









What we know about Turkey oak (*Quercus cerris* L.) — from evolutionary history to species ecology

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Abstract

Turkey oak (*Quercus cerris* L.) is a deciduous tree species of the genus *Quercus* section *Cerris* (Fagaceae), widely distributed in Europe and Asia Minor. Throughout its vast distribution range, the species carries high phenotypic and genetic variability. Due to its high drought tolerance, Turkey oak may have great potential to be a key tree species in Central and Western Europe under climate change conditions. However, more detailed information on its phylogeny, phylogeography, phenotypic, and genetic variability is still needed for a more careful and reliable assessment of the species' adaptation potential. To this end, based on 41 reviewed articles, we collected detailed information to support the evaluation of Turkey oak's adaptation potential under climate change. In the reviewed articles, we observed a significantly lower number of genetic studies of the members of the section *Cerris* (especially the Euro-Mediterranean species) relative to the subgenus *Quercus*. We also identified research gaps with respect to the functional and population genetics of the species that should be addressed in the future. Nevertheless, the different evolutionary background and adaptation strategies of Turkey oak as compared to Central European white oaks, as well as its high phenotypic and genetic variability, may indeed represent a great potential for this species to support the climate adaptation of forestry in Central and Western Europe.

Keywords: old-world oaks; paleobotany; section *Cerris*; adaptation; phenotypic variability; biogeography

Introduction

The genus *Quercus* comprises a number of key tree species in northern hemispheric forest ecosystems (e.g. *Quercus robur* L., *Quercus petraea* (Matt.) Liebl. and *Quercus cerris* L. in Europe). The distribution range of its species extends over four continents (North America, South America, Africa, Eurasia), from the Equator to 60°N; from sea level up to an elevation of 4000 m (Axelrod 1983, Menitsky 2005, Nixon 2006). Turkey oak (*Q. cerris* L.) is one of the over 400 species of the genus *Quercus* and the eponymous species of the subgenus and the section *Cerris*. According to different studies, section *Cerris* consists of ~13–15 species across Eurasia and North Africa (Menitsky 1984, Denk et al. 2017, Denk et al. 2023).

Over the last century, the ecological and economic importance of the genus has led to a number of studies related to taxonomy (e.g. Loudon 1838, Camus 1936–1954, Schwarz 1937, Menitsky 1984, Nixon 1993). Although oaks' phylogeny is among the best-resolved ones in plants, it is not yet fully resolved and remains a key issue in the genetic studies related to the genus *Quercus* (Denk and Grimm 2010, Hubert et al. 2014, Hipp et al. 2020, Manos and Hipp 2021) and its sections (Deng et al. 2018, Hipp et al. 2018, Jiang et al. 2019, Crowl et al. 2020, Denk et al. 2023). As high-resolution genetic data (e.g. in RAD-seq) and advanced computational approaches (e.g. Approximate Bayesian Computation)

become more widely available, more accurate reconstructions of phylogeny and biogeography are also becoming available (Holder and Lewis 2003, Davey and Blaxter 2011, Bagnoli et al. 2016, Parchman et al. 2018, Hipp et al. 2020).

Well-resolved phylogenies contribute to the understanding of evolutionary processes and adaptation of species to changing environmental factors and provide essential knowledge for developing effective climate change adaptation strategies in forestry (Senior et al. 2013, González-Orozco et al. 2016). In addition to molecular phylogenetic approaches, valuable evolutionary inferences can also be drawn from geology, palynology, palaeobotany, and palaeoclimatology (e.g. Denk and Grimm 2009, Barrón et al. 2017). Like most other genera in Fagales (e.g. *Fagus*, *Castanea*, *Carpinus*, etc.), the genus *Quercus* underwent a major differentiation during the Cenozoic (Manos et al. 2001, Barrón et al. 2017, Hipp et al. 2020) accompanied by fundamental geologic changes (e.g. orogeny of the Alpides, closure of Tethys) (Géczy 1972, Báldi 1979, Molnár 1984, Stampfli and Kozur 2006). In the case of oaks, these changes have had a major impact on their phylogenetic history, particularly on subgenus *Cerris* (Simeone et al. 2016, Jiang et al. 2019, Denk et al. 2023). Before this context and considering also climate change, the question whether the different evolutionary histories of the two subgenera led to pronounced differences in

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the species' adaptability and adaptation strategies seems relevant.

Currently, climate change adaptation is a pressing issue in forestry. According to the latest projections, besides temperature and precipitation extremes, the probability and amplitude of drought events will also increase in Central Europe (IPCC 2022). Under increasingly extreme site conditions, improving forest ecosystems' resilience is crucial [for more details see The European Green Deal (European Commission 2019), New EU Forest Strategy for 2030 (European Commission 2021)]. Although some species are predicted to be losers of climate change, other species such as Turkey oak, pubescent oak (*Quercus pubescens* Willd.), or the European white elm (*Ulmus laevis* Pall.) may gain wider distribution in response to global warming (Thurm et al. 2018). Although these winners may contribute to increase the resilience of forest ecosystems, the pace of changes might require human-assisted transfers of their wild populations. This is referred to as assisted migration (Crowe and Parker 2008, Vitt et al. 2010, Williams and Dumroese 2013). Although Turkey oak appears to be a promising species in Central Europe due to its ecological properties alone, successful assisted migration strategies will also benefit from more detailed information on the species' genetic attributes. This includes information related to the phylogeny and phylogeography of the species, the genetic structure of extant populations, its genetic variability, and the genetic characteristics, which make Turkey oak able to successfully adapt to changing environmental conditions. Although the number of studies in this general field of forestry research is increasing, detailed information on Turkey oak is only most recently becoming available.

The main objectives of this review are to provide detailed information on (i) the phylogeny and evolutionary history of the sections of subgenus *Cerris* with particular reference to the section *Cerris*; (ii) the existing genetic variability and population structure of Turkey oak; (iii) the population migrations in the past and corresponding predictions for the future; (iv) the phenotypic variability and (possibly associated) ecological characteristics of the species.

Methods

We reviewed 41 articles from the fields of ecology, phenotypic taxonomy, phylogenetics, phylogeography, population genetics, and palaeobotany (see Supplementary Table S1). To identify relevant literature, an extensive search was performed in the scientific databases of ISI Web of Science (Clarivate Analytics, Philadelphia, PA), Scopus (Elsevier, Amsterdam, Netherlands), and Google Scholar (Google, Mountain View, CA) by using the following keywords and different combinations of them: 'Q. cerris', 'phylogeny', 'population genetics', 'fossil history', 'ecology', 'drought tolerance', 'assisted migration', 'Cenozoic', 'last glacial maximum', 'refugia', 'phenotypic variability', 'climate envelope analysis'. In addition to English works, we also included studies published in local languages (e.g. Hungarian, Serbian, Russian, etc.). The cut-off date for publications to be included in this review was 11 May 2023.

Phylogeny of subgenus *Cerris* Phylogenetic studies of subgenus *Cerris* lag behind comparable studies in other oak clades

Over the last two decades, the development of molecular approaches has led to a large number of studies using different marker systems to investigate the phylogenetic relationships of oaks (Oh and Manos 2008, Hubert et al. 2014, Simeone et al.

2016, Deng et al. 2018, Hipp et al. 2020). However, perhaps due to the greater species diversity and wider distribution range of species of the subgenus *Quercus*, there are notably more studies on the phylogeny of the subgenus *Quercus* than *Cerris*. Although the phylogenetic backbone of the sections of subgenus *Quercus* is generally well resolved, comprehensive studies on the members of section *Cerris* lag behind in multiple aspects. On the one hand, only a few studies have addressed the phylogeny of the section *Cerris* relative to the section *Ilex* or *Cyclobalanopsis*. On the other hand, it is surprising that only two molecular studies deal exclusively and on a large geographical scale with Turkey oak (Özer 2014, Bagnoli et al. 2016), although it has the largest distribution in the Euro-Mediterranean range of its section [based on the distribution maps of Menitsky (1984), Schirone et al. (2015) and Caudullo et al. (2021)]. Meanwhile, for the only three species in the Asian range of the section (*Quercus acutissima* Carruth., *Quercus variabilis* Blume, *Quercus chenii* Nakai), there is a relatively long list of studies available (e.g. Li et al. 2019, Zhang et al. 2020, Chen et al. 2021). Moreover, the complete chloroplast genomes of *Q. acutissima* (Li et al. 2018), *Q. variabilis* (Pang et al. 2019), *Q. chenii* (Yang et al. 2018), and the mitochondrial genome of *Q. acutissima* (Liu et al. 2022) and *Q. variabilis* (Bi et al. 2019) have already been published.

Regarding the genetic approaches used, although more advanced genome-wide methods (such as RAD-seq) are relatively well-established for the members of subgenus *Quercus* (see e.g. Hipp et al. 2013, 2014, 2018, 2020), such studies with similar marker types dedicated to the members of section *Cerris* are rare so far (e.g. Jiang et al. 2019, Pina-Martins et al. 2019, Hipp et al. 2020, Denk et al. 2023).

As for complete nuclear reference genomes, there is also a delay for the section *Cerris*. Although several annotated genomes are already available for oak species to date [e.g. *Quercus lobata* Née (Sork et al. 2016a), *Q. robur* (Plomion et al. 2018), *Quercus rubra* L. (*Q. rubra* v2.1, DOE-JGI, https://phytozome-next.jgi.doe.gov/info/Quubra_v2_1)], there is only one draft genome belonging to a species of section *Cerris*, the cork oak (*Quercus suber* L.) (Ramos et al. 2018). Nevertheless, until more reference genomes are sequenced, the cork oak genome may provide an excellent opportunity for genome-wide association studies on other species of section *Cerris* such as Turkey oak.

Genotype–phenotype or genotype–environment associations could provide detailed information on, for example, the genetic background of drought adaptation. While for white oaks there are already countless studies dealing with related issues (Rellstab et al. 2016, Sork et al. 2016b, Gugger et al. 2021), again, for the members of the section *Cerris* such studies are still scarce (e.g. Pina-Martins et al. 2019).

Both nuclear and plastid DNA markers have been used in phylogenetic studies at different taxonomic levels of the members of section *Cerris*. However, it is difficult to make comparisons with the results even of this small number of studies because of the different marker systems and the different sampling strategies used.

In one of the first studies on the section *Cerris*, Bellarosa et al. (2005) applied nuclear ribosomal RNA and ITS sequences to infer phylogenetic relations of Italian oak species. Based on their results, they divided the Italian oak species into three individual groups corresponding to the sections *Quercus*, *Ilex*, and *Cerris*. Later, using amplified fragment length polymorphism (AFLP), internal transcribed spacer (ITS), and plastid restriction fragment length polymorphism (RFLP) methods, Lopez de Heredia et al. (2007) investigated the phylogeny of western Mediterranean evergreen oaks. In addition to suggesting a Miocene divergence date of the section *Cerris*, they also detected signatures of genetic contact in

the plastid genome between *Q. suber* and *Quercus ilex* L. In a study at a higher taxonomic level, Denk and Grimm (2010) separated western Eurasian oaks into three distinct groups, roburoid, ilicoid, and cerroid oaks, based on nuclear ITS and 5S intergenic spacer (5S-IGS) sequences. Simeone et al. (2016) suggested multiple origins of section *Ilex* by using three chloroplast markers (rbcL, trnK/matK, trnH-psbA). In addition, they pointed out a high versus mid-latitude separation of the two oak subgenera *Quercus* and *Cerris*, according to the deep phylogenetic split seen in the nuclear and plastid sequences of the two major groups. However, one of their most important results is that the Asian members of the section *Cerris* share the same plastid haplotype with an *Ilex* oak species (*Quercus phillyreoides* A. Gray), which points towards the Asian origin of the section *Cerris*. Later Simeone et al. (2018) provided the first comprehensive systematic and phylogeographic scheme of western Eurasian members of the section *Cerris*, based on plastid (trnH-psbA) and nuclear (5S-IGS) DNA variation. According to their results, they divided the western Eurasian members of the section *Cerris* into four evolutionary lineages, in which Turkey oak is a member of the 'Occidental' lineage together with *Quercus castaneifolia* C.A. Mey., *Quercus look* Kotschy, and *Quercus euboica* Papaioannou. In addition, western Eurasian members of section *Cerris* shared genetic signatures with the Mediterranean species of section *Ilex* but not with East Asian species of section *Cerris*, suggesting that this contact should have been established only after the section *Cerris* split into a Euro-Mediterranean and an Asian range. This phenomenon may also refer to an Asian origin of the section rather than a European one. Most recently, Denk et al. (2023) in a comprehensive phylogenetic study established a new phylogenetic and phylogeographic scenario for the section *Cerris* based on new fossil evidence and high-resolution restriction site-associated DNA sequencing (RAD-seq) data by including almost all the species of the section. According to this new scenario, the section *Cerris*' divergence date could be significantly earlier than previously estimated, as early as the Eocene. Furthermore, species of the section *Cerris* were divided into five subsections (*Campylolepidis*, *Suber*, *Aegilops*, *Libani*, *Cerris*), where Turkey oak is a member of subsection *Cerris* together with *Q. castaneifolia* and *Q. look*. In addition, the published new fossil evidence supports an East Asian origin for this section.

At the species level, in an extensive study, Bagnoli et al. (2016) mapped modern populations of Turkey oak to three distinct refugia and reconstructed their phylogeography using chloroplast microsatellites. Owing to these results, we now also have a relatively high-resolution map of the genetic structure of Turkey oak populations throughout the whole distribution range. Using these geographical patterns, it may be possible in the future to infer the origin of forest reproductive materials.

The system of the two subgenera

As a broader view (also considering the related phylogenetic groups of oaks) is essential to comprehend all the aspects forming Turkey oak's phylogeny, we should also shortly discuss the formation elements of the two subgenera, *Quercus* and *Cerris*.

Regarding the phylogenetic structure of the genus *Quercus*, recent phylogenetic studies consistently support two monophyletic groups within the genus (Oh and Manos 2008, Denk and Grimm 2010, Hipp et al. 2014, 2020, Hubert et al. 2014, Denk et al. 2017). The two main groups are *Quercus* and *Cerris*, which are treated as subgenera (Denk et al. 2017). The former group is also called the 'New World clade', while the latter is the 'Old World clade'. These refer to the deep biogeographic split between the two lineages. With a few exceptions, subgenus

Quercus is largely restricted to the Americas, and subgenus *Cerris* to Eurasia and North Africa (Manos and Hipp 2021). In addition, another interpretation of the major split as the 'mid-latitude clade' and 'high latitude clade' is also used referring to the initial biogeographic split between subgenus *Quercus* and *Cerris* (Simeone et al. 2016).

Recent studies suggest that the initial split between the two subgenera occurred during the Early Eocene soon after the divergence of the genus (Hubert et al. 2014, Hipp et al. 2020). Fossil data and molecular phylogenetic relationships between recent species support that the radiation from East Asia towards the New World occurred via the Beringian and North Atlantic land bridges, which played an important role in the intercontinental species exchanges during the Cenozoic (Denk and Grimm 2010, Denk et al. 2012, Hubert et al. 2014).

The two subgenera comprise eight monophyletic infrageneric groups, which are treated as sections (Denk et al. 2017). Subgenus *Quercus* involves sections *Quercus* (white oaks), *Lobatae* (red oaks), *Protobalanus* (golden-cup oaks), *Virentes* (live oaks), and *Ponticae*, while subgenus *Cerris* contains sections *Cyclobalanopsis* (cycle-cup oaks), *Ilex* (Holly oaks), and *Cerris* (*Cerris* oaks) (Denk et al. 2017, Hipp et al. 2020, Manos and Hipp 2021). In terms of species number, the subgenus *Quercus* contains more than twice as many species (284) as the subgenus *Cerris* (138). In the subgenus *Quercus*, *Quercus* and *Lobatae* are the most species-rich sections, with 146 and 124 species, respectively. In the subgenus *Cerris*, section *Cyclobalanopsis*, *Ilex*, and *Cerris* have 90, 35, and 13 species, respectively (Menitsky 2005, Denk et al. 2017, Manos and Hipp 2021) (Fig. 1). There are also marked differences in the distribution of the two subgenera. Subgenus *Cerris* is distributed only in Eurasia and North Africa, in tropical to mid-latitude, warm temperate areas (Menitsky 2005, Denk and Grimm 2010, Manos and Hipp 2021), whereas subgenus *Quercus* (mainly through section *Quercus*) is distributed throughout the whole Northern Hemisphere from a few degrees below the Equator (Sunda Islands) to 62–63 N° (Denisov 1970, Menitsky 2005, Manos and Hipp 2021).

The sections of subgenus *Cerris*

The initial split in subgenus *Cerris* is dated to the Eocene/Oligocene and was established between the two evergreen groups section *Cyclobalanopsis* and section *Ilex* (Hipp et al. 2020). Within subgenus *Cerris*, section *Cyclobalanopsis* is located at the basis of the phylogenetic tree (basal clade) (Hubert et al. 2014, Hipp et al. 2020). The species of this section are currently distributed in subtropical evergreen broadleaved forests of East and Southeast Asia. Cycle-cup oaks are typically evergreen trees or shrubs with entire leaves (Menitsky 2005, Deng et al. 2018). Currently, the centre of species diversity is in China, where 43 out of 69 species are endemic (Wu and Raven 1999). Nevertheless, fossil data from the Neogene of Europe (Portugal, Austria, Bulgaria) support a formerly significantly larger distribution; thus, the range contraction should be relatively recent (Pliocene) (Barrón et al. 2017, Vieira et al. 2023).

Based on RAD-seq data, Hipp et al. (2020) and Denk et al. (2023) suggest an Eocene divergence time for the two sister clades, section *Ilex* and *Cerris*. Group *Ilex* comprises typically evergreen, sclerophyllous-leaved, extratropical temperate to Mediterranean tree and shrub species. The current distribution is restricted to the Mediterranean regions of Europe, North Africa, and an Asian range throughout the Himalayan corridor to Southeast Asia (also referred to as 'Tethyan disjunction') (Jiang et al. 2019).

Previously, it has been suggested that the section *Cerris* is sister to the section *Ilex* and budded from the latter during the

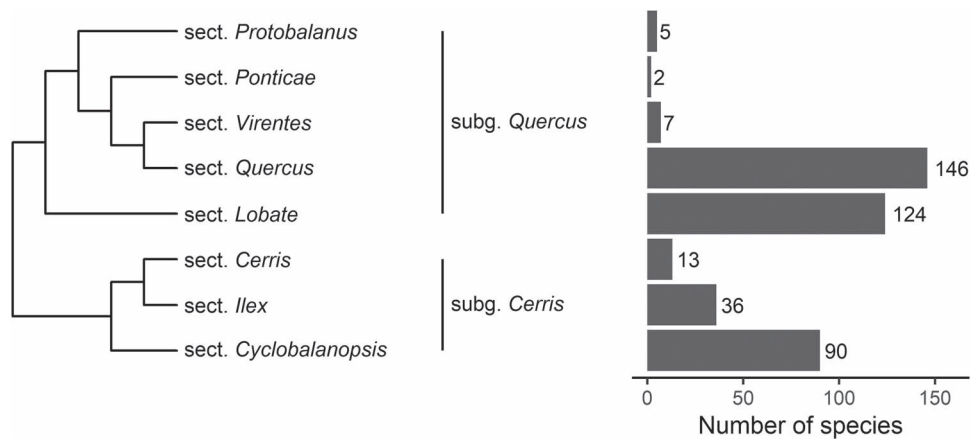


Figure 1. Phylogenetic relations of sections within genus *Quercus*, and the number of species inside sections (phylogenetic tree and species number based on Denk et al. 2017).

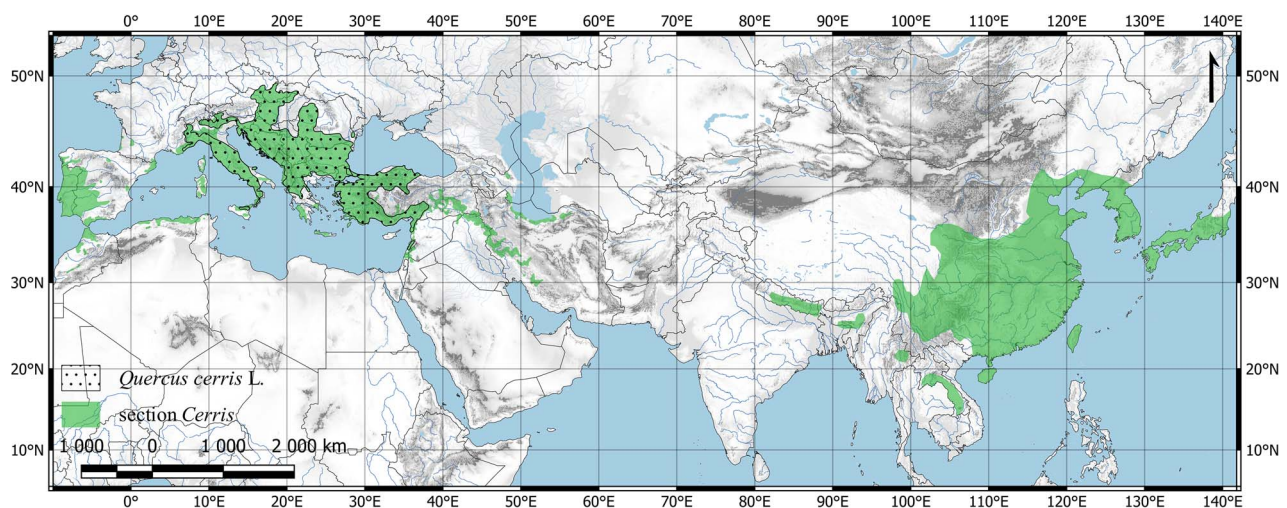


Figure 2. Geographical distribution of section *Cerris* and *Quercus cerris* L. based on Menitsky (1984), Schirone et al. (2015), and Caudullo et al. (2021).

Miocene (Bellarosa et al. 2005, Denk and Grimm 2010, Simeone et al. 2016). However, according to new fossil (Pavlyutkin 2015, Denk et al. 2017, Naryshkina and Evstigneeva 2020) and molecular evidence (Hipp et al. 2020, Denk et al. 2023), the divergence of the section is suggested to have occurred significantly earlier, already during the Eocene. Species of section *Cerris* introduced marked changes in the subgenus *Cerris* concerning their ecological properties. Unlike the two evergreen sections (*Cyclobalanopsis* and *Ilex*), the section *Cerris* contains mainly semi-evergreen and deciduous species with temperate characteristics (e.g. Turkey oak) (Menitsky 2005). According to the findings of Denk et al. (2023), the shift from evergreen to deciduous habit in section *Cerris* is coincident with the split between the section *Cerris* and *Ilex*. Furthermore, this may have been a consequence of the distribution of section *Cerris*, which was restricted to temperate biomes in higher latitudes at this time. Like section *Ilex*, the current distribution of the section *Cerris* is similarly restricted to a Euro-Mediterranean and an Asian range ("Tethyan disjunction") (Fig. 2), suggesting a more extensive, continuous area in the past where the three sections occurred together. Contemporary fossil evidence and shared plastid signatures support the occurrence of the three sections in Europe and Asia (Simeone et al. 2016, Barrón et al. 2017, Simeone et al. 2018, Vieira et al. 2023).

Despite the similar range of the sections *Ilex* and *Cerris*, there is a significant difference in the centre of their species' distribution. In the wild, 10 of the 13–15 species of the section *Cerris* occur only in the Euro-Mediterranean range. In contrast, this ratio is the opposite in the section *Ilex*, where only 4 species out of 35 occur in Europe and Asia Minor (Simeone et al. 2016, 2018, Denk et al. 2023). Despite the different recent species diversity hotspots of the sister sections, most recent molecular results combined with fossil evidence also suggest an East Asian origin for the section *Cerris* (Denk et al. 2023).

Considering the ecological profile, number, and current distribution of species in the three sections of subgenus *Cerris*, we can see a transition from tropical to temperate species. This trend is consistent with the large-scale geological and climatic changes of the Cenozoic (Denk et al. 2023).

A significant discrepancy appears when we consider the differences in the number of species between the Old World and New World oak clades. A possible reason for this phenomenon may be that the Old World clade distributed and evolved almost entirely in the Alpine-Himalayan orogenic belt, where fundamental geological events occurred through the Alpine cycle (major phases of orogeny during which the Alpine-Himalayan mountain chains were formed). In contrast, the New World clade had a

geologically undisturbed range for evolution (Simeone *et al.* 2016). Furthermore, the Pleistocene glaciations did not cause radical distribution contractions in the Americas (Kremer and Hipp 2020). The Alpine cycle coincides with the diversification of the genus *Quercus* and its geological changes altered the geomorphology of the range where subgenus *Cerris* diversified. The Tethys Ocean between Eurasia and Africa had been closed and ceased during the collision of continents. Later, the orogeny of the Alpine-Himalayan mountain chains from Western Europe to eastern Asia transformed the morphology of this region, forming east-west barriers. Simultaneously, the initial tropical character of the Tethyan realm gradually changed towards temperate conditions (Géczy 1972, Báldi 1979, Molnár 1984, Jiang *et al.* 2019, Denk *et al.* 2023). The first occurrences and the high diversity of fossil species of the section *Cerris* in western Eurasia (Miocene) coincide with a key period of the floristic development of Eurasia since the gradual retreat process of palaeotropical and neotropical broadleaved flora in favour of temperate Arcto-Tertiary elements began during the Oligocene and culminated in the Miocene (Géczy 1972, Utescher *et al.* 2007, Ivanov *et al.* 2011). Later several contraction and re-expansion events occurred during the glacial periods of the Pleistocene, especially in Europe. The latter may have resulted in numerous events (e.g. range contractions, bottleneck effects, extinctions) that negatively affected the diversity of Old World oaks (Bagnoli *et al.* 2016, Chen *et al.* 2021).

Species of the section *Cerris*

Today, according to different authors (e.g. Menitsky 1984, Simeone *et al.* 2018, Denk *et al.* 2023), ~13–15 species belong to the section *Cerris*, the majority from the Euro-Mediterranean region and only three species from East Asia. This uncertainty about the number of species is due to the fact that in some cases (e.g. *Quercus crenata* Lam., *Quercus macrolepis* Kotschy) it is controversial whether they should be considered as separate species or as subspecies or hybrids. Recently, in the most comprehensive phylogenetic study on the section *Cerris* so far, Denk *et al.* (2023) distinguished 15 individual species within the section (Table 1.). In addition to widely distributed species such as Turkey oak, this group also includes endemic and narrowly distributed species (e.g. *Quercus afares* Pomel, *Q. castaneifolia*, *Quercus brantii* Lindl., *Quercus libani* Oliv.). Today, Turkey oak is the most widespread and ecologically diverse taxon in the western Eurasian part of the section.

Based on chloroplast and nuclear ribosomal 5S-IGS sequences, Turkey oak shows higher diversity compared to the other taxa of the section (Bagnoli *et al.* 2016, Simeone *et al.* 2018). This is also reflected in high phenotypic variability (discussed below), contributing this species to filling countless ecological niches across its vast range. Like the other sections of the two subgenera, there is also interspecific gene flow among the members of section *Cerris*. Molecular studies suggest the interfertility in the wild of *Quercus trojana* and *Q. libani*, *Q. brantii* and *Q. macrolepis*, *Q. cerris* and *Q. suber*, *Q. trojana* and *Q. suber* (Bellarosa *et al.* 2005, Conte *et al.* 2007, Spada *et al.* 2009, Cristofolini *et al.* 2017, Simeone *et al.* 2018).

According to Kasaplıgil (1981) and Özer (2014), in Turkey, *Q. cerris* hybridizes with *Quercus infectoria* Oliv. (northern provinces), *Q. pubescens* (Konya), *Q. libani* (Kahramanmaraş), *Quercus aegilops* L. (northwest), *Q. trojana*, *Q. brantii*, and *Quercus ithaburensis*.

In addition, *Q. crenata* is a putative hybrid species of *Q. cerris* and *Q. suber*. Its hybrid nature has long been controversial. Although Conte *et al.* (2007) provided molecular evidence for the hybrid origin of *Q. crenata*, in the most recent study, Simeone *et al.* (2018) found no clear evidence for this and also Denk *et al.* (2023) considered *Q. crenata* as a separate species.

Table 1. Members of the section *Cerris* according to Denk *et al.* (2023).

Species	Distribution
<i>Quercus acutissima</i> Carruth.	East and Southeast Asia
<i>Quercus chenii</i> Nakai	East Asia
<i>Quercus variabilis</i> Blume	East and Southeast Asia, Japan
<i>Quercus crenata</i> Lam.	Endemic, Italian Peninsula
<i>Quercus suber</i> L.	Central and West Mediterranean
<i>Quercus brantii</i> Lindl.	South and Southeast Anatolia to Iran, Lebanon
<i>Quercus ithaburensis</i> Decne.	East Mediterranean, Southeast Italy to Palestine
<i>Quercus macrolepis</i> Kotschy	Southeast Italy and Balkans, Eastern Mediterranean
<i>Quercus afares</i> Pomel	Endemic, Algerian and Tunisian Tell Atlas
<i>Quercus libani</i> Oliv.	Southeast Anatolia to Iran
<i>Quercus trojana</i> Webb	Anatolia, Aegean to Southeast Italy
<i>Quercus euboica</i> Papaioannou	Endemic, Greece (Euboea)
<i>Quercus castaneifolia</i> C.A. Mey	Endemic, Hyrcania region, Azerbaijan to Iran
<i>Quercus look</i> Kotschy	Endemic, Lebanon to Anti-Lebanon Mountain Range
<i>Quercus cerris</i> L.	East and Central Mediterranean, Balkans



Figure 3. Fossil leaf attributed to *Quercus cerris* L. from Tortonien (Late Miocene) of Montagne d'Andance, France (Museum national d'Histoire naturelle).

At the inter-sectional level, there is evidence of bidirectional gene flow between the *Cerris* and *Ilex* sections. *Q. suber* and *Q. ilex* are proven to hybridize in nature (Burgarella *et al.* 2009, Lopez De Heredia *et al.* 2018). In addition, the identical plastid haplotypes of section *Cerris* and section *Ilex* indicate a deep contact between the two lineages (Simeone *et al.* 2016, 2018).

Fossil data help resolve phylogeny and infer biogeography

The first fossil record of the genus *Quercus* dates back to the Early Paleogene. Fossil *Quercoidites* pollen from the Late Paleocene of St. Pankraz (Austria)—ca. 55 Ma—is probably the earliest evidence of the occurrence of the genus *Quercus* (Hofmann *et al.* 2011). During subsequent epochs, the high number of fossil remains reflects the wide distribution and ecological significance of oaks across the Northern Hemisphere. Although leaves (Fig. 3) and pollen constitute most fossil remains, wood, flower, and acorn remains are also available. For a detailed review, see Barrón *et al.* (2017).

Although in earlier findings reliable and larger amounts of fossil evidence related to section *Cerris* began to appear only from the Oligocene, more recently, reliable fossil pollen confirms the existence of the section *Cerris* already from the Early Eocene of the Russian Far East (Denk et al. 2023). In recent times, in light of the new fossil and molecular evidence, the view on the geographic origin and the divergence time of the section has changed. Earlier studies (Denk and Grimm 2009, 2010, Hubert et al. 2014, Simeone et al. 2016, 2018) based on molecular and fossil pollen characteristics suggested that section *Cerris* established at the latest from the other two sections of the subgenus, by budding from section *Ilex*. Although previous studies dated the formation of the section *Cerris* to the Early Miocene (e.g. Denk and Grimm 2010, Hubert et al. 2014, Simeone et al. 2016), more recent results suggested a divergence already in the Oligocene (e.g. Simeone et al. 2018). A study on the genomic landscape of the global oak phylogeny (Hipp et al. 2020) suggested an even earlier, mid-Eocene—Early Oligocene divergence of the section *Cerris* (depending on whether it used crown or stem fossil calibration). Currently, according to the most recent phylogenetic study on the section *Cerris* (Denk et al. 2023), this section appears to be a contemporary and sister to section *Ilex* and the divergence of the two sections may have occurred during the Early Eocene. Thus, the initial Early Miocene scenario gradually transformed into an Early Eocene divergence time around 20 million years earlier.

In contrast to the other two sections of the subgenus (*Ilex* and *Cyclobalanopsis*), the most species-rich part of the distribution of the section *Cerris* now is in the Euro-Mediterranean region, not in Asia. This geographic dislocation of the species richness may support suggestions from previous studies that the section *Cerris* had been established in Europe, not in Asia. Earlier palaeobotanical studies also suggested that the section *Cerris* diversified in Europe during the Neogene, and this process resulted in several toothed or lobed leaf species (Knobloch and Velitzelos 1986, Shtefyrtsa 1990, Striegler 1992). According to Teodoridis and Kvaček (2006), Mai (2007), and Roiron (1992), members of the *Cerris* group with toothed leaves [e.g. *Quercus kubinyi* (Kováts ex Ettingsh.) Czeczott] inhabited the European region from the Early Miocene (Burdigalian, from 20.43 Ma) to the Late Pliocene (Piazencian, to 2.58 Ma). During this period, species of section *Cerris* were important elements of the Neogene European flora (Barrón et al. 2017).

However, if we assume that section *Cerris* originated during the Oligocene or the Eocene (as suggested by recent studies, e.g. Simeone et al. 2018, Hipp et al. 2020, Denk et al. 2023), then the European occurrence of the section and its divergence time are not consistent. Moreover, new fossil evidence confirms the occurrence of the section *Cerris* from the Eocene of the South of Primorskii Region, Russian Far East, which is well before the European occurrence in the Miocene (Pavlyutkin 2015, Naryshkina and Evstigneeva 2020, Denk et al. 2023). In addition, the common plastid haplotype of the western Eurasian species of the section *Cerris* and the Japanese species of the section *Ilex*, *Q. phillyreoides* also points to a northeast Asian origin of the section *Cerris* (Simeone et al. 2018).

In light of the new results (Denk et al. 2023), a new scenario may be set up, according to which the section *Cerris* diverged in Northeast Asia during the Early Eocene, from where it radiated towards Europe through a northern temperate climate migration route behind of the uplifting Qinghai–Tibet Plateau. After that, the distribution range split into a European and an Asian range, and the northeastern side of the section may have eroded e.g. as a result of geological and climatic changes.

Regarding the fossil occurrence of Turkey oak, fossil leaves and Turkey oak-like megafossils have been reported from the

Miocene and Pliocene (Dyjor et al. 1992, Bozukov and Tsenov 2012, Tanrattana et al. 2020), but reliable fossil evidence (leaves and pollen) assigned to Turkey oak appears only from the Early and Middle Pleistocene deposits (Martinetto and Sami 2001, Ollivier et al. 2010, Fletcher et al. 2013, Martinetto et al. 2014, Panagiotopoulos et al. 2014, Tonkov et al. 2014, Denk et al. 2021, Denk et al. 2022).

In the European Fossil Pollen Data Base, pollen records are available at 11 locations across Turkey oak's distribution range. Based on these records, the dynamics of the species' occurrence can be traced back to more than 12 000 years. For instance, according to the three Hungarian records [Neotoma Dataset 4486 (DOI: 10.21233/k0tg-pb80), 4487 (DOI: 10.21233/wn8a-n079), 4488 (DOI: 10.21233/vr8r-d168) (Nagy-Bodor et al. 1995)], the species occurs in the south-western region of the Carpathian Basin from around 3000–5000 years BP, about 8000–11 000 years after the appearance of local white oaks (*Q. robur* and *Q. petraea*). Thus, the northward recolonization of the Turkey oak after the Last Glacial Maximum (LGM) is delayed compared to the most widespread native white oaks in this region. This delay may indicate a higher temperature requirement for Turkey oak than local white oaks.

Phenotypic variability, forming phenotypic groups

Oaks generally display great phenotypic variability and this ability of phenotypic response to changing environments may be a fundamental key to its evolutionary success (Kremer and Hipp 2020). This is particularly true for Turkey oak.

One reason for the morphological plasticity of the oaks is the incomplete lineage sorting and consequently the ability of extensive gene flow (hybridization and introgression) between distinct species within sections (Kremer and Hipp 2020) and, more rarely, between members of different sections (Burgarella et al. 2009, Lopez De Heredia et al. 2018). Gene flow can also exchange adaptive alleles between different species (Kremer and Hipp 2020). In this way, oaks can even jump across adaptation stepping stones. The vast phenotypic variability—particularly in leaf morphology—sometimes makes it difficult to find stable diagnostic characters between species or even sections, let alone intraspecific units. According to Denk and Grimm (2009), pollen ornamentation is the most valuable attribute to the unequivocal separation of the members of the major infrageneric groups.

Currently, based on the Plants of the World Online database (accessed 26 October 2023), Turkey oak has no accepted intraspecific units, but its 80 homotypic and heterotypic synonyms may reflect the enormous phenotypic plasticity of the species. In Hungary, Mátyás (1970) assessed and described the phenotypic variability of Turkey oak based on more than a thousand herbarium specimens. The study described two varieties, var. *austriaca* and var. *cerris*, respectively. Within-variety units were organized into seven subvarieties. In addition, a total of 15 forms, 11 subforms, and 8 intermediate subforms were distinguished between the forms (Table 2).

In Serbia, Janković (1956) and Erdeši and Gajić (1977) dealt with the phenotypic variability of Turkey oak in detail, in the region of the Fruška Gora. Janković (1956) proposed the scientific question, which is still relevant today, what is the true taxonomic and ecological significance of leaf forms? He also noted that the use of leaf morphological traits to describe intraspecific groups can be controversial since it is not rare that all leaf variants occurring in a population can be found within a single tree as well. Finally, based on leaf morphology, Janković (1956) was able to divide Turkey oak individuals into a morphologically more consistent (with elongated leaf shapes and shallow lobes) and a

Table 2. Phenotypic classification of Turkey oak in Hungary according to Mátyás (1970).

var. <i>austriaca</i>	Formae transitoriae	var. <i>cerris</i>
subvar. <i>Castaniformae</i>		subvar. <i>pinnatae</i>
f. <i>Verae-Csapody</i>		f. <i>cerris</i>
f. <i>sinuato-lobata</i>		sf. <i>rotundilobata</i>
	sf. <i>mucronata</i>	sf. <i>basicordata</i>
subvar. <i>dentatilobatae</i>		sf. <i>acutiloba</i>
f. <i>dentatiloba</i>		sf. <i>mucronato-pinnata</i>
	sf. <i>acutilobata</i>	f. <i>bipinnata</i>
subvar. <i>austriacae</i>		sf. <i>subbipinnato-lobata</i>
f. <i>austriaca</i>		sf. <i>acuto-bipinnata</i>
	sf. <i>sublobata</i>	sf. <i>mucronato-bipinnata</i>
	sf. <i>acuto-mucronata</i>	subvar. <i>laciniatae</i>
f. <i>lancifolia</i>		f. <i>laciniata</i>
	sf. <i>rotundato-lobata</i>	sf. <i>lobato-laciniata</i>
	sf. <i>rinnatolobata</i>	f. <i>laciniato-lyrata</i>
	sf. <i>acuto-dentata</i>	sf. <i>rotundato-laciniata</i>
	sf. <i>submucronata</i>	sf. <i>acuto-laciniata</i>
subvar. <i>cyclolobatae</i>		sf. <i>dentato-laciniata</i>
f. <i>cycloloba</i>		
f. <i>Balátae</i>		subvar. <i>roburiformae</i>
f. <i>basi-cuneata</i>		f. <i>leviterlobata</i>
f. <i>macrophylla</i>		f. <i>roburolobata</i>

more variable (with variable leaf shapes and deeper lobes) group, group *typica* and group *pseudocerris*, respectively. Later, Erdeši and Gajić (1977) following the system of Mátyás (1970) described five new leaf forms from this area.

Despite the phenotypic groups are seeming well-defined, distinguishing these groups on the genetic basis is not a simple task. For instance, Özer (2014) failed to identify any distinctive difference based on 12 nuclear simple sequence repeat (SSR) markers between the two varieties, var. *austriaca* and var. *cerris*. Nevertheless, by using genome-wide methods, the analysis of thousands of polymorphisms throughout the genome may be effective in detecting genetic attributes behind phenotypic groups. In addition, to answer Janković's first question on the role of leaf shape in the species' taxonomy and ecology, it should also be tested whether the leaf types recognized by Mátyás (1970) can be correlated to particular environmental conditions. In other words, whether the different morphological groups could serve as indicators of Turkey oak's ecotypic variability.

Legacy of postglacial migrations in the genetic structure of modern Turkey oak populations

On a smaller temporal and spatial scale, the glacial periods of the Pleistocene also had a major impact on the section *Cerris*. Oaks in Europe survived the glacial periods in southern refugia, from where they migrated north and west during the favourable climatic conditions of the interglacials (Kremer 2010, 2016). The repeated phases of area disruption and expansion probably did not lead to macroevolutionary processes (e.g. speciation), since the Eurasian species mostly predate the Pleistocene (Kremer and Hipp 2020, Denk et al. 2023). However, the extinction and re-expansion processes contributed to oaks becoming the dominant species on the continent (Kremer and Hipp 2020).

Towards the end of the LGM, the distribution of oak forests in Europe was restricted to the Iberian, Italian, and Balkan peninsulas and Asia Minor (Near East) (Bennett et al. 1991, Petit et al. 2002). The northward migration of white oaks from these refugia started after the LGM and reached their current distribution by only 7000–6000 BP (Kremer 2016, Simeone et al. 2019). To explain the relatively fast rate of migration (500–1000 m per year) calculated on the basis of previous scenarios, the 'northern refugia' hypothesis suggests that oaks should have had a larger distribution northward towards the end of the LGM and that the rapid migration could have occurred simultaneously from the southern and northern populations (Brewer et al. 2002, Brewer et al. 2005, Svenning et al. 2008, Kremer 2016). Nevertheless, according to the new results on the population structure of Turkey oak (Bagnoli et al. 2016), this species may be an exception without northern refugia.

In the most detailed study on the phylogeography of Turkey oak, Bagnoli et al. (2016) studied the genetic diversity distribution and the genetic structure of modern Turkey oak populations with an extensive sampling of 192 populations covering almost the entire distribution range of the species. Based on six chloroplast SSR markers, they found 35 differing haplotypes, which, according to the Bayesian Analysis of Population Structure (BAPS), were clustered into three large genetically and geographically distinct groups, corresponding to the Italian and Balkan peninsulas and Asia Minor. In addition, a possible bottleneck effect was also suggested that would have finally caused the split between the eastern (Asia Minor) and central (Balkan) populations during the Early Pleistocene based on BAPS and fossil data. The split between the Italian and Balkan groups was assumed to have occurred later during the Middle Pleistocene, due to a marked population contraction caused by a glaciation phase. The number of detected haplotype variants shows a southward and eastward increasing variability gradient. Özer (2014) also observed this gradient for Turkish populations. Interestingly, according to the results of Bagnoli et al. (2016), almost all the sampled populations of the Carpathian Basin carry the same haplotype (QC10). This may indicate that Turkey oak completely disappeared from this region during the Pleistocene glacial periods and later migrated north almost exclusively from the direction of the Italian refuge. Another possible explanation for this phenomenon may be that Turkey oak maintained separate refugia in this region, in which the same ancestral haplotype was preserved. However, fossil pollen records from Lake Balaton confirm the presence of the species in this region only for 3000–5000 years BP [Neotoma Dataset 4486 (DOI: 10.21233/k0tg-pb80)], which is much later than the end of the LGM. The QC28 haplotypes on the eastern side of the Carpathian Basin (Fig. 4) suggest that a northward migration path of Balkan populations along the foothills of the eastern Carpathians could also have occurred, bypassing the Hungarian Great Plain. These routes fit with the postglacial movements of white oaks in this region [see Fig. 3. in Petit et al. (2002)].

Most recently, Bertolasi et al. (2023) provided the first fine-scale information from Italian Turkey oak populations. Based on eight nuclear microsatellite markers, they suggest four putative source gene pools and a rough subdivision of populations according to their geographical location.

As for the existing allelic diversity, we have only limited information so far. Limited in respect of the amount of data available and the represented area from the distribution range. At the moment, there are only a few studies in which results are available related to diversity at the population level. In addition,

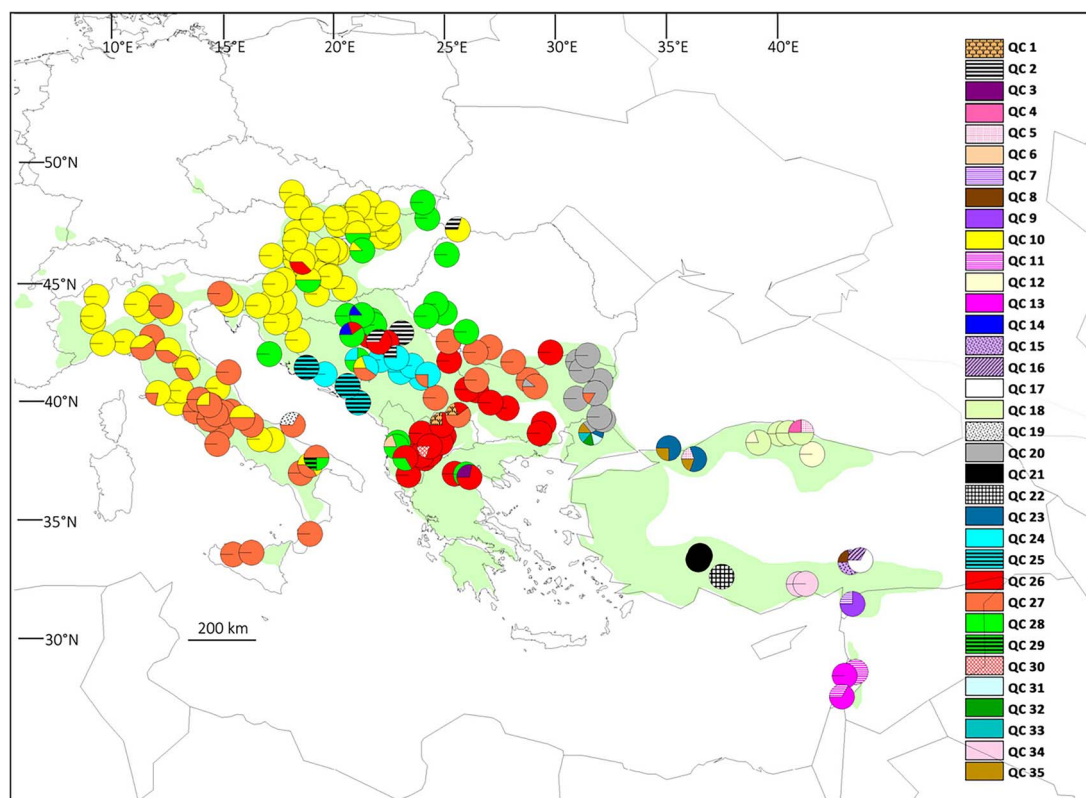


Figure 4. The chloroplast haplotype distribution of Turkey oak (the distribution range of Turkey oak in light green). From: “Combining molecular and fossil data to infer demographic history of *Quercus cerris*: Insights on European eastern glacial refugia.” By Bagnoli et al., 2016, *Journal of Biogeography* 43: 679–690. © 2015 John Wiley & Sons Ltd.

it is also hard to make comparisons with them because of the differing genetic markers and sample sizes used. Nevertheless, the above-mentioned study of Bertolasi et al. (2023) in Italy and the thesis of Özer (2014) in Turkey investigated, among others, the allelic diversity within and among populations.

In Italy, Bertolasi et al. (2023) found a relatively high diversity of nuclear SSR loci. In this study, they identified a total of 265 allele variants at eight loci in 809 sampled Turkey oak individuals. This corresponds to an average of 35 alleles/locus and the values of alleles/locus/population seem almost constant among populations (10–14 alleles/locus/population). As for the measure of genetic diversity, they found relatively high values, the computed average expected heterozygosity values ranged between 0.65 and 0.81 by populations.

In Turkey, Özer (2014) investigated a total of 172 Turkey oak individuals from 13 populations. In this thesis, 12 nuclear SSR markers were used for population genetic analyses. For allelic diversity, the average of alleles/locus was 12.58 and the mean number of alleles/population ranged between 2.75 (± 0.08 standard deviation) and 6.33 (± 0.21 standard deviation). As for the genetic diversity, the value of the expected heterozygosity ranged between 0.38 (± 0.03 standard deviation) and 0.73 (± 0.02 standard deviation). According to the values of the F_{st} statistics, 26% of genetic variation was between ($F_{st} = 0.26$) and 74% within populations.

Concerning the above results, Turkey oak populations in the study regions have relatively high genetic diversity on the investigated loci. However, these findings of course may not be relevant in each part of the distribution range. One reason for this is that each study investigated populations in the central areas of the

main refugia, where genetic diversity may have remained higher than in the northern part of the range.

Ecological properties

According to Mátyás (1970), Turkey oak is a colline-prealpine species of south-eastern Europe and Asia Minor. It is a warmth- and light-demanding, mesophilic-subcontinental tree species, reaching its climatic optimum in the Mediterranean region, in the transition zone between evergreen and deciduous forests (Bellarosa et al. 2003, Simeone et al. 2019). The scattered foliage and the lack of shade leaves indicate its pronounced light demand. Turkey oak is relatively tolerant to temperature extremes and drought (Bellarosa et al. 2003). According to Majer (1983), in the eastern part of its distribution, in Turkey, the species grows even with 350 mm annual precipitation and tolerates not only drought periods but also extremely wet conditions of pseudogley soils in the spring. Contrarily, Simeone et al. (2019) describe Turkey oak as water-demanding and only moderately resistant to temperature extremes and claim its competitive ability decreases significantly under xeric conditions.

Turkey oak is quite tolerant to different physical and chemical soil properties and occurs on several soil types (Keresztesi 1967, Simeone et al. 2019). In the southern regions of its range (possibly due to the competitive pressure of more extreme tolerating species), Turkey oak avoids calcareous soils and mainly occupies silicate and volcanic soils (except in Central and Northern Turkey, Menitsky 2005). In contrast, in the northern part of its distribution, Turkey oak occurs in a variety of soils, including calcareous soils; soils formed from limestone, loess, dolomite, andesite, Pannonian

clay, shale, Pleistocene gravel, and even river sediments. In terms of soil hydrology, Turkey oak also has a wide ecological spectrum, occurring both on dry and wet soils. The restriction to extreme sites is partly the consequence of the strong competition of shade-tolerant species in better conditions (Keresztesi 1967).

Natural stands of Turkey oak are generally mixed with other oak species depending on the site conditions. In Hungary, Turkey oak usually coexists with Daléchamp's oak (*Quercus dalechampii* Ten.) (member of the complex *Q. petraea* sensu lato), with pubescent oak (*Q. pubescens*) on dry sites, and with pedunculate oak (*Q. robur*) on gravel sediments of West Hungary (Keresztesi 1967). In northwestern and northern Turkey, Turkey oak is a component of the oak-hornbeam lowland forests of *Q. cerris*, *Quercus frainetto* Ten., *Quercus hartwissiana* Steven, and *Carpinus betulus* L. In addition, Turkey oak forms mixed stands with several species in the eastern Mediterranean region, including conifers such as *Abies cilicica* (Antoine and Kotschy) Carrière or *Pinus nigra* Aiton in Inner Anatolia. The characteristic species of these stands are also *Q. libani*, *Acer monspessulanum* L., *Castanea sativa* Mill., *Fraxinus ornus* L., and *Ostrya carpinifolia* Scop. (Menitsky 2005). In southern Europe, Turkey oak forms mixed stands with cork oak (*Q. suber*). Additionally, *Q. crenata*, the formerly presumed hybrid of the latter two species, also occurs in this region (Italy, southern France, Slovenia, and Croatia) (Simeone et al. 2019). In the westernmost part of its distribution, Turkey oak occurs in pure stands or mixed with *Q. petraea*, *Q. robur*, *Q. pubescens*, *Q. frainetto*, and *Q. suber*, depending on site conditions. Due to the loose canopy, the above-mentioned stands are generally characterized by a dense, species-rich shrub layer as well (Keresztesi 1967).

Mert et al. (2016) found that the most deterministic bioclimatic factors for Turkey oak's occurrence in Sütçüler District (Turkey) are the mean annual precipitation and the minimum temperature of the coldest month. Inside the Carpathian Basin in Hungary, the occurrence of the species is connected to temperature conditions only. The species here is absent from sites where the mean annual temperature falls below 8 and 8.5°C, and the mean temperature of the vegetation period is below 15.5°C. Topographic and other climatic factors (e.g. higher humidity) may also modify the latter threshold (Keresztesi 1967).

Compared to other local oak species (e.g. *Q. petraea* s.l., *Q. robur*), Turkey oak is generally considered to be a drought-tolerant species (Keresztesi 1967, Majer 1983, Mórícz et al. 2013, Simeone et al. 2019, Kostić et al. 2022). Based on the association of dendrochronological and climatic data, Mórícz et al. (2021) compared the response to drought periods of Turkey oak and sessile oak (*Q. petraea*) along a precipitation gradient in southwestern Hungary. According to their results, Turkey oak and sessile oak have different responses to drought periods. Sessile oak responded to the increasing drought stress with a slight growth reduction, while Turkey oak responded with a significant growth reduction. In addition, the recovery of Turkey oak after the drought periods was faster than that of sessile oak. Therefore, Turkey oak could cope with drought periods in Hungary better than sessile oak, which may provide competitive advantages for Turkey oak under projected climate change. In the future, this resistance of Turkey oak to drought may increase its importance in forestry (Mórícz et al. 2013).

Recently, Mészáros et al. (2022) also showed in a low-altitude xeric site that Turkey oak had better long-term radial growth, growth recovery, and resilience after severe drought events than the coexisting sessile oak. In addition, earlier works suggest that the different responses to drought by these two species could be

explained by different water use strategies (Tognetti et al. 1996, Mészáros 2011).

Kostić et al. (2022), analysing tree-ring width, stable carbon isotope ratio, and intrinsic water use efficiency, found that Turkey oak is more drought-tolerant and more sensitive to climate variations in terms of tree ring width and stable carbon isotope ratio compared to pedunculate oak (*Q. robur*) in northwestern Serbia. In Italy, a study based on a comparative study of leaf traits and tree rings (Tognetti et al. 2007) suggested that Turkey oak has a different water use and carbon assimilation strategy compared to *Q. pubescens*. Although both species are drought-tolerant, pubescent oak had more competitive advantages on xeric ridges due to easier access to soil water (may be due to different rooting) and the more conservative use of it (Tognetti et al. 2007).

Current distribution and projections for the future range

Today, Turkey oak is an eastern Mediterranean-Pontic species distributed from south-eastern France across the Italian and Balkan peninsulas to Anatolia and extending south to Lebanon and Israel. The westernmost occurrence of the species is in France, where it is only found in the Var and Alpes-Maritimes départements (based on the distribution map of Silene Nature data base; <https://nature.silene.eu/espece/116670>). In the northernmost part of its range, Turkey oak penetrates deeply into the Pannonian floristic province throughout the Carpathian Basin (Gencsi and Vancsura 1992). The line of Myjava—Trenčín—Prievidza—Kremnica—Zvolen—Tisovec—Dobšiná—Rožňava—Hidasnémeti—Sátoraljaújhely—Sighetu-Marmăției represents the northern limit of the distribution (Fekete and Blattny 1913, Mauri et al. 2017). Turkey oak is therefore not only the most northerly species in section *Cerris* but also the entire subgenus [based on the distribution maps of Menitsky (1984), Schirone et al. (2015) and Caudullo et al. (2021)] (see Fig. 2).

The centre of the distribution of Turkey oak is in the Balkan Peninsula and the species is most abundant in Italy and the Balkan Peninsula. Turkey oak prefers mainly mountainous or hilly areas and generally avoids lowland locations. Its vertical distribution ranges from near sea level (e.g. in Italy) up to 2200 m above sea level (e.g. in the Nur (Amanus) Mountains, Turkey). In the southern and southeastern regions, the species has a montane character. In the Lebanese mountains, for example, Turkey oak stands occur between 1300 and 2200 m above sea level and generally between 500 and 2200 m a.s.l. in the eastern Mediterranean region (Bellarosa et al. 2003, Menitsky 2005). However, in the northern part of its range, Turkey oak is absent above 1000 m a.s.l. (Fekete and Blattny 1913, Bölöni et al. 2011).

Turkey oak has a large distribution range and a significant proportion of the forested area compared to the other European members of the section *Cerris*. The species covers 280 000 ha in Italy (Bellarosa et al. 2003), 205 000 ha in Slovenia (Komjanac 2005), 216 000 ha in Hungary (Nemzeti Földügyi Központ 2022), 50 000 ha in Slovakia (Barka et al. 2018), 261 000 ha in Romania (Marin et al. 2019), 270 000 ha in Serbia (Banković and Nenad 2009), 35 900 ha in Montenegro (Dees et al. 2013), 133 000 ha in Albania (Stafasani and Toromani 2015), and 350 000 ha in Bulgaria (Stoeva et al. 2018).

In view of projected climate change including more frequent drought periods, thermophilous and xerophilous species are likely to become more abundant and extend their range. Turkey oak may be one of these species. In response to climate change, Turkey oak is expected to shift its distribution. This range shift

is expected to include the northward expansion of its current distribution (Hlásny et al. 2014, Illés and Mórićz 2022). In addition, Turkey oak may also extend its distribution regionally (e.g. in Italy) by colonizing sites at higher altitudes that are no longer suitable for mesophilic species (Attorre et al. 2008). In Hungary, for example, it is predicted that Turkey oak will almost completely maintain its current distribution, with an additional expansion into sessile oak habitats during this century (Führer et al. 2011, Mórićz et al. 2013). According to the results of Thurm et al. (2018), it is suggested that Turkey oak could increase its area in Europe by 5%–44% by 2070 (depending on whether the RCP 4.5 or RCP 8.5 global emission scenario was used for estimation). Similarly, based on the climate envelope analysis of Illés and Mórićz (2022), the suitable habitats for the species may increase by more than 40% in Europe by 2100. However, in parallel, other sympatric oak species (with more xerophilous characteristics) could also benefit from climate change. Hence, these species are expected to become competitors of Turkey oak. Such species could be the pubescent oak (*Q. pubescens*), the holly oak (*Q. ilex*), and the cork oak (*Q. suber*) in central and southern Europe. According to Attorre et al. (2008), Illés and Mórićz (2022), and Thurm et al. (2018), these oak species, together with other forest tree taxa (e.g. *U. laevis* Pall.), are predicted to extend their distribution in parallel with Turkey oak.

However, in addition to the northward expansion, the southernmost populations of European tree species may be threatened with extinction due to increased temperatures and prolonged dry periods. In the case of Turkey oak, a significant habitat loss is expected in Sütçüler District, Turkey, in the southern region of the species distribution (Mert et al. 2016). During contractions, the fragmentation of populations could lead to less efficient gene flow and finally, the reduction of local diversity, which would be the basis of its adaptability. Therefore, it is important to develop strategies for the conservation of local genetic diversity to ensure *in situ* adaptation. To this end, assessing Turkey oak gene pools and population structure (by studying its phylogeny, phylogeography, intra- and interspecific gene flow, etc.) would be of great importance.

Moreover, the projected area 'expansion' mentioned above does not automatically imply that Turkey oak will be able to reach the new suitable habitats by natural migration. If we take into account the migration speed of oaks (500–1000 m per year), Turkey oak populations can only move 100 km within the next 100 years. However, this assumption is rather unlikely due to natural and artificial barriers and human disturbance. Furthermore, according to the prediction of Thurm et al. (2018), the centroid of Turkey oak's distribution area should shift about 445–667 km northwards by 2070 (based on RCP 4.5 or RCP 8.5). Nevertheless, human-assisted movements of natural populations (e.g. by forestry reproductive material transfers) could accelerate this process in the future. In some cases, it does not necessarily mean the need for long-distance movements of selected populations. For example, a recent study (Karrer et al. 2022) found that there are provenances of Turkey oak within Austria's borders considered drought-tolerant among the existing populations.

Conclusions

This review aimed to synthesize findings from different scientific disciplines to provide a deeper insight into the extent of knowledge on Turkey oak. This species may be a potential candidate for assisted migration efforts in the near future due to its drought-tolerating characteristics. Therefore, revealing its genetic structure throughout its range is a key issue. In addition, a thorough

assessment of its present ecological amplitude may help to select populations that are best suited for assisted migration under climate warming.

According to the reviewed material, Turkey oak is the only species in the subgenus *Cerris*, which penetrates deeply into the temperate zone. Nevertheless, this species still has a mainly southeast European-Pontic distribution. In the native range, Turkey oak often co-occurs with several important species of the section *Quercus* (e.g. *Q. petraea*, *Q. frainetto*). However, due to their different geographical origins and the different evolutionary pathways that formed modern species, Turkey oak may exhibit adaptation strategies that are absent in the species of the section *Quercus*. The reviewed dendrochronological studies indicate such differing strategies (e.g. in water use or recovery after a drought period).

Based on the available information, Turkey oak has high genotypic and phenotypic variability throughout its range. Consequently, this high level of variability may make this species more plastic to environmental changes such as recent climate change and may be the key to its long-term adaptability. Promisingly, projections based on future climate scenarios suggest that Turkey oak could be a winner of climate change in Central and Western Europe, where a significant expansion of suitable habitats is expected.

On the other hand, the pace of environmental change makes it unlikely that natural populations will be able to keep up. Therefore, human-assisted movement of selected populations (assisted migration) would be an effective way to speed up natural migration. However, to select the appropriate populations for assisted migration, more information would be needed on the genetic constitution of the species and the genetic background of its adaptation to environmental conditions. To obtain such information, detailed genetic studies on adaptation and traditional provenance trials for Turkey oak would be needed in the future. In addition to these, it would also be important to take into account competition from other (oak) species when predicting future distribution and abundance. Species such as *Q. pubescens* could exert significant competitive pressure on Turkey oak.

Furthermore, it should also be noted that despite the increase in distribution in the northern part of the range, southern populations may be threatened with extinction. Population fragmentation could limit the efficiency of gene flow. As a result, locally adapted populations could lose the genetic diversity that is the basis of their adaptability. Therefore, further studies on local genetic diversity and ecological properties of populations are important to develop strategies to conserve local genetic diversity.

During the literature review, we found several local studies related to the ecology and phenotypic variability of Turkey oak (and also many other oak species). These are often difficult to access and written in local languages. However, these local studies usually provide very detailed and unique observations of the local phenotypic characteristics, ecology, distribution, etc. These may contain key information for a deeper understanding of the species. Further research would therefore be needed in the future to identify these studies and make them available to a wider international research community.

From a forest management perspective, the mentioned high-level variability of Turkey oak is interesting since it allows the species to adapt to a wide range of ecological conditions due to its drought-tolerant nature and unique drought adaptation strategy that sets it apart from local white oaks. These properties make it a valuable species for forestry in Central and Western Europe. Although only a relatively small number of scientific

results are available for Turkey oak so far, some of them could already be implemented in forestry practice. For example, the geographic distribution of Turkey oak's chloroplast haplotypes may enable more objective identification of the origin of forestry reproductive materials in the future. In addition, the strong genetic structures of Turkey oak populations throughout its distribution range may project potential risks associated with long-distance reproductive material movements (Hewitt et al. 2011, Williams and Dumroese 2013). Namely, although imported reproductive materials can increase local genetic diversity and enhance adaptability, these can simultaneously blur differences between natural genetic groups through introgression over the long term. Consequently, it is crucial to carefully manage future assisted migration initiatives, ensuring the preservation of local diversity. Additionally, addressing the current research gaps is equally essential. For example, the use of genome-wide technologies in studying the genetic basis of adaptation could enable a more precise assessment of the adaptability of natural populations. Furthermore, selecting reproductive materials based on knowledge of genetic traits that promote drought resilience (such as 'drought-tolerant alleles') may prove more effective in enhancing the resilience of forest ecosystems in the future.

Author contributions

The first draft of the paper was written by Botond B. Lados. All authors contributed critical readings and suggestions to the final version.

Supplementary data

Supplementary data are available at *Forestry* online.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that might appear to have influenced the work reported in this paper.

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Data availability

No new data were generated or analysed in support of this research.

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