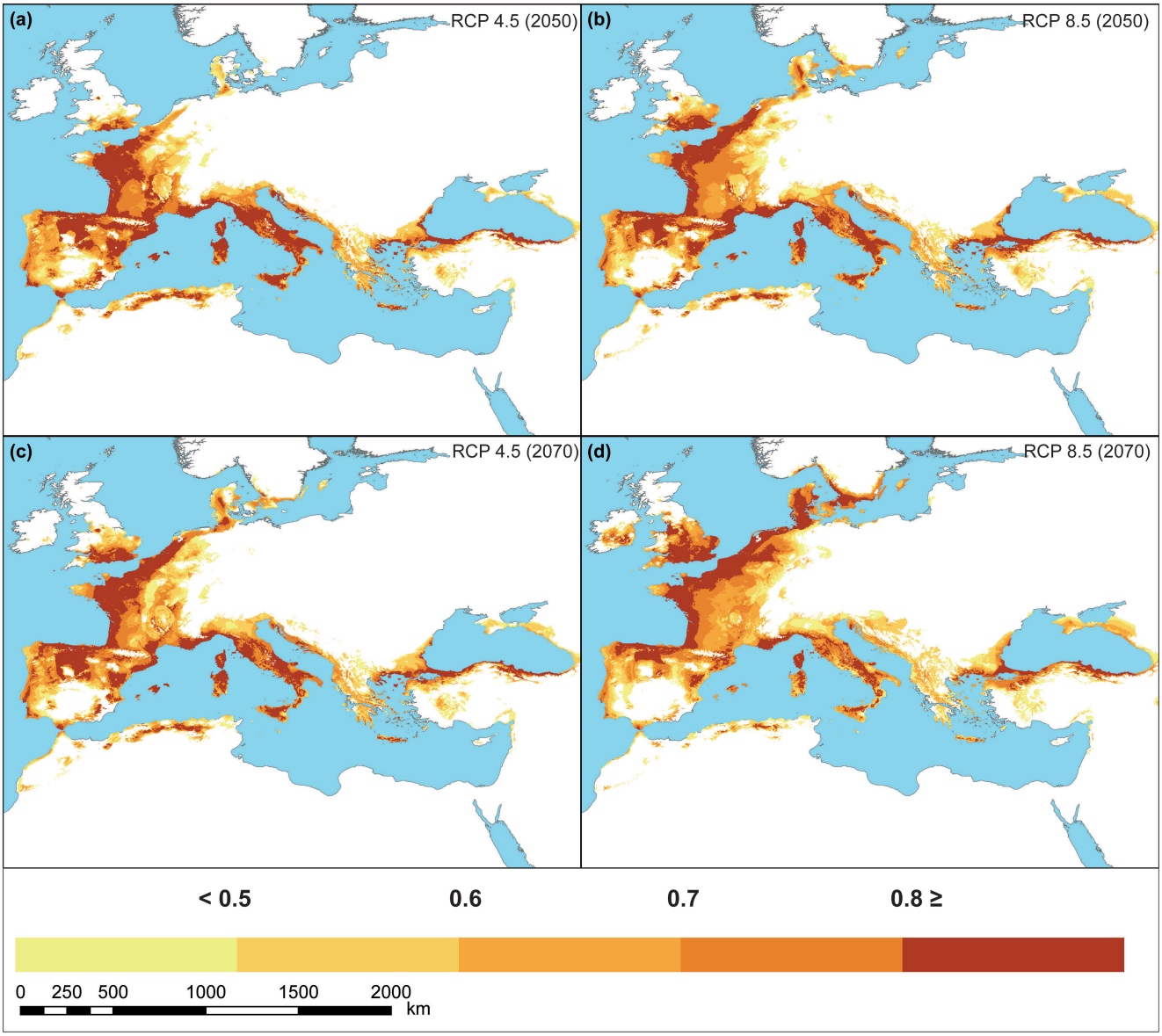


FIGURE 3 Potential distribution of *Quercus ilex* under climate change scenarios from the mean of all repetition for random forest algorithm outputs, here only CCSM4 displayed (for MIROC-ESM see Figures S15–S24). Darker colors indicate a higher probability of occurrence.

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

indicating LDD. Fifty-six of the eighty-one pollen records indicating abundant and continuous *Q. ilex* presence overlap and validate our model predictions.

3.5 | Future predictions

Based on future predictions, the main geographic shift of *Q. ilex* will be toward the north-northwest of its current distribution. Moreover, our model revealed potential suitable areas in the Inner-west Anatolia region for *Q. ilex* under both climate scenarios, despite the species not currently occupying these areas. However, these areas are predicted to have relatively lower levels of suitability. In addition, a serious range contraction is expected in the *Q. ilex* distribution under these scenarios (Figure 3). These contractions are larger in the models obtained with the 2070 RCP 8.5 scenario. Changes in the range of *Q. ilex*, including habitat loss, habitat gain, and habitat stability over time, are shown in Figure 4, Tables S6,S7 for both CCSM4 and MIROC-ESM GCM. In both climate scenarios (RCP 4.5 and RCP 8.5) and in both models produced for 2050–2070, areas that act as refugia for *Q. ilex* against the effects of the Quaternary climate oscillation in the past on the southern Mediterranean coasts (southern Iberian Peninsula, Sicily, Corsica, Sardinia, and Crete) were predicted by our model to act as a climate refuge in future scenarios (Figure 4), even though the suitability have decreased compared to current prediction (brighter colors in Figure 3). In the RCP 4.5 scenario, a high probability of predicted range change toward northwestern France is observed, whereas in the RCP 8.5 scenario, there is a decrease in the likelihood of suitable areas, leading to a contraction in their extent. (Figure 3d).

4 | DISCUSSION

The results indicated that the models successfully distinguished occurrence data from the background based on their AUC and TSS values varying from 0.829 to 0.946 for AUC, and from 0.659 to

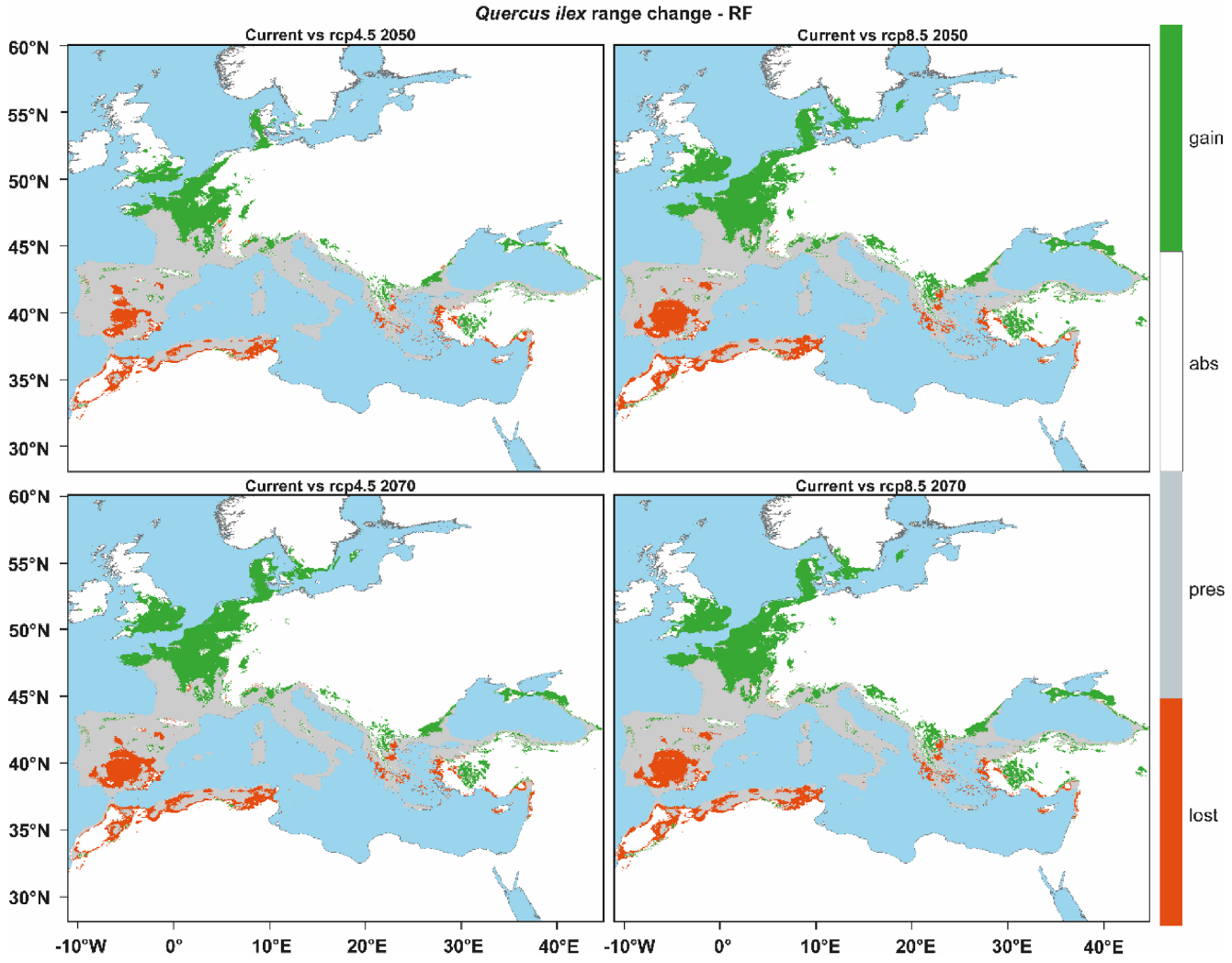


FIGURE 4 Range change maps of *Quercus ilex* produced from the current and future projections binary map of the RF algorithm outputs. Green areas refer to the expansion of species occurrence based on current predictions and future projections, red areas refer to the contraction, white areas refer to areas predicted to be absent in the future, gray areas refer to the areas predicted to be present in the future.

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

0.834 (all >0.7 except BIOCLIM, Table 1, Elith et al., 2011) for TSS. Also, consistent results between modeling performances from different algorithms, low standard deviations are noteworthy (Table 1, Figure S25), which is a clue for reproducibility. It is worth mentioning that our past predictions are in agreement with pollen data, suggesting that the ecological niche of *Q. ilex* is species-climatic equilibrium based on bioclimatic data (Nogués-Bravo, 2009). This justified us to use the trained model for past and future simulations. The known distribution of *Q. ilex* in Anatolia is characterized by scattered occurrences and does not form pure forests (Barbero et al., 1992; Browicz & Zieliński, 1982; de Rigo & Caudullo, 2016; Zohary, 1973). Nevertheless, our model predicts a continuous distribution of the species along the Black Sea coast of Anatolia (Figure 2d), indicating that it is subjected to significant human impact in this region. Indeed, the observed distributions in Samsun and Zonguldak were limited to urban areas, and the two occurrences near Sinop were fragmented by anthropogenic activities, as reported by Akkemik et al. (2020). The potential presence of *Q. ilex* in the Levant is questionable because the species is not currently found in that region. On the other hand, there is information in the literature that the species exists in Lebanon with fragmented distribution (Menitsky, 2005).

The model outputs indicate that the distribution of the species encompasses regions characterized by the Mediterranean climate, following a significant range contraction during the LIG-LGM transition from the distribution observed on the Atlantic coast. According to Vessella et al. (2015), based on the average results of seven different algorithms, the distribution of *Q. suber*, another evergreen oak species in the Mediterranean Basin, was found to have extended along the Atlantic coast (from the western Iberian Peninsula to northwestern France) during the LIG period. Subsequently, its distribution contracted to suitable areas in the southern Mediterranean due to the cooling climate during the LGM period, which is in line with the findings of our model. The results concerning the LIG period are reinforced by pollen data, which show continuous pollen values along the southern and eastern coastlines of the Iberian Peninsula, offshore the western shores of North Africa, as well as at the Valle di Castiglione and Lago Grande di Monticchio sites in central Italy, along with the southern Balkans region (Figure 2a, Table S5). This evidence indicates the presence of the *Q. ilex* during LIG period across southern Iberia, western North Africa, the central Mediterranean, and the southern Balkans.

The potential area of *Q. ilex* predicted by our model during LGM was limited to suitable areas in southern Europe along the Mediterranean coast due to the colder and drier climate during LGM (Figure 2b). These areas are consistent with the areas identified as glacial refugia during the LGM (Médail & Diadema, 2009) and support our model predictions. Our findings are further supported by molecular studies. Lumaret et al. (2002) revealed that the recolonization of *Q. ilex* following the last glacial period originated from the three Mediterranean peninsulas. Additionally, our model predicted suitable areas for the species in the south and southeast of the Iberian Peninsula, which is consistent with both molecular and palynological data (López de Heredia et al., 2007) and modeling studies (Benito Garzón et al., 2007) as well. Continuous and abundant pollen records are available from the southern Iberian Peninsula and the Balearic Islands, which are consistent with the areas predicted by our model. In addition, continuous but low pollen records from southern France, southern Italy, southern Greece, and the Black Sea coast of Turkey suggest the presence of nearby refugia during the LGM. Although there are no pollen records from Crete and Sicily, our model predicts these regions as refugia. This prediction is supported by molecular studies (Fineschi et al., 2005; Lumaret et al., 2002), which indicate the diversity of haplotypes in Sicily and its role as one of the colonization centers. Additionally, abundant pollen records from the MH demonstrate the dispersal of the species from refugia to the surrounding environment after the LGM, further supporting our predictions (Table S5). Our models predicted the role of refugia in the Aegean, Black Sea, and Mediterranean coasts, and Amanos Mountains in Anatolia. However, these predictions lack support from both pollen records and molecular studies, with the exception of the Black Sea coast where discontinuous low pollen records exist.

Our model predicted a *Q. ilex* distribution during the MH period that was similar to the present day. As anticipated, the more favorable climatic conditions during the MH allowed for an expansion of the *Q. ilex* range, in contrast to the LGM. However, our model predicted a northward extension along the northwestern coast of France during the MH, which is not observed in the present distribution. Furthermore, our model predicted a more restricted distribution of *Q. ilex* in southern Europe, including the central Iberian Peninsula, Italy, the southern Balkans, and Anatolia, compared to its current range. Moreover, the model was constrained in its ability to predict areas of high climate suitability during the MH period, resulting in a more limited projection compared to the present distribution. Paleoclimatic reconstructions indicate that the MH had a warmer climate than the present, varying by season and region (Mauri et al., 2015; Strandberg et al., 2022). Specifically, in northern Europe, winter temperatures were higher than today, which may have led to a shift in the predicted distribution of *Q. ilex* further northwest into France. Moreover, drier conditions in the Mediterranean region due to reduced summer precipitation and relatively stable winter precipitation (Strandberg et al., 2022) may have contributed to the predicted distribution of *Q. ilex* being more similar to its current distribution. These findings are supported by numerous continuous and discontinuous pollen records obtained from various locations spanning northwest France and the entire Mediterranean Basin (Figure 2c, Table S5). The continuous and abundant pollen records found in the Ammiq and Chamsine locations in Lebanon, Steerenmoos in Germany, and the low but continuous pollen records in Qarun Lake in Egypt do not match the output of our model for the MH period. These records indicate the presence of evergreen oaks in the Levant region, while the records from Germany and Egypt reflect human impact rather than the natural occurrence of the species. Therefore, it is natural that our model outputs do not match these records (Cheddadi & Khater, 2016; Hajar et al., 2010; Hamdan et al., 2020; Rösch et al., 2012).

Our model projections suggest that the distribution of *Q. ilex* in the Mediterranean Basin will experience significant range

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

contractions as a result of climate change, with the southern and central Iberian Peninsula, North Africa, and the Aegean coast of Anatolia being particularly vulnerable under the RCP 4.5 scenario. Under the more severe RCP 8.5 scenario, the contractions are predicted to be even more severe and widespread throughout the basin. These results are consistent with other modeling studies that also predicted range contractions in North Africa. For example, in Algeria, Tabet et al. (2018) predicted a strong negative impact of climate change on *Q. ilex*, resulting in a substantial contraction of its distribution in Algeria. Our results on the distribution of *Q. ilex* in the Iberian and Italian Peninsula contradict the predictions made by López-Tirado et al. (2018) and López-Tirado and Hidalgo (2018), who suggested that evergreen oak species, including *Q. ilex*, may expand their range of distribution and benefit from climate change in the western Mediterranean region. However, our approach takes into account the ecological requirements of *Q. ilex* and eliminates highly correlated variables, which helps to prevent overestimation by producing more simple models. Furthermore, by incorporating the *Q. ilex*'s entire range distribution in the model, we established the climate equilibrium for current conditions, which may provide a more realistic prediction of its potential response to future climate change. However, there is an agreement in our mutual prediction that *Q. ilex* will expand its distribution in France, which is a result of other modeling studies in literature (Cheaib et al., 2012). Climate projections for the central and southern regions of the Iberian Peninsula, particularly under the RCP8.5 scenario, indicate a significant decrease in annual precipitation, pointing to pronounced summer droughts (Andrade et al., 2021; Cardoso Pereira et al., 2020). Furthermore, these projections forecast a striking increase in temperatures in these same regions compared to those in others (Viceto et al., 2019). Despite *Q. ilex* being known for its resistance to summer droughts, the increasing temperatures and more frequent occurrences of extreme drought events may strain its capacity for recovery, leading to an increase in its sensitivity to climate change (Barbeta & Peñuelas, 2016; Gea-Izquierdo et al., 2009). In addition, experimental studies have shown that the drought-adaptive characteristics of *Q. ilex* leaves increase their tolerance to moderate drought, but do not confer resistance to severe water stress (Limousin et al., 2022). Furthermore, the percentage of seed germination and the development of normal seedlings are closely related to the water content of the seeds after winter, and it has been suggested that drying in situ is a significant cause of seed mortality. Findings reveal that seed drying sensitivity is an important functional trait that may affect the propagation success in temperate climate resistant seed species. Furthermore, reduced winter precipitation can negatively impact the germination success of seeds (Joët et al., 2013, 2016). Moreover, (Martínez-Vilalta et al., 2003; Ogaya & Peñuelas, 2003) suggest that *Q. ilex* could gradually be replaced by other species that are better adapted to summer droughts. The model outputs for the central and southern regions of the Iberian Peninsula align with these findings and are supported by this information within the context of future scenarios. Therefore, the increase in temperature in the western Mediterranean Basin, the decrease in precipitation, and the changes in the seasonality of precipitation may result in severe suitable area contractions in the southern Iberian Peninsula in our models, in Africa, and in the reduction of high suitable areas along the Mediterranean Basin. Based on future predictions, the main geographic shift of *Q. ilex* will be toward the north-northwest of its current distribution (Figure 4). It is worth emphasizing that *Q. ilex* is an introduced species in these newly acquired areas in northwestern Europe, especially in southern England (Fisher et al., 1994; Southwood et al., 2004). Regarding the Atlantic coast of France, Delzon et al. (2013) suggest that the rates of *Q. ilex* dispersion and establishment may not keep up with the velocity of climate change, thus limiting its ability to expand into emerging suitable areas. Additionally, our model predicts only moderate levels of suitability for *Q. ilex* in the Inner West Anatolia subregion (Figure 4), which is not currently occupied by the species. Due to the effect of climate change, including increasing temperatures, decreasing frost days, and an extended vegetation period in the region, it is likely that new species, especially evergreen oaks, may colonize the area (Sar et al., 2019). However, considering the precipitation conditions, the colonization of *Q. ilex* in this region appears unlikely. Indeed, our model predictions also show low probability.

In our past period predictions, areas that are consistently predicted as suitable are noteworthy as long-term refugia (Figure 5) correspond with modeling studies, phylogeographic studies, and DNA studies specific to *Q. ilex* (López de Heredia et al., 2007; Lumaret et al., 2002; Médail & Diadema, 2009). Furthermore, our model suggests that the Black Sea coast in Anatolia and around Iskenderun Bay may serve as a long-term refugium for *Q. ilex*. The identification of multiple oak species, subspecies, and varieties in Anatolia suggests its role as a refugia (Hedge & Yaltırık, 1982; Rokas et al., 2003) such that genetic evidence and ecological niche modeling have further supported the notion that Anatolia may have served as a refuge for several evergreen and deciduous oak species during the LGM period (Di Pasquale et al., 2020; Tekpinar et al., 2021; Toumi & Lumaret, 2010; Ülker et al., 2018; Vessella et al., 2015). Unfortunately, there is no evidence of the existence of *Q. ilex* in Anatolia during the LIG period. Nevertheless, Anatolia is considered the origin of the eastern populations of another evergreen oak species, *Q. coccifera* (Toumi & Lumaret, 2010), and is also believed to be one of the possible origins of the deciduous oak species *Q. cerris* (Bagnoli et al., 2016), suggesting that Anatolia may have served as a founding population for *Q. ilex*. Therefore, more detailed molecular studies, particularly in Anatolia, are required to gain a better understanding of the phylogeography of *Q. ilex*.

A noteworthy difference is detected in the long-term refugia areas observed between the CCSM4 and MIROC-ESM models in the southern and central parts of the Iberian Peninsula. This difference may arise due to uncertainties within the models themselves or, considering the resemblance of the two climate models' outputs at other locations in the Mediterranean region, be linked to the inclusion/exclusion of the LIG period. The predictions from CCSM4 climate models indicate unsuitable habitats for the LIG period in the southern and central Iberian Peninsula, aligning with

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

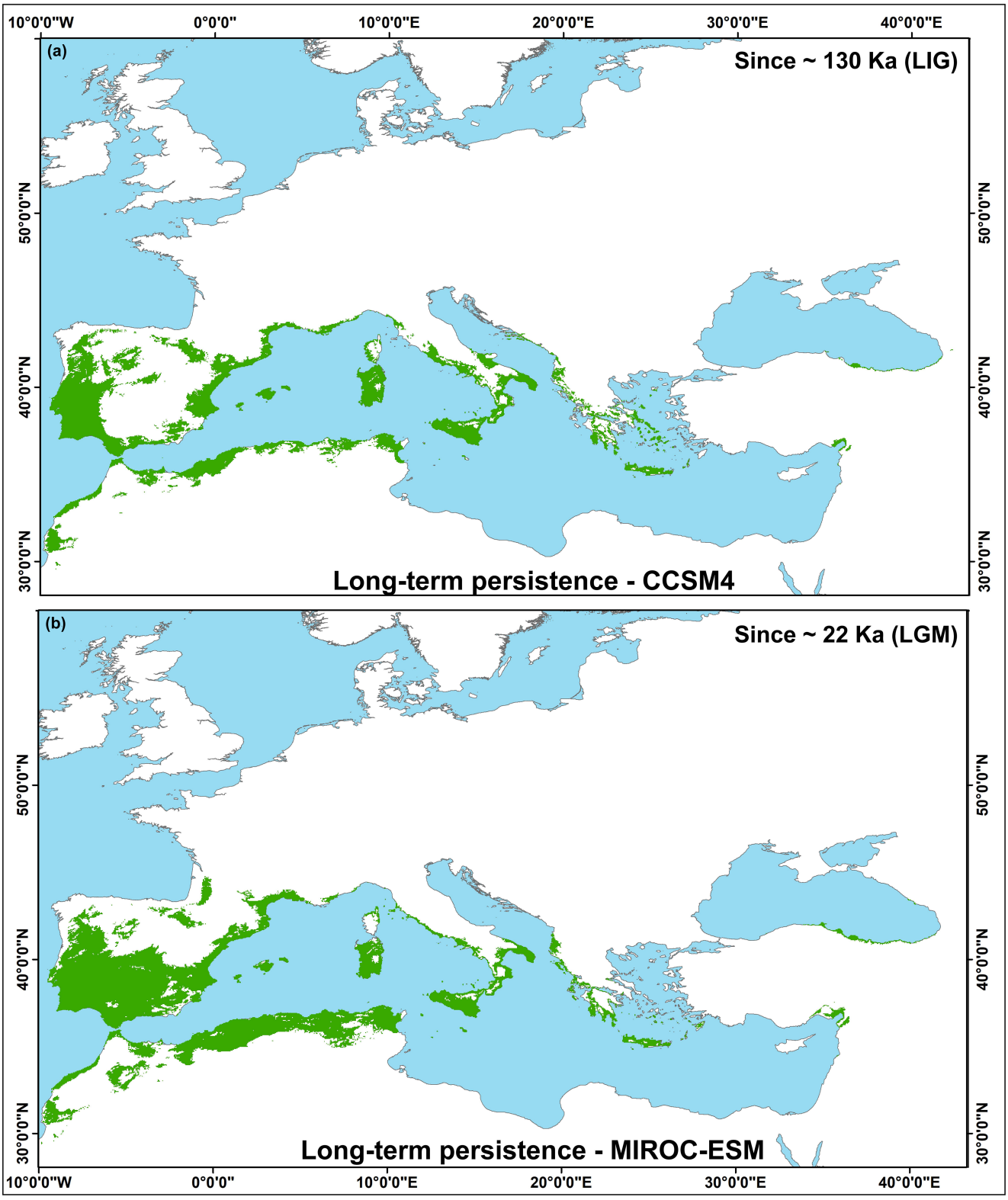


FIGURE 5 The areas identified as continuously suitable for *Quercus ilex* under the LIG, the LGM, the MH, and the current climate conditions have been inferred as long-term persistence or putative "long-term refugia". This inference was based on the outputs of the random forest (RF) algorithm, using global climate models CCSM4 (a) and MIROC-ESM (b).

the outputs under future climate scenarios. It is known that the ecological trends and responses of the LIG period are recognized as a potential analog to enhance future climate change projections (Kukla et al., 2002; Otto-Bliesner et al., 2021). The long-term pollen record from Villarquemado, an area in the interior of the Iberian Peninsula, indicated the presence of *Juniperus* and *Artemisia* pollen

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

records during the LIG period, demonstrating suitability for intense evapotranspiration conditions triggering higher soil water deficit and high thermal seasonality in the region (González-Sampériz et al., 2020); in contrast, pollen records from Padul, a location in the southern Iberian Peninsula characterized by oceanic influences and mountainous areas, revealed the emergence of both evergreen and deciduous oak species, and *Pistacia*, as well as moisture-demanding species such as *Betula*, *Alnus*, and *Fraxinus* during the LIG period, indicating warm and humid interglacial climate conditions (Camuera et al., 2019). Climate projections covering the Iberian Peninsula notably point to a significant decrease in annual precipitation and an increase in precipitation seasonality in the central region (Andrade et al., 2021; Cardoso Pereira et al., 2020), positioning it as an area with the highest projected increase in annual mean temperatures on the Iberian Peninsula (Viceto et al., 2019). The similarities in model predictions within the central Iberian Peninsula between the LIG period and future climate change scenarios can be attributed to decreased precipitation and increased evapotranspiration due to rising temperatures and continental conditions.

5 | CONCLUSIONS

In this study, we investigated the late Quaternary range changes of *Q. ilex* by ecological niche modeling and predicted the future distribution of the species in response to global climate change. For that we applied 10 different algorithms provided by "biomod2" among them, the RF algorithm performed best with more plausible results for both past and future distributions. We then compared the model outputs with palynological records from LIG, LGM, and MH to validate that the results were in agreement with the palynological data. Our model defined a long-term refugia role for *Q. ilex* in the Mediterranean Basin (Figure 5) in past prediction. These areas overlap with chloroplast DNA studies. In addition, the long-term refugia role of the east Black Sea coast in Anatolia and around Iskenderun Bay has been observed. While our model predictions do not have sufficient genetic or pollen data to support the potential role of Anatolia as a long-term refuge for *Q. ilex* populations, they do emphasize the need for further, more detailed molecular studies involving Anatolia to gain a better understanding of the phylogeography of *Q. ilex*. The results of our future projection analyses indicate that both RCP 4.5 and RCP 8.5 scenarios will have a considerable impact on the distribution range of *Q. ilex*. While significant reductions in suitable areas were observed in the central and southern regions of the Iberian Peninsula and North Africa, the model predicts a general contraction of suitable areas in northern Italy, southern Greece, and the Aegean coasts of Anatolia, due to less favorable climate conditions. Notably, our model predicts a substantial contraction of suitable areas in the maps produced for the year 2070, particularly under the RCP 8.5 scenario, in regions that were identified as long-term refugia in the past period. It should be noted that the current study excludes local adaptation. Although the correlative modeling approach has been emphasized in the literature for potentially underestimating species range dynamics (Benito Garzón et al., 2019; Hoffmann & Sgrò, 2011; Waldvogel et al., 2020), we would like to emphasize that this study identifies areas within the entire distribution range of *Q. ilex* where the species may be susceptible to the consequences of climate change, even if there is some potential for underestimation. These findings identify regions that require prioritization for conservation efforts. Indeed, the observed habitat losses in genetically diverse areas that exhibit high suitability for the species, acting as long-term refugia, underscore the need for studies that integrate local adaptation and ENM approaches at a local level in these regions. Our models predicted a range shift toward the north and northwest of the current *Q. ilex* distribution under both scenarios, resulting in a significant increase in available area for the species in these regions in the future. However, the ability of *Q. ilex* to migrate to these potential suitable areas remains uncertain due to the limitations of dispersal and establishment in the relatively short time frame considered. This study may be extended by incorporating additional environmental variables, such as soil type, elevation, and aspect, in addition to climate variables, and by employing alternative climate models, as appropriate. Nevertheless, the inclusion of these variables in ecological niche models is subject to the availability of data within the range of the species, which may be lacking or require certain assumptions that may affect the reliability of the results, particularly for distant past time periods. Despite being an older data version, we utilized WorldClim v.1.4 for all the periods included in the study. However, it is important to note that WorldClim v.2.1 has benefited from data recorded by a higher number of meteorological stations, especially at higher latitudes and different elevations. As a result, there is a possibility of inconsistencies in model predictions compared to those generated by WorldClim v.1.4 across Europe (Cerasoli et al., 2022). Once WorldClim v.2.1 version for past periods becomes available, it would allow the study to be replicated using more up-to-date data, thereby strengthening the representation of outputs within future scenarios. The Mediterranean Basin is one of the most vulnerable climate change hotspots in the world, and thus, understanding how climate change will affect the distribution of plant species in the Mediterranean Basin allows better species risk assessment and conservation management to be prepared. This study reveals important findings about the sensitivity of the *Q. ilex* species, which can be considered as a key species for the Mediterranean ecosystem, future climate change, and points out the importance of Anatolia for the species and our study suggests that more detailed molecular studies involving Anatolia are needed to understand the phylogeography of *Q. ilex*.

AUTHOR CONTRIBUTIONS

Burak Suicmez: Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); resources (equal); software (lead); validation (equal); visualization (equal); writing – original draft (lead). **Meral Avci:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); project

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

administration (lead); resources (equal); supervision (lead); validation (equal); visualization (equal); writing – review and editing (lead).

ACKNOWLEDGEMENTS

The authors are grateful to Prof. Dr. Nüzhet Dalfes (ITU) for organizing the trainings for the R Studio program used in data processing and model creation; to Prof. Dr. Sedat Avci (IU) for fruitful discussions on maps generated for the study; as well as to the creators of the open-source "ENM2020: a free online course and set of resources on modeling species niches and distributions" course.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Datasets and programming codes are available in Supporting Information.

ORCID

Burak Suicmez https://orcid.org/0009-0008-2113-1022
Meral Avci https://orcid.org/0000-0003-4367-3021

REFERENCES

Akkemik, Ü., Genç, S., Yilmaz, O. Y., Selvi, E., Yilmaz, H., Sevgi, E., Sevgi, O., & Akarsu, F. (2021). Effects of growing site parameters on vessel elements of *Quercus ilex* through Turkey and evaluating in respect of forestry. *Turkish Journal of Agriculture and Forestry*, *45*(5), 599–616. https://doi.org/10.3906/TAR-2011-65

Akkemik, Ü., Yılmaz, O., Yılmaz, H., Sevgi, O., Sevgi, E., Akarsu, F., & Doğan, H. (2020). Current distribution of *Quercus ilex* species in Turkey, detection and evaluation of new distribution areas. *Eurasian Journal of Forest Science*, *8*, 195–220. https://doi.org/10.3195/ejejfs.786041 (in Turkish).

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Almeida, A. M., Martins, M. J., Campagnolo, M. L., Fernandez, P., Albuquerque, T., Gerassis, S., Gonçalves, J. C., & Ribeiro, M. M. (2022). Prediction scenarios of past, present, and future environmental suitability for the Mediterranean species *Arbutus unedo* L. *Scientific Reports*, *12*(1), 84. https://doi.org/10.1038/s41598-021-03996-0

Andrade, C., Contente, J., & Santos, J. A. (2021). Climate change projections of aridity conditions in the Iberian Peninsula. *Water*, *13*(15), 2035. https://doi.org/10.3390/w13152035

Araújo, M. B., & Rahbek, C. (2006). How does climate change affect biodiversity? *Science*, *313*(5792), 1396–1397. https://doi.org/10.1126/science.1131758

Avci, M. (2005). Diversity and endemism in Turkey's vegetation. *Istanbul University Journal of Geography*, *13*, 27–55.

Badgley, C., Smiley, T. M., Terry, R., Davis, E. B., DeSantis, L. R. G., Fox, D. L., Hopkins, S. S. B., Jezkova, T., Matocq, M. D., Matzke, N., McGuire, J. L., Mulch, A., Riddle, B. R., Roth, V. L., Samuels, J. X., Strömberg, C. A. E., & Yanites, B. J. (2017). Biodiversity and topographic complexity: Modern and geohistorical perspectives. *Trends in Ecology & Evolution*, *32*(3), 211–226. https://doi.org/10.1016/j.tree.2016.12.010

Bagnoli, F., Tsuda, Y., Fineschi, S., Bruschi, P., Magri, D., Zhelev, P., Paule, L., Simeone, M. C., González-Martínez, S. C., & Vendramin, G. G. (2016). Combining molecular and fossil data to infer demographic history of *Quercus cerris*: Insights on European eastern glacial refugia. *Journal of Biogeography*, *43*(4), 679–690. https://doi.org/10.1111/jbi.12673

Barber, R. A., Ball, S. G., Morris, R. K. A., & Gilbert, F. (2022). Target-group backgrounds prove effective at correcting sampling bias in Maxent models. *Diversity and Distributions*, *28*(1), 128–141. https://doi.org/10.1111/ddi.13442

Barbero, M., Loisel, R., & Quézel, P. (1992). Biogeography, ecology and history of Mediterranean *Quercus ilex* ecosystems. In F. Romane & J. Terradas (Eds.), *Quercus ilex L. ecosystems: Function, dynamics and management* (pp. 19–34). Springer Netherlands. https://doi.org/10.1007/978-94-017-2836-2_2

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Barbeta, A., & Peñuelas, J. (2016). Sequence of plant responses to droughts of different timescales: Lessons from holm oak (*Quercus ilex*) forests. *Plant Ecology and Diversity*, *9*(4), 321–338. https://doi.org/10.1080/17550874.2016.1212288

Barcikowska, M. J., Kapnick, S. B., & Feser, F. (2018). Impact of large-scale circulation changes in the North Atlantic sector on the current and future Mediterranean winter hydroclimate. *Climate Dynamics*, *50*(5), 2039–2059. https://doi.org/10.1007/s00382-017-3735-5

Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2013). Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics*, *19*, 10–15. https://doi.org/10.1016/j.ecoinf.2013.11.002

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Benito Garzón, M., Robson, T. M., & Hampe, A. (2019). ΔTraitSDMs: Species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, *222*(4), 1757–1765. https://doi.org/10.1111/nph.15716

Benito Garzón, M., Sánchez De Dios, R., & Sáinz Ollero, H. (2007). Predictive modelling of tree species distributions on the Iberian Peninsula during the last glacial maximum and mid-Holocene. *Ecography*, *30*(1), 120–134. https://doi.org/10.1111/j.0906-7590.2007.04813.x

Bennett, K. D., & Provan, J. (2008). What do we mean by 'refugia'? *Quaternary Science Reviews*, *27*(27), 2449–2455. https://doi.org/10.1016/j.quascirev.2008.08.019

Bennett, K. D., Tzedakis, P. C., & Willis, K. J. (1991). Quaternary refugia of North European trees. *Journal of Biogeography*, *18*(1), 103–115. https://doi.org/10.2307/2845248

Bhagwat, S. A., & Willis, K. J. (2008). Species persistence in northerly glacial refugia of Europe: A matter of chance or biogeographical traits? *Journal of Biogeography*, *35*(3), 464–482. https://doi.org/10.1111/j.1365-2699.2007.01861.x

Bilgin, R. (2011). Back to the suture: The distribution of intraspecific genetic diversity in and around Anatolia. *International Journal of Molecular Sciences*, *12*(6), 4080–4103. https://doi.org/10.3390/ijms12064080

Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, *275*, 73–77. https://doi.org/10.1016/j.ecolmodel.2013.12.012

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Browicz, K., & Zieliński, J. (1982). *Chorology of trees and shrubs in southwest Asia and adjacent regions* (Vol. 1). Polish Scientific Publishers.

Brown, J. L., Bennett, J. R., & French, C. M. (2017). SDMtoolbox 2.0: The next generation python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ*, *2017*(12), e4095. https://doi.org/10.7717/peerj.4095

Campelo, F., Nabais, C., García-González, I., Cherubini, P., Gutiérrez, E., & Freitas, H. (2009). Dendrochronology of *Quercus ilex* L. and its potential use for climate reconstruction in the Mediterranean region. *Canadian Journal of Forest Research*, *39*(12), 2486–2493. https://doi.org/10.1139/X09-163

Camuera, J., Jiménez-Moreno, G., Ramos-Román, M. J., García-Alix, A., Toney, J. L., Anderson, R. S., Jiménez-Espejo, F., Bright, J., Webster, C., Yanes, Y., & Carrión, J. S. (2019). Vegetation and climate changes during the last two glacial-interglacial cycles in the western Mediterranean: A new long pollen record from Padul (southern Iberian Peninsula). *Quaternary Science Reviews*, *205*, 86–105. https://doi.org/10.1016/j.quascirev.2018.12.013

Cardoso Pereira, S., Marta-Almeida, M., Carvalho, A. C., & Rocha, A. (2020). Extreme precipitation events under climate change in the Iberian Peninsula. *International Journal of Climatology*, *40*(2), 1255–1278. https://doi.org/10.1002/joc.626

Caudullo, G., Welk, E., & San-Miguel-Ayanz, J. (2017). Chorological maps for the main European woody species. *Data in Brief*, *12*, 662–666. https://doi.org/10.1016/j.dib.2017.05.007

Cerasoli, F., D'Alessandro, P., & Biondi, M. (2022). Worldclim 2.1 versus Worldclim 1.4: Climatic niche and grid resolution affect between-version mismatches in habitat suitability models predictions across Europe. *Ecology and Evolution*, *12*(2), e8430. https://doi.org/10.1002/ece3.8430

Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E. S., Legay, M., Pagé, C., Thuiller, W., Viovy, N., & Leadley, P. (2012). Climate change impacts on tree ranges: Model intercomparison facilitates understanding and quantification of uncertainty. *Ecology Letters*, *15*(6), 533–544. https://doi.org/10.1111/j.1461-0248.2012.01764.x

Cheddadi, R., & Khater, C. (2016). Climate change since the last glacial period in Lebanon and the persistence of Mediterranean species. *Quaternary Science Reviews*, *150*, 146–157. https://doi.org/10.1016/j.quascirev.2016.08.010

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, *28*(8), 482–488. https://doi.org/10.1016/j.tree.2013.04.003

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, *292*(5517), 673–679. https://doi.org/10.1126/science.292.5517.673

de Rigo, D., & Caudullo, G. (2016). Quercus ilex in Europe: distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European Atlas of forest tree species*. European Union Publication Office.

Delzon, S., Urli, M., Samalens, J.-C., Lamy, J.-B., Lischke, H., Sin, F., Zimmermann, N. E., & Porté, A. J. (2013). Field evidence of colonisation by holm oak, at the northern margin of its distribution range, during the Anthropocene period. *PLoS One*, *8*(11), e80443. https://doi.org/10.1371/journal.pone.0080443

Di Pasquale, G., Saracino, A., Bosso, L., Russo, D., Moroni, A., Bonanomi, G., & Allevato, E. (2020). Coastal pine-oak glacial Refugia in the mediterranean basin: A biogeographic approach based on charcoal analysis and spatial modelling. *Forests*, *11*(6), 673. https://doi.org/10.3390/F11060673

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Elith, J. (2000). Quantitative methods for modeling species habitat: Comparative performance and an application to Australian plants. In S. Ferson & M. Burgman (Eds.), *Quantitative methods for conservation biology* (pp. 39–58). Springer. https://doi.org/10.1007/0-387-22648-6_4

ESRI. (2020). *ArcGIS Desktop: Release 10.8*. Environmental Systems Research Institute.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Fineschi, S., Cozzolino, S., Migliaccio, M., Musacchio, A., Innocenti, M., & Vendramin, G. G. (2005). Sicily represents the Italian reservoir of chloroplast DNA diversity of *Quercus ilex* L. (Fagaceae). *Annals of Forest Science*, *62*(1), 79–84. https://doi.org/10.1051/forest:2004085

Fisher, P. J., Petrini, O., Petrini, L. E., & Sutton, B. C. (1994). Fungal endophytes from the leaves and twigs of *Quercus ilex* L. from England, Majorca and Switzerland. *New Phytologist*, *127*(1), 133–137. https://doi.org/10.1111/j.1469-8137.1994.tb04267.x

Fyllas, N. M., Sazeides, C. I., & Spyroglou, G. (2019). Potential impacts of climate change on the distribution of seven dominant tree species in Greece. *Plants*, *11*(12), 1–2. https://doi.org/10.3390/plants11121616

Günal, N. (2003). Türkiye'de Sınırlı Yayılışa Sahip Bir Meşe Türü: *Quercus ilex* (Pırnal Meşesi). *Öneri Dergisi*, *5*(19), 191–197. https://doi.org/10.14783/maruoneri.682744 (in Turkish).

Gea-Izquierdo, G., Martín-Benito, D., Cherubini, P., & Cañellas, I. (2009). Climate-growth variability in *Quercus ilex* L. west Iberian open woodlands of different stand density. *Annals of Forest Science*, *66*(8), 802. https://doi.org/10.1051/forest/2009080

Giorgi, F. (2006). Climate change hot-spots. *Geophysical Research Letters*, *33*, L08707. https://doi.org/10.1029/2006GL025734

Global Biodiversity Information Facility (GBIF). (2022). *GBIF Occurrence Download*. https://doi.org/10.15468/dl.mxppy7

González-Sampériz, P., Gil-Romera, G., García-Prieto, E., Aranbarri, J., Moreno, A., Morellón, M., Sevilla-Callejo, M., Leunda, M., Santos, L., Franco-Múgica, F., Andrade, A., Carrión, J. S., & Valero-Garcés, B. L. (2020). Strong continentality and effective moisture drove unforeseen vegetation dynamics since the last interglacial at inland Mediterranean areas: The Villarquemado sequence in NE Iberia. *Quaternary Science Reviews*, *242*, 106425. https://doi.org/10.1016/j.quascirev.2020.106425

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). Habitat suitability and distribution models: With applications in R. In *Ecology, biodiversity and conservation*. Cambridge University Press. https://doi.org/10.1017/9781139028271

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., Regan, T. J., Brotons, L., Mcdonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., … Buckley, Y. M. (2013). Predicting

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

species distributions for conservation decisions. *Ecology Letters*, *16*(12), 1424–1435. https://doi.org/10.1111/ele.12189

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*(2–3), 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Guo, W.-Y., Serra-Diaz, J. M., Schrodt, F., Eiserhardt, W. L., Maitner, B. S., Merow, C., Violle, C., Anand, M., Belluau, M., Bruun, H. H., Byun, C., Catford, J. A., Cerabolini, B. E. L., Chacón-Madrigal, E., Ciccarelli, D., Cornelissen, J. H. C., Dang-Le, A. T., de Frutos, A., Dias, A. S., … Svenning, J.-C. (2022). High exposure of global tree diversity to human pressure. *Proceedings of the National Academy of Sciences*, *119*(25), e2026733119. https://doi.org/10.1073/pnas.2026733119

Hajar, L., Haïdar-Boustani, M., Khater, C., & Cheddadi, R. (2010). Environmental changes in Lebanon during the Holocene: Man vs. climate impacts. *Journal of Arid Environments*, *74*(7), 746–755. https://doi.org/10.1016/j.jaridenv.2008.11.002

Hamdan, M. A., Flower, R. J., Hassan, F. A., & Leroy, S. A. G. (2020). Geochemical and palynological analysis of Faiyum Lake sediments, Egypt: Implications for holocene paleoclimate. *Journal of African Earth Sciences*, *167*, 103864. https://doi.org/10.1016/j.jafrearsci.2020.103864

Hampe, A., & Jump, A. S. (2011). Climate relicts: Past, present, future. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 313–333. https://doi.org/10.1146/annurev-ecolsys-102710-145015

Hedge, I. C., & Yaltırık, F. (1982). Quercus L. In P. H. Davis, J. R. Edmondson, R. R. Mill, & K. Tan (Eds.), *Flora of Turkey and the East Aegean Islands Vol. 7* (pp. 659–683). Edinburgh University Press.

Hernández-Agüero, J. A., Ruiz-Tapiador, I., & Cayuela, L. (2022). What feeds on *Quercus ilex* L.? A biogeographical approach to studying trophic interactions in a Mediterranean keystone species. *Diversity and Distributions*, *28*(1), 4–24. https://doi.org/10.1111/ddi.13413

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*(3), 247–276. https://doi.org/10.1006/bijl.1996.0035

Hewitt, G. M. (1999). Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, *68*(1–2), 87–112. https://doi.org/10.1006/bijl.1999.0332

Hewitt, G. M. (2000). The genetic legacy of the quaternary ice ages. *Nature*, *405*(6789), 907–913. https://doi.org/10.1038/35016000

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the quaternary. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *359*(1442), 183–195. https://doi.org/10.1098/rstb.2003.1388

Hijmans, R. J. (2023). *_terra: Spatial Data Analysis_*. (R package version 1.7-18). https://cran.r-project.org/package=terra

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(7335), 479–485. https://doi.org/10.1038/nature09670

Hughes, P. D., Gibbard, P. L., & Ehlers, J. (2013). Timing of glaciation during the last glacial cycle: Evaluating the concept of a global 'last glacial maximum' (LGM). *Earth-Science Reviews*, *125*, 171–198. https://doi.org/10.1016/j.earscirev.2013.07.003

IPCC. (2021). Summary for policymakers. In V. Masson-Delmotte, P. Zhai, A. Pirani, T. K. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, B. Zhou, T. K. Maycock, T. Waterfield, O. Yelekçi, & R. Yu (Eds.), *Climate change 2021: The physical science basis. contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change* (pp. 3–32). Cambridge University Press.

Joët, T., Ourcival, J. M., Capelli, M., Dussert, S., & Morin, X. (2016). Explanatory ecological factors for the persistence of desiccation-sensitive seeds in transient soil seed banks: *Quercus ilex* as a case study. *Annals of Botany*, *117*(1), 165–176. https://doi.org/10.1093/aob/mcv139

Joët, T., Ourcival, J.-M., & Dussert, S. (2013). Ecological significance of seed desiccation sensitivity in *Quercus ilex*. *Annals of Botany*, *111*(4), 693–701. https://doi.org/10.1093/aob/mct025

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122. https://doi.org/10.1038/sdata.2017.122

Kukla, G. J., Bender, M. L., de Beaulieu, J. L., Bond, G., Broecker, W. S., Cleveringa, P., Gavin, J. E., Herbert, T. D., Imbrie, J., Jouzel, J., Keigwin, L. D., Knudsen, K. L., McManus, J. F., Merkt, J., Muhs, D. R., Müller, H., Poore, R. Z., Porter, S. C., Seret, G., … Winograd, I. J. (2002). Last interglacial climates. *Quaternary Research*, *58*(1), 2–13. https://doi.org/10.1006/qres.2001.2316

López de Heredia, U., Carrión, J. S., Jiménez, P., Collada, C., & Gil, L. (2007). Molecular and palaeoecological evidence for multiple glacial refugia for evergreen oaks on the Iberian Peninsula. *Journal of Biogeography*, *34*(9), 1505–1517. https://doi.org/10.1111/j.1365-2699.2007.01715.x

López-Tirado, J., & Hidalgo, P. J. (2018). Predicting suitability of forest dynamics to future climatic conditions: The likely dominance of holm oak [*Quercus ilex* subsp. ballota (Desf.) Samp.] and Aleppo pine (*Pinus halepensis* Mill.). *Annals of Forest Science*, *75*(1), 19. https://doi.org/10.1007/s13595-018-0702-1

López-Tirado, J., Vessella, F., Schirone, B., & Hidalgo, P. J. (2018). Trends in evergreen oak suitability from assembled species distribution models: Assessing climate change in South-Western Europe. *New Forests*, *49*(4), 471–487. https://doi.org/10.1007/s11056-018-9629-5

Limousin, J.-M., Roussel, A., Rodríguez-Calcerrada, J., Torres-Ruiz, J. M., Moreno, M., Garcia de Jalon, L., Ourcival, J.-M., Simioni, G., Cochard, H., & Martin-StPaul, N. (2022). Drought acclimation of *Quercus ilex* leaves improves tolerance to moderate drought but not resistance to severe water stress. *Plant, Cell & Environment*, *45*(7), 1967–1984. https://doi.org/10.1111/pce.14326

Lisiecki, L. E., & Raymo, M. E. (2007). Plio-Pleistocene climate evolution: Trends and transitions in glacial cycle dynamics. *Quaternary Science Reviews*, *26*(1–2), 56–69. https://doi.org/10.1016/j.quascirev.2006.09.005

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, *40*(4), 778–789. https://doi.org/10.1111/jbi.12058

Lumaret, R., Mir, C., Michaud, H., & Raynal, V. (2002). Phylogeographical variation of chloroplast DNA in holm oak (*Quercus ilex* L.). *Molecular Ecology*, *11*, 2327–2336. https://doi.org/10.1046/j.1365-294X.2002.01611.x

Médail, F., & Diadema, K. (2009). Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography*, *36*(7), 1333–1345. https://doi.org/10.1111/j.1365-2699.2008.02051.x

Médail, F., & Myers, N. (2004). Mediterranean Basin. In R. A. Mittermeier, M. R. Gil, M. Hoffmann, J. Pilgrim, T. Brooks, G. C. Mittermeier, J. Lamoreaux, & G. A. B. Da Fonseca (Eds.), *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions* (pp. 144–147). CEMEX, Monterrey, Conservation International, Washington and Agrupación Sierra Madre.

Martínez-Vilalta, J., Mangirón, M., Ogaya, R., Sauret, M., Serrano, L., Peñuelas, J., & Piñol, J. (2003). Sap flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. *Tree Physiology*, *23*(11), 747–758. https://doi.org/10.1093/treephys/23.11.747

Mauri, A., Davis, B. A. S., Collins, P. M., & Kaplan, J. O. (2015). The climate of Europe during the Holocene: A gridded pollen-based reconstruction and its multi-proxy evaluation. *Quaternary Science Reviews*, *112*, 109–127. https://doi.org/10.1016/j.quascirev.2015.01.013

Menitsky, Y. (2005). *Oaks of Asia*. Science Publishers.

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Mittermeier, R. A., Gil, P. R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., Lamoreux, J., & Da Fonseca, G. A. (2004). Hotspots revisited. Earth's biologically richest and most endangered terrestrial ecoregions. *Conservation International*, *315*, 392.

Nogués-Bravo, D. (2009). Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, *18*(5), 521–531. https://doi.org/10.1111/j.1466-8238.2009.00476.x

Ogaya, R., & Peñuelas, J. (2003). Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: Photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany*, *50*(2), 137–148. https://doi.org/10.1016/S0098-8472(03)00019-4

Otto-Bliesner, B., Brady, E., Zhao, A., Brierley, C., Axford, Y., Capron, E., Govin, A., Hoffman, J., Isaac, E., Kageyama, M., Scussolini, P., Tzedakis, C., Williams, C., Wolff, E., Abe-Ouchi, A., Braconnot, P., Buarque, S., Cao, J., de Anne, V., & Zheng, W. (2021). Large-scale features of last interglacial climate: Results from evaluating the lig127k simulations for the coupled model Intercomparison project (CMIP6)-paleoclimate modeling Intercomparison project (PMIP4). *Climate of the Past*, *17*, 63–94. https://doi.org/10.5194/cp-17-63-2021

Otto-Bliesner, B. L., Marshall, S. J., Overpeck, J. T., Miller, G. H., & Hu, A. (2006). Simulating arctic climate warmth and icefield retreat in the last interglaciation. *Science*, *311*(5768), 1751–1753. https://doi.org/10.1126/science.1120808

Pacifici, M., Foden, W., Visconti, P., Watson, J., Butchart, S., Kovacs, K., Scheffers, B., Hole, D., Martin, T., Akcakaya, H. R., Corlett, R., Huntley, B., Bickford, D., Carr, J., Hoffmann, A., Midgley, G., Pearce-Kelly, P., Pearson, R., Williams, S., & Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, *5*, 215–224. https://doi.org/10.1038/nclimate2448

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*(5), 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Quinto, L., Navarro-Cerrillo, R. M., Palacios-Rodriguez, G., Ruiz-Gómez, F., & Duque-Lazo, J. (2021). The current situation and future perspectives of *Quercus ilex* and *Pinus halepensis* afforestation on agricultural land in Spain under climate change scenarios. *New Forests*, *52*(1), 145–166. https://doi.org/10.1007/s11056-020-09788-0

R Core Team. (2022). *R: A language and environment for statistical computing* (4.2.2). R Foundation for Statistical Computing. https://www.r-project.org/

Rösch, M., Fischer, E., Lechterbeck, J., & Wick, L. (2012). Pollenanalysen an drei Bohrkernen aus dem Profundal des Ortasees (Piemont, Italien). In A. Stobbe & U. Tegtmeier (Eds.), *Verzweigungen - eine Würdigung für A. J. Kalis und J. Meurers-Balke* (Vol. *18*, pp. 225–247). *Frankfurter Archäologische Schriften*.

Randall, D. A., Wood, R. A., Bony, S., Colman, R., Fichefet, T., Fyfe, J., Kattsov, V., Pitman, A., Shukla, J., Srinivasan, J., Stouffer, R. J., Sumi, A., & Taylor, K. E. (2007). Cilmate models and their evaluation. In M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, & H. L. Miller (Eds.), *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (pp. 589–662). Cambridge University Press.

Rokas, A., Atkinson, R. J., Webster, L. M. I., Csóka, G., & Stone, G. N. (2003). Out of Anatolia: Longitudinal gradients in genetic diversity support an eastern origin for a circum-Mediterranean oak gall-wasp Andricus quercustozae. *Molecular Ecology*, *12*(8), 2153–2174. https://doi.org/10.1046/j.1365-294X.2003.01894.x

Rull, V. (2020). *Quaternary ecology, evolution, and biogeography*. Academic Press.

Salvà-Catarineu, M., Romo, A., Mazur, M., Zielińska, M., Minissale, P., Dönmez, A. A., Boratyńska, K., & Boratyński, A. (2021). Past, present, and future geographic range of the relict Mediterranean and Macaronesian *Juniperus phoenicea* complex. *Ecology and Evolution*, *11*(10), 5075–5095. https://doi.org/10.1002/ece3.7395

Sar, T., Avcı, S., & Avci, M. (2019). Evaluation of the vegetation period according to climate change scenarios: A case study in the inner West Anatolia subregion of Turkey. *Journal of Geography*, *39*, 29–39. https://doi.org/10.26650/JGEOG2019-0018

Schmitt, T. (2007). Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers in Zoology*, *4*(1), 11. https://doi.org/10.1186/1742-9994-4-11

Şekercioğlu, Ç. H., Anderson, S., Akçay, E., Bilgin, R., Can, Ö. E., Semiz, G., Tavşanoğlu, Ç., Yokeş, M. B., Soyumert, A., İpekdal, K., Sağlam, İ. K., Yücel, M., & Nüzhet Dalfes, H. (2011). Turkey's globally important biodiversity in crisis. *Biological Conservation*, *144*(12), 2752–2769. https://doi.org/10.1016/j.biocon.2011.06.025

Southwood, T. R. E., Wint, G. R. W., Kennedy, C. E. J., & Greenwood, S. R. (2004). Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. *European Journal of Entomology*, *101*(1), 43–50. https://doi.org/10.14411/eje.2004.011

Strandberg, G., Lindström, J., Poska, A., Zhang, Q., Fyfe, R., Githumbi, E., Kjellström, E., Mazier, F., Nielsen, A. B., Sugita, S., Trondman, A.-K., Woodbridge, J., & Gaillard, M.-J. (2022). Mid-Holocene European climate revisited: New high-resolution regional climate model simulations using pollen-based land-cover. *Quaternary Science Reviews*, *281*, 107431. https://doi.org/10.1016/j.quascirev.2022.107431

Svenning, J. C., Normand, S., & Kageyama, M. (2008). Glacial refugia of temperate trees in Europe: Insights from species distribution modelling. *Journal of Ecology*, *96*(6), 1117–1127. https://doi.org/10.1111/j.1365-2745.2008.01422.x

Svenning, J.-C., & Skov, F. (2007). Ice age legacies in the geographic distribution of tree species richness in Europe. *Global Ecology and Biogeography*, *16*, 234–245. https://doi.org/10.1111/j.1466-8238.2006.00280.x

Tabet, S., Belhemra, M., Francois, L., & Arar, A. (2018). Evaluation by prediction of the natural range shrinkage of *Quercus ilex* L. in Eastern Algeria. *Forestist*, *68*(1), 7–15. https://doi.org/10.5152/forestist.2018.002

Tekpinar, A. D., Aktaş, C., Kansu, Ç., Duman, H., & Kaya, Z. (2021). Phylogeography and phylogeny of genus *Quercus* L. (Fagaceae) in Turkey implied by variations of trnT(UGU)-L(UAA)-F (GAA) chloroplast DNA region. *Tree Genetics & Genomes*, *17*(5), 40. https://doi.org/10.1007/s11295-021-01522-x

Terradas, J., & Savé, R. (1992). The influence of summer and winter stress and water relationships on the distribution of *Quercus ilex* L. *Vegetatio*, *99–100*(1), 137–145. https://doi.org/10.1007/BF00118219

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A.,

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145–148. https://doi.org/10.1038/nature02121

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD – A platform for ensemble forecasting of species distributions. *Ecography*, *32*(3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Toumi, L., & Lumaret, R. (2010). Genetic variation and evolutionary history of holly oak: A circum-Mediterranean species-complex [*Quercus coccifera* L./*Q. Calliprinos* (Webb) Holmboe, Fagaceae]. *Plant Systematics and Evolution*, *290*(1/4), 159–171. http://www.jstor.org/stable/43558068

Tramblay, Y., Koutroulis, A., Samaniego, L., Vicente-Serrano, S. M., Volaire, F., Boone, A., Le Page, M., Llasat, M. C., Albergel, C., Burak, S., Cailleret, M., Kalin, K. C., Davi, H., Dupuy, J.-L., Greve, P., Grillakis, M., Hanich, L., Jarlan, L., Martin-StPaul, N., … Polcher, J. (2020). Challenges for drought assessment in the Mediterranean region under future climate scenarios. *Earth-Science Reviews*, *210*, 103348. https://doi.org/10.1016/j.earscirev.2020.103348

Turkes, M., Turp, M. T., An, N., Ozturk, T., & Kurnaz, M. L. (2020). *Impacts of climate change on precipitation climatology and variability in Turkey BT – Water resources of Turkey* (N. B. Harmancioglu & D. Altinbilek (eds.); pp. 467–491). Springer International Publishing. https://doi.org/10.1007/978-3-030-11729-0_14

Ülker, E. D., Tavşanoğlu, Ç., & Perktaş, U. (2018). Ecological niche modelling of pedunculate oak (*Quercus robur*) supports the 'expansion–contraction' model of Pleistocene biogeography. *Biological Journal of the Linnean Society*, *123*(2), 338–347. https://doi.org/10.1093/biolinnean/blx154

Varela, S., Rodríguez, J., & Lobo, J. M. (2009). Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. *Journal of Biogeography*, *36*(9), 1645–1655. https://doi.org/10.1111/j.1365-2699.2009.02125.x

Vessella, F., Simeone, M. C., & Schirone, B. (2015). *Quercus suber* range dynamics by ecological niche modelling: From the last interglacial to present time. *Quaternary Science Reviews*, *119*, 85–93. https://doi.org/10.1016/j.quascirev.2015.04.018

Viceto, C., Cardoso Pereira, S., & Rocha, A. (2019). Climate change projections of extreme temperatures for the Iberian Peninsula. *Atmosphere*, *10*(5), 229. https://doi.org/10.3390/atmos10050229

Waldvogel, A.-M., Feldmeyer, B., Rolshausen, G., Exposito-Alonso, M., Rellstab, C., Kofler, R., Mock, T., Schmid, K., Schmitt, I., Bataillon, T., Savolainen, O., Bergland, A., Flatt, T., Guillaume, F., & Pfenninger, M. (2020). Evolutionary genomics can improve prediction of species' responses to climate change. *Evolution Letters*, *4*(1), 4–18. https://doi.org/10.1002/evl3.154

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(6879), 389–395. https://doi.org/10.1038/416389a

Yates, K. L., Bouchet, P. J., Caley, M. J., Mengersen, K., Randin, C. F., Parnell, S., Fielding, A. H., Bamford, A. J., Ban, S., Barbosa, A. M., Dormann, C. F., Elith, J., Embling, C. B., Ervin, G. N., Fisher, R., Gould, S., Graf, R. F., Gregr, E. J., Halpin, P. N., … Sequeira, A. M. M. (2018). Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution*, *33*(10), 790–802. https://doi.org/10.1016/j.tree.2018.08.001

Zohary, M. (1973). *Geobotanical foundations of the Middle East* (Vol. *2*). Gustav Fisher Verlag.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Suicmez, B., & Avci, M. (2023). Distribution patterns of *Quercus ilex* from the last interglacial period to the future by ecological niche modeling. *Ecology and Evolution*, *13*, e10606. https://doi.org/10.1002/ece3.10606

20457758, 2023, 10, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.10606 by Turkey Cochrane Evidence Aid, Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License