# THE COMPARISON OF CLIMATIC NICHES, PLANT FUNCTIONAL TRAITS AND THE LATE QUATERNARY REFUGIA OF OAKS (*QUERCUS*) DISTRIBUTED IN DIFFERENT BIOMES OF THE WESTERN PALEARCTIC REGION

# BATI PALEARKTİK BÖLGENİN FARKLI BİYOMLARINDA DAĞILIM GÖSTEREN MEŞELERİN (*QUERCUS*) İKLİMSEL NİŞ, FONKSİYONEL BİTKİ KARAKTERLERİ VE GEÇ KUVATERNER DÖNEM SIĞINAKLARI BAKIMINDAN KARŞILAŞTIRILMASI

**ELİF DENİZ ÜLKER**

**PROF. DR ÇAĞATAY TAVŞANOĞLU**
**Supervisor**

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# ABSTRACT

## THE COMPARISON OF CLIMATIC NICHES, PLANT FUNCTIONAL TRAITS AND THE LATE QUATERNARY REFUGIA OF OAKS (*QUERCUS*) DISTRIBUTED IN DIFFERENT BIOMES OF THE WESTERN PALEARCTIC REGION

**Elif Deniz ÜLKER**

**Doctor of Philosophy, Department of Biology**

**Supervisor: Prof. Dr. Çağatay Tavşanoğlu**

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Various factors have impacts of species' distributions on a global scale. The genus *Quercus* (oaks) has many widespread species whose distributionhas changed significantly with the global climate changes that occurred in the late Quaternary period. However, the fact that it has many subspecies, high hybridization capacity, and the fact that many species are sympatric in the same area shows that apart from climate the plant functional traits shaped by environmental differences also contribute to their geographical distribution. The objectives of this thesis are to determine the differentiation of oak species distributed in the Western Palearctic region between different climate zones and to determine the differences in plant functional traits among these climate zones and among sections, to interpret their climatic niches in the Western Palearctic oak species, and to reveal the biogeographic patterns of these species. For this purpose, we used ecological niche modeling to test both wide-ranged and endemic species' response to climate fluctuations, also revealed their possible refugia during the late Quaternary refugia. Additionally, we assessed the variabilities in ten functional plant traits among 23 oak species under the four oak sections (*Quercus, Ilex, Cerris, Ponticae*) in three different climatic conditions by using general linear mixed models. The results of the functional traits analyses show that Mediterranean zone species' response patterns against climatic changes, and trait variabilities has a difference compared to other climatic zone species. Therefore, climate zone shapes trait variability in oaks of the western Palearctic, but the evolutionary legacy in plant traits may have also played a role. Our results reveal out that the distribution ranges and functional traits of Mediterranean oak species are more conservative under climate changes and this pattern is important to consider climatic zones in conservation and management plannings. Our findings contributed to the scientific literature regarding the climatic niche variability of oak species in the western Palearctic region and contributed the effects of the plant functional traits shaping the species distribution ranges, and the importance of Anatolia as a host for the diverse of oak species.

**Keywords:** Western Palearctic oaks, climatic niche, plant functional traits, Anatolia, *Quercus*, Late Quaternary refugia, biogeography.

# ÖZET

## BATI PALEARKTİK BÖLGENİN FARKLI BİYOMLARINDA DAĞILIM GÖSTEREN MEŞELERİN (*QUERCUS*) İKLİMSEL NİŞ, FONKSİYONEL BİTKİ KARAKTERLERİ VE GEÇ KUVATERNER DÖNEM SIĞINAKLARI BAKIMINDAN KARŞILAŞTIRILMASI

**Elif Deniz ÜLKER**

**Doktora, Biyoloji Bölümü**

**Tez Danışmanı: Prof. Dr. Çağatay TAVŞANOĞLU**

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Türlerin coğrafi dağılım desenlerini şekillendirmede çeşitli faktörler küresel ölçekte etkilidir. Geniş bir coğrafyada dağılan ve birçok türü bulunan *Quercus* (meşe) cinsine ait türlerin coğrafi dağılımının, Geç Kuvaterner dönemde meydana gelen küresel iklim değişiklikleri ile önemli ölçüde değiştiği bilinmektedir. Bununla birlikte, birçok alt türe sahip olması, yüksek hibritleşme kapasitesi ve birçok türün simpatrik olması, bitki fonksiyonel karakterlerinin iklimden bağımsız olarak çevresel farklılıklar tarafından şekillendirildiğini ve coğrafi dağılımlarına katkıda bulunduğunu göstermektedir. Bu tezin hedefleri, Batı Palearktik bölgesinde yayılış gösteren meşe türlerinin farklı iklim kuşakları arasındaki farklılaşmasını belirlemek, bu iklim kuşakları ve cins içi seksiyonlar arasındaki bitki fonksiyonel karakterlerindeki farkları belirlemek, Batı Palearktik meşe türlerindeki iklimsel nişlerini yorumlamak ve bu türlerin biyocoğrafik desenlerini ortaya çıkarmaktır. Bu amaçla, geniş yayılışlı ve endemik türlerin iklim değişikliğine tepkisini test etmek için ekolojik niş modellemesini kullandık ve olası buzul sığınaklarını ortaya çıkardık. Ayrıca, üç farklı iklim bölgesinde (Akdeniz, Geçiş ve Ilıman) yayılış gösteren ve dört seksiyona (*Quercus, Ilex, Cerris, Ponticae*) ait 23 meşe türünde on fonksiyonel karakterin değişkenliklerini genel lineer karışık modeller kullanarak değerlendirdik. Sonuçlarımız, Akdeniz bölgesi türlerinin iklim değişikliklerine karşı cevap örüntülerinin ve fonksiyonel karakterlerindeki değişkenliklerinin diğer iklim bölgeleri türlerine göre farklı olduğunu göstermektedir. Bu nedenle, iklim kuşağı Batı Palearktik meşelerinde fonksiyonel karakterleri şekillendirmekte, ancak bitki karakterlerinde evrimsel mirasın da dikkate alınması gerekmektedir. Sonuçlarımız, Akdeniz türlerinin dağılım aralıkları ve fonksiyonel karakterlerinin iklim değişiklikleri altında daha korumacı olduğunu ve bu örüntünün, koruma ve yönetim planlamalarında iklim bölgelerini dikkate almanın önemini göstermektedir. Bulgularımız, Batı Palearktik bölgesinde meşe türlerinin iklimsel niş değişkenliği ve türlerin dağılımını şekillendiren bitki işlevsel özelliklerinin etkileri konusunda bilimsel literatüre katkıda bulunmuş ve Anadolu'nun meşe çeşitliliği konusundaki önemini ortaya koymuştur.

**Anahtar Kelimeler:** Batı Palearktik bölge, iklimsel niş, bitki fonksiyonel karakterleri, Anadolu, *Quercus*, Geç Kuvaterner sığınakları, biyocoğrafya

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# CHAPTER 1: GENERAL INTRODUCTION

*Quercus* stands as the largest genus within the Fagaceae family and is renowned for its broad distribution, spanning from equatorial to boreal regions, and encompassing elevations ranging from sea level to 4000 meters, and is recognized as one of the most diverse tree genera in the Northern Hemisphere. (Menitsky, 2005; De Beaulieu & Lamant, 2010; Kremer & Hipp, 2019). Their current global geographical and ecological diversification results from the evolution of wide-ranging lineages over 56 million years in the early Eocene climatic optimum (Hipp et al., 2020). According to the most recent estimates, oaks are represented by approximately 435 species, where America and Asia have numerous species, and Europe exhibits lower species richness (up to 30) (Denk et al., 2017; Kremer & Hipp, 2019). They inhabit a wide range of habitats and are recognized as significant components of temperate and subtropical forests, as well as steppes, maquis, and open woodlands.

*Quercus* is a genus with a high interspecies hybridization rate; with meachanisms behing the occurrence of sibling and sympatric species are questioned (Cavender-Bares & Pahlich, 2009). As a result of the difference between the pollen dispersal and seed dispersal rates, both ecological and genetic structures effected, thus induces the gene sharing between two oak species, which causes a result of high hybridization in oaks (Petit et al., 2003). Due to these circumstances, the biological species concept is generally not applicable to oaks (Coyne, 1994). Moreover, oaks are recognized as significant indicator species, demonstrating the crucial role of introgression in the evolution of plants (González-Rodríguez et al., 2004). For *Quercus* genus, for which the biological species concept is insufficient, different classifications have been made by various authors over history, and this has often led to confusion for this genus, whose systematics is already troubled (Linné (1753), Loudon (1838); Ørsted (1871), Trelease (1924), Schwarz (1936), Camus (1936–1954), Menitsky (1984), Nixon (1993)) as cited in (Denk et al., 2017). Today, several major lineages we recognize as sections are divided into eight sections (*Cerris*, *Cyclobalanopsis*, *Ilex*, *Lobatae*, *Ponticae*, *Protobalanus*, *Quercus*, and *Virentes*) under two major subgenera (Denk et al., 2017). Fossil data suggest that the diversification of the genus was rapid into geographically structured clades, and as the temperature cooled, they diversified ecologically within each region over the past 40 Myr (Kremer & Hipp, 2020). The global diversification of oak species is the outcome of multiple instances of diversification occurring within similar geographic and ecological spaces. These diversification events are primarily driven by fluctuations in climate and variations in topography.

Quaternary is one of the most important periods in which significant short and long-term climate changes have occurred. The most interesting period in understanding the evolutionary processes of modern communities and taxa is the late Quaternary (approx. 2 mya.), due to the well-known geomorphological and climatological records. The temperate-region species in the Western Palearctic Region contracted their distributions towards southern regions into the climatically suitable areas as the glaciers started to expand with the cooling and drying of the climate in the Late Quaternary (Hewitt 1996; Taberlet 1998; Hewitt, 1999; Petit et al., 2002; Svenning & Skov 2007; Waltari & Guralnick 2009; Médail & Diadema 2009 During this period, the Iberian Peninsula, Italy, the Balkans, and Anatolia were revealed as an important glacial refugium for temperate species, and the existence of the habitats with suitable micro-climatic conditions in the north and Anatolia were determined as the extra-Mediterranean refugium (Hewitt, 1996; Bennett & Provan, 2008; Ülker et al., 2018; Perktaş & Quintero, 2013; Perktaş et al., 2015). It was observed that temperate species expanded their distribution during the interglacial periods, but species adapted to continental and harsh climates maintained in the interglacial refugium in areas dominated by continental-oceanic climate (Schmitt & Varga, 2012; Gür, 2013).

Molecular and palynological studies were conducted for temperate oak species distributed in Europe to identify glacial refugia in southern parts of Europe (Olalde et al., 2002; Brewer et al., 2002; Petit et al., 2002; Carrión et al., 2003; Svenning et al., 2008). Due to the lack of moisture, temperate oak species in the western Palearctic region could not form extensive forests in the glacial refugia during LGM, but when the climatic conditions began to improve, they quickly expanded their distribution towards the north. However, the Younger Dryas slowed the expansion of these populations again, causing them to retreat to secondary refugium suitable for them (Petit et al., 2002). From the Middle Holocene onwards, when climatic conditions stabilized for these species, a rapid distribution from secondary refugium to the northwest began, and a somewhat slower distribution towards central and eastern Europe occurred (Petit et al., 2002). In the spread of deciduous oaks to Europe, which started about 15,000 years ago, it is seen that the first recolonizations were shaped according to the climate, and the secondary recolonizations were shaped by geographical barriers, interspecies competition, and various edaphic factors. It has been observed that deciduous oaks naturally reached their widest distribution in Europe 6,000 years ago, and after this period, their expansion and spread to different regions accelerated with human activities (Turner et al., 2008).

Climate changes are more effective in sensitive areas such as the Mediterranean Basin, where evergreen oaks are distributed. According to the macrofossil records, southern Anatolia and the Middle East have been displayed as sheltering regions and diversification areas for *Ilex* section since Miocene (Vitelli et al., 2017). The hypothesis of multiple refugia for this group in the Mediterranean Region is emphasized (de Heredia, 2007). Since they are less competitive than temperate oaks, highly tolerant to drought, and have different ecological needs from each other, the impact of fires, herbivores, pathogen attacks, and the arrival of new competitors in the Mediterranean Basin, evergreen oaks have been limited in the Mediterranean coasts in the historical process (Carión, 2002; Turner et al., 2008).

Global climate changes are widely known as an important factor in shaping the species' geographical distribution patterns. However, environmental differences depending on climatic conditions, land use, and biotic interactions shape demographic processes, and ecological and physiological traits of species, and the contribution of these traits to the geographical distribution and the ecological niche differences of species should not be ignored (Lian et al., 2022).

Plant traits encompass a range of measurable characteristics at the individual level, including morphology, anatomy, physiology, biochemistry, and phenology. These traits influence the growth, reproduction, and survival of plants, as well as their ability to adapt and thrive in dynamic environmental conditions (Violle et al., 2007, Garnier et al., 2016). Basically, trait-based approach is mostly used in ecological and evolutionary research from individual level to community level (Violle et al.,2007). To understand more about the functional traits, would provide a better understanding about the ecological processes and ecosystem functioning in the communities (Tavşanoğlu & Pauses, 2018). Among their wide range of usage, trait-based approaches is using also to explain the biogeographic history of the species. Numerous studies have shown that these traits shape the geographical distribution of plants.

The Mediterranean Basin hosts numerous plant species with high endemism rate and considered as one of the biodiversity hotspots. Besides played as a role of glacial refugium during the LGM, faced several environmental and climatic changes, and faced disturbances during its history that has been mostly used to predict the critical importance of the functional traits, and responses of the populations, species and communities. The response of oak species against fires, drought, and frozen stress, competitive interactions between sympatric or sibling species, limited gene flow and niche differentiation, and the strategies they developed against environmental factors have been studied in several biomes and mostly in Mediterranean region (Cavender-Bares et al., 2004; Cavender-Bares et al., 2005; Cavender-Bares & Pahlich, 2009; Moles et al., 2014), yet still not enough studies for the Western Palearctic region oaks.

*Quercus* is ecologically, economically, and culturally a valuable genus (Carrero, 2020). Although their significance in terms of ecology and the economy is well recognized, preserving them poses a challenge as they cannot be stored in seed banks under typical conditions characterized by low levels of humidity and temperature, besides they also faced globally major threats include land-use change, climate change, non-native pests and diseases, logging, habitat conversion for urbanization or agriculture, and changes in fire regimes (Kramer & Pence, 2012; Carrero et al., 2020). Therefore, urgent and collaborative conservation plans and actions are necessary on global and regional scales.

Europe has the lowest oak species richness (30 species and several subspecies and hybrids) compared to other regions, but Anatolia consists of 18 *Quercus* species, due to its topographical and climatic diversity (Olson & Dinerstein, 2002; Şekercioğlu et al., 2011; Simeone et al., 2018). In this diverse and disturbed geography, Anatolia hosts of 3 biodiversity hotspots (Mediterranean Basin, Irano-Turanian, Caucasus) (Mittermeier et al., 2005), and where three regional endemic oak species (*Q. aucheri, Q. pontica, Q. vulcanica*) distributes in these regions. Among them, *Q. pontica* is assessed as Endangered according to the IUCN definitions (Carrero, 2020). These Anatolian endemic oak species, each located in different climatic zone, with different ecological requirements and vulnerable populations, and facing different environmental and anthropological threats (Yaltırık, 1984). As one of the main goals of this thesis, the effective conservation and viability of their populations require a better understanding of their ecological and population status.

## 1.1.The Objectives of the Study

The objectives of this study are as follows:

- To determine the population status, possible glacial refugia, and future distribution areas of three regional endemic *Quercus* species in Anatolia,
- To determine the differences in plant functional traits of the temperate and Mediterranean zone *Quercus* species in the Western Palearctic region
- To determine the climate-based ecological niche differences and the LGM refugia of the temperate and Mediterranean zone *Quercus* species in the Western Palearctic region.

## 1.2.The Importance of the Study

This thesis constitutes the most comprehensive study on *Quercus* genus about evaluating the climatic niches and functional traits of oak species in different climatic zones in the Western Palearctic region. The highest unique value of this study for literature is its research on the differences in the response of plant species in different biomes to climatic changes in the Pleistocene period. In addition, this thesis is the first study that comparatively evaluates the plant functional traits of oak species in the Western Palearctic region based on climatic zones and taxonomic sections. Finally, determining the LGM refugia, predicting their future distribution, and developing conservation measurements accordingly for the endemic oak species in Anatolia reveals the importance of this thesis.

## 1.3. Research Questions

In this study, I compared niche difference and plant trait variability in *Quercus* in different climatic zones in the Western Palearctic region. I also determined the past and future distributional patterns of regionally endemic oak species in Anatolia and the oaks of the Western Palearctic region. In this context, the following specific questions were asked:

- Do the distributional patterns in LGM and climatic niches differ between the Mediterranean and temperate oaks,
- Do the plant functional traits differ between the Mediterranean and temperate oaks, and among taxonomic sections,
- Do climatic niches of Anatolian regional endemic oak species differ from each other?

The below-mentioned hypothesis about the results of the study related to those questions are as follows:

- The distributional patterns in LGM and climatic niches of Mediterranean and temperate oak species are different,
- Functional traits are significantly different among the sections of *Quercus* and between climate zones (Mediterranean versus Temperate).
- Three endemic oak species have a strong response to climate, different climatic niches, and their distribution range will significantly contracted in the near future due to climate change.

## 1.4.The Structure of the Thesis

The thesis consists of five chapters in total, including the “General Introduction”, and "Conclusions" chapters, where the results of each chapter are briefly evaluated. The second, third, and fourth chapters of the thesis are prepared in the scientific paper format.

In the first chapter, “General Introduction”, general information about oaks, the effect of the Late Quaternary period on the species’ distributions, the effects of plant functional traits, and the environmental impacts on oaks species are briefly described. The study's purpose, importance, and research hypotheses are mentioned accordingly.

In the second chapter of the thesis, the responses of Anatolian endemic oaks to environmental changes by determining their past and future distribution patterns in relation to climate is provided. Moreover, the most vulnerable populations of each species using *in situ* observations about the threats faced by the species are provided, accordingly, conservation measures are proposed.

The third chapter of the thesis provides the results on the role of different climate zones in shaping functional trait variability in Western Palearctic region oaks. The sections of *Quercus* are also considered to reveal the trait variability among different taxonomic groups within the genus.

In the fourth chapter of the thesis, the niche differences between the Mediterranean and temperate zone oaks, their possible LGM refugia and recolonization routes under the climatic conditions of the Late Pleistocene in the Western Palearctic region are revealed.

The last chapter, “Conclusions”, briefly summarizes the general results of the thesis presented in previous chapters and emphasizes the uniqueness of the thesis.

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# CHAPTER 2: THE PAST AND FUTURE OF REGIONALLY ENDEMIC OAKS IN ANATOLIA: CLIMATE CHANGE AND ANTHROPOGENIC IMPACTS*

## Abstract

Understanding species' responses to the drivers of global environmental changes is the key contemporary element for better conservation of species. In this study, we aimed to reveal possible threats on three regionally endemic oaks in Anatolia (*Quercus aucheri*, *Q*. *pontica*, and *Q*. *vulcanica*) by examining the status of several populations and projecting the distributional patterns under the Last Glacial Maximum (LGM), the Present, and a warmer future. We made observational assessments on anthropogenic impacts and natural disturbances in 39 populations belonging to three oak species in the field and conducted ENM approach to predict the effect of climatic changes on the studied species. Models predicted that the range of *Q. pontica* and *Q. vulcanica* contracted towards climatically suitable areas within their current distribution ranges during LGM, while *Q. aucheri* showed an opposite pattern and displayed a broader range in LGM than the Present. The future (2081-2100) predictions gave narrower distribution ranges than the current predictions for *Q. pontica* and *Q. vulcanica*, but models predicted a broader range for *Q. aucheri* in this warmer future period. The type of anthropogenic impact was species-specific, but the populations of the studied species suffered a few common threats, such as land-use change and pest damage. In conclusion, our results revealed the existence of different climate responses and threats faced by the studied regionally endemic oak species. These differences should be considered for developing and implementing the conservation and management plans for forests and shrublands dominated by these oak species.

**Keywords:** Anatolia; climate change; ecological niche modeling; *Quercus*; threat assessment

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## 2.1. Introduction

*Quercus* stands out as a genus within the Fagaceae family, known for its abundant species and ecological diversity, and it holds a significant position as one of the largest genera among all tree families in the Northern Hemisphere (Manos & Stanford, 2001; Valencia-Ávalos, 2004). Recent phylogenetic studies suggest that there are 430 species of oaks worldwide (Denk et al., 2017; Hipp et al., 2020), and still, new species are being described. Throughout their evolutionary journey spanning 56 million years, oaks have emerged as dominant species in the Northern Hemisphere. (Hipp, 2020) Notably, they exhibit the highest diversity of species in Southeast Asia and Central America, while Europe showcases comparably lower species richness, with approximately 30 identified species (Denk & Grimm, 2010; Hipp, 2020; Carrero et al., 2020).

Geographical and ecological variations impact the global oak diversity (Hipp, 2020). The European oak flora was driven by the Late Pleistocene glacial and interglacial climatic changes and the recolonizations from southern refugium of Europe (Ferris et al., 1998; Petit et al., 2002b; Ülker et al., 2018). Moreover, the distribution of at least 18 oak species considerably overlaps with the biodiversity hotspots globally (Carrero, 2020). The Anatolian peninsula serves as a convergence and interaction point for three notable biodiversity hotspots: the Caucasus, Irano-Anatolian, and Mediterranean hotspots (Conservation International, 2021). Anatolia has high biodiversity for a medium-sized temperate country due to its location between three continents, the past geological and climatic dynamics, and its long human history (Şekercioğlu et al., 2011). Anatolia hosts the most oak species, 19 taxa, in the western Palearctic region, and three of seven regionally endemic oaks in the region (namely *Q. aucheri*, *Q. pontica*, and *Q. vulcanica*) are only found in Anatolia or its surroundings. Their range corresponds to three distinct phytogeographic regions (Mediterranean, Euro-Siberian, Irano-Turanian) and biodiversity hotspots within Anatolia. These patterns of oak species richness and distribution in the western Palearctic region make the Anatolian peninsula a unique biogeographical region for oak diversity. Yet, it has remained unexplored for many aspects of oak distribution and ecology (Bagnoli et al., 2016).

As stated in The Red List of Oaks 2020 (Carrero, 2020), significant challenges faced by oak species include land use transformation, climate change, as well as the presence of both native and non-native pests and diseases. The impact on oaks at a landscape level is frequently a result of habitat conversion for agricultural purposes or urbanization, logging activities, and modifications in fire patterns (De Rigo et al., 2016; Conrad et al., 2020; Carrero, 2020). Knowledge of threats to oak species is critically important for developing conservation and management plans, and without information on threats and population status, evaluations for conservation or management would have shortcomings. For instance, although Asian oaks are threatened by agriculture and aquaculture at most, and the red list of oaks 2020 suggests that Turkey has only one threatened oak species due to biological resource use such as logging and wood harvesting, the impacts of agricultural activities are underestimated (Carrero, 2020). Fortunately, specific IUCN assessments (Carrero, 2020) for oak species of Turkey include more threatened oaks and define more threats, including agriculture, but data for IUCN assessments is also imperfect for a complete evaluation of the status of Anatolian oaks, especially of those that are regionally endemic (Stephan, 2018; Güner et al., 2019; Strijk & Carrero, 2020). Therefore, there is an urgent need to collect more data on threatened oak species in Turkey for efficient conservation and management.

Historical climatic fluctuations have had major impacts on oaks by altering their altitudinal and latitudinal range shifts, and the global oak diversity is the result of the changing climate (Gómez-Mendoza & Arriaga, L., 2007; Hipp et al., 2018; Deng et al., 2018; Cavender-Bares, 2019). Climate-dependent range shifts are predicted to be more noticeable at higher latitudes now and in future, moreover, pathogens (invasion on oaks) have increased, and the productivity of the forests has declined due to climate warming (Bakkenes et al., 2002). An ‘expansion–contraction’ model has suggested that the distribution of temperate species contracted through glacial refugia during the glacial periods and then expanded in interglacial periods in Pleistocene (Taberlet et al., 1998; Hewitt, 1999). Western Palearctic *Quercus* species also used glacial refugia in the Mediterranean region (Taberlet et al., 1998; Brewer et al., 2002; Petit et al., 2002b; Habel et al., 2010; Bagnoli et al., 2015; Ülker et al., 2018) or some cryptic refugium in the relatively north (Provan & Bennett, 2008) during the Last Glacial Maximum (LGM; ca. 22000 ybp). Climate is the main ecological driver of the distribution of oak species in Anatolia (Ülker et al., 2018; Kenar & Kikvidze, 2019). Moreover, Anatolia has also been suggested as an important glacial refugium for many European taxa (Krebs et al., 2014; Korkmaz et al., 2014; Perktaş et al., 2015a, 2015b; Rokas et al., 2016). There are also signals for that Anatolian displays as a glacial refugium for *Quercus* species obtained from studies using ecological niche modeling (Ülker et al., 2018) or genetic approaches (Dizkirici-Tekpinar et al., 2021).

Our research endeavors to enhance comprehension regarding how Anatolian endemic oaks respond to environmental changes, achieved by analyzing their historical and prospective distribution trends concerning climate variations. In addition, we also aimed to contribute to conservation implementations regarding these endemic oaks by determining the most vulnerable populations using *in situ* observations about the threats faced by several populations. Considering the current climate change negatively affects many tree species worldwide, we hypothesized that three endemic oak species have a strong response to climate, and their range will significantly decrease in the near future due to climate change. Similarly, we expected to find a prediction of range contractions during the LGM for the studied species. We also expected that many populations of three endemic oaks are under strong human pressure. To test these hypotheses, we used an ecological niche modeling approach using occurrence data of the studied species and climatic data of three endemic oak species.

## 2.2. Materials and Methods

### 2.2.1. Study Species

We studied three endemic oak species in the Anatolian Peninsula (Turkey): *Quercus aucheri, Q. pontica*, and *Q. vulcanica* (Figure 2.1). These species are distributed in three distinct biomes and are considered elements of different phytogeographic regions (Mediterranean, Euro-Siberian, and Irano-Turanian, respectively), therefore reflecting the high-level biodiversity and climatic variability of Anatolia. These species also represent three different taxonomic sections in the global oak phylogeny: *Ilex* (Ilicoid oaks), *Ponticae,* and *Quercus* (White oaks), respectively (Manos et al., 2001; Denk & Grimm, 2010; Simeone et al., 2016; Denk et al., 2017; Simeone et al., 2018).

**Figure 2.1.** General view and leaves with acorns of the studied endemic species: a. *Quercus aucheri*, b. *Q. pontica*, c. *Q. vulcanica*. Photos from Turkey by Elif D. Ülker.

*Q. aucheri* can be found distributed along the southern inclines of elevated hills in southwestern Anatolia and certain eastern Aegean islands, ranging from sea level to an altitude of 500 meters above sea level. The distributional range of *Q. aucheri* is restricted to areas where the Mediterranean climate dominates and occurs in the Mediterranean biodiversity hotspot. *Q. aucheri* is an evergreen species resistant to higher temperatures and sensitive to frost. This species prefers fertile soils and generally appears in shrub form under environmental stress conditions or disturbances (Yaltırık, 1984). The species is an element of the Mediterranean phytogeographic region (Yaltırık, 1984).

*Q. pontica* is a deciduous species with a shrub-like growth habit, capable of reaching heights between 3 to 5 meters. It is commonly found in the mountainous regions of the Eastern Black Sea Region, occupying elevations ranging from 800 meters up to 2100 meters above sea level. (Hedge & Yaltırık, 1982). This area has an oceanic climate and falls within the Caucasus biodiversity hotspot. *Q. pontica* occurs in small groups in the mixed forests of *Fagus orientalis- Picea orientalis* in areas with abundant rainfall and high relative humidity (Yaltırık, 1984). The species is considered as a Colchic sub-zone element of the Euro-Siberian phytogeographic region Yaltırık, 1984).

The main distribution area of *Q. vulcanica* is the central Anatolia - upper Mediterranean Turkey region (i.e., "Turkish Lakes Region"), and a few isolated populations in the southwestern Black Sea region and Eastern Mediterranean (Yaltırık, 1984; Birol et al., 2020). Because of the heterogeneous topography in the region, the climate is spatially variable and characterized by both a Mediterranean climate and the central Anatolian semi-arid climate. *Q. vulcanica* frequently forms mixed forests with *Cedrus libani, Acer hyrcanum, Quercus cerris,* and *Pinus* species or sometimes pure stands between 1100-2000 m altitude ranges according to our field observations. *Q. vulcanica*'s distribution range falls into several Key Biodiversity Areas recognized for central Anatolia due to the climatic and topographic diversity, besides one of the most remarkable habitat feature is the volcanic bedrock (Yaltırık, 1984; Eken et al., 2006). Although the species is considered as an element of the Irano-Turanian phytogeographic region, some populations are also found in the Mediterranean phytogeographic region (Yaltırık, 1984).

### 2.2.2. Occurrence Data

We compiled the occurrence data from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), published literature, personal communications with researchers from the study area, and the field surveys between 2018 and 2021. Since GBIF has limited data especially for *Q. vulcanica* and *Q. pontica* occurrence, we conducted field surveys based on the reference locations stated in the *Quercus* section of the Turkish Flora (Davis, 1982; Hedge & Yaltırık, 1982) for each species. We carried out these field surveys between August and September 2018 for *Q. pontica* and *Q. aucheri*, and between July and October 2021 for *Q. vulcanica.* After confirming geolocations of the places roughly stated in the Turkish flora, we carried out the field studies accordingly and compiled a total of 64, 52, and 101 occurrence records for *Q. aucheri, Q. pontica* and *Q. vulcanica*, respectively, for this study (Figure 2.2).

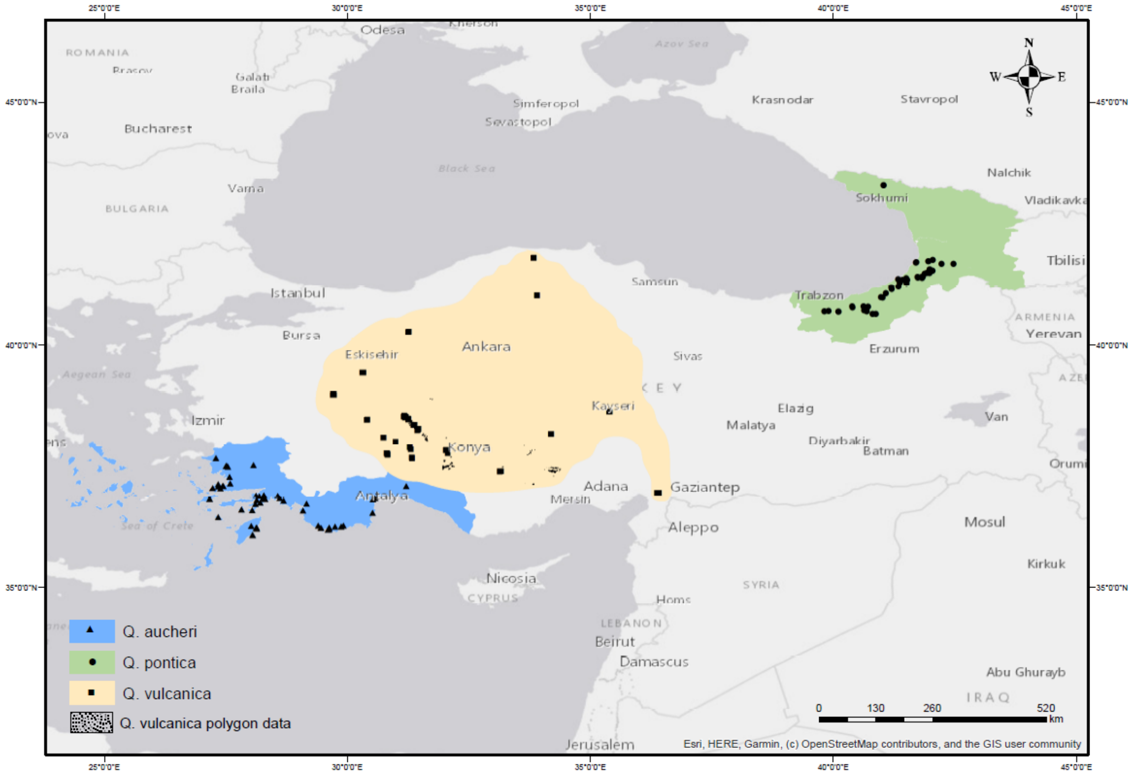

**Figure 2.2.** Calibration area of each species (colored area), and occurrence data (points) compiled from field studies and literature. For *Q. vulcanica*, additional distribution data obtained from map polygons were added to better represent species ranges (this polygon data were not included in models). The map centered on the Anatolian peninsula (Türkiye).

### 2.2.3. Field Observations

During the field surveys to confirm the location of *Quercus* populations, we also made observations on the abundance, forest health conditions, and current threats to the studied species. Specifically, we surveyed six, 12, and 21 populations for *Q. pontica*, *Q. aucheri*, and *Q. vulcanica*, respectively. During these field surveys, we examined several individuals in each population for pest damage, grazing effect, or fire scars and made observations on anthropogenic threats. Moreover, we also conducted casual interviews with the local people to record their usage, attitude, and observations about the study species. The abundance of the individuals among the distribution area of each population, growth form, and vegetation structure were determined to characterize the habitat properties. For each of the three species, we identified the intensity of threats in four categories (no, low, moderate, and high) according to our observations in the field, including natural disturbances such as fire and pest damage and anthropogenic impacts such as logging, land-use change, and domestic grazing.

### 2.2.4. Ecological Niche Modeling

Ecological niche modeling (ENM) is a statistical approach that utilizes a range of tools to estimate geographic distribution patterns. It involves analyzing the correlations between known occurrences of species and environmental variables to make estimations (Simões et al., 2020). We performed an ecological niche modeling (ENM) approach to predict the possible impacts of climatic changes on the distribution patterns of study species under different time periods and climate scenarios. In this study, ENMs were employed to assess the relationship between present climatic conditions and the current distribution range of the studied species. Additionally, we predicted the distribution range of these species by considering past climatic conditions during the Last Glacial Maximum (approximately 22,000 years ago) as well as potential future warmer climates (for 2081-2100).

Bioclimatic variables were downloaded from the WorldClim database version 2.1 (Fick et al., 2017) at a spatial resolution of 2.5’ (~4.63 km at the equator) (Table A1). SDMToolbox is used to remove duplicates from the dataset, reducing spatial autocorrelation and delimiting the calibration area (*M*) (Brown, 2014) in ArcGIS version 10.6.1 (ArcGIS, 2010). After the cleansing process, 31 occurrence points for *Q. pontica*, 39 for *Q. aucheri* and 20 for *Q. vulcanica* were left for subsequent ENM analyses.

We defined the calibration area (M) for each species by considering the biology, dispersal ability of the species, the environmental conditions represented in the area BAM diagram approach (Peterson et al., 2015), and additionally, the habitat continuity and topographic patterns. After creating the M shapefiles, the bioclimatic variables were masked to represent the calibration areas for each species. Due to the artifacts in some of the bioclimatic variables (bio8, 9, 18, and 19; Simões et al., 2020), they were excluded from climatic data before building the models. To reduce multicollinearity among bioclimatic variables, we used Pearson correlation analysis by calculating the correlation coefficients within the area where the models are being calibrated. Following the correlation analysis, we only kept one climatic variable for further analysis among highly correlated ($r > 0.70$) variables, while we removed others from the dataset. For correlation analysis, we used the “corrplot” package (Wei and Simko, 2021) implemented in the R environment (R Core Team, 2021).

For the model calibration, we used the “kuenm” package (Cobos et al., 2019) in the R environment (R Core Team, 2021) to create ENMs and describe the calibration, evaluation, and processing of the models. To choose the climatic variables that best reflect the species' distribution, we determined alternative climate variable sets for each species. During the calibration process of the models, various combinations of regularization multipliers, feature classes, and climate variables were employed (Table 2.1). Since distributional patterns differ for each studied species, we initially tested different regularization multipliers before running the models. Similarly, we determined the feature classes according to the number of occurrence points in each species. For each species, we selected the best models based on model explanatory power, specifically using the partial ROC, omission rate, and AICc values. In total, we tested 20, 48, and 54 candidate models, including combinations of regularization multipliers, feature classes, and sets of climatic predictors for *Q. aucheri*, *Q. pontica*, and *Q. vulcanica*, respectively.

We run the final models in the “kuenm” R package according to the selected best parameters combination for the past, current, and future periods (Philips, Anderson & Schapire, 2006) for each species. We considered future projections (2081-2100) under three different models (BCC-CSM2-MR, CNRM-CM6-1, MIROC6) with two different climate scenarios (ssp126 and ssp585). We considered the LGM projections under three different models (CCSM, MPI, MIROC). These models used were chosen since they contain data from both optimistic and pessimistic scenarios of the tested climatic period. We ran each model 10 times and implemented the raster calculation and visualization of the final outputs in ArcGIS version 10.6.1 (ArcGIS, 2010).

**Table 2.1.** Parameters of the candidate models for each species.

| **Species** | **Regularization multipliers** | **Feature class** | **Sets of predictors** |
|---|---|---|---|
| *Quercus aucheri* | 0.5, 1, 2 | l, lq, lqp, | Set1 (bio3, bio5, bio16, bio17) |
| | | lqpt, lqpth | Set2 (bio3, bio5, bio12, bio15) |

| | | | |
|---|---|---|---|
| *Quercus pontica* | 0.5, 1, 2 | l, lq, lqp, lqpt, lqpth | Set1 (bio3, bio5, bio15)<br>Set2 (bio3, bio5, bio13, bio15) |
| *Quercus vulcanica* | 0.5, 1, 2 | l, lq, lqp, lqpt, lqpth | Set1 (bio1, bio7, bio17)<br>Set2 (bio1, bio4, bio7, bio17) |

## 2.3. Results

### 2.3.1. Ecological Niche Models

The set of final model parameters best predicted the climatic suitability for each species is given in Table 2.2. The outcomes of the modeling appear encouraging, and the models demonstrated high performance across all study species, as indicated by the area under the curve (AUC) values (mean AUC > 0.75, Table 2.2), indicating a better prediction than a null (random) model (Phillips & Dudik, 2008). Since diagnostic thresholds were not specicified, AUC values preferred to use instead on AIC. According to partial ROC statistics (Figure A4), the model results and the distributions of all species exhibited considerable improvement compared to random predictions. Additionally, the response curves of the bioclimatic variables clearly illustrate the significant impact of each variable on the MaxEnt outputs for individual species (Figure A1-A3). These curves illustrate the individual influence of each variable and demonstrate how the predicted probability fluctuates with changes in each environmental factor.

**Table 2.2.** The best parameters and mean AUC values of the final models for studied species.

| **Species** | **Regularization multipliers** | **Feature class** | **Predictors** | **Mean AUC** | **Variable percent contributions (respectively)** |
|---|---|---|---|---|---|
| *Quercus aucheri* | 1 | lqp | Set_2 (bio3, bio5, bio12, bio15) | 0.751 | (2.8, 0.3, 2.5, 94.4) |

| | | | | | |
|---|---|---|---|---|---|
| *Quercus pontica* | 0.5 | lqp | Set_2 (bio3, bio5, bio13, bio15), | 0.836 | (3.1, 41.3, 5.2, 50.4) |
| *Quercus vulcanica* | 1 | lqp | Set_1 (bio1, bio7, bio17) | 0.849 | (32.1, 46, 21.9) |

The ENM predictions were concordant with the known distributions, which were supported by occurrence data from the literature and observation data from the field surveys of each species. Extensive calibration areas according to these known distribution ranges were designated, and even so, some regions where the species are not currently distributed were also projected as climatically suitable areas for the species by the models. These outcomes show the species-climate equilibrium based on the bioclimatic data for determining the ecological niches of the study species (Nogués-Bravo, 2009). Besides, according to the model results, for example, northeastern Anatolia, Caucasus regions and Lake Van, and the Levant seem to be suitable areas for *Q. vulcanica* and *Q. aucheri*, respectively, under the current climatic conditions. However, considering these areas have not been accessible for these species due to dispersal constraints related to climatic or geographic barriers, we interpret these results as an overprediction of the geographical range of species under different climatic conditions (the LGM, Present, and future).

The variables that most affect the current distribution of *Q. aucheri* were the precipitation seasonality (bio15), annual precipitation (bio12), and isothermality (which reflects temperature fluctuation trends; bio3) (Table 2.2). Consequently, precipitation-related variables had the most contribution (over 90%) in projecting the distribution of this species. On the other hand, *Q. vulcanica* was mainly affected by temperature annual range (bio7), mean annual range (bio1), and precipitation of the driest quarter (bio17) (Table 2.2). Temperature annual range (bio7) alone contributed the most to the distribution of *Q. vulcanica* (over 90%). Similarly, *Q. pontica* mainly was affected by precipitation of seasonality (bio15), maximum temperature of the warmest period (bio5), precipitation of wettest period (bio13) and isothermality (bio3) (Table 2.2). Precipitation-related variables contributed the most (over 55%) to projecting the distribution of *Q. pontica*.

Under the LGM, the range of *Q. pontica* and *Q. vulcanica* showed a contraction towards climatically suitable areas within their distribution ranges (Figure 2.3a, 2.4a). In contrast, *Q. aucheri* showed an opposite pattern and had a broader range in the LGM than the Present (Figure 2.5a). The future (2081-2100) predictions has much narrower distribution ranges compared the current predictions for *Q. pontica* and *Q. vulcanica* (Figure 2.3b, 2.4b), while *Q. aucheri* showed a broader distribution range than its current prediction compatible with the bioclimatic conditions (Figure 2.5b). Specifically, *Q. pontica* had suitable climatic conditions around Abkhazia region of Georgia, and Rize and Artvin provinces of Turkey during the LGM (Figure 2.3a). On the other hand, the contraction of *Q. vulcanica* range during the LGM was more prominent as climatically suitable areas were only found in anti-Taurus mountains and a few volcanic mountains in the south of Central Anatolia (Figure 2.4a).

Future models also predicted significant range contradictions in *Q. pontica* (Figure 2.3c, 2.3d) and *Q. vulcanica* (Figure 2.4c, 2.4d) but not in *Q. aucheri* (Figure 2.5c, 2.5d). According to the optimistic future scenario for the 2081-2100 period (ssp126), *Q. pontica* was predicted to contract its distribution in northeastern Anatolia in the next 80 years, but the species will maintain its distribution in higher elevations in mountainous areas (Figure 2.3c). However, the worst-case future climate scenario (ssp585) suggests that distribution range of *Q. pontica* will dramatically reduce in the native distribution area, as its distribution will be limited to the Kaçkar Mountains, northern Georgia, and the mountainous regions of the Abkhazia region (Figure 2.3d). *Q. vulcanica* was also predicted to suffer range contraction in both future climate scenarios (Fig. 2.4c, 2.4d). However, the ENM model under the worst-case future climate scenario (ssp585) predicted a dramatic loss of *Q. vulcanica* populations, in west central parts of Anatolia and possibly in the southern mountainous parts of southern Kayseri (Figure 2.4d). In contrast to *Q. pontica* and *Q. vulcanica*, the future models predicted that *Q. aucheri* will not only have its current distribution areas but also expand towards high elevation areas above 500 m where the species is not found today (Figure 2.5b). The overall model result suggests a slight increase in the range of *Q. aucheri* in at the end of the 21$^{st}$ century (Figure 2.5c, 2.5d).

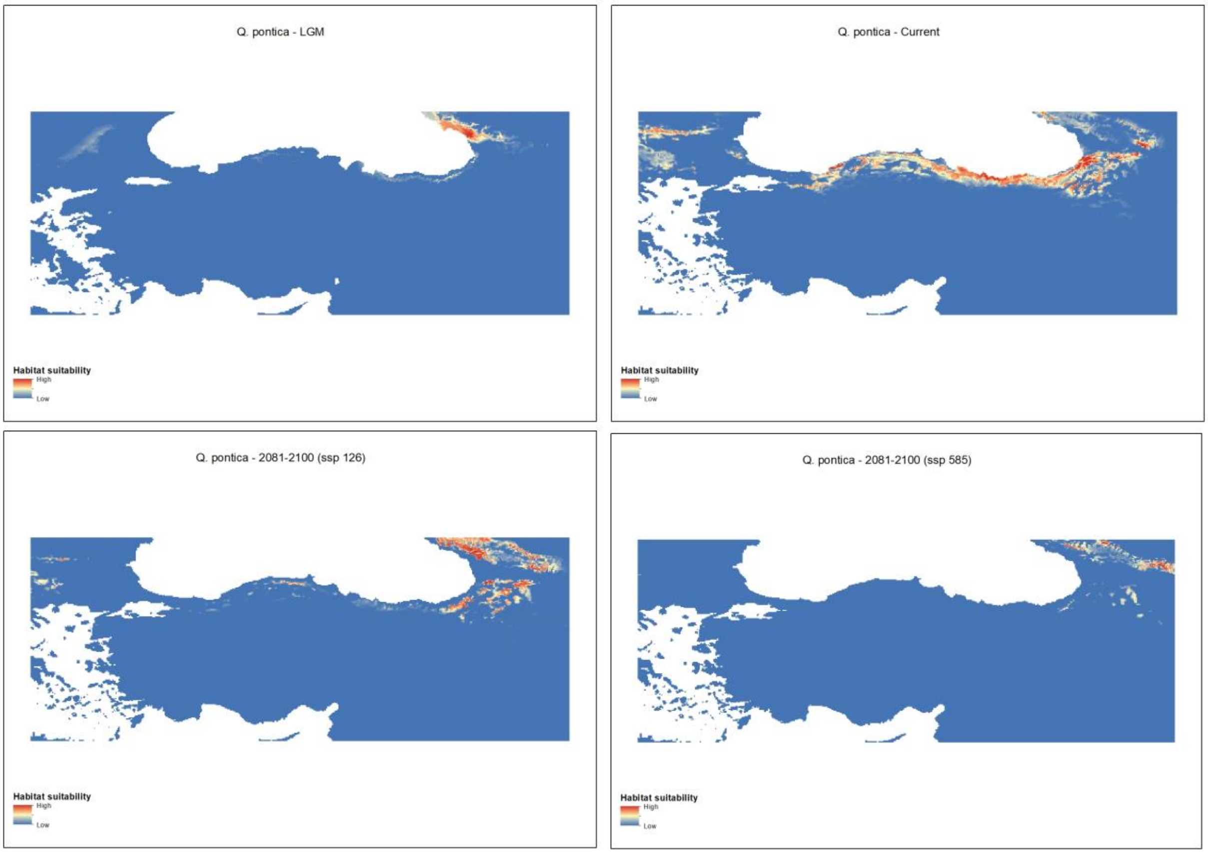

**Figure 2.3.** Ecological niche modeling projections showing the distribution of *Q. pontica* under a. the Last Glacial Maximum (22000 YBP) b. the Present, c. future (2081-2100 ssp126), and d. future (2081-2100 ssp585) bioclimatic conditions.

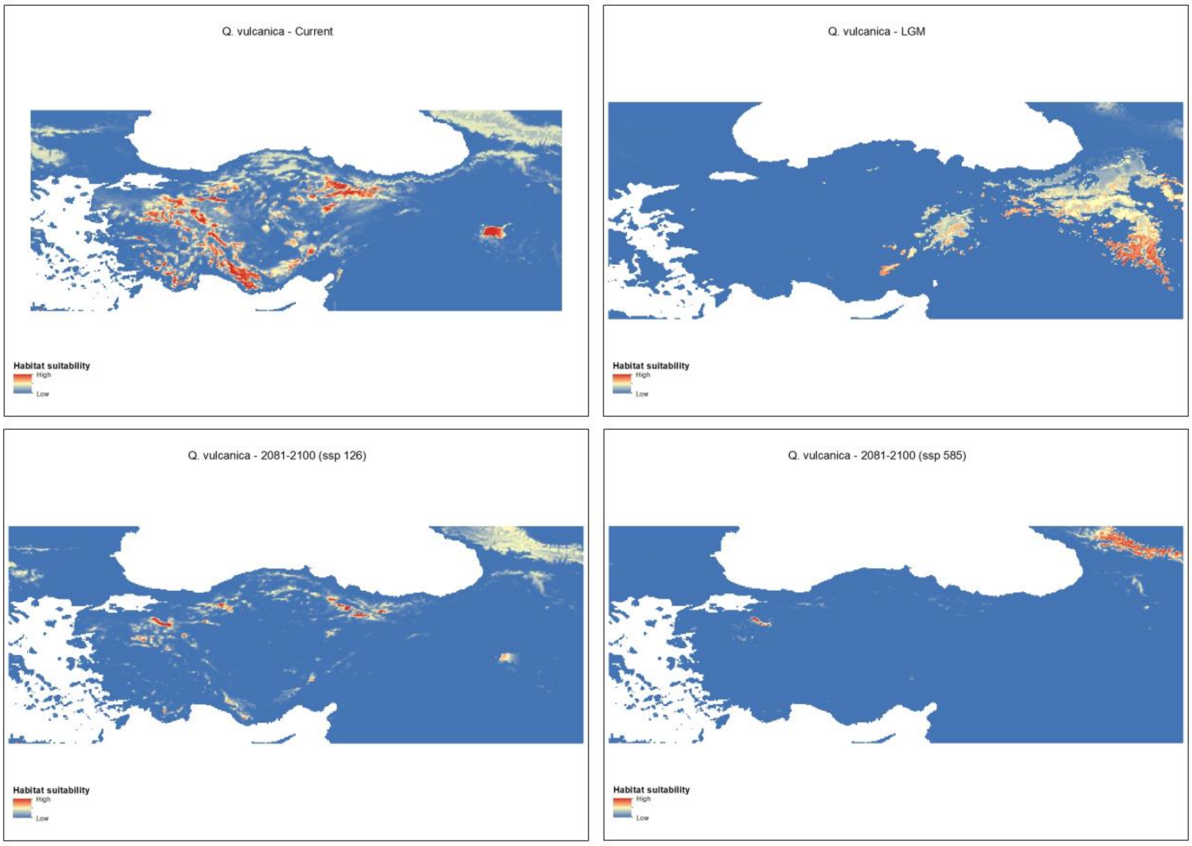

**Figure 2.4.** Ecological niche modeling projections showing the distribution of *Q. vulcanica* under the a. Last Glacial Maximum (22000 YBP) b. current, c. Future (2081-2100 ssp126), and d. Future (2081-2100 ssp585) bioclimatic conditions.

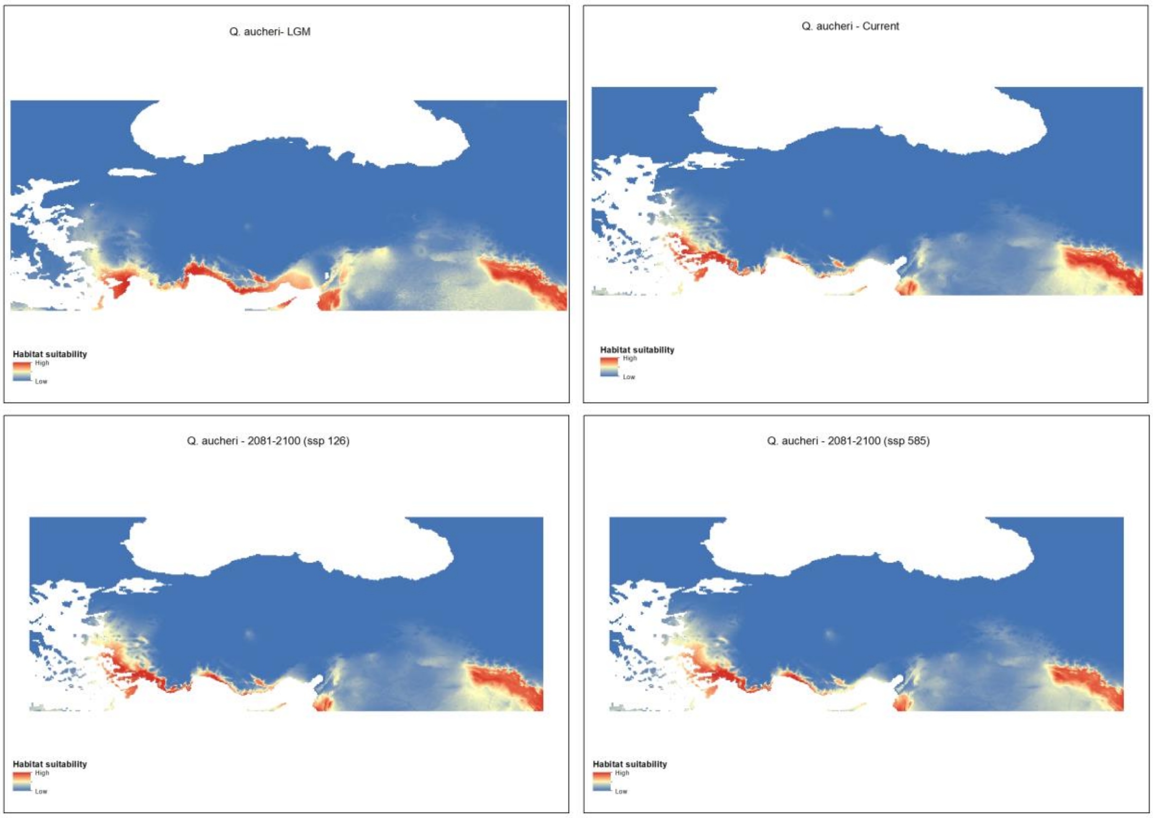

**Figure 2.5.** Ecological niche modeling projections showing the distribution of *Q. aucheri* under the a. Last Glacial Maximum (22000 YBP) b. current, c. Future (2081-2100 ssp126), and d. Future (2081-2100 ssp585) bioclimatic conditions**.**

### 2.3.2. Current Threats on Populations

Although anthropogenic impacts were generally species-specific, we observed that all the studied *Quercus* species also suffered a few common threats according to the interviews and direct observations during the field surveys (Table 3). Overall, the intensity of these impacts and disturbances was relatively higher in *Q. aucheri* and *Q. vulcanica* than *Q. pontica* (Table 2.3). Land-use change was the most frequently observed impact on the populations of all three species, although the drivers of land-use change differ among species. Moreover, insect and fungal damage on trees were also observed in all species, even though they had relatively less impact on population health in comparison to the land-use change.

**Table 2.3.** Main anthropogenic impacts and natural disturbances occurring on the species studied. Logging includes both illegal and legal activities; land-use change means deforestation; domestic herbivory identifies the grazing and browsing by sheep and goats, fires are both of anthropogenic and natural origin, and pest damage include insect and fungal damages.

| **Species** | **Logging or coppicing** | **Land-use change** | **Domestic herbivory** | **Fire** | **Pest damage** |
|---|---|---|---|---|---|
| *Quercus aucheri* | Moderate | High | High | High | Moderate |
| *Quercus pontica* | Low* | High | No* | No | Moderate |
| *Quercus vulcanica* | High | High | Moderate | Low | Moderate |

* Assessment is only for Turkish populations. Georgia populations are under pressure of overgrazing and overharvesting (Strijk & Carrero, 2020).

We observed pest damage and land-use change as the most prominent impacts on *Q. pontica* populations. In all *Q. pontica* populations except the Camili population of Artvin province of Turkey, individuals had brown spots on leaves, indicating fungal damage. However, apart from the discoloration of leaves, the trunks of the individuals were not damaged, and whole acorns were detected. According to local accounts, the primary factor leading to habitat loss in *Q. pontica* stands has been land-use change, with a significant portion of forests transformed into tea orchards in the past. Illegal logging was only observed in one population in Cimil uplands in Rize province of Turkey, therefore, it seems that illegal logging is not a significant threat for *Q. pontica*, at least in Turkey.

The damage on individuals due to domestic herbivory (mainly domestic goats) was higher in *Q. aucheri* in contrast to *Q. pontica* and *Q. vulcanica*. Moreover, fire is also a significant factor for *Q. aucheri* populations since the species distributes in fire-prone Mediterranean ecosystems. As most *Q. aucheri* populations were found within different protected areas, we did not identify any anthropogenic impacts, such as logging, as a current threat for these populations. However, the converted shrublands into olive groves and tourism areas are the significant land-use change impact in the distribution area of *Q. aucheri*. Possibly due to these reasons, we observed that the abundance of *Q.*

*aucheri* was higher in the populations within the protected areas than that outside. Various insect larvae were detected on the leaves, but it was observed that they did not entirely damage individuals.

*Q. vulcanica* is the one that was subjected to both domestic grazing and logging pressures most among the studied species. According to available literature, the species has primarily been utilized for purposes such as firewood and within the wood industry. It finds applications in various areas including coverings, floor parquet, furniture, building materials, tool handles, and charcoal production (Yaltırık, 1984; Kargıoğlu et al., 2009). Our local interviews in the Beyşehir district of Turkey suggest that *Q. vulcanica* lost its dominance in the region due to intensive logging pressure in the past. In the field surveys, we observed that nearly all populations in the Sultan Mountains ranges had been exposed to legal logging pressure by the Turkish forest service. In addition, we observed the impact of domestic herbivory by sheep, cattle, and goats in several *Q. vulcanica* populations.

## 2.4. Discussion

Our results revealed the existence of different climate responses and threats faced by the studied regionally endemic oak species. Our models suggest that *Quercus aucheri*, the only Mediterranean oak in our study, had a broader distributional range during the LGM than the Present. On the other hand, *Q. pontica* and *Q. vulcanica* displayed a shrinking pattern towards climatically favorable areas within their current distributional range during the LGM. The predicted future climate will also negatively affect the distribution of the latter two species, but *Q. aucheri* will favor the warmer climatic conditions of the end of the century. Therefore, *Q. aucheri* seems to be the least vulnerable to climate change among three oak species. Our observations suggest that anthropogenic activities severely affect all species even if they have high resilience to various disturbances such as fire, herbivory, and logging (due to the resprouting ability of oaks). However, land conversions from forest or shrublands to agricultural areas (for *Q. aucheri* and *Q. pontica*) and touristic and residential facilities (for *Q. aucheri* and *Q. vulcanica*) are the main threats for the studied oak species creating fragmented populations for them. Our observations on threats are consistent with IUCN assessments of these species (Stephan, 2018; Güner et al., 2019; Strijk & Carrero, 2020).

Dramatic climate changes during the Late Quaternary and the future climate under different scenarios strongly impact the range of tree species' dynamics (Svenning, 2003; Svenning et al., 2008; Thuiller et al., 2011). Besides, anthropogenic impacts have significant and equivalent impacts as much as the climate on the species' range dynamics. Our model predictions show that *Q. aucheri* does not follow the ‘expansion–contraction’ model as in several other *Quercus* species in the western Palearctic (Ferris et al., 1998; Brewer et al., 2002; Ülker et al., 2018). Throughout the Late Pleistocene glacial-interglacial cycle, when assessing the species' reactions to climate change, Anatolia acted as a conventional southern refugium for numerous temperate species. Nevertheless, *Q. aucheri* exhibited unique behavior, expanding its geographical range both latitudinally and longitudinally in response to the climate changes during the LGM (Bennet & Provan, 2008; Stewart et al., 2010). Undoubtedly, the region of southern Anatolia is acknowledged as a significant area of concentrated plant biodiversity within the Mediterranean Basin, boasting the recognition of five recognized potential refugia. (Medail & Diadema, 2009). The projections for the Last Glacial Maximum (LGM) align with the paleoecological evidence of enduring vegetation in the Mediterranean Basin, providing evidence of the presence of oak species in this area throughout extended periods of climatic fluctuations (Petit et al., 2002; Tzedakis et al., 2006; Şenkul & Doğan, 2013; Bouchal et al., 2018). Therefore, we conclude that *Q. aucheri* possibly has a long history in the area covering the present-day distribution range of the species, as similar to other Mediterranean tree species. It is suggested that Mediterranean refugia were less affected than European temperate refugia during the past climate changes, conserving long-term genetic and species diversity (Cowling et al., 2005; Medail & Diadema, 2009). Our predictions of the broad distribution of *Q. aucheri* during the LGM are consistent with this idea and also suggest that Mediterranean plant species might have responded differently to Pleistocene climate changes in comparison to European temperate plants. Under the future climate projections, *Q. aucheri* showed a broader distribution range than its current prediction and expand their ranges through higher elevations. Besides the northern parts of Zagros Mountains is predicted as climatically suitable areas for *Q. aucheri* for each time period that were tested. The Zagros Mountain range, situated in the Irano-Turanian biogeographical region, exhibits a continental climate, but researchers suggest a precipitation regime as Mediterranean (Noroozi et al., 2020). This region hosts other oak species, which most of them are belong to section Cerris, such as *Q. libani*, and *Q.*

*brantii*, and *Q. ithaburensis* from section *Quercus*. Although this region is an important host to different oak species due to its climatic diversity, the known distribution of *Q. aucheri* has never been this far east and in a partially continental region.

Unlike *Q. aucheri*, *Q. pontica* and *Q. vulcanica* displayed a shrinking pattern towards climatically favorable areas within their current distributional range during the LGM. Precipitation seasonality was the most critical variable for *Q. pontica* according to the projection results, which also reflects the unseasonal precipitation characteristics of the Black Sea coastal region of northeastern Anatolia (Türkeş, 1996). Moreover, it can be said that *Q. pontica* adapted to prominent climatic oscillations as it is a Tertiary relict species in this region. The Caucasus Mountain range which constitutes the northernmost limit of the distribution of *Q. pontica*, is a major biogeographical barrier limiting the movement and dispersal of several temperate plant and animal taxa but served as a glacial refugium for a variety of species during the LGM (Hewitt, 1999; Perktaş et al., 2015a; Aradhya et al., 2017; Parvizi et al., 2019). *Q. pontica* also presented a contraction pattern towards climatically suitable areas according to the LGM projections and has been able to survive in the Abkhazia region in the Present, which inferred that this area displays a possible glacial refugium as for many other Caucasian forest species (Tarkhnishvili et al., 2011). Although our predictions under a warmer future climate suggest a large climatically suitable region in the south of Caucasus mountains in Georgia for *Q. pontica*, no record of this species are known from this region. The lack of the presence of the species in this area makes the northeastern Anatolian mountains the only possible area for the future survival of *Q. pontica* as a species by the end of the century in the case of the worst-case climate scenario. However, the populations of *Q. pontica* in northeastern Anatolia are currently severely fragmented and found only in specific highlands. Therefore, conservation measures should be taken for these fragmented populations where many are found in areas lacking any protection status.

Temperature-related variables had the most contribution to the *Q. vulcanica* models. The bioclimatic niche of *Q. vulcanica* is characterized by a highly heterogeneous climate, and the tolerance range varies from arid to humid (Kargıoğlu et al., 2009). Our model predictions suggest more than one and disconnected suitable distribution areas for *Q. vulcanica* during the LGM, where the postglacial expansion occurred during the Late Pleistocene. As such, this pattern could be reputed as multiple refugia for this species. Anatolia stands as the exclusive habitat for *Q. vulcanica*, renowned as a glacial refugium for numerous temperate species during various climatic oscillations (Ülker et al., 2018; Bilgin, 2011; Perktaş et al., 2015b), these multiple refugia occurred in different climatic and topographic regions support the refugia-within-refugia hypothesis, but this conclusion strictly needs for further phylogenetic analysis (Gomez & Lucas, 2007). The future models predicted a contraction in the potential distribution range in *Q. vulcanica*, and this contraction was more dramatic under the worst-case scenario, bringing possible extinction. Even though it was modeled for the period of 2050-2070 and with different bioclimatic variables, Sarıkaya et al. (2022) revealed a similar future distribution pattern for *Q. vulcanica* that will face a dramatic loss in its distribution range. Our models indicated that the places where potential LGM refugia and potential remnant populations under a warmer future are the same for *Q. vulcanica*, namely anti-Taurus mountains and a few specific long-dormant volcanoes in the south of central Anatolia. The findings hold considerable importance for the enduring preservation of this species, as the majority of its genetic diversity, in accordance with the 'expansion-contraction' model during the Pleistocene glacial cycles, is safeguarded within glacial refugia (Petit et al., 2002a). Certainly, *Q. vulcanica* exhibits notable levels of genetic diversity, and despite its isolation in various populations within Turkey, there is minimal genetic differentiation among them. This is attributed to recent fragmentation caused by human activity, which has had only a restricted impact on the genetic variation patterns within this species (Yücedağ et al., 2021). On the other hand, since *Q. vulcanica* populations distributed in places where are potential for LGM refugia and potential remnant locations (the eastern part of its main distribution range) has not been genetically studied yet, conservation decisions should carefully be made, especially after more genetic analysis of the species including populations in potential LGM refugia.

In the era known as the 'Anthropocene', alterations in land and sea use, direct exploitation, climate change, pollution, and the presence of invasive alien species are intricately connected to human activities (IPBES, 2019), which causes direct loss of biodiversity and ecosystems in local, regional, and global extents. Among 35 global biodiversity hotspots, Anatolia hosts three of them and all the study species are distributed in one of them. The natural vegetation of these habitats was extremely destroyed by the human impact over thousands of years (Mittermeier et al., 2011). The biodiversity in the Mediterranean Basin, mainly along the coastal areas, is under threat due to human impacts as well (Medail & Diadema, 2006), and Turkey is one of the regions which is under disproportionate threat from human activities (Medail & Diadema, 2009; Şekercioğlu et al., 2011). Although a dramatic contraction is not foreseen for *Q. aucheri* under future climate scenarios, forestry practices in relation to the species should be carried out carefully, and land use should be limited to a certain extent in its distributional range since the severely fragmented population structure of the species (Güner et al., 2019). *Q. vulcanica* was used as a parquet material and wood fuel for several years (Genç et al., 2021), and during the field surveys in the area, it was learned from the foresters that the species faced logging in the past 50 years. It was also stated that the fragmental distribution of this species is due to anthropic disturbance (Aydınözü, 2004). Therefore, it was observed that the closure of *Q. vulcanica*, and the number of individuals in a region is relatively lower than the other species, if it was a mixed stand, and it is not successful in competing with the other species. *Q. vulcanica* still suffers from land-use change, logging, and domestic grazing and needs to be protected with convenient forestry implementations not just in its known conservation areas but in each population. Unlike *Q. aucheri* and *Q. vulcania, Q. pontica* is classified by IUCN as the only regionally endemic oak species for Anatolia as endangered (EN) status. For *Q. pontica*, the Georgia populations are threatened by overgrazing and logging (Strijk & Carrero, 2020), while Anatolian populations have been faced with land-use changes at most, and pest damage in some populations according to our observations.

In conclusion, our study revealed the possible glacial refugia during the LGM and their possible remnant populations under the future climate for three regionally endemic oak species from different climatic zones of Anatolia. Our observations also documented the possible threats these species face due to anthropogenic and natural disturbances. Combining these two findings, climate change, and anthropogenic pressure may result in dramatic declines in the distribution range of these species in the future. Therefore, immediate conservation action is required for at least *Q. pontica* and *Q. vulcanica* to make proper management decisions about their populations by considering the future warmer climate and current human activities. The differences in the responses of studied oak species to climate change and the anthropogenic pressures they are subjected to should be considered for developing and implementing the conservation and management plans for forests and shrublands dominated by these oak species.

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## Supplementary Material to the Chapter 2

**Table A1.** Bioclimatic variables used in ENMs that were downloaded from the WorldClim database version 2.1 (Fick et al., 2017).

| Bioclimatic variable | Definition |
|---|---|
| BIO1 | Annual mean temperature |
| BIO2 | Mean diurnal range (max temp/min temp) (monthly average) |
| BIO3 | Isothermality (BIO1/BIO7) × 100 |
| BIO4 | Temperature seasonality (Coefficient of variation) |
| BIO5 | Max. temperature of warmest period |
| BIO6 | Min. temperature of coldest period |
| BIO7 | Temperature annual range (BIO5-BIO6) |
| BIO8 | Mean temperature of wettest quarter |
| BIO9 | Mean temperature of driest quarter |
| BIO10 | Mean temperature of warmest quarter |
| BIO11 | Mean temperature of driest quarter |
| BIO12 | Annual precipitation |
| BIO13 | Precipitation of wettest period |
| BIO14 | Precipitation of driest period |
| BIO15 | Precipitation of seasonality (Coefficient of variation) |
| BIO16 | Precipitation of wettest quarter |
| BIO17 | Precipitation of driest quarter |
| BIO18 | Precipitation of warmest quarter |
| BIO19 | Precipitation of coldest quarter |

**Table A2.** Coordinate data used for ecological niche modeling for each species.

| Species | Longitude | Latitude |
|---|---|---|
| *Q_aucheri* | 28.14386 | 36.79743 |
| *Q_aucheri* | 28.22187 | 36.74617 |
| *Q_aucheri* | 27.55145 | 37.4886 |
| *Q_aucheri* | 27.58489 | 37.28009 |
| *Q_aucheri* | 27.39839 | 37.04572 |
| *Q_aucheri* | 27.35150 | 37.13419 |
| *Q_aucheri* | 27.23606 | 37.0545 |
| *Q_aucheri* | 28.20000 | 36.88333 |
| *Q_aucheri* | 28.13333 | 36.90000 |
| *Q_aucheri* | 28.30000 | 36.83333 |
| *Q_aucheri* | 28.05336 | 36.58674 |
| *Q_aucheri* | 29.17130 | 36.72293 |
| *Q_aucheri* | 30.53754 | 36.81084 |
| *Q_aucheri* | 27.29974 | 37.65908 |
| *Q_aucheri* | 27.45710 | 37.09193 |
| *Q_aucheri* | 28.07708 | 37.52220 |
| *Q_aucheri* | 28.57827 | 36.89159 |
| *Q_aucheri* | 29.60675 | 36.19161 |
| *Q_aucheri* | 31.22415 | 37.09482 |
| *Q_aucheri* | 27.34951 | 37.08695 |
| *Q_aucheri* | 29.46326 | 36.22721 |
| *Q_aucheri* | 29.92945 | 36.27347 |
| *Q_aucheri* | 30.52966 | 36.53607 |
| *Q_aucheri* | 28.29150 | 36.89730 |

| | | |
|---|---|---|
| *Q_aucheri* | 27.59930 | 37.14460 |
| *Q_aucheri* | 29.75280 | 36.25180 |
| *Q_aucheri* | 29.41580 | 36.27320 |
| *Q_aucheri* | 29.09590 | 36.58460 |
| *Q_aucheri* | 28.11840 | 36.71680 |
| *Q_aucheri* | 28.61570 | 36.83600 |
| *Q_aucheri* | 28.69650 | 36.78430 |
| *Q_aucheri* | 27.17670 | 36.81670 |
| *Q_aucheri* | 28.15000 | 36.21670 |
| *Q_aucheri* | 27.83330 | 36.60000 |
| *Q_aucheri* | 28.06670 | 36.08330 |
| *Q_aucheri* | 28.03330 | 36.26670 |
| *Q_aucheri* | 27.35000 | 36.45000 |
| *Q_aucheri* | 29.63330 | 36.23330 |
| *Q_pontica* | 39.90870 | 40.69280 |
| *Q_pontica* | 40.11300 | 40.68260 |
| *Q_pontica* | 40.39840 | 40.79200 |
| *Q_pontica* | 40.63170 | 40.79150 |
| *Q_pontica* | 40.64790 | 40.70750 |
| *Q_pontica* | 41.02260 | 40.96820 |
| *Q_pontica* | 41.20250 | 41.17690 |
| *Q_pontica* | 41.37430 | 41.27650 |
| *Q_pontica* | 41.42700 | 41.33760 |
| *Q_pontica* | 41.74320 | 41.39950 |
| *Q_pontica* | 41.83480 | 41.40480 |
| *Q_pontica* | 41.93490 | 41.47980 |

|  |  |  |
|---|---|---|
| *Q_pontica* | 40.72610 | 40.78170 |
| *Q_pontica* | 39.82190 | 40.68830 |
| *Q_pontica* | 41.34190 | 41.35330 |
| *Q_pontica* | 41.51080 | 41.37330 |
| *Q_pontica* | 41.71040 | 41.69090 |
| *Q_pontica* | 42.04500 | 41.52890 |
| *Q_pontica* | 40.88330 | 40.63330 |
| *Q_pontica* | 41.96670 | 41.71670 |
| *Q_pontica* | 42.04970 | 41.74750 |
| *Q_pontica* | 41.04400 | 43.27800 |
| *Q_pontica* | 40.82000 | 40.63300 |
| *Q_pontica* | 41.08510 | 41.05610 |
| *Q_pontica* | 41.51730 | 41.26480 |
| *Q_pontica* | 42.23330 | 41.66670 |
| *Q_pontica* | 42.48330 | 41.66670 |
| *Q_pontica* | 41.99060 | 41.54950 |
| *Q_pontica* | 41.35000 | 41.20000 |
| *Q_pontica* | 40.70060 | 40.68680 |
| *Q_vulcanica* | 30.82467 | 37.75763 |
| *Q_vulcanica* | 31.47579 | 38.26792 |
| *Q_vulcanica* | 31.38562 | 38.34846 |
| *Q_vulcanica* | 31.26194 | 38.47528 |
| *Q_vulcanica* | 30.41194 | 38.44806 |
| *Q_vulcanica* | 32.03006 | 37.82260 |
| *Q_vulcanica* | 31.34028 | 37.66000 |
| *Q_vulcanica* | 31.29194 | 37.88611 |

| | | |
|---|---|---|
| *Q_vulcanica* | 29.73250 | 38.96194 |
| *Q_vulcanica* | 30.34222 | 39.43111 |
| *Q_vulcanica* | 30.74666 | 38.08635 |
| *Q_vulcanica* | 31.00000 | 38.00000 |
| *Q_vulcanica* | 36.41722 | 36.94889 |
| *Q_vulcanica* | 35.39361 | 38.61750 |
| *Q_vulcanica* | 34.19681 | 38.16564 |
| *Q_vulcanica* | 33.16753 | 37.39116 |
| *Q_vulcanica* | 33.84778 | 41.79083 |
| *Q_vulcanica* | 33.91694 | 41.00889 |
| *Q_vulcanica* | 31.27333 | 40.27111 |

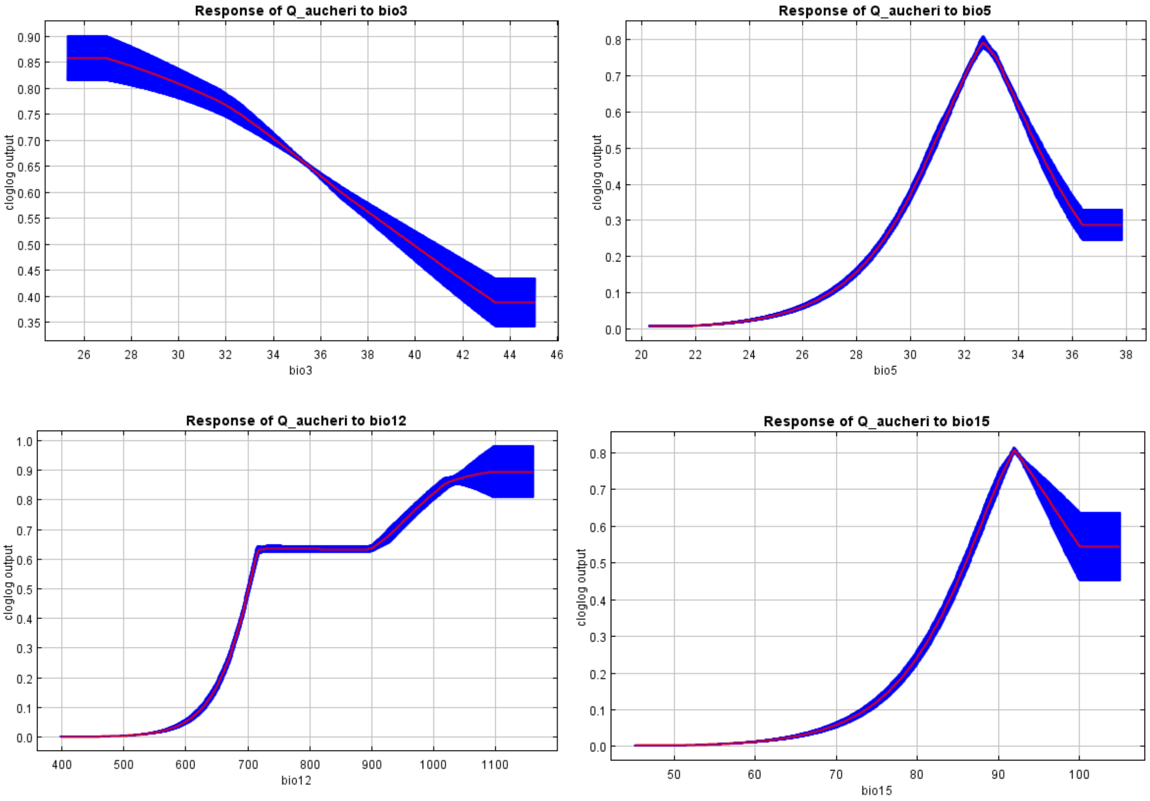


**Figure A1.** Response curves of the bioclimatic variables affected the model projections for *Quercus aucheri*.

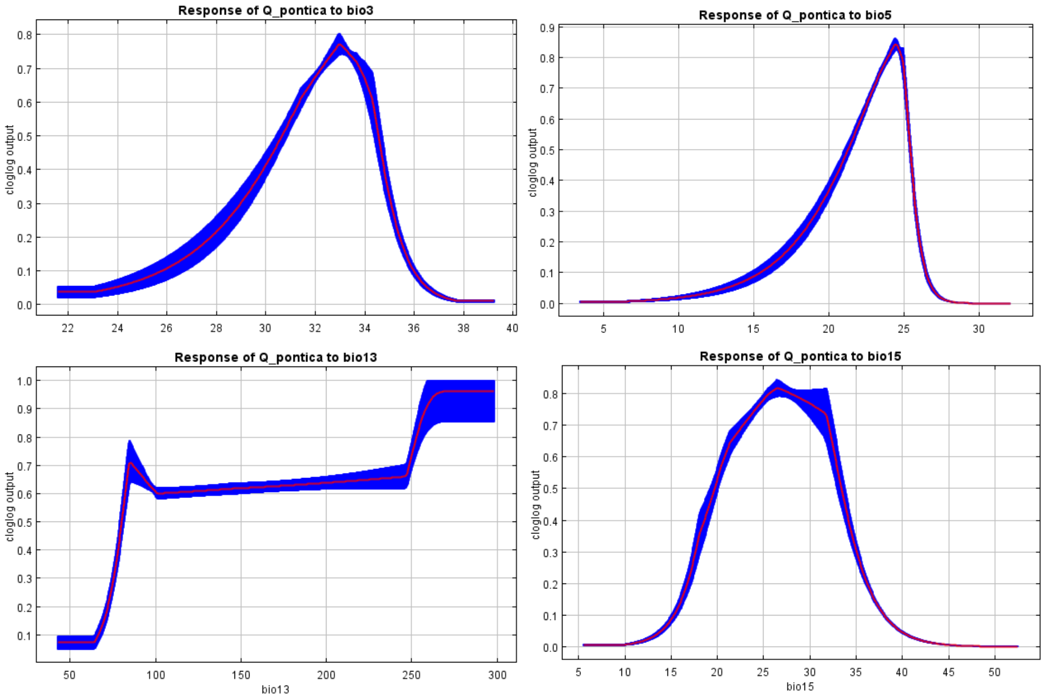


**Figure A2.** Response curves of the bioclimatic variables affected the model projections for *Quercus pontica*.

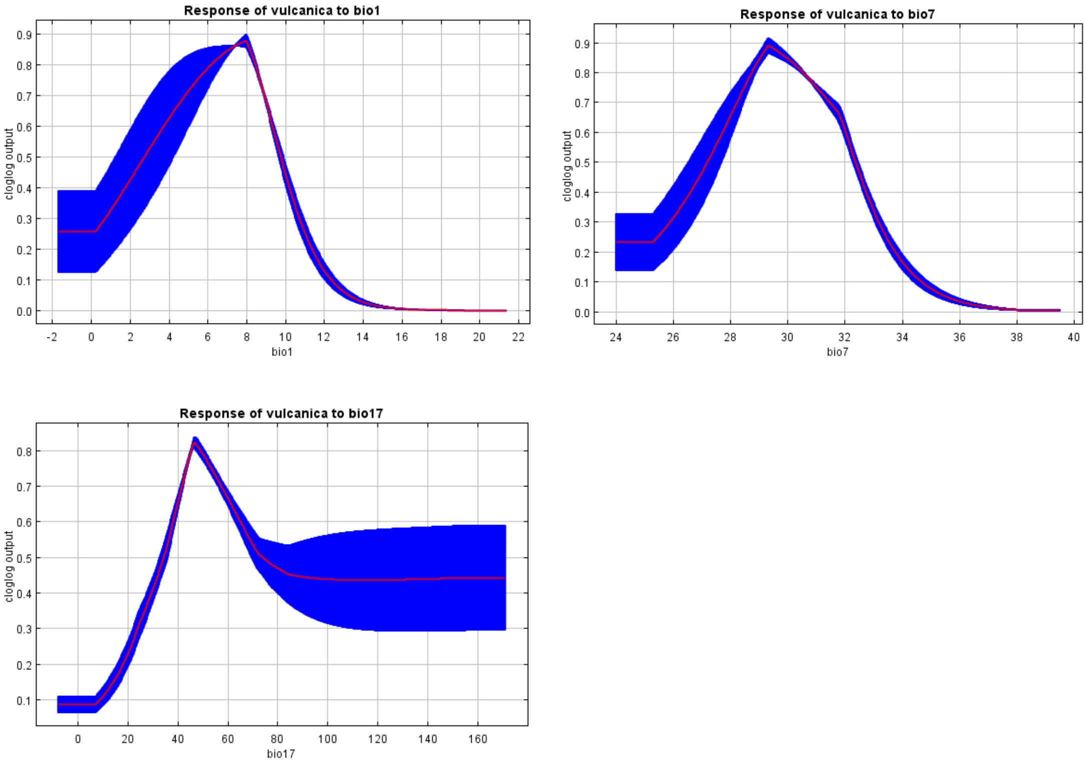
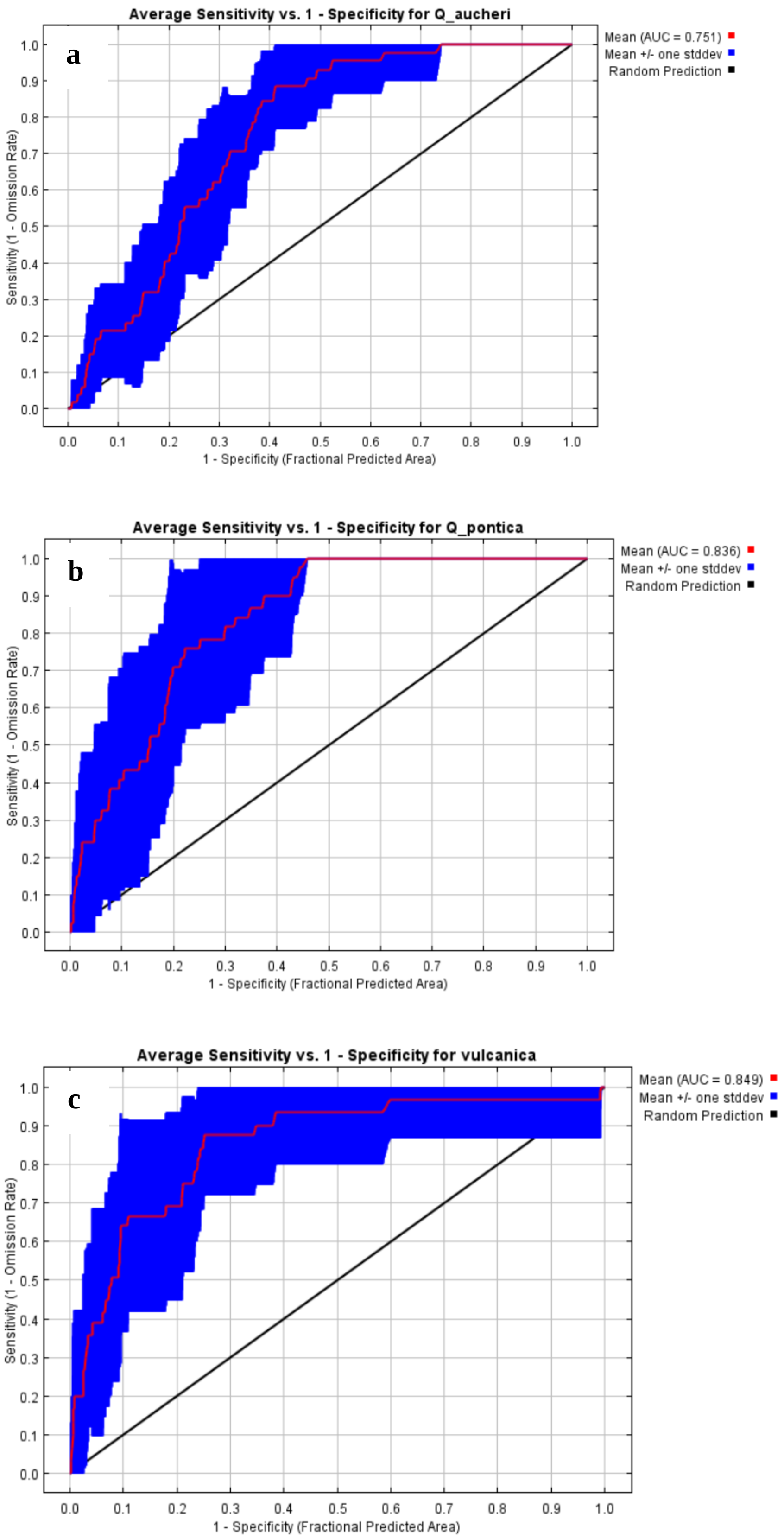


**Figure A3.** Response curves of the bioclimatic variables affected the model projections for *Quercus vulcanica*.



**FigureA4.** ROC statistics of the model projections for **a.** *Q. aucheri*, **b.** *Q. pontica*, **c.** *Q. vulcanica*

# CHAPTER 3. CLIMATE ZONE AND INFRAGENERIC SECTIONS EXPLAINS TRAIT VARIABILITY IN OAKS OF THE WESTERN PALEARCTIC REGION

## Abstract

Climate changes are considered as one of the main drivers of the oak flora in western Palearctic region. Environmental differences arising from climatic conditions and evolutionary processes shape demographic processes, as well as ecological and physiological traits of species. In order to enhance comprehension of the biogeographic history, a trait-based approach was used to reveal functional trait variability between different climatic zones and sections of the western Palearctic oaks. We assessed the differences and similarities in ten functional traits among 23 oak species belonging to four oak sections (*Ilex, Cerris, Quercus*, and *Ponticae)* and distributed across three climatic zones (Mediterranean, Transition, and Temperate) using general linear mixed models. Many traits, mainly those related to the leaf economics spectrum, exhibited high-level variability among climate zones and infrageneric groups (i.e., sections). The most striking differences in traits were directly and prominently related to the climate response of species, such as leaf thickness and leaf area. Our results showed that temperate zone oak traits differ from transition and Mediterranean oaks. Moreover, an association between climate zones and sections was found through a chi-square analysis. In other words, the main differentiation occurs between *Quercus* and *Ilex/Cerris* sections, with all species in the *Ilex* and *Cerris* sections comprising Mediterranean species. Our results suggest that climate zone shapes trait variability in oaks of the western Palearctic, but evolutionary legacy may have played a role in plant traits as well.

**Keywords:** *Quercus,* western Palearctic, climatic gradients, infrageneric sections, leaf thickness, leaf area, trait variability

## 3.1. Introduction

Climate is a major factor determining vegetation types in many regions worldwide. Humboldt was the first scientist to highlight the effects of climate elements such as temperature, humidity, and altitude on different vegetation zones (Jackson, 2009). The most widely used global climate classification system, Köppen-Geiger, is based on this idea, dividing climates into five main groups based on precipitation, temperature patterns, and regional vegetation types (Peel, et al., 2007). Although the current climate has shaped extant vegetation belts, climate change has begun to have phenological and distributional impacts on species at regional and global scales (Walther et al., 2002; Parmesan & Yohe, 2003).

Global climate changes are widely recognized as a crucial factor in shaping species' geographical distribution patterns. Advancements in biogeographic research have illuminated the climate fluctuations during the Quaternary period, particularly the last glacial maximum, which played a transformative role in reshaping the vegetation-climate interactions in North America and Europe (Hewitt, 1996; Taberlet et al, 1998, Provan & Bennet, 2008). For instance, European oak flora has been driven by climate changes (Petit et al., 2002; Hipp et al., 2020).

Species distribution models are commonly employed to predict shifts in the distributional range of species, built upon the fundamental assumption of niche theory (Hutchinson, 1957; Maguire, 1973; Holt, 2009). However, in recent years, this approach has been subject to questioning, as theoretical niches do not always dictate species abundance (Sporbert et al., 2020). The reasons behind why a species' distribution might deviate from the niche optimum are numerous, but the underlying mechanisms governing these relationships are still under investigation. For instance, the concept of niche mismatch has revealed that the recolonization of temperate oak species from glacial refugia occurred in two stages: primary refugia and secondary refugia (Brewer et al., 2002; Petit et al., 2002). Accordingly, while the first recolonizations were mostly related to the changes in climate; topography, interspecific competition, and edaphic factors were effective during the secondary colonization. Additionally, a multilayered seed dispersal mechanism suggests that the ecological needs of the species and interspecies variability may affect the direction and speed of colonization of the temperate oaks in Europe (Petit et al., 2002). For Mediterranean oaks, the multiple refugia hypothesis is applicable, as these species have been limited to Mediterranean coastlines due to factors such as being less competitive, adaptability to drought, different ecological requirements, wildfires in the Mediterranean Basin, herbivores, pathogen attacks, and the arrival of new competitors (de heredia, 2007; Carrión, 2002; Turner et al., 2008). While global climate change plays a major role in shaping the geographical distribution patterns of species, it is important to acknowledge that the environmental variations resulting from climatic conditions also shape the ecological and physiological traits of species, which in turn contribute to their geographical distributions.

At the global scale, plant functional traits are primarily shaped by annual mean temperature, but annual mean total precipitation has also affected plant growth. Moreover, the mean annual temperature is mainly effective in the plant growth in temperate regions (Moles et al., 2014). Functional traits, such as leaf thickness, leaf area, and seed mass, are critical to plant growth, survival, and reproduction (Díaz et al., 2022), and functional traits determines how plants perform and respond to changing environments (Violle et al., 2007, Garnier et al., 2016). Numerous studies have demonstrated that the geographical distribution of plants is influenced by their functional traits (Cavender-Bares et al., 2005; Cavender-Bares & Pahlich, 2009). When evaluated on a community basis, the sympatric distribution of many *Quercus* species or the coexistence of sibling species in close geographies suggest that factors other than climate are important in determining their ecological niches. Considering its wide distribution across various regions and ecosystems in the Northern Hemisphere (Carrero et al., 2020), it emerges as an interesting group in the evaluation of functional plant traits (Sakai et al., 1981; Cavender-Bares et al. 2004; Cavender-Bares et al., 2005; Cavender-Bares & Pahlich, 2009). Gaining insights into the connections among climate zones, functional traits, and the distribution of oak species can provide valuable information for effective oak management and conservation endeavors.

In this study, we aimed to reveal the role of climate zones in shaping trait variability in western Palearctic *Quercus*. Also, considering the infrageneric groups (i.e., sections) in *Quercus* (Ilex, Cerris, Quercus, and Ponticae), we hypothesized that oak sections from the Mediterranean and temperate zones should differ in many plant functional traits. To test this hypothesis, we compiled trait data from databases of oak species in the western Palearctic region and complemented it with field observations for Anatolian endemic oaks) and compared the traits of oaks growing in different climate zones and belonging to different infrageneric groups.

## 3.2. Materials and Methods

### 3.2.1. Species

We studied oak (*Quercus*) species distributed in the western Palearctic region. We followed Denk et al. (2017) for the nomenclature and taxonomic classification of oak species. We selected 23 oak species among the listed 28 oaks from the western Palearctic region since the lack of trait data in five species. The selected species are representatives of different climate zones of the region and infrageneric groups (i.e., sections) within the *Quercus* genus (Table 1). In summary, the selected oaks belong to *Cerris* (7 species), *Ilex* (3 species), *Ponticae* (1 species), and *Quercus* (12 species) sections. Mainly, the distribution of oaks in the western Palearctic region falls into two distinct climate zones: the ‘Mediterranean’ (13 species) and ‘temperate’ (5 species). Consequently, we further grouped the studied species according to their main distribution ranges in these climate zones. We assigned the 5 species found in both regions to a third group, which we defined as 'transition'. (Table 1; Figure 1).

**Table 3.1.** The list of the western Palearctic oak species studied. Section and climate zone (*ClimZone*) are given for each species. The species are sorted alphabetically according to species epithets.

| **Species** | **Section** | **ClimZone** |
|---|---|---|
| *Quercus afares* Pomel | Cerris | Med |
| *Quercus aucheri* Jaub. & Spach | Ilex | Med |
| *Quercus brantii* Lindl. | Cerris | Med |
| *Quercus canariensis* Willd. | Quercus | Med |
| *Quercus cerris* L. | Cerris | Trans |
| *Quercus coccifera* L. | Ilex | Med |
| *Quercus faginea* Lam. | Quercus | Med |
| *Quercus frainetto* Ten. | Quercus | Trans |
| *Quercus hartwissiana* Steven | Quercus | Temp |
| *Quercus ilex* L. | Ilex | Med |

|  |  |  |
|---|---|---|
| *Quercus infectoria* Oliver | Quercus | Med |
| *Quercus ithaburensis* Decne. | Cerris | Med |
| *Quercus libani* Oliver | Cerris | Med |
| *Quercus lusitanica* Lam. | Quercus | Med |
| *Quercus macranthera* Fisch. & C.A.Mey ex Hohen. | Quercus | Temp |
| *Quercus petrae*a (Matt.) Liebl. | Quercus | Temp |
| *Quercus pontica* K.Koch | Ponticae | Temp |
| *Quercus pubescens* Willd. | Quercus | Trans |
| *Quercus pyrenaica* Willd. | Quercus | Trans |
| *Quercus robur* L. | Quercus | Temp |
| *Quercus suber* L. | Cerris | Med |
| *Quercus trojana* Webb. | Cerris | Med |
| *Quercus vulcanica* Boiss. & Heldr. | Quercus | Trans |

**Figure 3.1.** The geographic range of the three studied oaks, representative of (a) the Mediterranean (*Quercus coccifera*), (b) transition (*Q. pubescens*), and (c) temperate (*Q. petraea*) species. The maps were derived from Caudullo et al. (2017).

### 3.2.2. Trait Data

We selected traits that are significant determinants of the ecological and physiological requirements of plant species, but also considered the availability of data in the literature. We obtained trait data mainly from the TRY (Kattge et al., 2020) and BROT (Tavşanoğlu & Pausas, 2018) databases. For some traits, we also included trait records from regional flora books (Hedge & Yaltırık, 1982; Tutin et al.,1964, Franco, 1990; Vila-Viçosa et al., 2022) and FEL (Functional Ecology Laboratory, Hacettepe University, Turkey) trait datasets (Aktepe, 2021; Coşgun, 2022; Tüfekcioğlu, 2022). Finally, we did fieldwork to obtain data on height, leaf area, and specific leaf area traits for Anatolian endemic oaks (*Quercus pontica*, *Q. vulcanica*, and *Q. aucheri*), species with missing information in many traits. We followed the protocols mentioned in PérezHarguindeguy et al. (2013) to select individuals for collecting, storing, and measuring leaf samples. In the field, we selected five mature and healthy-looking individuals and sampled five leaves from each individual in each population. In the laboratory, we scanned the leaves to calculate their one-sided area by using the program ImageJ program (Rasband, 2012). To obtain specific leaf area values for each individual, we measured the oven-dried mass of leaves, then divided it by the average leaf area of the individual.

We did not include traits with few data records in our dataset. We also removed redundant trait data that existed both in the TRY and BROT databases. We filtered extreme trait values before analyses based on the reference publications indicating the standardized range of trait values (Reich et al., 1997; Garnier et al., 2001; Maherali et al., 2004; Díaz et al., 2022). Thus, we could exclude trait values from individuals growing in extreme conditions or possibly biased measurements. Finally, in our dataset, we included 7949 data records of ten traits for 23 oak species (Table 3.2). These traits represent the leaf economic spectrum (leaf area, specific leaf area, mass-based leaf nitrogen content, leaf dry matter content, leaf thickness, and leaf lifespan), reproductive success (seed mass), light acquisition (height), plant durability and physical resistance (stem specific density), and drought resistance (resistance to xylem cavitation) of plant species (Garnier et al., 2001; Reich et al., 2004; Pérez-Harguindeguy et al., 2013; Díaz et al., 2022).

**Table 3.2.** Short definitions, units, and the number of taxa, records, and trait databases used in the study. Definitions, abbreviations, and units are based on Pérez-Harguindeguy et al. (2013) and Tavşanoğlu & Pausas (2018).

| | | | | **N** | | |
|---|---|---|---|---|---|---|
| **Trait** | **Abbreviation** | **Definition** | **Units** | **Species** | **Record** | **Databases** |
| Height | H | The shortest distance between the ground level and the upper boundary of the vegetative tissues. | m | 21 | 143 | 7 |
| Leaf Dry Matter Content | LDMC | The ratio of oven-dry mass (mg) to its water-saturated fresh mass (g) of a leaf. | mg/g | 10 | 1139 | 4 |
| Leaf Area | LA | Area of the one-sided or projected area of an individual leaf based on its length and width. | $mm^2$ | 15 | 1390 | 6 |
| Leaf Life Span | LLS | Physiologically active or alive time period of an individual leaf | months | 11 | 39 | 2 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| Leaf Thickness | L*th* | Determines the physical strength of leaves and a key component of SLA. | mm | 14 | 308 | 2 |
| Leaf Nitrogen Content Mass | LNCm | The total amount of N per unit of dry leaf mass. | mg/g | 11 | 1964 | 2 |
| Hydraulic Conductivity | P50 | Xylem resistance to drought-induced cavitation. | Mpa | 7 | 27 | 1 |
| Seed Mass | SM | The dry mass of an average seed of a species. | mg | 15 | 132 | 2 |
| Specific Leaf Area | SLA | The ratio of the one-sided area of a fresh leaf to its oven-dry mass. | $mm^2$/mg | 19 | 2503 | 5 |
| Stem Specific Density | SSD | The oven-dry mass of a section of the main stem divided by the fresh volume of the related section. | $g/cm^3$ | 9 | 310 | 1 |

### 3.2.3. Data Analysis

General linear models were performed to assess the differences in the studied functional traits among climate zones and sections. In these analyses, traits were considered as response variables and the climate zone or the section as fixed factors. Conducting two-way analyses including both climate zone and section as fixed factors were not possible due to the lack of enough combinations between climate zones and sections, therefore, we made separate analyses for each factor for evaluating each trait.

Since there are unequal sampling sizes among species for many traits, most data records came from only a few species for some traits. To reduce the possible bias in data analysis due to such aggregation in data, linear mixed model analyses were also performed for each trait to reveal the differences among climate zones and sections. In these analyses, traits were considered as response variables, the climate zone or the section as fixed factors, and the species included in the model as the random factor. A likelihood ratio test was performed for the comparison among climate zones or sections for each trait in linear mixed models.

Prior to conducting each analysis, the data underwent normality testing using the Shapiro-Wilk test. In cases where normality was not met, a logarithmic transformation was applied to achieve a better approximation of normality. Following each analysis, the model's residuals were also visually inspected using residual plots. Subsequently, multiple comparisons following the general linear model or linear mixed model analyses were carried out by estimating marginal means for the climate zone or section pairs.

All analyses were conducted in the R environment (R Core Team, 2022). For linear mixed models, we utilized the *nlme* package (Pinheiro et al., 2022). Multiple group comparisons were performed using the *emmeans* package (Lenth et al., 2022) for both linear and linear mixed models. Violin plots were generated using the *ggplot2* package (Wickham et al., 2022).

### 3.4. Results

Trait values varied among the studied *Quercus* species. According to individual data records in our dataset, many traits showed high level variability among species but in some traits, there were also variability among populations (Supp. Figure A1). Namely, the maximum height varied between 1 m (*Q. coccifera*) and 45 m (*Q. robur*), LDMC between 76.68 mg $g^{-1}$ (*Q. petraea*) and 886.44 mg $g^{-1}$ (*Q. coccifera*), leaf area between 38.23 $mm^2$ (*Q. coccifera*) and 16935.96 $mm^2$ (*Q. frainetto*), leaf lifespan between 2.2 months (*Q. frainetto*) and 37.6 months (*Q. ilex*), leaf thickness between 0.092 mm (*Q. robur*) and 1.290 mm (*Q. coccifera*), leaf nitrogen content between 7.066 mg g-1 and 49.410 mg g-1 (both for *Q. petraea*), SLA between 2.010 $mm^2$ $mg^{-1}$ (*Q. vulcanica*) and

78.64 $mm^2$ $mg^{-1}$ (*Q. petraea*), and stem specific density between 0.079 g $cm^{-3}$ and 1.290 g $cm^{-3}$ (both for *Q. ilex*).

Despite high level trait variability among species, the variation in data in many traits could be explained by the climate zone (Mediterranean, transition, and temperate) and infrageneric group (Table 3.3 & 3.4, Figure 3.2 & 3.3). Specifically, temperate oaks had higher SLA, were taller, had thinner leaves, had larger leaves, and contained more nitrogen and dry matter content in their leaves, and had a shorter leaf lifespan than Mediterranean oaks (Table 3.3, Figure 3.2, $P < 0.01$). Oaks in the transition and temperate zones had relatively similar mean values in comparison to Mediterranean oaks in many traits (Table 3.3, Figure 3.2). However, temperate oaks had significantly higher SLA and height than oaks both from Mediterranean and transition zones (Table 3.3). Among the studied traits, we found no significant difference among climate zones in seed mass and P50 ($P > 0.05$).

Regarding infrageneric groups, *Quercus* section had higher SLA, were taller, were heavier in seed mass, had thinner leaves, had larger leaves, had shorter leaf lifespan, and contained less nitrogen and dry matter in their leaves than both section *Cerris* and section *Ilex* (Table 3.4, Figure 3.3, $P < 0.01$). *Ilex* section had the extreme values (min/max) as regards other groups in almost all traits; had the smallest SLA, had the narrowest leaves, had the smallest SSD, had the least dry matter and nitrogen content, but the had the thickest leaves and the longer leaf lifespan. Section *Ponticae* was the shortest group but had the largest leaves among these sections (Table 3.4). The oaks in the *Cerris* section had significantly heavier seeds than other sections ($P < 0.05$).

The primary findings of our study were obtained through general linear models. However, upon reanalyzing the data using linear mixed models, with species considered as the random factor, the significant differences in trait values among climate zones diminished for several traits. The disparities between the results of fixed-effect models and mixed models primarily arose from the abundance of data records originating from only a few species, particularly in certain traits. Consequently, considering the species as a random factor reduces the possibility of finding significant differences among tested groups in statistical terms. However, leaf thickness and leaf area (and somewhat LNCm) were still significantly different among climate zones, showing that the effect of climate zone is still higher for shaping these traits even in the data records for the same species controlled in the analysis. The frequency of the reduction in significance due to mixed models was relatively lower in infrageneric group analysis than climate zone. Specifically, all traits except LDMC, seed mass, and SLA had significantly different values among sections.

In our dataset, all six species in the *Cerris* section and three of four species in the *Ilex* section were distributed in the Mediterranean climate zone, whereas eight of 12 species in the *Quercus* section were distributed in non-Mediterranean climate zones (i.e., transition and temperate zones) (Supp. Table A1). A chi-square analysis indicated a significant association between climate zone (Mediterranean versus non-Mediterranean) and infrageneric groups in our dataset (X2 = 7.9, d.f.= 2, P = 0.020; *Ponticae* section was excluded in the analysis).

**Table 3.3.** Mean values and the standard errors (in parenthesis) of functional traits in three climate zones. The results of the general linear models and linear mixed models testing the differences in functional traits among climate zones are given. LR is the likelihood ratio and estimated by comparing the model with a null model only including species as the random factor.

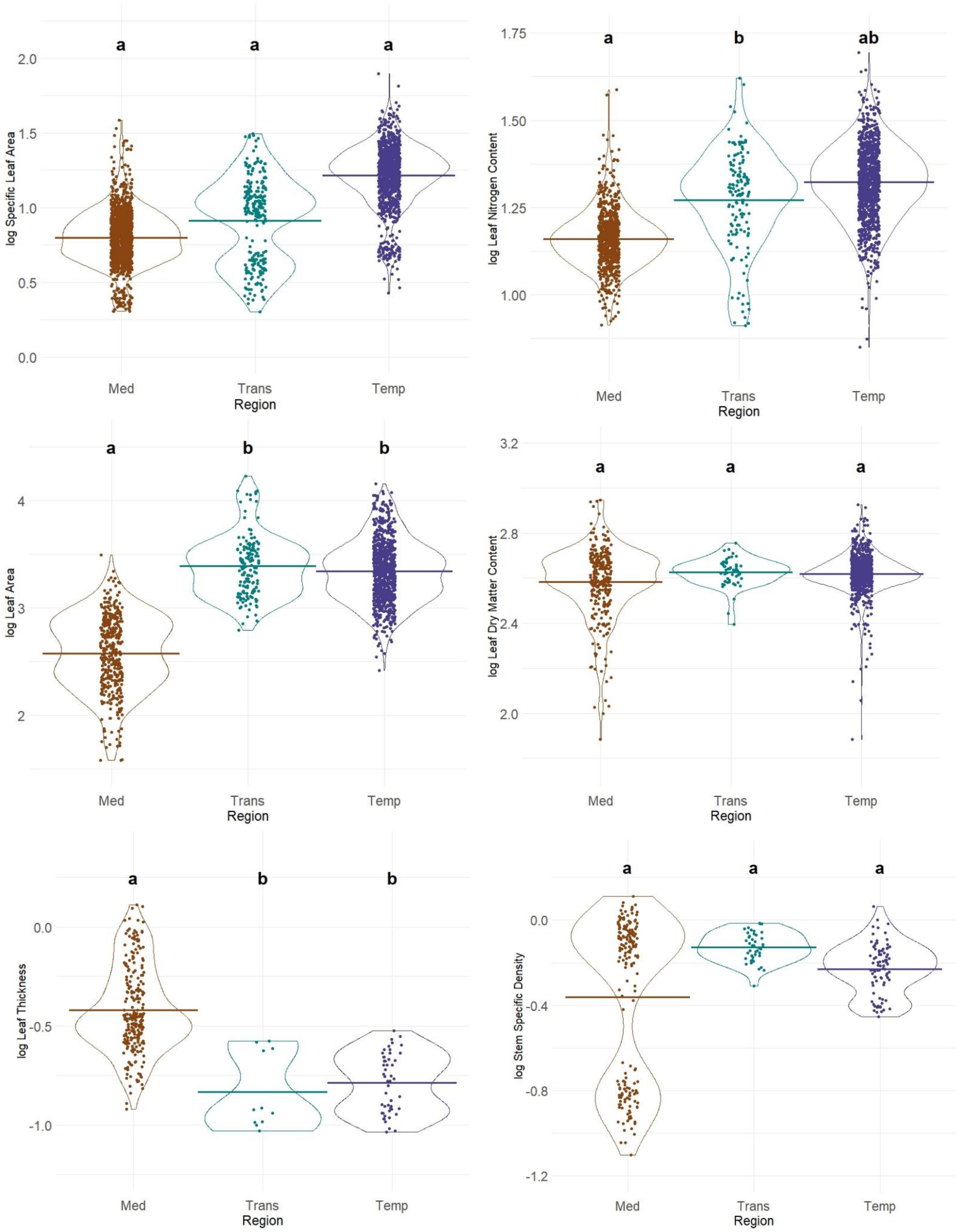
| | Mean | | | Linear models | | Linear mixed models | |
|---|---|---|---|---|---|---|---|
| | Med | Trans | Temp | F | P | LR | P |
| **SLA** | **6.94 (0.1)** | **9.97 (0.4)** | **18.26 (0.2)** | **1049** | **<0.0001** | 2.03 | 0.36 |
| Height | 9.90 (0.8) | 14.32 (1.6) | 21.15 (3.4) | 7.27 | 0.0009 | 2.77 | 0.25 |
| SeedMass | 2907.9 (197.4) | 3029.32 (295.8) | 2675.1 (221.0) | 0.516 | 0.5981 | 0.82 | 0.66 |
| **Leaf Thickness** | **0.43 (0.02)** | **0.16 (0.02)** | **0.17 (0.01)** | **82.0** | **<0.0001** | 10.1 | 0.0063 |
| LDMC | 405.82 (7.3) | 426.78 (7.4) | 425.24 (2.9) | 4.75 | 0.008 | 0.42 | 0.80 |
| **Leaf Area** | **504.36 (19.6)** | **3115.15 (221.2)** | **2744.23 (71.0)** | **901.1** | **<0.0001** | **16.78** | **<0.0001** |
| **Leaf Lifespan** | **17.99 (1.9)** | **5.68 (0.3)** | **7.20 0.7)** | **7.73** | **0.001** | 2.03 | 0.36 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **LNCm** | **14.71 (0.1)** | **19.61 (0.5)** | **21.63 (0.2)** | **491.8** | **<0.0001** | 5.55 | 0.06 |
| P50 | -4.17 (0.6) | -3.18 (0.4) | -3.12 (0.1) | 1.448 | 0.25 | 2.56 | 0.27 |
| SSD | 0.58 (0.02) | 0.75 (0.01) | 0.61 (0.01) | 5.81 | 0.003 | 1.45 | 0.48 |

**Table 3.4** Mean values and the standard errors (in parenthesis) of functional traits for three sections. The results of the general linear models and linear mixed models testing the differences in functional traits among climate zones are given. LR is the likelihood ratio and estimated by comparing the model with a null model only including species as the random factor.

| | Mean | | | | Linear model | | Linear-mixed model | |
|---|---|---|---|---|---|---|---|---|
| | *Ilex* | *Cerris* | *Quercus* | *Ponticae* | F | P | LR | P |
| **SLA** | **6.36 (0.07)** | **10.94 (0.46)** | **16.74 0.23)** | **NA** | **827.4** | **<0.0001** | 3.36 | 0.18 |
| **Height** | **7.16 (0.91)** | **16.16 (1.91)** | **17.27 (1.42)** | **3.50 (0.39)** | **24.35** | **<0.0001** | 12.60 | 0.0056 |
| SeedMass | 2530.21 (215.18) | 3592.7 (282.02) | 2759.36 (189.15) | NA | 4.298 | 0.015 | 0.50 | 0.77 |
| **Leaf Thickness** | **0.49 (0.018)** | **0.23 (0.01)** | **0.19 (0.008)** | **NA** | **115.7** | **<0.0001** | **14.0** | **<0.0001** |
| LDMC | 402.47 (7.54) | 432.36 (8.15) | 425.97 2.86) | NA | 6.93 | 0.001 | 1.68 | 0.43 |
| **Leaf Area** | **464.75 (19.84)** | **2288.80 (190.30)** | **2710.86 (68.65)** | **9407.85 (365.16)** | **598** | **<0.0001** | **16.70** | **<0.0001** |
| **Leaf Lifespan** | **23.30 (1.99)** | **13.32 (1.83)** | **6.23 0.42)** | **NA** | **38.64** | **<0.0001** | **14.83** | **<0.0001** |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| **LNCm** | **14.91 (0.11)** | **16.78 (0.24)** | **21.39 (0.15)** | **NA** | **504.2** | **<0.0001** | **16.48** | **<0.0001** |
| P50 | -4.08 (0.65) | -5.20 (NA) | -3.15 (0.21) | NA | 1.71 | 0.20 | 2.49 | 0.28 |
| SSD | 0.48 (0.03) | 0.79 (0.02) | 0.66 (0.01) | NA | 26.12 | <0.0001 | 8.1 | 0.01 |



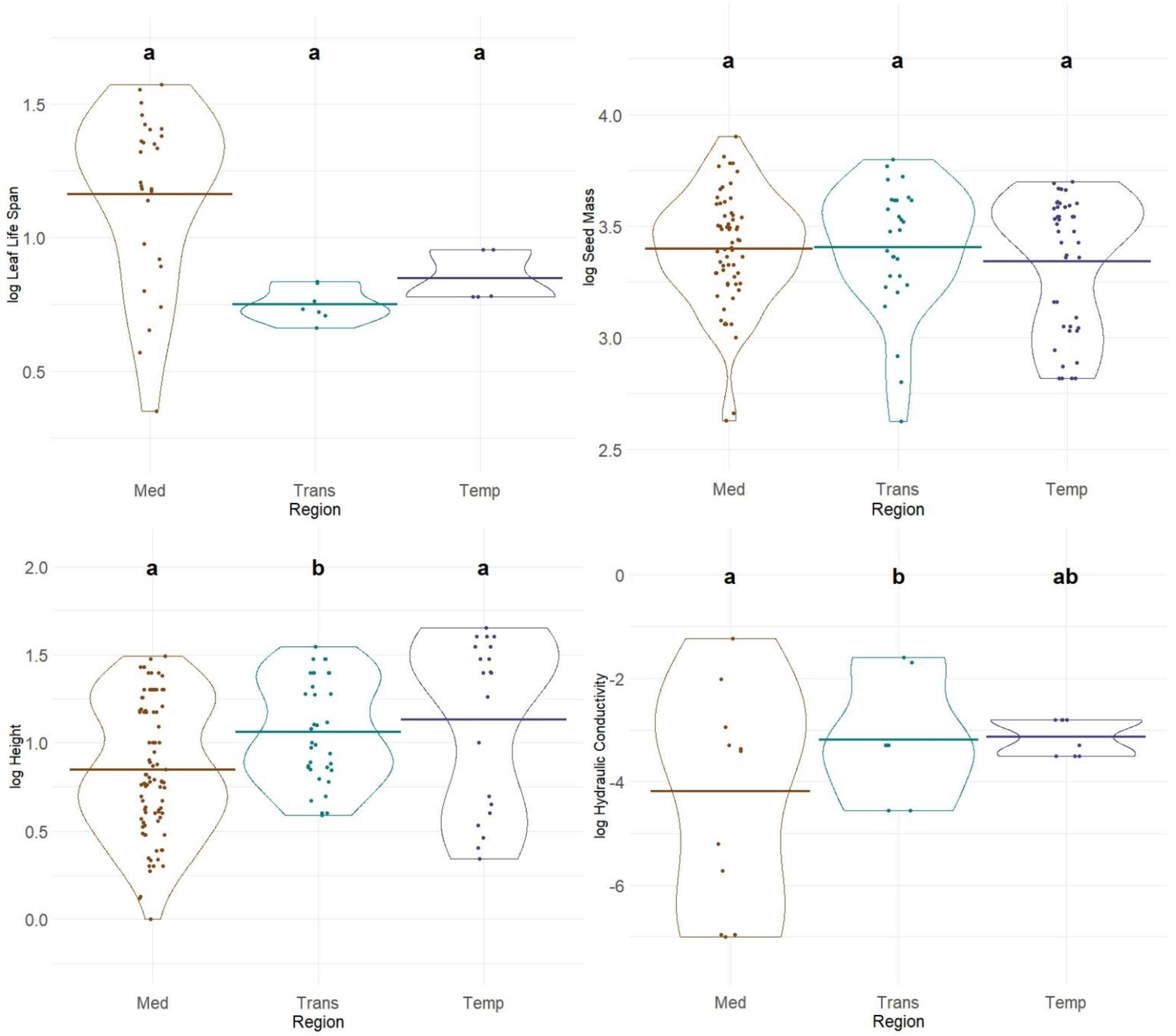
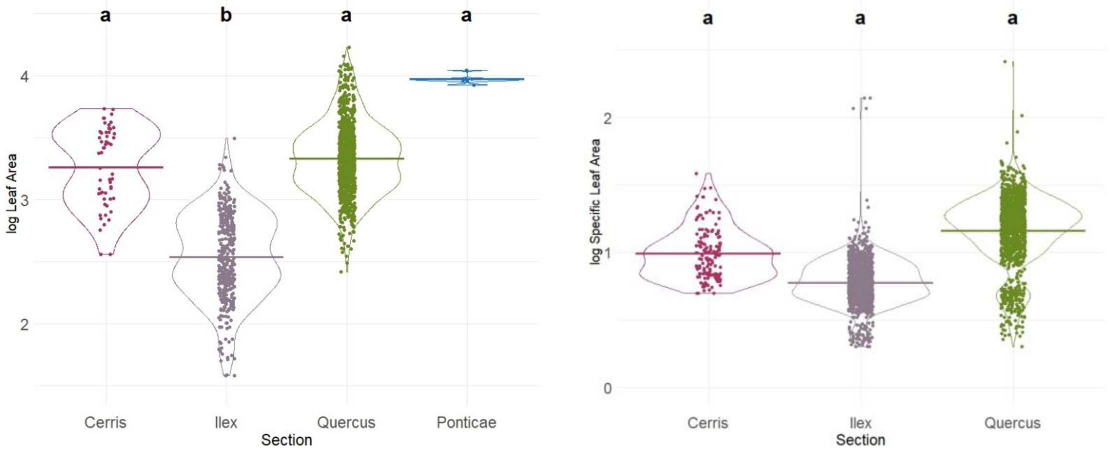


**Figure 3.2.** Comparison of oak species in different climate zones regarding the studied plant traits. Violin graphs show data distributions, each point is one trait record, the horizontal line is the mean, and the width of the violin is relative to the number of data points corresponding to trait values. Distinct letters above the graphs indicate significant differences between the two groups, as determined by a pairwise comparison test using the linear mixed model.



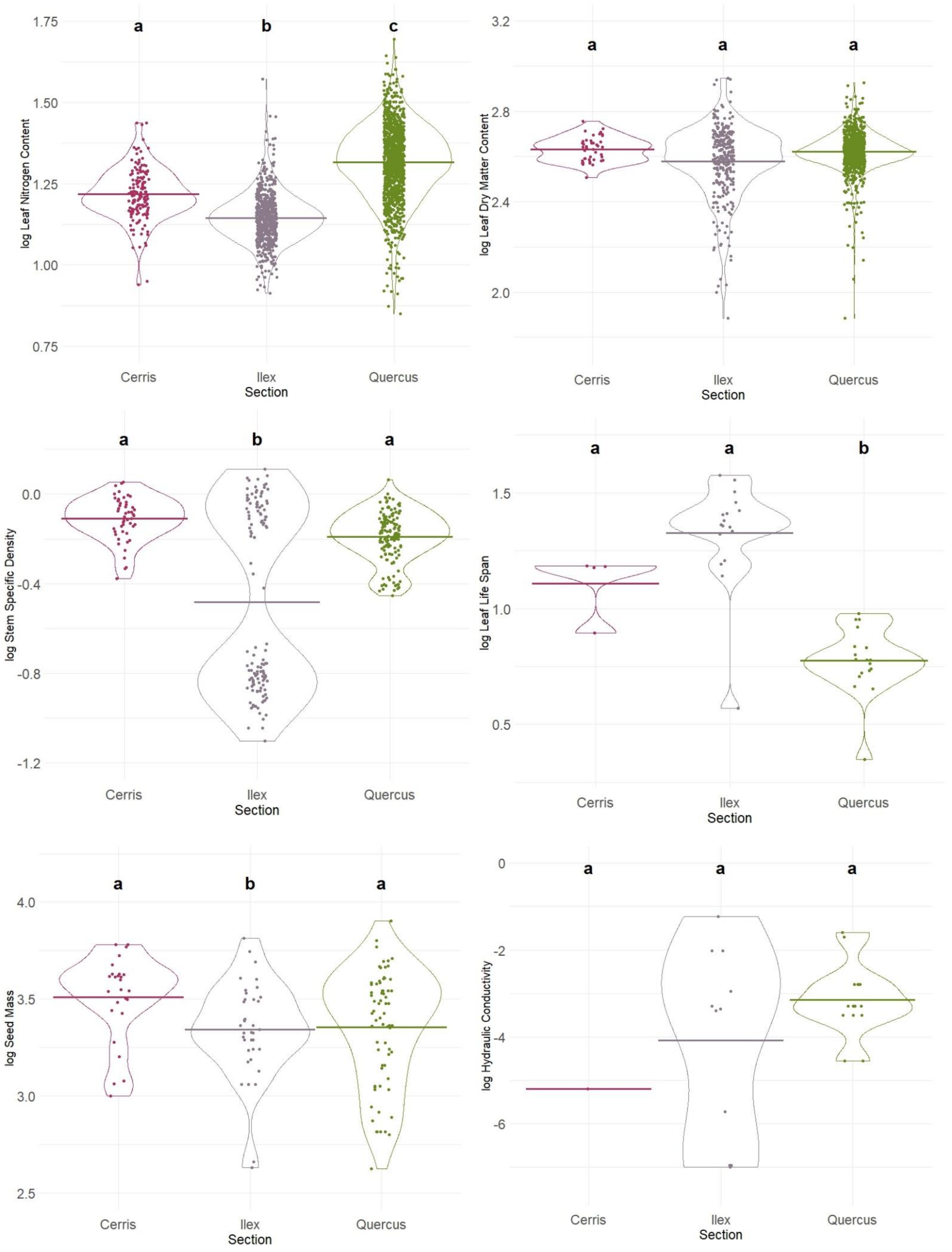


**Figure 2.** Comparison of oak species in different sections regarding the studied plant traits. Violin graphs show data distributions, each point is one trait record, the horizontal line is the mean, and the width of the violin is relative to the number of data points corresponding to trait values. Distinct letters above the graphs indicate significant differences between the two groups, as determined by a pairwise comparison test using the linear mixed model.

## 3.4. Discussion

This study marks the first attempt to assess the functional traits of oaks in the western Palearctic region in relation to climate zones and infrageneric groups. Our research provided evidence of substantial interspecific variability in the functional traits of the western Palearctic oaks, particularly in traits representing leaf economics spectrum. Additionally, our analyses revealed that climate zone and infrageneric group (i.e., section) account for a considerable amount of trait variability. Furthermore, we found a possible relationship between the sections of *Quercus* and the climatic zones in which they are predominantly found. Consequently, our results support our hypothesis.

Based on their distributional ranges (Denk et al., 2010; Caudollo et al., 2017) we defined three climatic zones (Mediterranean, transition, and temperate) for the oaks of the western Palearctic region. According to our findings, the traits of temperate zone oaks are comparable to those of transition and Mediterranean oaks. In other words, the main differentiation occurs between the *Quercus* and *Ilex/Cerris* sections, with almost all the members of the *Ilex* and *Cerri*s sections comprising Mediterranean species. Indeed, the association between climate zone and section regarding the number of species assigned to each group was significant. Mediterranean species have evolved under hot and dry climate conditions, especially during the summer, while temperate species have adapted to warm and relatively humid conditions. Temperate species are also exposed to more intense and prolonged cold periods than Mediterranean species, particularly during winters in the northern Hemisphere. Among the traits examined, the most notable differences we observed were directly and prominently associated with the species' response to climate, particularly in traits like leaf thickness and leaf area. Leaf thickness is known to be one of the most sensitive plant functional traits to environmental gradients and is directly related to leaf nitrogen content and abiotic conditions (Read & Stokes, 2006; Onoda et al., 2011; Pérez-Harguindeguy et al., 2013). Leaf area affects water consumption and energy expenditure of a leaf (Díaz et al., 2016). In our study, another trait that differed between climate zones was LNCm, a trait known to vary from temperate to tropical regions and constrain plant growth (Reich & Oleksyn, 2004; Chen et al, 2013). In our dataset, seed mass was significant only in the section group, where the *Cerris* section had substantially heavier seeds than others. This might result from phylogenetic effects and the ancestral backgrounds of the sections (Denk et al., 2023). Therefore, our findings suggest that climate is a driver of trait differentiation between oaks of temperate and Mediterranean climate zones in the western Palearctic region, as previously shown before with different species in other biomes (Cavender-Bares et al., 2004; Cavender-Bares et al., 2005; Cavender-Bares & Pahlich, 2009). Additionally, our results support the interaction between the leaf economic spectrum and changing climate and land-use (Wright et al., 2004).

The biogeographic origins of plant lineages can have a legacy effect on species' functional traits in some regions, influencing community assembly, diversity, and ecosystem functioning of the modern flora (Cavender-Bares et al., 2016). Our results also suggest an evolutionary legacy in plant traits can be observed among western Palearctic oaks. This implies that ancestral characteristics and adaptations of these oak lineages have persisted over time, shaping the functional traits observed in present-day species. As a result, understanding the historical context of these oaks can provide valuable insights into their current ecological roles and the processes driving their trait evolution. The conventional infrageneric oaks classification was historically dependent on their reproductive and leaf traits. However, two significant challenges arose during this classification process: the accurate weighting of characters and the consideration of geographic regions. These challenges were attributed to the prevalence of convergent morphological evolution within the *Quercus* genus (Denk et al., 2017). Therefore, the more their evolutionary background is understood, the more interpretable the functional traits they evolved within the study regions become.

Throughout the oak's evolutionary history, paleoclimatic and paleogeographic conditions have a significant role in influencing their diversification and distribution. According to fossil pollen records, the diversification of oaks can be traced back to the early Eocene, approximately 56 million years ago (Hofmann et al., 2011). During this period, a major vicariance event occurred between Eurasia and North America, leading to the emergence of primary lineages due to a climate cool-down. Over the next 20 million years, temperate biomes dominated by oaks began to take shape (Hipp et al., 2020; Zhou et al., 2022). Today, *Quercus* occupies a wide range in the Northern Hemisphere, from tropics to highlands and temperate zone to boreal regions (Peel, Finlayson & McMahon, 2007; Simeone et al., 2016). Sections *Quercus* and *Ilex* are recognized as the most genetically diverse groups within the *Quercus* genus when compared to section *Cerris* (Simeone et al., 2016). However, recent findings indicate that section *Cerris* is now acknowledged as the sole oak section to achieve its greatest species richness and absolute phylogenetic diversity in Western Eurasia (Denk et al., 2023). Due to the geographic heterogeneity in its widespread distributional range, section *Ilex* is currently found in extra-tropical regions, high mountainous regions, sub-alpine, subtropical forests, and warm, summer-dry winters in the Mediterranean region (Simeone et al., 2018; Denk et al., 2023). European fossil lineages, despite their differences in leaf morphology compared to later lineages, suggest local adaptation and the impacts of climate change in this region (Jiang et al., 2019). Although the molecular differentiation of section *Cerris* based on the fossil records remains debatable (Simeone et al., 2018), this section is most diverse in western Eurasia today, and throughout its distribution in the Mediterranean, it overlaps with the section *Ilex.* Section *Cerris*, spanning across its east-west and north-south range in the western Palearctic region, has shown adaptability to diverse climate types, including cold-steppe, warm-temperate climates with varying precipitation patterns, and predominantly arid summer-dry Mediterranean climates (Peel et al., 2007; Simeone et al., 2018). As inferred from the latest paper that uncovers the phylogenetic background of section *Cerris*, its ecological variability is the evidence of both niche and trait convergence, in particular to leaf morphology (Denk et al., 2023), which could be supported by our leaf area results significantly varied from section *Ilex* but not from section *Quercus*. For the section *Quercus*, the root of the white oaks ('roburoids') is nested within a fully temperate clade with similar leaf morphology from North America and diverged from here around 25-30 Mya (Hipp et al., 2017; McVay et al., 2017, Denk et al., 2017). Again, the climatic evolutionary background helps to explain the significant divergence in leaf area for section *Quercus*. Section *Ponticae*, considered a Holarctic group, evolved entirely in temperate regions (only *Q. pontica* is considered in this paper) and forms the earliest branch of white oaks in this region, being recognized as a relic of a widespread species group (McVay et al., 2017). Besies their geographical dispersal processes and the effect of climate, the oak sections at high latitudes (*Quercus*) underwent evolution in tectonically stable regions, whereas the ones at low latitudes (*Ilex, Cerris*) evolved in tectonically unstable regions. (Simeone et al., 2016). The interplay of these factors, along with the tendency of oaks to undergo introgression, resulted in elevated genetic diversity in southern regions and reduced diversity in northern regions. To gain deeper insights into the historical biogeography of the *Quercus* genus, it is imperative to take into account the influence of these geological processes and the variation in functional trait.

In conclusion, our study demonstrates that western Palearctic oaks from Mediterranean and temperate climate zones, as well as those belonging to distinct infrageneric groups, exhibit differences in their functional traits, particularly those related to the climate response of species. These findings suggest that both evolutionary legacy and regional climate shape trait variability among oak species, at least for those distributed in the western Palearctic region. Consequently, functional traits can be employed to predict the climate response of oaks, potentially aiding in the development of conservation plans, especially for narrowly distributed or endemic oak species, such as *Q. afares, Q. aucheri, Q. hartwissiana, Q. lusitanica, Q. vulcanica*, and *Q. pontica* in the western Palearctic region.

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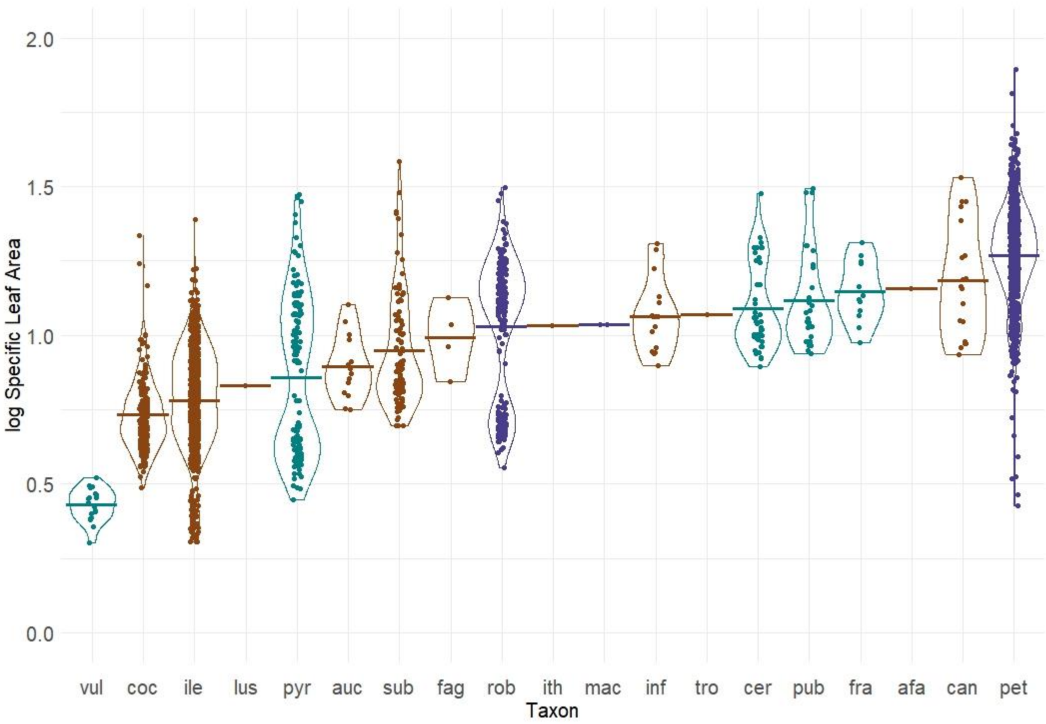
## Supplementary Material to the Chapter 3

**Table A1.** The association between the number of species belonging to different sections and distribution in different climate zones.

|  | **Section** |  |  |  |
|---|---|---|---|---|
| **Climate zone** | ***Cerris*** | ***Ilex*** | ***Quercus*** | ***Ponticae*** |
| **Mediterranean** | 6 | 3 | 4 | 0 |
| **Transition** | 0 | 0 | 4 | 0 |
| **Temperate** | 0 | 0 | 4 | 1 |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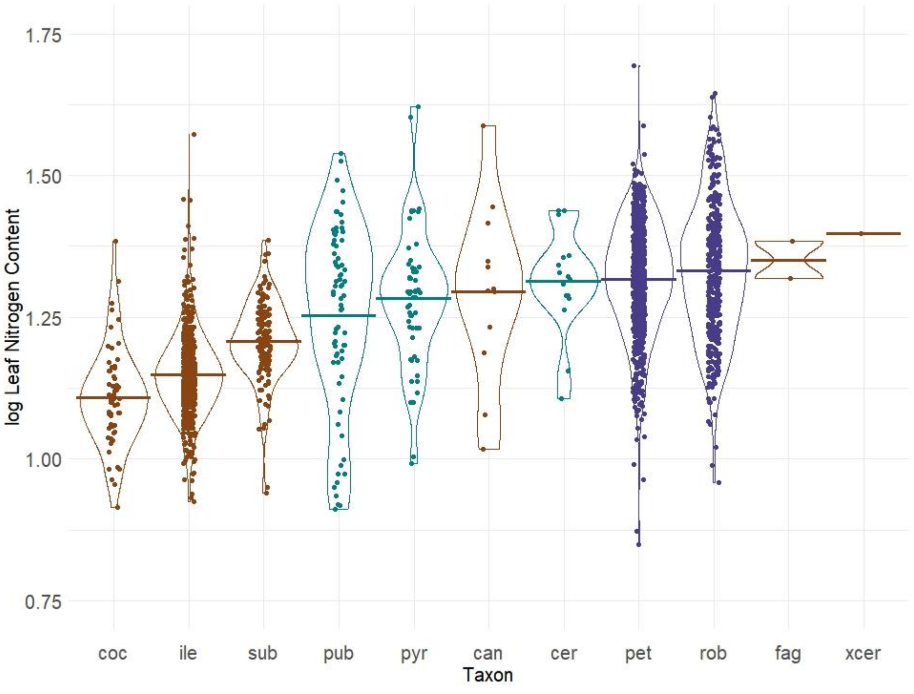
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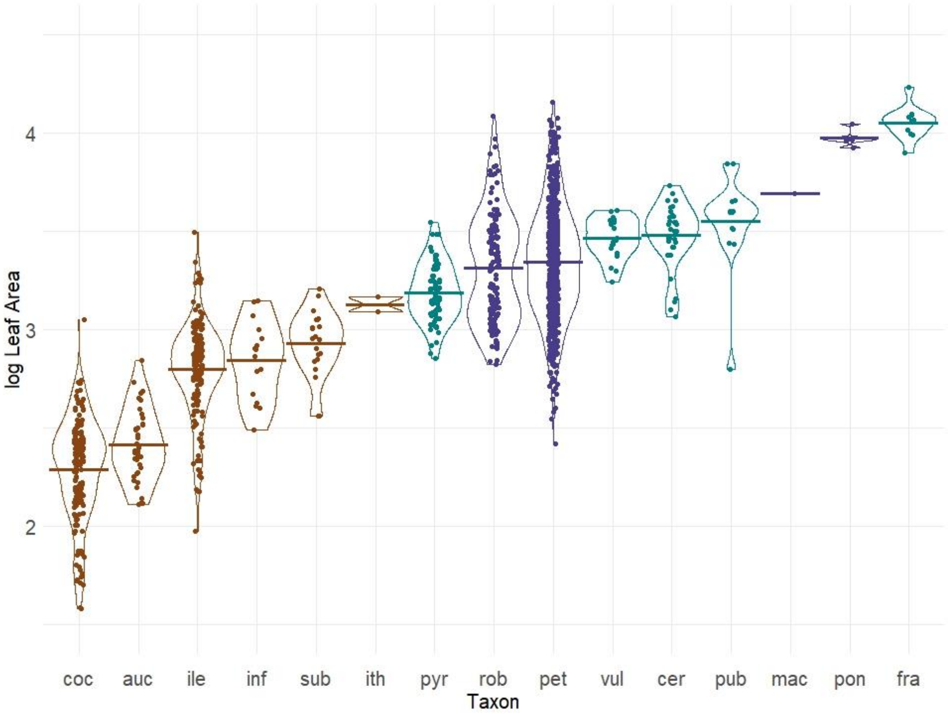
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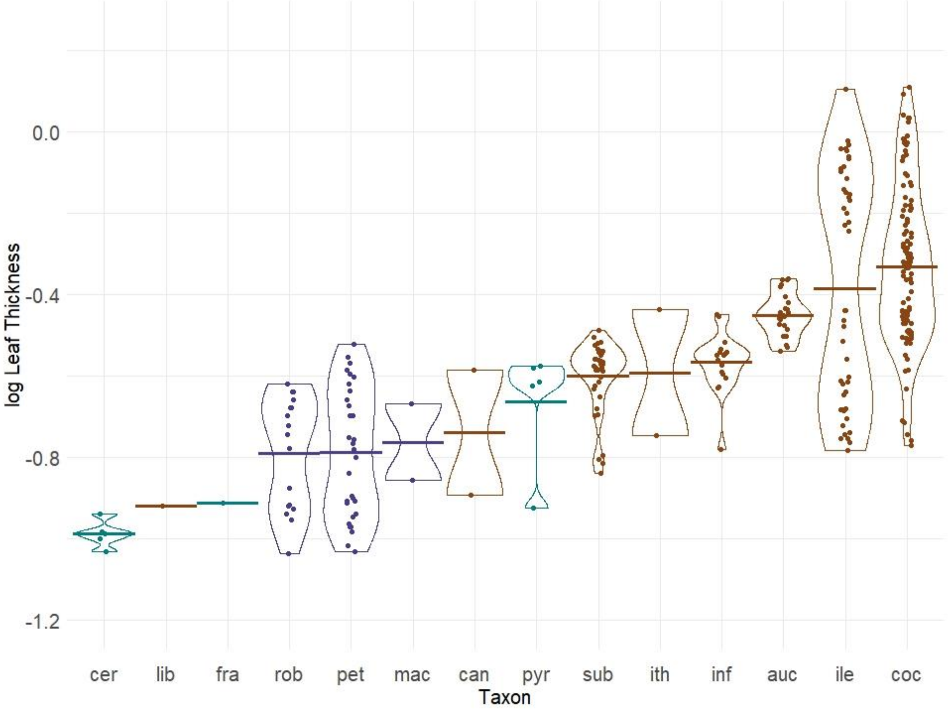
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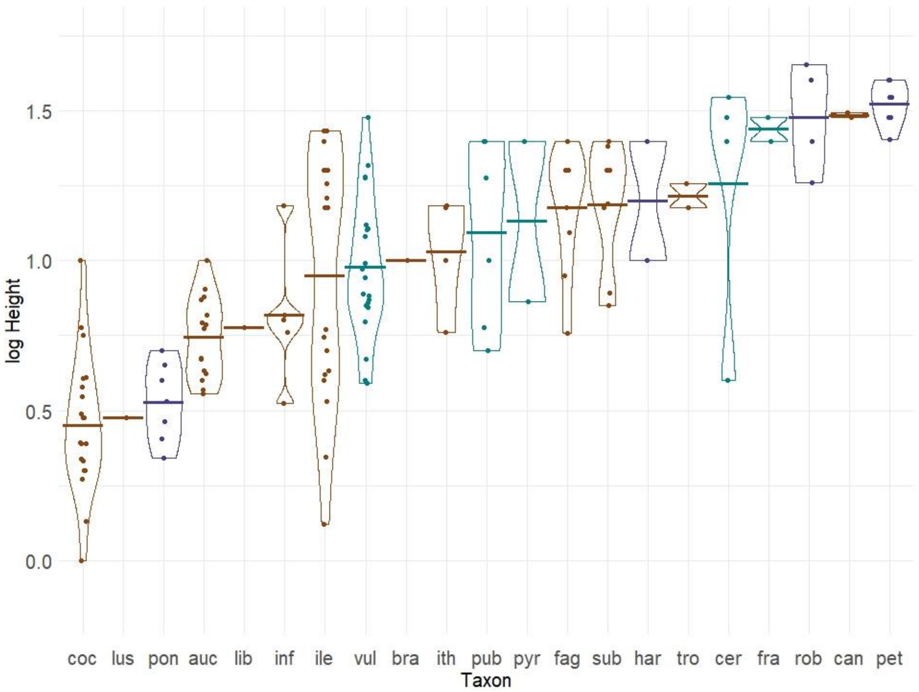
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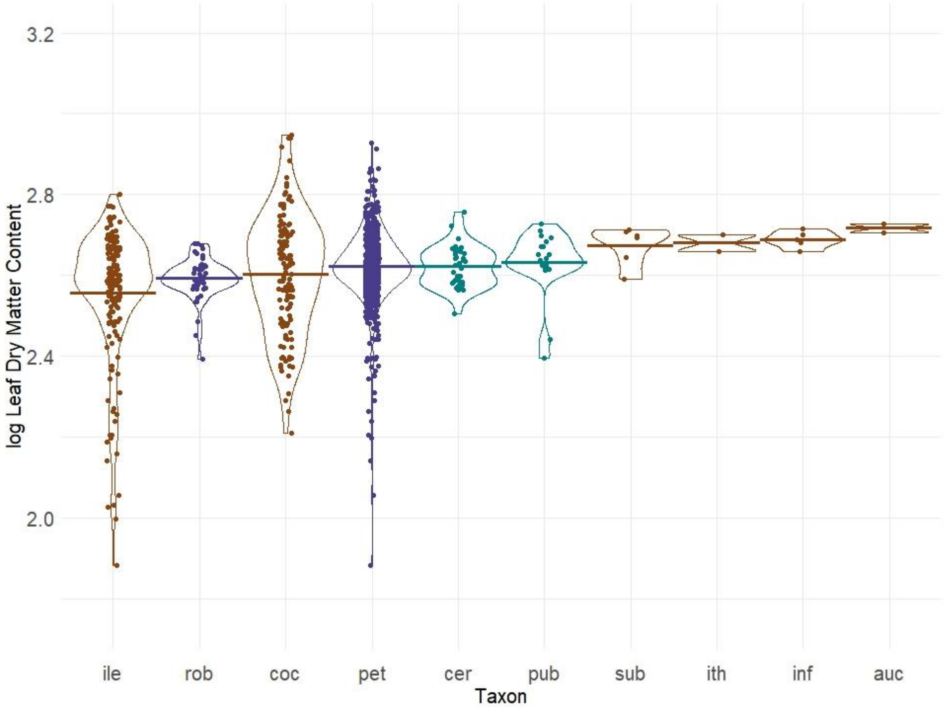
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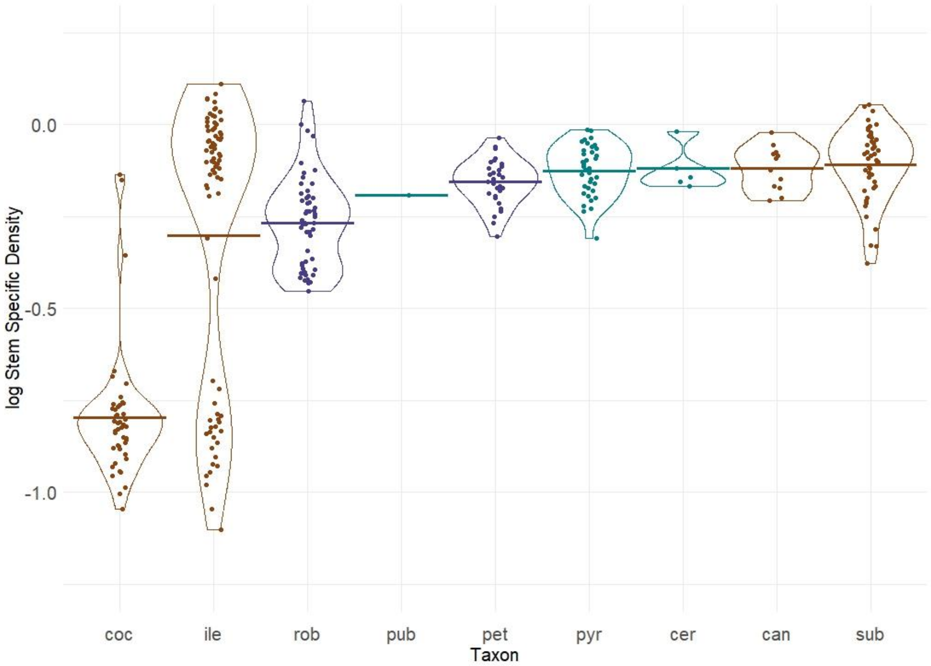
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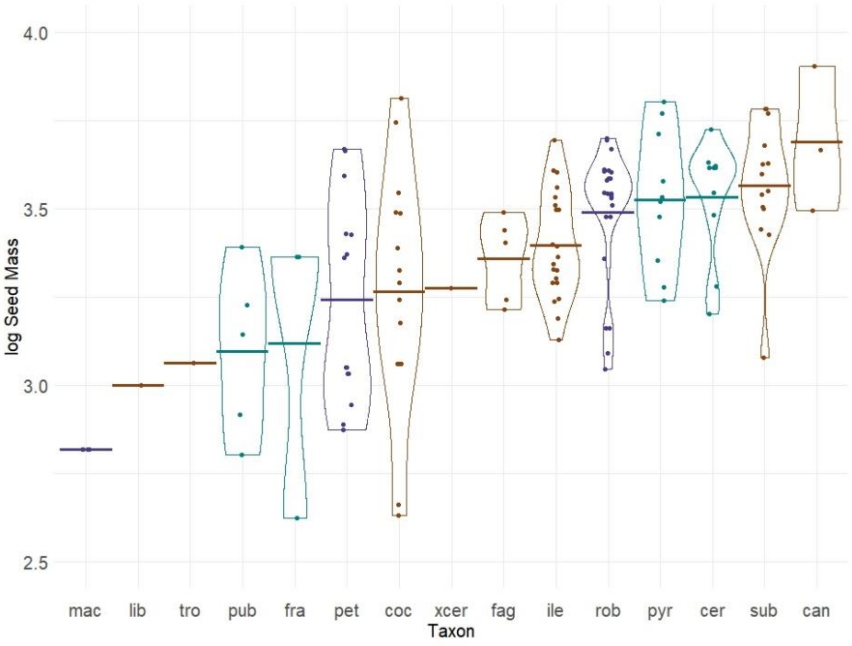
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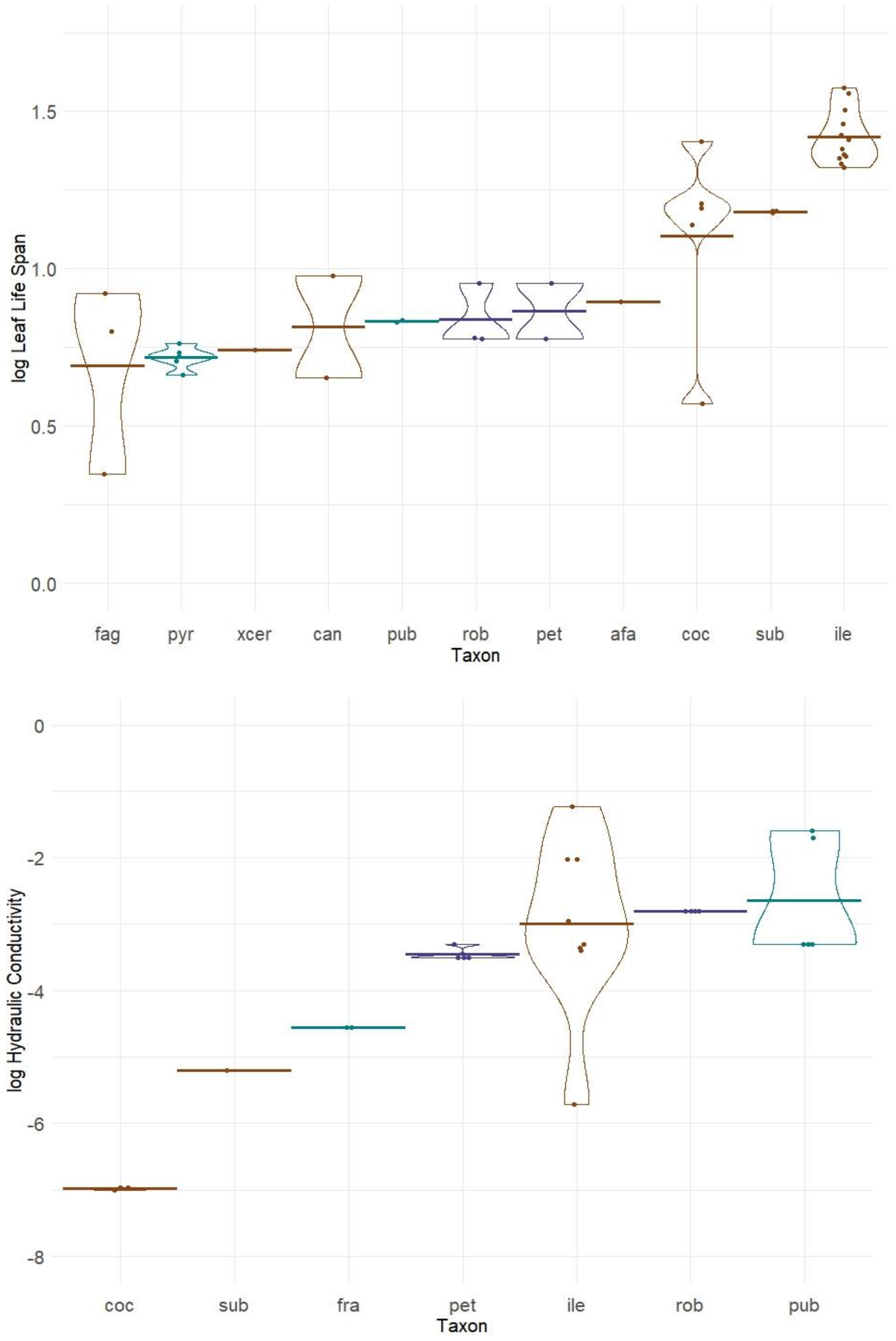

**Figure A1.** Comparison of oak species regarding the studied plant traits. Violin graphs show data distributions, each point is one trait record, the horizontal line is the mean, and the width of the violin is relative to the number of data points corresponding to trait values.

# CHAPTER 4. OAKS AND CLIMATE CHANGE: DISTINCT RANGE RESPONSES OF MEDITERRANEAN AND TEMPERATE OAKS IN THE WESTERN PALEARCTIC

## Abstract

Over the late Quaternary period, the geographic distributions of oak species within the *Quercus* genus have experienced notable shifts in response to global climate changes. This study aims to investigate the biogeographic patterns of six oak species found in various climatic zones within the western Palearctic region, considering both past and future climatic conditions. The primary goal is to discern the variations in species' responses to climate change and identify potential refugia during the Last Glacial Maximum (LGM). We employed an ENM approach, running three separate models for the past and three models for the future 2081-2100 period (with optimistic and pessimistic scenarios). Under the climatic conditions for all the different time periods analyzed, temperate and transition-zone species exhibited a similar pattern, while Mediterranean zone species showed the opposite. Based on these patterns, it can be inferred that temperate and transition-zone species have contracted their distributions during the LGM, surviving in habitats with suitable climatic conditions in southern latitudes. Apart from the recognized areas in the southern latitudes, northern Anatolia and southern France have also been identified as significant glacial refugia for these groups. Although some populations of Mediterranean species in the south may have been lost during the LGM, their distribution has remained relatively stable within their distribution ranges in comparison to the studied transition-zone and temperate oaks. Under future scenarios, temperate and transition-zone species have significantly reduced their known distribution ranges, surviving mainly in northern latitudes and higher elevations. In contrast, Mediterranean species have expanded their distribution under these conditions. The results highlighted a significant distinction between Mediterranean oaks and those from temperate and transition-zones in terms of their distributional range responses to climate changes, particularly in areas of LGM refugia and potential ranges under future warming scenarios.

**Keywords:** *Quercus*, western Palearctic region, climate change, Mediterranean oaks, temperate oaks

## 4.1. Introduction

The Quaternary period, commencing approximately 2.5 million years ago, encompasses the most significant climate changes in the Earth's history. Given the extensive information on the geomorphological and climatological records of this period, Late Quaternary has emerged as a crucial period for understanding the evolutionary dynamics of contemporary communities and taxa (Hewitt 1996; Taberlet 1998; Hewitt, 1999; Petit et al., 2003; Svenning & Skov 2007; Waltari & Guralnick 2009; Médail & Diadema 2009). The effects of these global climatic fluctuations have occurred in different ways on different continents, depending on the distance to the ocean, ocean currents, continental mass, and topographic characteristics of the regions. European forests had undergone major changes due to alternating climate in the Quaternary (Taberlet et al., 1998; Brewer et al., 2002; Petit et al., 2002). As the climate cooled and dried, glaciers began to expand from the poles to south, particularly in LGM, fragmented the distribution of the temperate and broad-leaved forests of the western Palearctic Region and causing their ranges to contract towards the climatically suitable regions such as coastal areas, mountainous regions, and southern parts of the Mediterranean basin (Taberlet 1998; Hewitt, 1999; Svenning & Skov 2007; Schmitt & Varga, 2012). Nevertheless, the pace of climate change is accelerating, and the most recent projections for Europe indicate that temperatures are expected to rise by approximately 2-5ºC in Europe and certain areas of the Mediterranean region by the year 2100 (Christensen et al., 2007; IPCC, 2022).

The ongoing global warming is already altering the functional traits, phenology, biotic interactions, and geographic ranges of the species (Cavender-Bares et al., 2004; Parmesan, 2006). Because trees have long lifespans, forests are especially vulnerable to climate change, as they cannot quickly adapt to environmental shifts. Climate change is exerting notable impacts on forest ecosystems in both the Mediterranean zone and temperate zone within the western Palearctic region (Resco de Dioas et al., 2007; Nunes et al., 2021; www.efi.int). The Mediterranean forests are at risk of degradation and species loss because of the combined impacts of increased temperatures, water scarcity, and altered precipitation patterns that can lead to habitat loss, species shifts, increased fire and drought risk, ecological disruptions, pests, and invasive species (Lindner et al., 2010). In the temperate zone forests, which include diverse habitats of deciduous forests in the western Palearctic, are altering the timing of seasonal events, and mainly constrained the water availability due to decreasing annual precipitation than today (Marrachi et al., 2005).

Temperate deciduous broadleaf and mixed forests constitute the largest terrestrial biome type in western Palearctic region and genus *Quercus*, commonly known as oaks, is one of the dominant tree groups in these ecosystems (San-Miguel-Ayanz et al., 2016). Oaks are characterized by their extensive distribution and diversity, encompassing approximately 430 species found across the Northern Hemisphere, spanning North America, Europe, Asia, and certain regions of North Africa (Carrero, 2020). Within this global diversity, oaks are less represented in Europe (28 species), however it is the most dominant tree genus in Europe (Carrero, 2020). The evolutionary history of *Quercus* can be traced back to the Eocene epoch, around 55 mys, where oaks experienced a major rapid diversification, likely impacted by climate changes and the opening of new habitats (Hipp et al., 2020). Over time, *Quercus* species colonized different regions, adapting to various ecological niches. Continental drift and geological events played a crucial role in shaping the current distribution patterns of oaks. Furthermore, glaciations during the Pleistocene period influenced the migration and diversification of oaks, resulting in the formation of localized species and subspecies. Therefore, climate change is accepted as the major driving force of shaping the European oak flora (Petit et al., 2002; Hipp et al., 2020).

Sinde of many oak species widely distributed, the presence of subspecies, fragmented population structures observed in their distributions, the hybridization capacity and the occurrences in different climatic zones, the genus *Quercus* is of great interest in ecological and evolutionary biology research and offers ample opportunities to address numerous research questions in biogeography. In line with this, this study aims to uncover the climate-based ecological niches of six oak species that occur in the western Palearctic region and occupy different climatic zones (Mediterranean, temperate, and transition). Using an ecological niche modeling approach, we aimed to assess the suitable distribution areas and potential refugia of *Quercus* species in these climatic zones during the LGM. Furthermore, the study also aims to predict the potential distribution areas under the future climate changes. Considering their differences in life history traits between Mediterranean and temperate oaks (see; the third chapter of this thesis), we hypothesized that the climatic niches of these groups should differ from each other, and accordingly, we expected that they give different distributional responses to climatic changes in different periods, including the LGM and future. We also expected that the location of LGM refugia should have differed between Mediterranean and temperate oaks. Our expectation was that transition-zone oaks should be in-between Mediterranean and temperate oaks regarding the tested hypotheses.

## 4.2. Materials and Methods

### 4.2.1. Study Area and Species

We selected the western Palearctic Region (12ºW-52ºE and 20-72ºN) to test our hypothesis. In this region, there are vast plains extending to Russia in the north, and mountainous areas located in the east-west direction such as the Alps, Pyrenees, and Transylvania in the south and connected to Asia (Hewitt, 1996). Anatolia, situated in the Asian part of this region, exhibits remarkable topographic and climatic variations (Şekercioğlu et al., 2011). Further south is the Mediterranean region. This region includes four main Köppen-Geiger climate types; cold D is the dominant climate type, followed by arid B, temperate C and polar E (Peel et al., 2007).

Western Palearctic Region has 28 *Quercus* (oak) species and several subspecies and hybrids, which is the lowest oak species richness compared to other regions in the northern Hemisphere, represented under four sections (*Quercus, Cerris, Ilex, Ponticae*). Here we grouped the studied species according to their main distribution ranges in these climate zones, however some species found in both zones, therefore we defined a third 'transition-zone' group. We selected two species from each group for temperate (*Q. robur, Q. petraea*), Mediterranean (*Q. coccifera, Q. suber*) and transition-zone (*Q. cerris, Q. pubescens*). We followed Denk et al. (2017) for the nomenclature and taxonomic classification of these species.

### 4.2.2. Occurrence and Climate Data

The occurrence data were mostly compiled from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), regional flora books (Hedge & Yaltırık, 1982; Tutin et al.,1964, Franco, 1990;6 Vila-Viçosa et al., 2022), and the European Forest Genetic Resources Program (EUFORGEN) (https://www.euforgen.org/species/). In the data we obtained from GBIF, we did not include the data grouped as 'herbarium specimens', since the coordinates reflect the related herbariums and specimens from regions outside the distribution ranges of the species. A total of 19 bioclimatic variables for each time period were obtained from WorldClim version 2.1 (Fick et al., 2017) at a spatial resolution of 2.5’ (~4.63 km at the equator) (Table A1). We considered three different models (BCC-CSM2-MR, CNRM-CM6-1, MIROC6) and two different climate scenarios (ssp126 and ssp585) for the future projections (2081-2100). According to these scenarios, the mean annual temperature will be expected to increase 0.2-1.8ºC and 2.6-4.8ºC, and the expected $CO_2$ level will be 450 ppm and 1350 ppm in 2100, for optimistic (ssp126) and pessimistic (ssp585) scenarios, respectively (IPCC, 2022). Additionally, we considered three different models (CCSM, MPI, MIROC) for Last Glacial Maximum (LGM) projections.

### 4.2.1. Ecological Niche Modeling

hrough an ecological niche modeling (ENM) approach, we made predictions regarding the potential impact of climate change on the distribution patterns of the studied species across different time frames and climate scenarios. Our study entailed predicting the distribution range of the species under past climatic conditions during the LGM (approximately 22,000 ybp), present conditions, and two distinct future climate scenarios for the period 2081-2100 (ssp126 and ssp585).

During the preparation stage, *SDMToolbox* (Brown, 2014) was utilized to remove the duplicate occurrence records, reduce spatial autocorrelation and delimiting the calibration area (M) in ArcGIS version 10.6.1 for each species. After the cleansing process, 276 occurrence points for *Q. robur*, 438 for *Q. petraea*, 390 for *Q. coccifera*, 338 for *Q. suber*, 108 for *Q. cerris* and 392 for *Q. pubescens* left for subsequent ENM analyses.

The calibration area (M) for each species was determined by considering the species' biology, dispersal ability, environmental conditions represented in the area (using the BAM diagram approach, Peterson et al., 2015), as well as considering the continuity of habitat and topographic patterns. Due to the artifacts of bio8, 9, 18, and 19, these variables were excluded from the bioclimatic variables set, then the climate variables were masked according to the M calibration area, and to reduce multicollinearity among climate variables Pearson correlation analysis used by calculating the correlation coefficients. We used the “*corrplot*” package version 0.92 (Wei and Simko, 2021) implemented in the R environment (R Core Team, 2022), and one climatic variable among the related highly correlated ones (r > 0.70) and removed others (Figure A1-6).

We ran models under MaxEnt version 4.3.3, which uses presence-only data (Phillips et al., 2006). For assessing the model's performance, we employed the Area Under the Curve (AUC), a metric that ranges between 0 and 1. Since there were enough occurrence data for each species, we used default feature classes. We initially tested different regularization multipliers, however since the AUC values didn’t differ the results, we preferred to use 1 (the default value) as regularization multiplier for each species. To obtain replicates, we executed each model 10 times. To evaluate the potential distributions, we utilized the sensitivity-specificity equality method to establish a threshold criterion for the minimum predicted occurrence values of each species. These values, which varied from 0.5 to 0.6, were calculated individually for each species. Then, we conducted raster calculations and visualization of the final outputs using ArcGIS version 10.6.1 (ArcGIS, 2010).

### 4.3. Results

The ENM predictions demonstrated strong agreement with the known current distributions of each species, which were corroborated by occurrence data from EUFORGEN (Caudullo et al., 2017) and GBIF (https://www.gbif.org/) databases. Besides, the current projections were highly concordant with the estimated maximum habitat suitability maps from the European Atlas of Tree Species for each species (San-Miguel-Ayanz et al., 2016). The modeling outcomes hold significant importance, evident from the high performance of the models, as reflected by the area under the curve (AUC) values, across all study species for each projected time period. (mean AUC > 0.75, Table A2). This suggests a high predictive capability compared to a null (random) model (Phillips & Dudik, 2008). Due to the designated extensive calibration areas according to these known distribution ranges, some climatically suitable regions were also projected as for the species by the models, such as the Aegean and southern coasts of Anatolia for *Q. suber* (Figure 4.3f), northwestern parts of Europe and Britain for *Q. pubescens* (Figure 4.2f), and Iberian Peninsula for *Q. cerris* (Figure 4.2b). This illustrates the equilibrium between species and climate, as inferred from the bioclimatic data, enabling the identification of ecological niches for the study species. (Nogués-Bravo, 2009). However, recognizing the limitations of species' dispersal capacity and geographical barriers in accessing certain regions, we interpreted the distribution of species in various periods to avoid overestimating their geographical range under different climatic conditions. Furthermore, the model predictions and the geographic distribution of all species were found to be significantly superior to random expectations, as verified by partial ROC statistics. Moreover, the response curves of the bioclimatic variables (Figure A7-12) demonstrate the significant influence of each variable on the MaxEnt outputs for each species. These curves illustrate the marginal impact of each variable and how the predicted probability changes with variations in environmental factors.

The current climate models have been successful in identifying the optimal environmental conditions for each species and have been used to predict their possible distributions under different time periods. Temperature-related variables have shown the greatest contribution in projecting the distribution of both temperate and transition zone species, accounting for over 80% of the impact for both groups. Specifically, temperature variability-related variables like bio4 and bio7 have had the most significant impact on the current distribution of species. In contrast, both precipitation and temperature-related variables have nearly equal contribution in projecting the distribution of species in the Mediterranean zone. However, temperature-related variables, such as bio6 (minimum temperature of the cold period), appear to have a limiting effect on species in the Mediterranean zone.

### 4.3.1. LGM Projections

Under the LGM conditions temperate-zone and transition-zone species showed similar patterns and contracted towards climatically suitable areas within the distribution ranges (Figure 4.1a,4.1e & 4.2a,4.2e). Within these areas, Caucasus, coastal regions of Black Sea, inner parts of Aegean coasts and Taurus Mountains in Anatolia, Balkans, Italy, southern parts of France and southern parts of Pyrenees showed up as climatically suitable regions during LGM. In contrast, the Mediterranean zone species showed more consistent distribution in the Mediterranean Region, and showed less change or expanded their populations as regards temperate and transition-zone species during LGM (Figure 4.3a,4.3e).

### 4.3.2. Future Projections

The future model results under different scenarios show that the temperate and transition-zone species will still have similar patterns and their main geographical ranges will shift towards northern parts of western Palearctic (Figure 4.1c, 4.1d & 4.2g, 4.2h). However, under both scenarios the transition-zone species showed more consistency in their current populations and relatively expansion under future climate changes than temperate zone species. Besides, under the pessimistic scenarios temperate zone species will drastically contract their populations and become almost extinct in their current populations. On the contrary, the Mediterranean zone species will expand their populations towards the terrestrial biomes of the Palearctic region even in the most pessimistic scenario, although their southernmost distribution will narrow relatively.

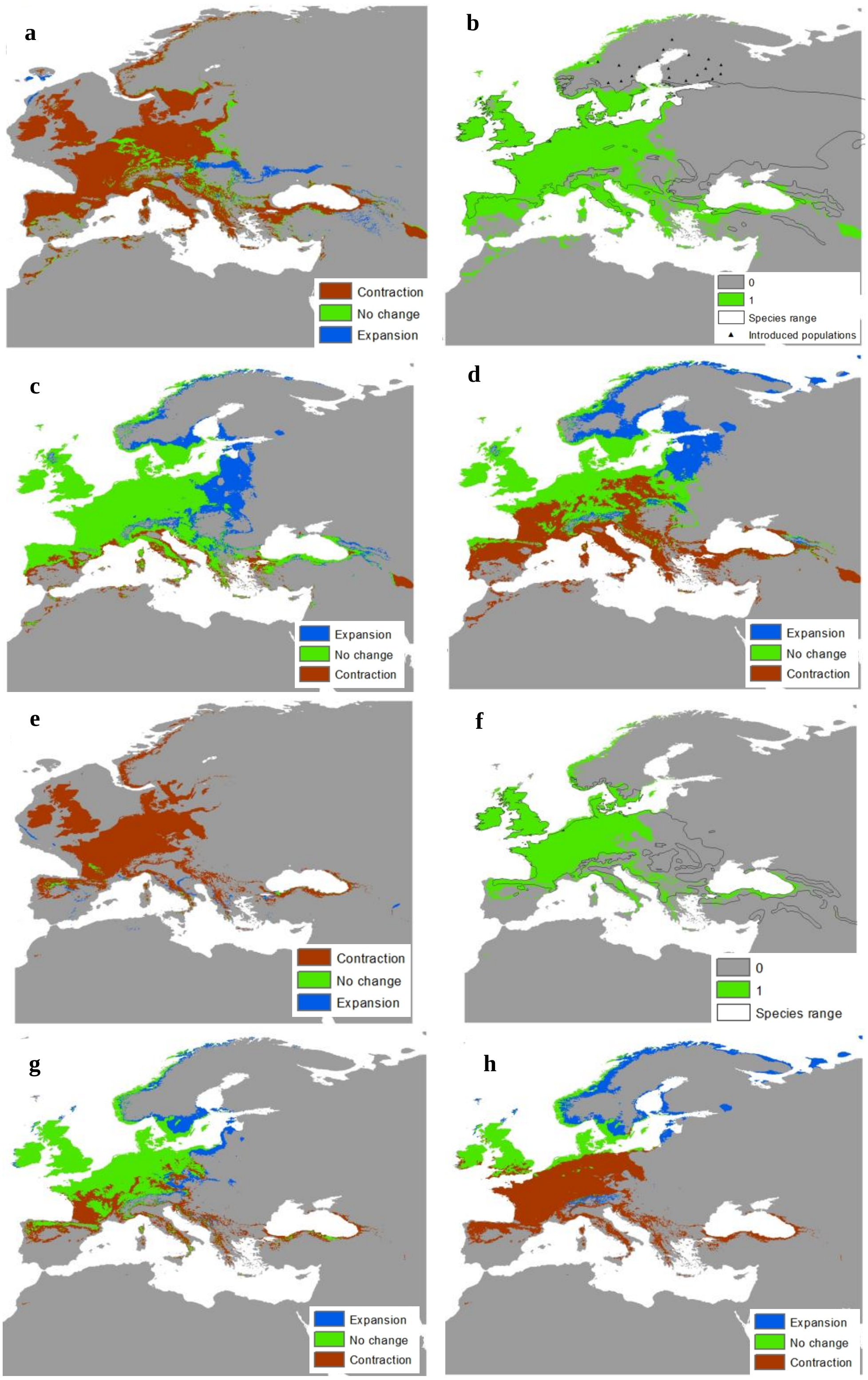

**Figure 4.1.** Model projections of temperate zone species under a. the Last Glacial Maximum (22000 YBP) b. Current, c. future (2081-2100 ssp126), and d. future (2081-2100 ssp585) of *Q. robur*; and e. the Last Glacial Maximum (22000 YBP), f. Current, g. future (2081-2100 ssp126), and h. future (2081-2100 ssp585) of *Q. petraea*

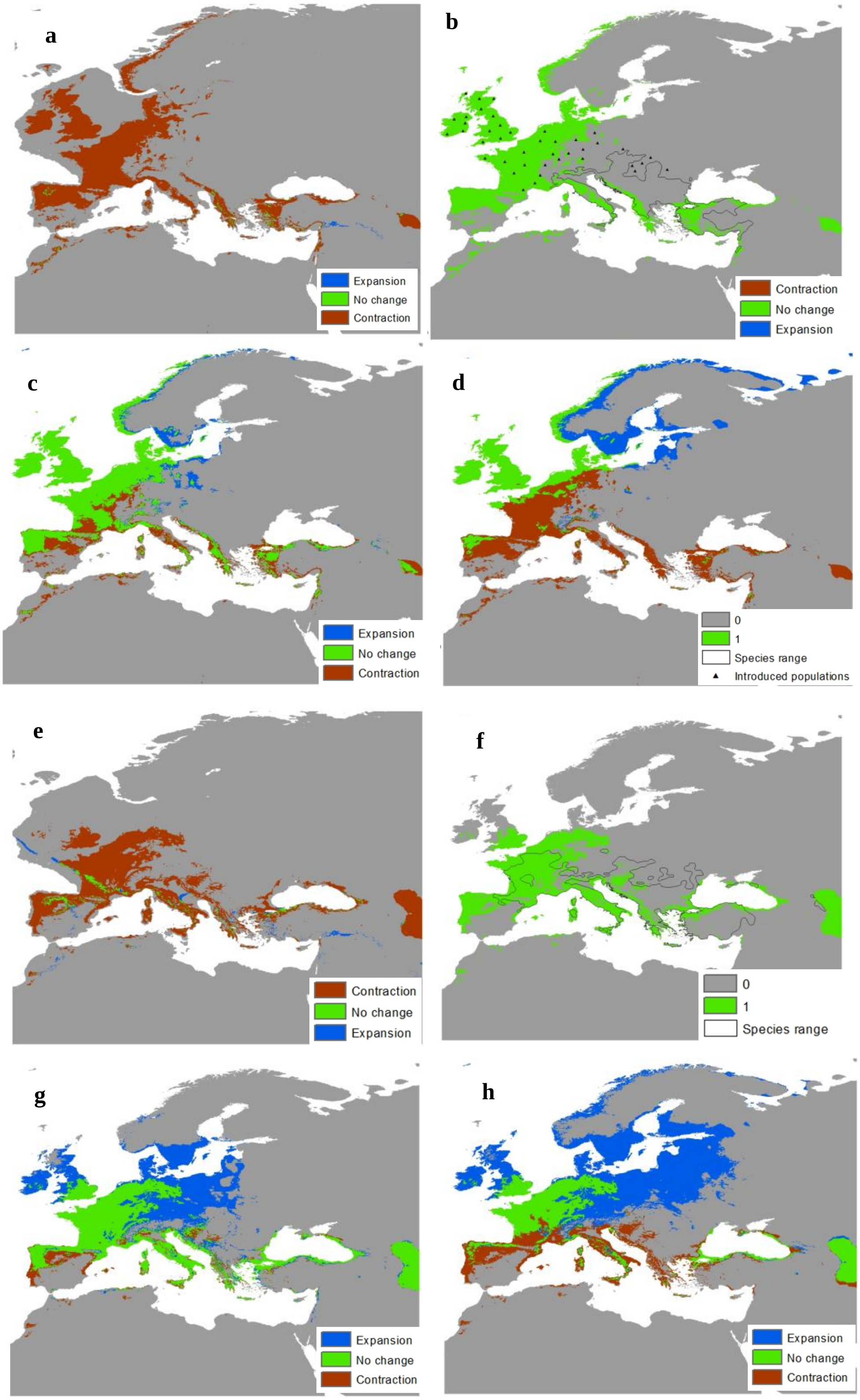

**Figure 4.2.** Model projections of transition-zone species under a. the Last Glacial Maximum (22000 YBP), b. Current, c. future (2081-2100 ssp126), and d. future (2081-2100 ssp585) of *Q. cerris*; and e. the Last Glacial Maximum (22000 YBP), f. Current, g. future (2081-2100 ssp126), and h. future (2081-2100 ssp585) of *Q. pubescens*

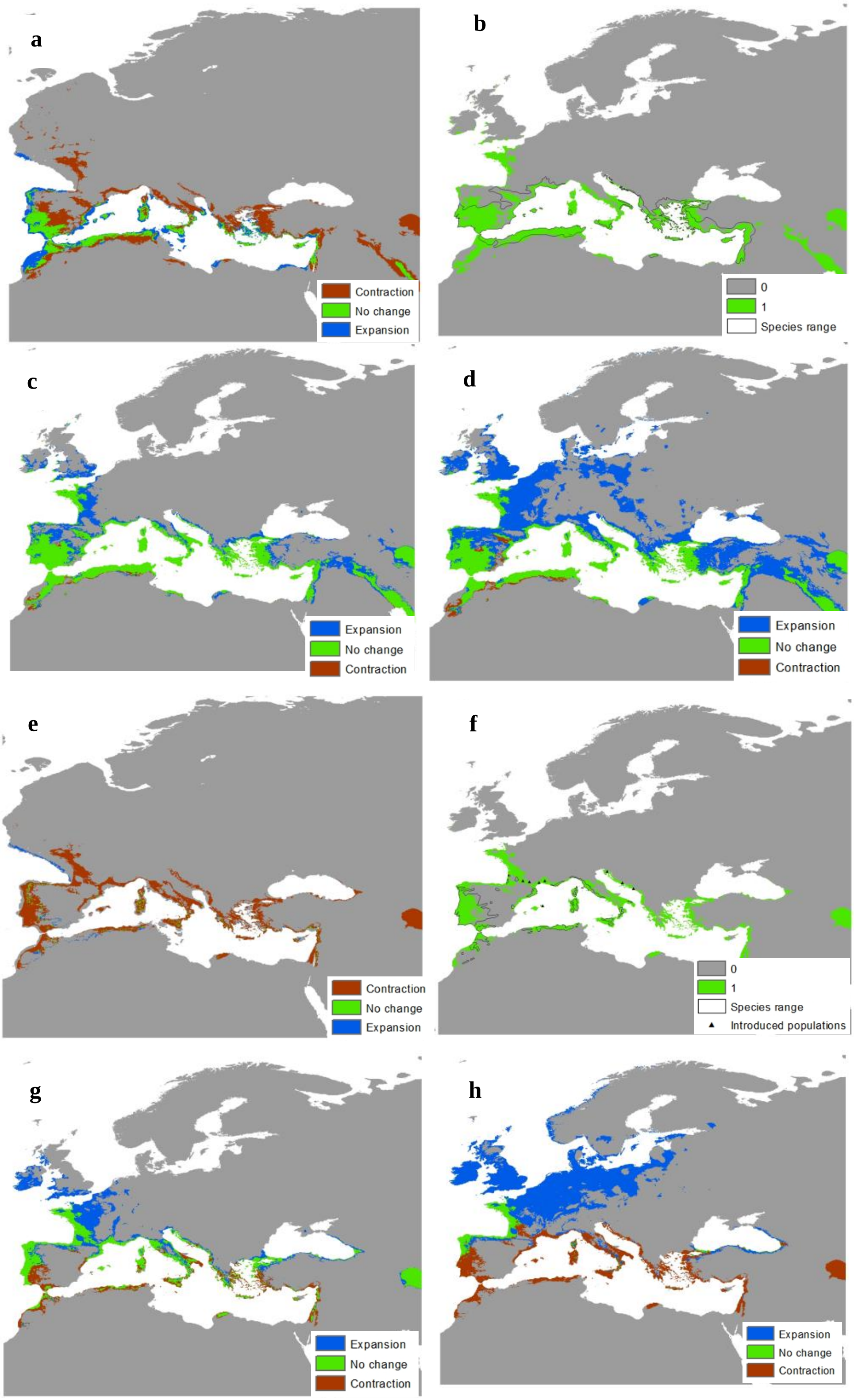

**Figure 4.3.** Model projections of the Mediterranean zone species under a. the Last Glacial Maximum (22000 YBP), b. Current, c. future (2081-2100 ssp126), and d. future (2081-2100 ssp585) of *Q. coccifera*; and e. the Last Glacial Maximum (22000 YBP), f. Current, g. future (2081-2100 ssp126), and h. future (2081-2100 ssp585) of *Q. suber*.

## 4.4. Discussion

Since the current model projections are compatible with the known occurrence of the species distributions, besides the projected introduced populations and climatically suitable habitats out of the ranges, we were able to emphasize the trained models for the past and future climate conditions. Our findings showed that oak species distributed in different climatic zones of the western Palearctic have distinct range responses to climatic changes. The results supported our initial hypothesis that Mediterranean and temperate oaks should differ regarding their responses, but we failed to show transition-zone oaks lie in-between Mediterranean and temperate ones, as transition-zone species had more similar responses to temperate oaks. These results distinctly position Mediterranean species among western Palearctic oaks in terms of their distributional range response to climate change. Consequently, our study underscores those western Palearctic oaks, currently distributed across diverse climatic zones (i.e., the Mediterranean versus temperate and transition-zones), will be differentially affected by future climate changes. This suggests that distinct conservation measures should be implemented for oaks in different climatic zones.

Our results show that both temperate-zone species (*Q. robur, Q. petraea*) and transition-zone species (*Q. cerris, Q. pubescens*) showed a similar pattern against climatic changes and contracted their northern distribution ranges towards climatically suitable regions of southern Europe during LGM, as suggested for many temperate species (Bennett, Tzedakis & Willis, 1991; Hewitt, 1996; Bennett & Provan, 2008; Médail & Diadema, 2009). These results are consistent with the Provan-Bennet's (2008) expansion-contraction model, and these areas that species survived during the climatic conditions of LGM were potential glacial refugia for these species. Apart from the accepted glacial refugia such as Iberian Peninsula, Italy, Balkans, and the latest Anatolia for temperate oak species in southern Europe (Bennet et al., 1991; Taberlet et al., 1998; Brewer et al., 2002; Bagnoli et al., 2015; Ülker et al., 2018), Anatolia is also revealed as an important plausible glacial refugia for the transition-zone oak species in this study. During this period, it is known that certain regions in the northern part of the main mountainous areas had suitable microclimatic conditions, indicating the presence of refugia outside the Mediterranean region (Schmitt & Varga, 2012; Perktaş et al., 2015). The projected areas in the southern parts of France, and the coastal areas of Black Sea region might indicate an extra-Mediterranean refugium for these species. Due to moisture deficiency, temperate oak species were unable to form extensive forests in glacial refuges during the LGM. However, as climatic conditions started to improve, they rapidly expanded their distribution northward. It is known that the spread of these species from glacial refugia to different regions, particularly during the Middle Holocene (approximately 6000 years ago), was accelerated by human activities (Turner et al., 2008).

Compared to temperate and transition-zone species, Mediterranean species have narrowed their distribution ranges to a lesser extent during the LGM. They have experienced a noticeable expansion in their populations towards the southern regions of their distribution ranges. The suggested biodiversity hotspots for plant species in the Mediterranean region (Medail & Diadema, 2009) are also projected as possible glacial refugia for both *Q. suber* and *Q. coccifera* during the LGM, these predictions also support the paleoecological evidence of long-term vegetation persistence in the Mediterranean Basin, demonstrating the presence of oak species in this region during long-term climate changes. These results offer additional evidence for the enduring sustainability of oak species in the region. However, based on the species-specific analysis, both *Q. suber* and *Q. coccifera*, the Mediterranean species in our study, displayed a comparable response pattern to climate conditions during this period. Nonetheless, *Q. coccifera* exhibited a more effective preservation of its distribution area in the Mediterranean Basin compared to *Q. suber*. Indeed, this situation could be attributed to the fact that these two species, classified as Mediterranean species, belong to different sections (*Q. suber* belongs to *Cerris* section and *Q. suber* belongs to section *Ilex* section) and thus have different evolutionary origins (Simeone et al., 2016; Simeone et al., 2018; Denk et al., 2023). Based on the examination of macrofossil records, it has been unveiled that evergreen oaks have been present in the Eastern Mediterranean region since the Miocene period (Vitelli et al., 2017). When considering the global distribution of the *Ilex* section, both southern Anatolia and the Middle East have played dual roles as refugia and centers of diversification for this particular group. Therefore, it is emphasized that the hypothesis of only a few refugia in the south during the LGM is not applicable to this group, but rather a multiple refugia hypothesis (López de Heredia, 2007) should be considered, which is supported by our results. Moreover, evergreen oaks, compared to temperate oaks, have remained limited to the coastal areas of the Mediterranean due to several factors throughout the historical process. These factors include their lower competitiveness, higher tolerance to drought, distinct ecological requirements, the impact of fires, herbivores, pathogen attacks, and the arrival of new competitors in the Mediterranean Basin (Carrión, 2002; Turner et al., 2008). These factors have collectively contributed to the restricted distribution of evergreen oaks along the Mediterranean coast, besides the impact of climate.

According to optimistic and pessimistic climate future scenarios (ssp126 and ssp585), temperate-zone and transition-zone species were expected to exhibit a similar pattern in response to climate change. It is predicted that within the next 60-80 years, they will lose their southern populations, but expand through more terrestrial parts, higher elevations through mountainous areas, and the northern regions of Europe, in particular to Scandinavia. The habitat loss is expected to be less pronounced in transition-zone species compared to temperate-zone species, according to our projections. It is also predicted that transition-zone species will be limited by climate and also declined in the introduced regions, but relatively more capable of preserving their populations in the southern regions compared to temperate-zone species. In the pessimistic scenario (ssp585), it is indeed anticipated that temperate-zone species will experience a more significant loss. The fact that *Q. petraea* and *Q. robur*, which are the most dominant and economically important species of European forests (Cottrell et al., 2002), are subject to such a rapid decline, revealing the necessity of developing protection strategies for these widely distributed species in terms of European forestry practices. In contrast, the Mediterranean species are predicted to slightly contract their current known distribution areas in the south, yet still they are expected to exhibit distributions in wider areas compared to the present climatic conditions. Indeed, even under the pessimistic scenario where the climate is projected to become warmer and regions in the middle latitudes of Europe gradually acquire Mediterranean climate characteristics (IPCC, 2022), it is predicted that *Q. coccifera*, in particular, will expand its distribution towards central Europe. This suggests that *Q. coccifera* may extend its range further northward in response to the changing climatic conditions. According to the pessimistic scenario, *Q. suber* indeed diverges from *Q. coccifera* in its response to climate. While it may expand its distribution towards the northeast, it is expected to experience some population loss in the south. This suggests that *Q. suber* may face challenges in maintaining its populations in the southern regions under the changing climatic conditions. The novel fire regimes expected in temperate Europe in upcoming decades (Grünig et al., 2023; Sayedi et al., 2023) may further ease the expansion of the range of Mediterranean oaks towards more northern latitudes, as they are well resprouters even after intense crown fires (Tavşanoğlu & Pausas, 2018).

The distribution of the study species across various regions in the western Palearctic (Mediterranean, temperate, and both) explains the notable diversity in the climatic variables influencing their geographical distribution. Consequently, they respond differently to climatic changes. The findings of this study indicate that temperate and transition-zone species display more pronounced responses to climate change compared to Mediterranean species. It is evident that the Mediterranean species have experienced and are expected to encounter lesser impacts from past and future climatic changes. This suggests that the temperate and transition-zone species are more sensitive and vulnerable to climate variability, while the Mediterranean species have certain adaptations or tolerances that enable them to withstand and persist under changing climatic conditions.

In general, our findings for each climate-zone species pattern align with the widely acknowledged correlation between ecological niches and spatial characteristics of species in future projections (Thuiller et al., 2005), therefore the variations under each group could be explained by these arguments. This study revealed that (1) the species inhabiting colder regions are anticipated to experience greater habitat loss compared to those found in warmer regions, which explains the situation between the Mediterranean-zone species and the other; (2) species characterized by limited occurrences were projected to undergo substantial reductions in suitable habitat, which explains the situation between *Q. coccifera* and *Q. suber*; and (3) species displaying a narrow tolerance to temperature were projected to experience significant habitat loss, whereas species exhibiting high tolerance to aridity were anticipated to exhibit greater stability under future conditions, which supports the slight difference between the temperate and transition zone species projections.

The European climate exhibited a dominant temperature gradient, complemented by a secondary gradient in precipitation (Thuiller et al., 2005; Peel et al., 2007). Consequently, considering the identified species niche positions, the potential effects of climate change can be more accurately estimated. This study has made a substantial contribution to advancing our comprehension of the biogeographical patterns exhibited by temperate and Mediterranean oak species in the western Palearctic Region. This contribution is particularly important for the scientific literature concerning the impact of late Quaternary climate changes on the formation of present-day oak diversity. Lastly, we have highlighted the importance of including Anatolia in such studies, as it has been found to have significant potential refugia.

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## Supplementary Material to the Chapter 4

**Table A1.** Bioclimatic variables used in ENMs were downloaded from the WorldClim database version 2.1.

| **Bioclimatic Variable** | **Definition** |
|---|---|
| BIO1 | Annual mean temperature |
| BIO2 | Mean diurnal range (max temp/min temp)(monthly average) |
| BIO3 | Isothermality(BIO1/BIO7)X100 |
| BIO4 | Temperature seasonality (Coefficient of Variation) |
| BIO5 | Max. temperature of warmest period |
| BIO6 | Min. temperature of coldest period |
| BIO7 | Temperature annual range (BIO5-BIO6) |
| BIO8 | Mean temperature of wettest quarter |
| BIO9 | Mean temperature of driest quarter |
| BIO10 | Mean temperature of warmest quarter |
| BIO11 | Mean temperature of driest quarter |
| BIO12 | Annual precipitation |
| BIO13 | Precipitation of wettest period |
| BIO14 | Precipitation of driest period |
| BIO15 | Precipitation of seasonality (Coefficient of Variation) |
| BIO16 | Precipitation of wettest quarter |
| BIO17 | Precipitation of driest quarter |
| BIO18 | Precipitation of warmest quarter |
| BIO19 | Precipitation of coldest quarter |

**Table A2.** Mean AUC values of the study species

| Species | Mean AUC values |
|---|---|
| *Q. robur* | 0.737 |
| *Q. petraea* | 0.830 |
| *Q. coccifera* | 0.817 |
| *Q. suber* | 0.840 |
| *Q. cerris* | 0.772 |
| *Q. pubescens* | 0.789 |

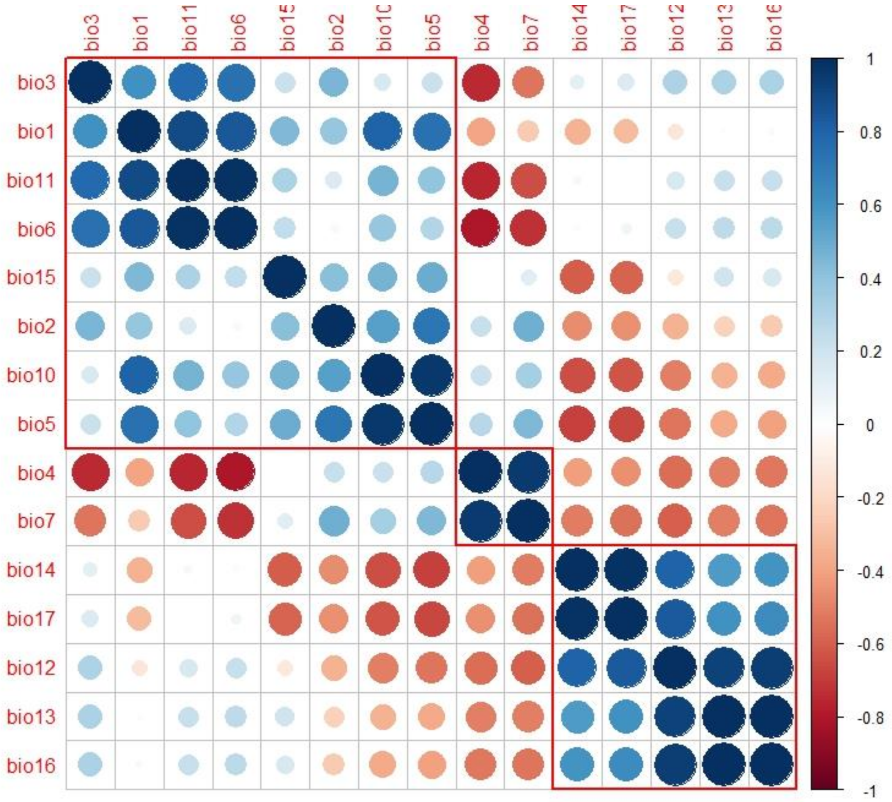

**Figure A1.** Correlation matrix between 15 bioclimatic variables of *Q. robur*

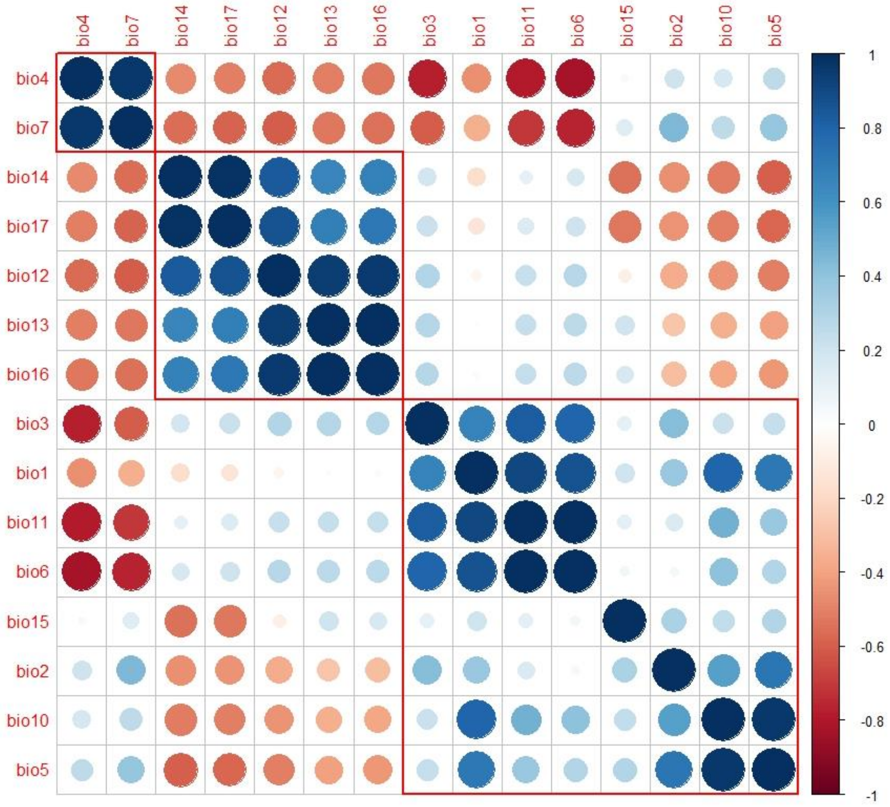

**Figure A2**. Correlation matrix between 15 bioclimatic variables of *Q. petraea*

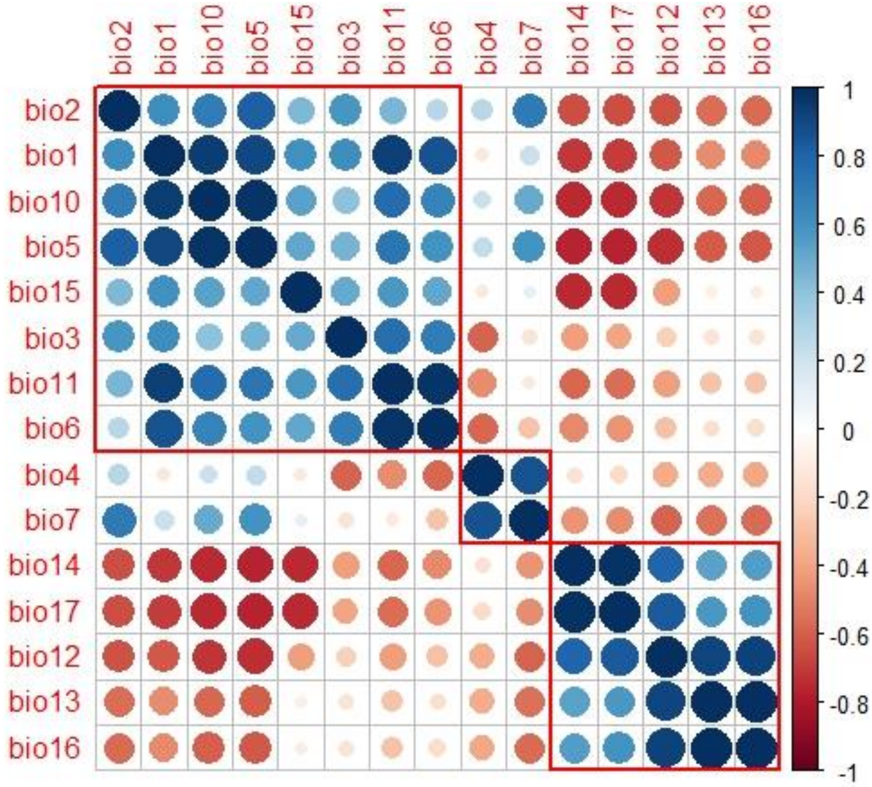

**Figure A3.** Correlation matrix between 15 bioclimatic variables of *Q. coccifera*

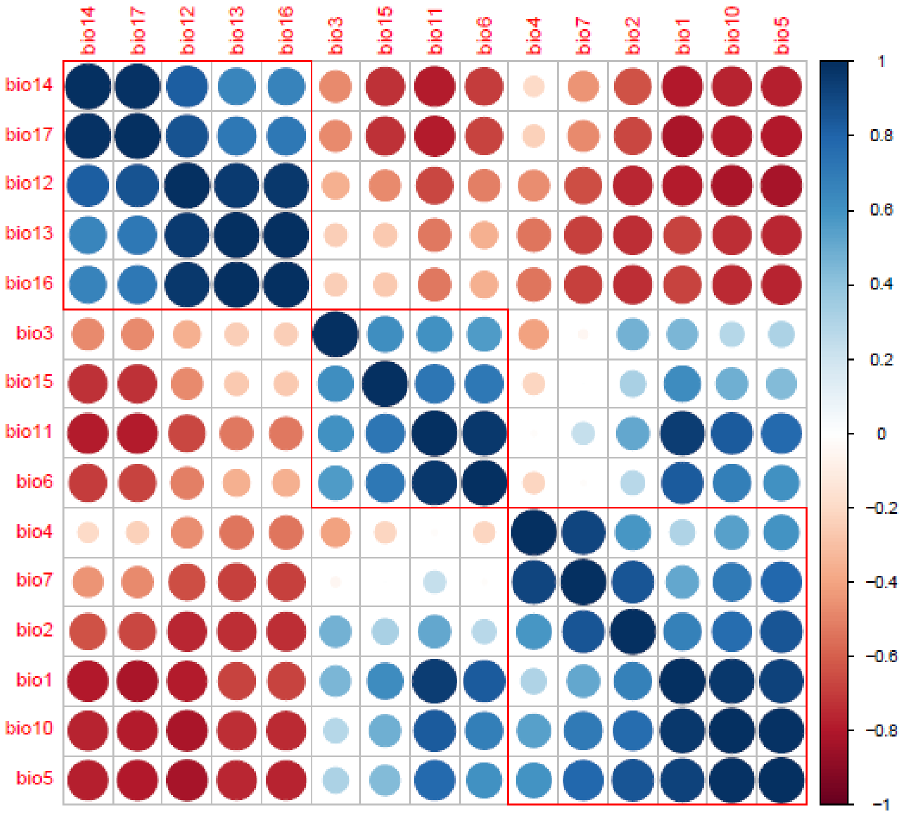

**Figure A4.** Correlation matrix between 15 bioclimatic variables of *Q. suber*

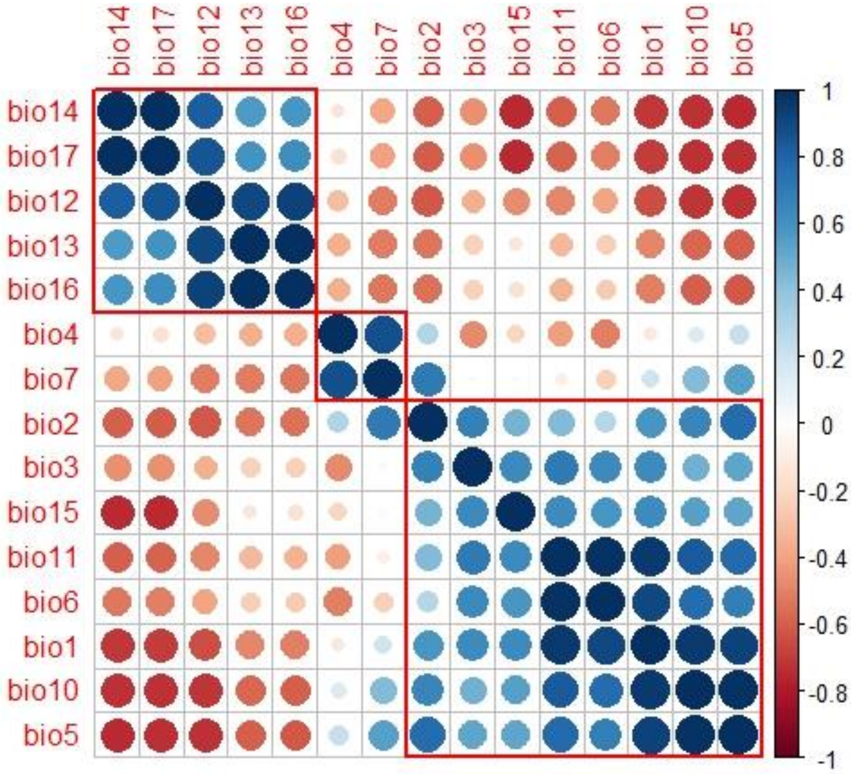

**Figure A5.** Correlation matrix between 15 bioclimatic variables of *Q. cerrris*

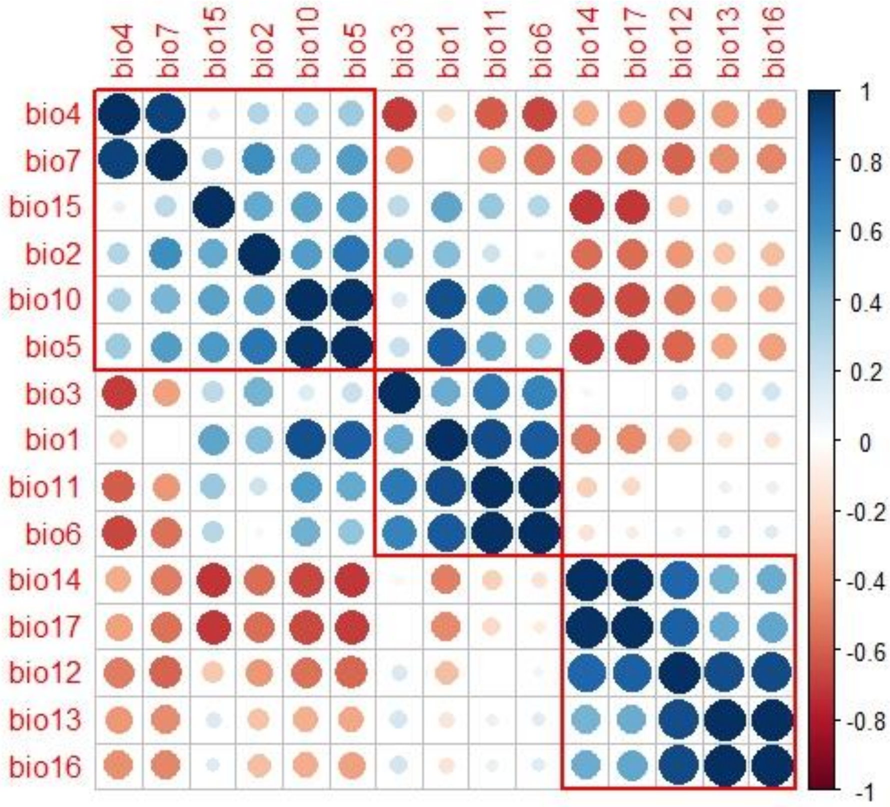

**Figure A6.** Correlation matrix between 15 bioclimatic variables of *Q. pubescens*

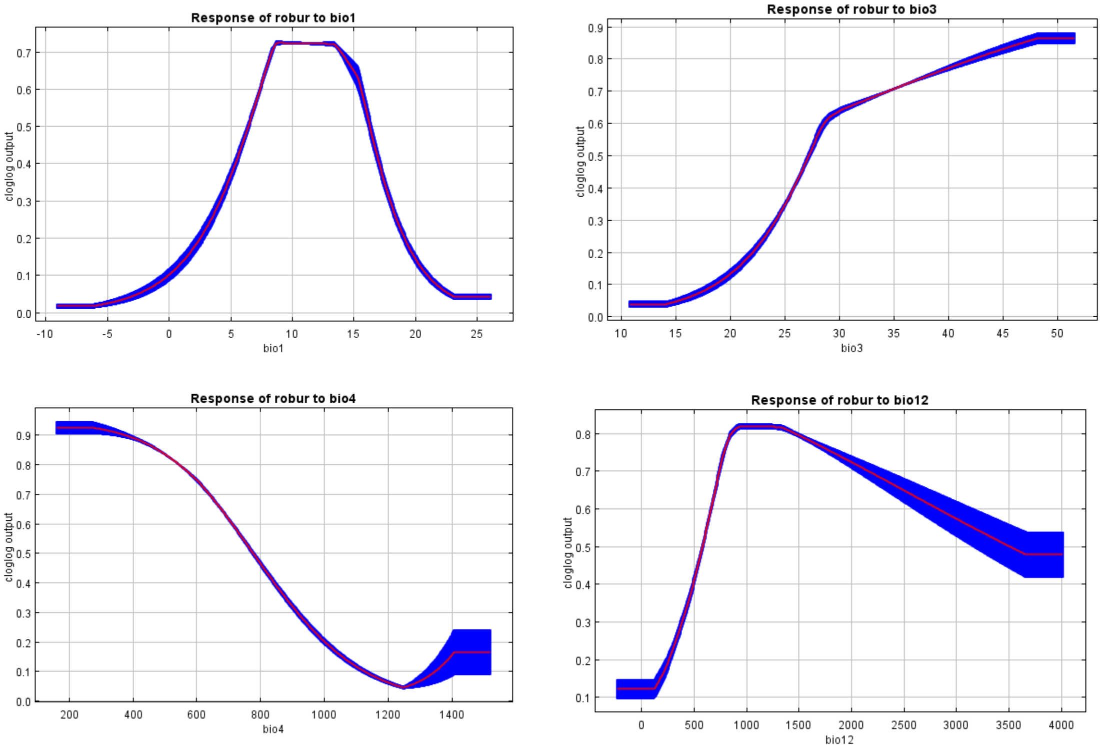

**Figure A7.** Response curves of the bioclimatic variables affected the model projections for *Q. robur*

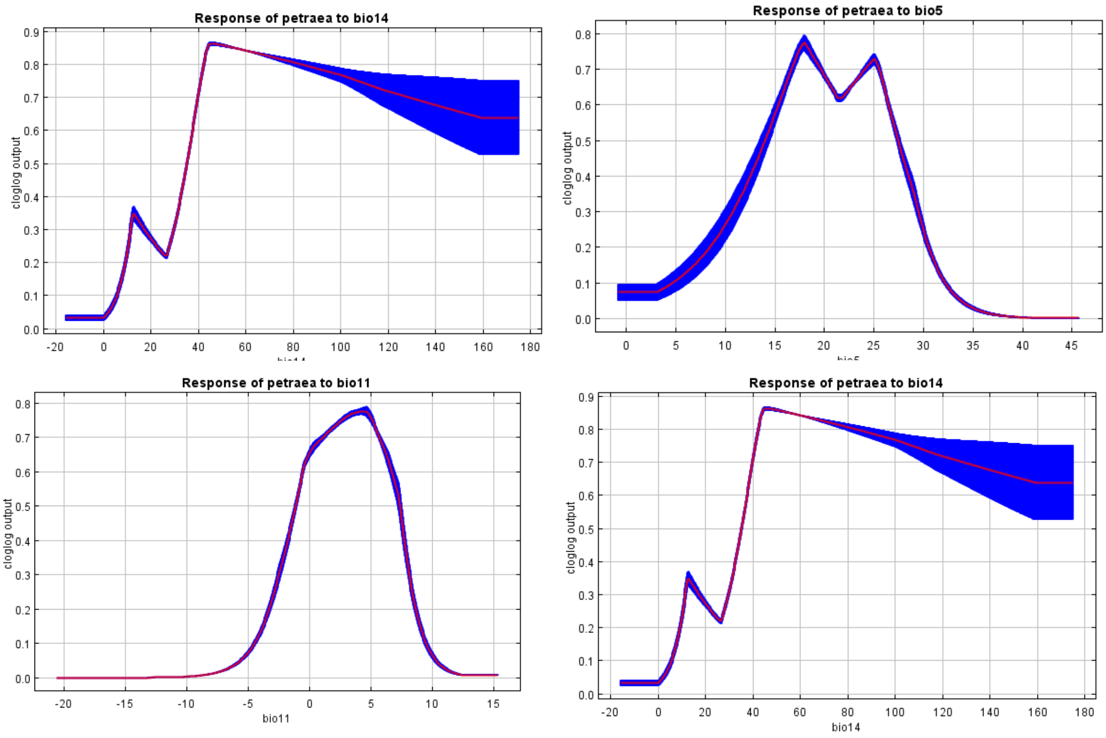

**Figure A8.** Response curves of the bioclimatic variables affected the model projections for *Q. petraea*

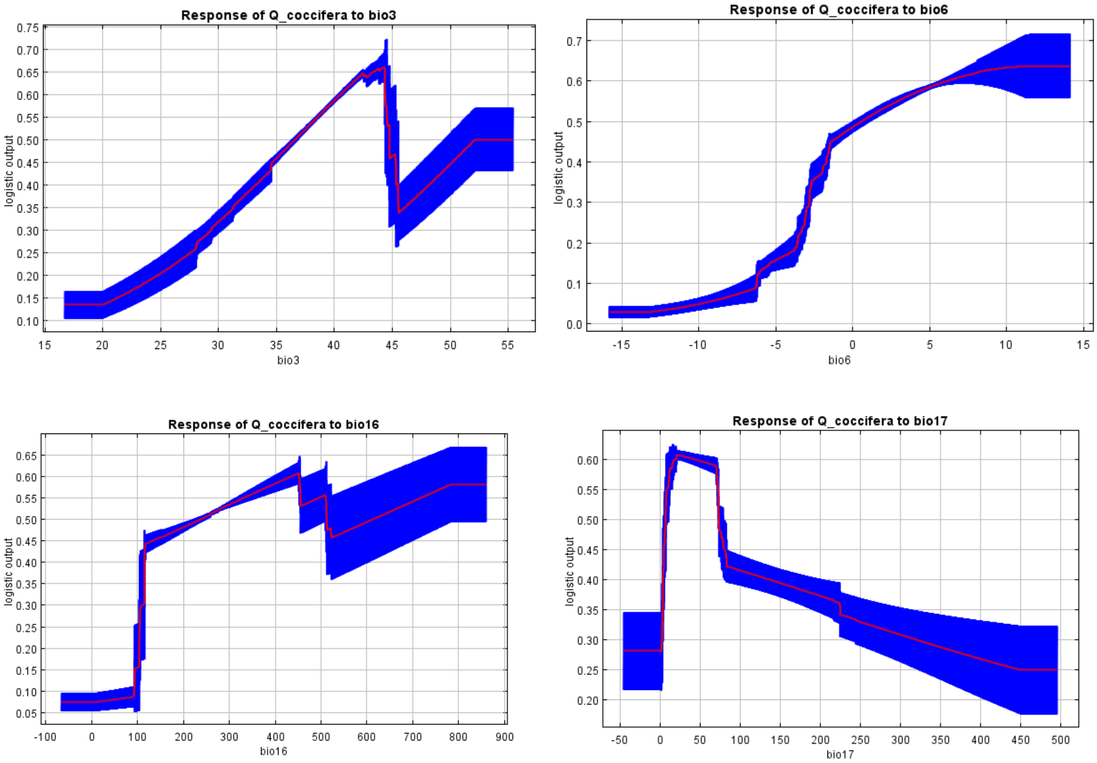

**Figure A9.** Response curves of the bioclimatic variables affected the model projections for *Q. coccifera*

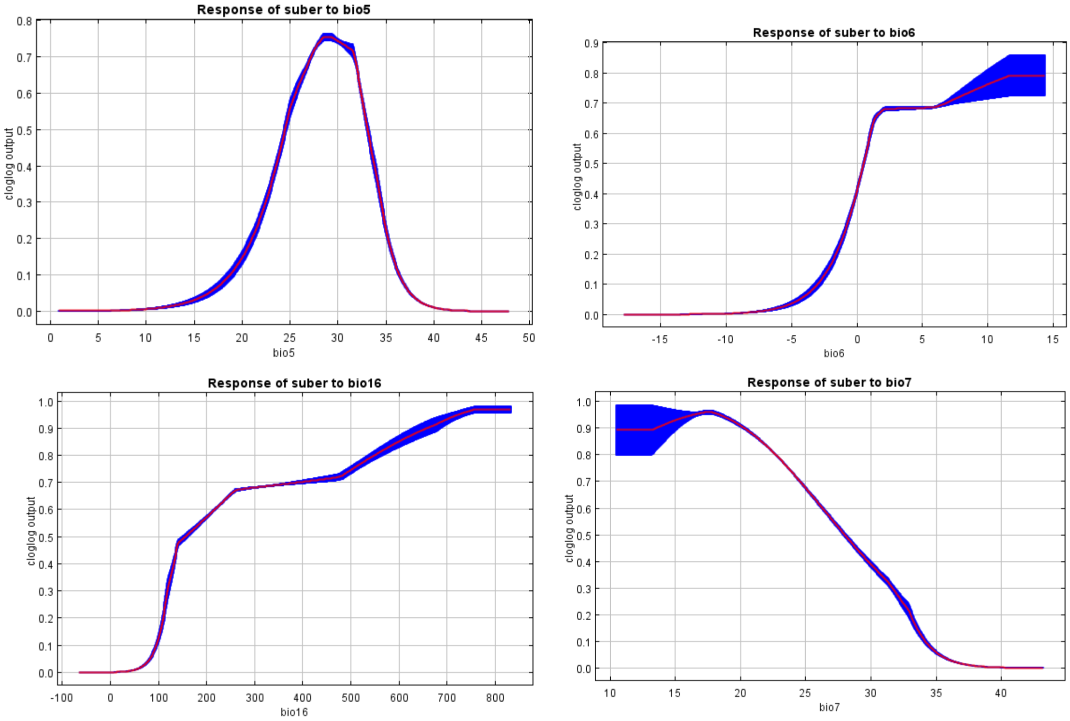

**Figure A10.** Response curves of the bioclimatic variables affected the model projections for *Q. suber*

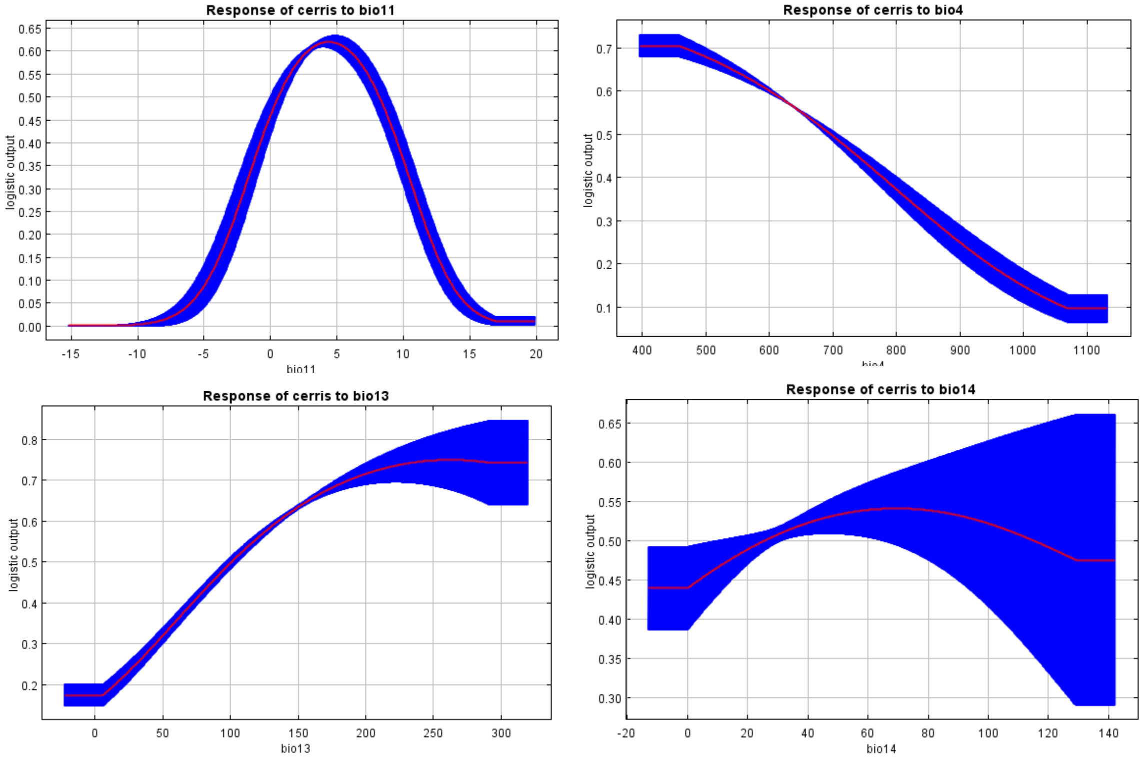

**Figure A11.** Response curves of the bioclimatic variables affected the model projections for *Q. cerris*

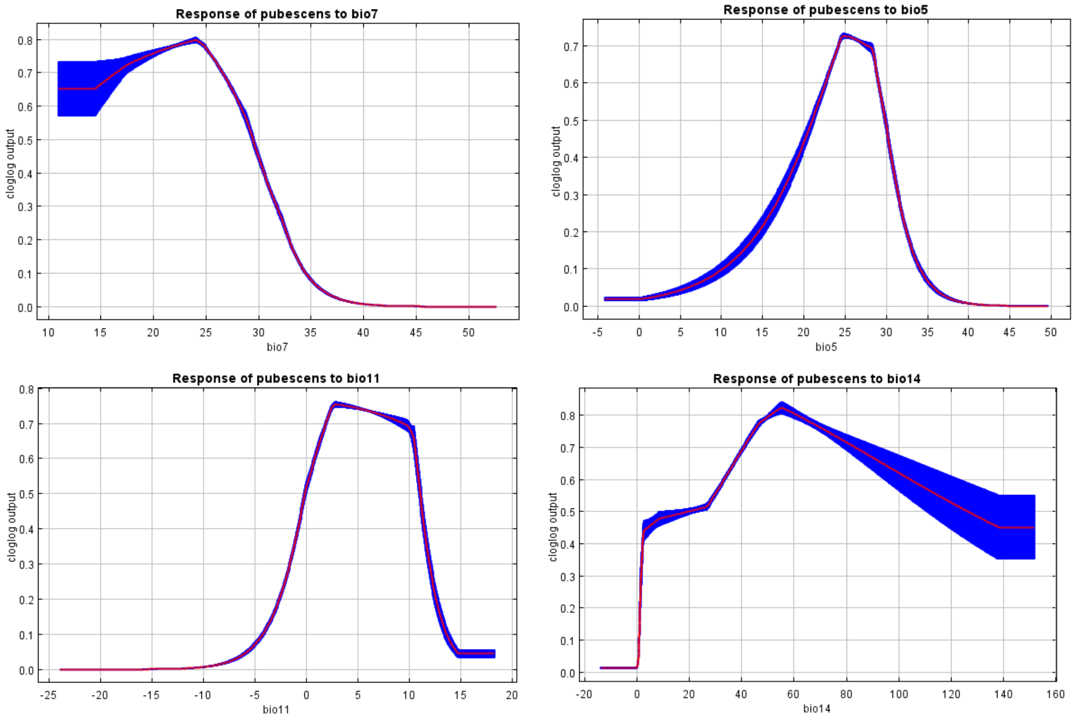

**Figure A12.** Response curves of the bioclimatic variables affected the model projections for *Q. pubescens*

# CHAPTER 5. CONCLUSION

This thesis presents the most in-depth examination to date of oak species within the Western Palearctic region, focusing specifically on their climatic niches. A primary emphasis has been on elucidating the distinct responses of oak species across varied climatic zones, accomplished through highlighting differential functional trait manifestation. The findings generated through this work have established that oak species within the Mediterranean climate zone display unique patterns of climatic responses and functional traits when contrasted with those from temperate and transition-zones outside the Mediterranean climate area.

Upon further exploration into the phylogenetic lineages of *Quercus*, these variations in specific traits and geographic distributions could be more comprehensively interpreted within the context of their respective taxonomic sections. Patterns observed in the geographical distributions of widely distributed species, with regards to climatic alterations, also held true for narrowly distributed and endemic species residing in different climatic zones.

Moreover, significant functional trait disparities within species occupying different climatic zones suggest two possible theories: either species adapt their functional characteristics according to their climatic contexts ('climate-first'), or species distribute themselves across climatic zones based on pre-existing functional traits ('trait-first'). Our findings, when examined through the lens of species' evolutionary origins and phylogenetic divergences, provide a more cogent understanding of where different taxonomic sections have evolved.

This research underscores both distributional and trait-based response patterns of western Palearctic oak species in relation to climate change. It reveals a significant convergence between functional traits and past and future ecological niche model projections, thereby substantiating climatic niche assumptions for species, even in regions such as Anatolia that have traditionally been underestimated. However, for a more profound understanding of the captivating evolutionary journey of oaks, further molecular analyses are necessary.

From the vantage point of conservation and management, it is critically important to consider the climatic zones in which plant species, such as those within the genus *Quercus*, are situated. Applying a blanket assumption of universal range shift responses to climate change could yield biased interpretations, particularly for species that diverge from this generalized model. It is noteworthy that Mediterranean oak taxa appear to deviate from the standard range contraction-expansion paradigm typically ascribed to temperate species. As such, these Mediterranean oaks warrant a separate analysis from temperate oak species in the context of their responses to climatic fluctuations. This tailoring of approach ensures a more nuanced and precise understanding of these species' resilience and adaptability in the face of climate change.

### ***Implications for practitioners***

While the results of the analysis obtained at the regional scale highlight the threat of climate change, it has also revealed that pressures such as illegal logging, land destruction, fires, invasive species, and grazing pose an increasing threat to endemic species at the local scale. Therefore, various steps can be taken with forestry practices to protect oak species and to sustain their habitats in the future.

- Maintaining microclimates (i.e., small-scale climate) in areas where oak species grow can help species better adapt to climate change. For example, soil management that increases water holding capacity can increase longer-term moisture retention and drought tolerance.
- Identify and protect important habitats and populations with higher biodiversity and ecological significance. If possible, restore converted habitats back to suitable oak forest conditions, especially in the case of endemic species.
- Collaborate with local communities, stakeholders and researchers to develop sustainable land-use practices that are less damaging to oak populations.
- Encourage practices that support mixed land-use systems, combining agriculture or tourism with conservation,
- Monitor and manage invasive insect species and fungal pathogens that affect oak health. Although they may not have a severe impact currently, proactive management can prevent future outbreaks,
- Develop and implement fire management plans for the populations in fire-prone Mediterranean ecosystems,
- Implement measures to control domestic herbivory (e.g., grazing by goats) in areas,

- Strengthen monitoring and law enforcement to prevent illegal logging, particularly in areas where endemic populations are at risk. If timber harvesting is necessary for *Q. vulcanica,* promote sustainable and selective practices to minimize negative impacts on the species' populations.
- Engage local communities and raise awareness about the importance of oak conservation. Involve local people in conservation efforts and utilize traditional knowledge for sustainable management.
- Conduct regular monitoring of oak populations, including assessments of pest and disease prevalence, population dynamics, and regeneration rates. Support research to better understand the specific threats to each species and their respective habitats. It is important to conduct regular surveys to monitor changes in the distribution of oak species and to understand their causes. This helps evaluate the effectiveness of forestry practices and revise practices as needed.

It is important for forest managers, forestry personnel to recognize the oak species in the area for which they are responsible. In addition, educating and raising awareness about the effects of climate change on oak species is critical to the success of conservation efforts. It is essential to implement the management practices in a collaborative manner, involving local communities, government agencies, and conservation organizations to ensure their effectiveness and long-term sustainability. Flexibility in approach and adaptive management will be crucial given the specific challenges each species faces and the changing dynamics of their habitats and threats over time.