



Genetic and morphological variation in taxonomically critical populations of *Quercus petraea* s.l. in Southern Europe

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Abstract

This study investigated the genetic and morphological variability of critical populations of *Quercus petraea* s.l. in southern Europe considering taxonomic and biogeographical issues. Ten EST-SSR markers were applied on sixteen populations of *Q. petraea* s.l., including *Q. petraea* subsp. *petraea*, *Q. petraea* subsp. *austrotyrrhenica*, *Q. dalechampii* auct. non Ten., and *Q. banatus*, to assess genetic variation within and among populations using specific indices. Genetic structure was analysed using Bayesian clustering. Eight populations of potentially interfertile white oaks such as *Q. pubescens* (5) and *Q. robur* (3) were included in the overall dataset (24 populations) for comparison. Multivariate analysis procedures were applied to analyse genetic relationships among populations. The morphological variability of oak individuals was assessed only on the *Q. petraea* s.l. populations based on traits observed in leaves, twigs, and acorns. The patterns of covariation between morphological traits, taxonomic identity, and the geographical distribution of sessile oak populations were also investigated. The analysis on the overall dataset revealed four main genetic clusters for *Q. petraea* s.l.: one of possible ancestral origin, one occurring mainly in the Balkans, one spread across southern Italy, and one distributed primarily in western and central Europe. From a morphometric perspective, only a few leaf morphological traits exhibited variation trends correlated with the genetic structure pattern. Considerable overlap was found among populations within the *Q. petraea* collective group from both the genetic and morphological side. The variability observed was insufficient to distinguish species other than *Q. petraea* (Matt.) Liebl. (i.e. *Q. dalechampii* auct. non Ten., *Q. banatus* Kučera). However, all *Q. petraea* s.l. populations were found to be clearly distinguishable from the *Q. robur* subsp. *robur* and *Q. pubescens* subsp. *pubescens* populations included in the dataset as outgroups.

Keywords Genetic diversity · Morphological traits · *Quercus dalechampii* · Sessile oak · Taxonomy · White oaks

Introduction

The forest heritage of central and southern Europe is largely characterised by oak woodlands belonging to various phytosociological classes, orders, and alliances (e.g. *Quercetea pubescentis*, *Quercetea ilicis*, *Quercetea robori-petraeae*, *Quercetalia calliprini*, *Quercion frainetto*, etc.) which constitute a significant portion of the syntaxonomic framework of European forests (Mucina et al. 2016). Europe is home to numerous oak species (genus *Quercus* L.), including

both evergreen and deciduous species. These are distributed within two subgenera, the subgen. *Cerris*, comprising a group of deciduous oaks from the central and eastern Mediterranean (e.g. *Q. cerris* L., *Q. ithaburensis* Decne, *Q. trojana* Webb, etc.) together with some evergreen sclerophyllous species (e.g. *Q. ilex* L., *Q. suber* L., *Q. coccifera* L.), and subgen. *Quercus*, which mainly comprises deciduous species (the so-called “white oaks”) (Denk et al. 2017). In Europe, the subgen. *Quercus* is the most species-rich and has the widest geographical distribution. However,

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taxonomists still disagree on the exact number of taxa that should be included in the European white oak group at the species level. This is primarily due to the lack of consensus on the taxonomic assessment of a significant number of “critical” taxa, most of which belong to the collective groups of *Quercus pubescens* and *Q. petraea*. Among the European white oaks, *Quercus petraea* (Matt.) Liebl (commonly known as sessile oak) together with *Q. robur* L., is the only other European oak species whose current centre of distribution is central Europe (Fig. 1) where it exhibits a wide ecological amplitude enabling it to colonize dry sandy or moraine soils as well as podsolized oligotrophic and acidic soils alongside *Q. robur*.

It can also be found on steep slopes with thin neutral arenaceous soils alongside *Q. pubescens* and *Q. cerris*, or on deep, eutrophic soils, where it plays a dominant role in various types of mesic forest (Mucina et al. 2016). In southern Europe, *Q. petraea* s.l. has a much more restricted and fragmented distribution, though it exhibits an even wider ecological amplitude. In peninsular Italy for example, *Q. petraea* gives rise to mixed communities with *Fagus sylvatica* in the montane belt or with *Quercus ilex* and *Q. suber* in

the much drier, warmer conditions of the Meso-Mediterranean bioclimate. It is also associated with all other deciduous oaks and broadleaf trees in the colline and submontane belts (Blasi et al. 2004; Di Pietro et al. 2010; Viciani et al. 2016). From a chorological perspective, *Q. petraea* s.l. is widely distributed throughout central Europe from the northern slopes of the Alps to the British Isles, southern Scandinavia and western Ukraine. In southern Europe and southwestern Asia, the species still has a wide longitudinal range (from western Spain to western Iran), although there are large gaps between populations. It occurs in the northern part of the Iberian Peninsula (Amaral Franco 1990), throughout the whole of Italian Peninsula, up to northern Sicily (Gianguzzi et al. 2016; Bartolucci et al. 2018) and in the Balkan Peninsula, up to the southern border of continental Greece (Horvat et al. 1974; Dimopoulos et al. 2013). Given the average mesophilic characteristics of *Q. petraea* at its ecological optimum, its current fragmented range in southern Europe is attributed to its poor ability to cope with the long summer droughts that are characteristic of the Mediterranean climate (Rivas-Martínez et al. 2004). However, despite being highly fragmented, *Q. petraea* populations in southern Europe



Fig. 1 Distribution range of *Quercus petraea* (after Caudullo et al. 2024 modified). Dashed area: continuous range. Dots: isolated populations

are important for reasons that extend beyond their current abundance. Until a few years ago, it was widely accepted that during the periods of glacial maximum, forest cover in central Europe was greatly reduced and replaced by periglacial steppe-like grasslands and tundra communities (Frenzel 1992; van Andel and Tzedakis 1996; Magri 2010; Tzedakis et al. 2013). Deciduous oaks and other thermophilous woody species were restricted to glacial refugia in the Iberian, Italian, and Balkan peninsulas (Bennet et al. 1991; Brewer et al. 2002; Petit et al. 2002b). At the end of each glacial cycle, these species migrated northwards again to recolonise central and northern Europe. This theory was partially questioned by Willis and van Andel (2004), who, advanced the hypothesis that, based on macrofossil charcoal wood from central and eastern Europe, restricted populations of coniferous and deciduous trees managed to survive much further north and east during the last full-glacial than previously assumed. Similar arguments are presented in a recent study by Hošek et al. (2024) who argued that temperate tree species, such as *Quercus*, *Tilia*, *Corylus*, and *Fraxinus* survived the last glacial maximum in sites north of the Alps located near geothermal springs. While the hot spring refugia theory and the persistence of cryptic refugia for boreal forest species far north during the glacial period are both plausible (see Parducci et al. 2012; Robin et al. 2016), it is also likely that genetic drift and bottlenecks have significantly impacted these surviving northern outposts of temperate forest. Phylogenetic and phylogeographic studies of plastid DNA have shown that most of the current European haplotype diversity in white oaks is concentrated in the south of the continent (Petit et al. 2002a; Semerikova et al. 2023; Di Pietro et al. 2024; Fortini et al. 2024). However, white oak populations in central Europe exhibit comparatively high diversity of haplotype lineages, which is the result of the convergence of postglacial migration routes (covered at unexpectedly high speed) and reproduction within large, continuous populations over many generations (Petit et al. 2002a, b; Kremer 2016). Therefore, the southern European sessile oak forests should be regarded as harbouring the oldest genetic heritage to survive the glaciations. This heritage has been shaped not only by paleo-ecological vicissitudes, but also by intense and millennia-long human management and exploitation, as well as the negative effects of climate change (Milad et al. 2011; Conte et al. 2019; Tóth et al. 2021). This combination of ecological and anthropogenic pressures, may have played a significant role in increasing the phenotypic variability of *Q. petraea* s.l., fuelling a heated debate on the possible presence of multiple species (e.g. *Q. aurea* Wirzb., *Q. dalechampii* auct. non Ten., *Q. polycarpa* Schur, *Q. banatus* Kučera) and subspecies in both southern and eastern Europe (Pignatti 1982; Stevanovic 2012; Kaplan et al. 2022) (Fig. 2).

While a significant body of literature exists on the genetic diversity and extent of hybridization of *Q. petraea* in central Europe (Zanetto et al. 1994; Zanetto and Kremer 1995; Cottrel et al. 2002; Neophytou et al. 2010; Dostálek et al. 2011; Lang et al. 2020), much less is known about southern Europe where information is fragmented and based on local-scale research (Bruschi et al. 2003; Antonecchia et al. 2015; Lupini et al. 2019; Popović et al. 2022). Studies examining the genetic and morphological variability of European white oak populations have also been geographically limited and offered only a partial picture of the overall variation (Viscosi et al. 2009; Antonecchia et al. 2015; Di Pietro et al. 2016; Pietro et al. 2020a, b, 2021; Semerikova et al. 2023; Neophytou et al. 2024).

This research project examines the genetic and morphological variability of certain taxonomically critical populations within the *Q. petraea* collective group that are found in southern Europe and are currently associated under a different binomial than *Quercus petraea* (Matt.) Liebl, namely *Q. dalechampii* auct. non Ten., *Q. banatus* Kučera, *Q. petraea* subsp. *austrotyrrhenica* Brullo, Guarino & Siracusa. The genetic diversity of these populations was evaluated by comparing them with populations currently classified as *Q. petraea* subsp. *petraea*, as well as with additional populations of sympatric white oaks (i.e. *Q. robur* subsp. *robur* and *Q. pubescens* subsp. *pubescens*) across central and southern Europe. This was done to verify whether pattern of genetic diversity identified in taxonomically critical *Q. petraea* s.l. populations corresponded to patterns of morphological diversity and to establish whether trends in genetic and morphological variation could provide diagnostic information from a phylogeographic and taxonomic perspective.

Materials and methods

Study area and plant material

The study was carried out across southern Europe involving eight countries (Austria, Croatia, the Czech Republic, France, Italy, Romania, Serbia, and Spain). A total of 444 individuals belonging to 24 natural populations of six white oak taxa were collected. Sixteen populations of *Quercus petraea* s.l. (including: *Q. banatus* P. Kučera, *Q. dalechampii* auct. non Ten., *Q. petraea* (Matt.) Liebl. subsp. *petraea*, and *Q. petraea* subsp. *austrotyrrhenica* Brullo, Guarino & Siracusa) were sampled in natural forest communities where these taxa were dominant in the absence of other possible taxa belonging to the *Q. petraea* collective group. Additionally, five populations of *Q. pubescens* Willd. subsp. *pubescens* and three populations of *Q. robur* L. subsp. *robur* coming from surrounding areas were included

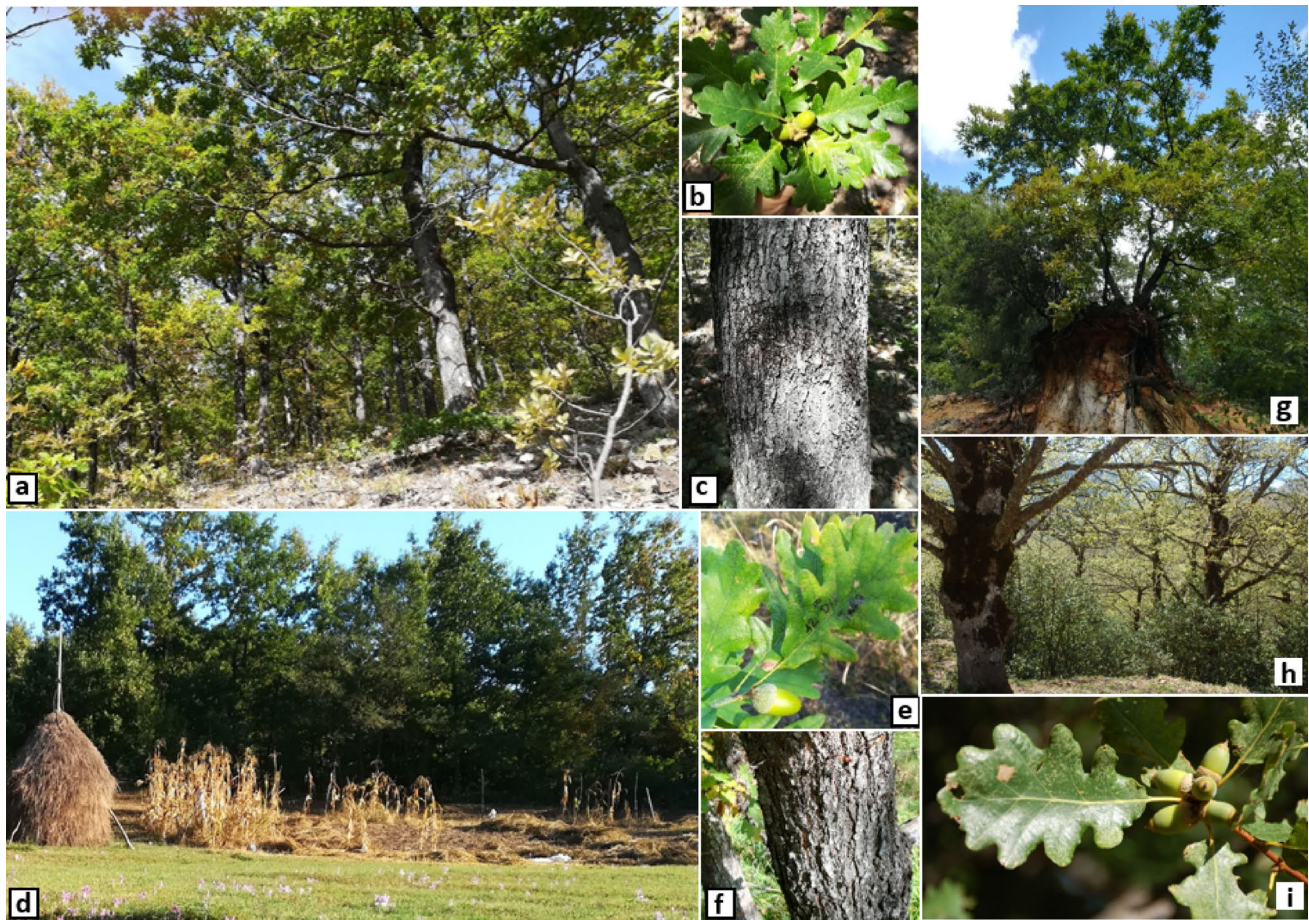


Fig. 2 Pictures **a–i** show some critical taxa within the complex of *Quercus petraea* s.l. **a–c** *Q. banatus* Kučera from Orovitza (Banat Region – Romania), **a**: Forest community on thin shallow and stony soils, **b**: leaf and fruit, **c**: bark; **d–f** *Q. dalechampii* auct. non Ten. from Mt. Tara (SW-Serbia), **d**: Forest edge at the border of a traditional mown meadow, **e**: leaf and fruit, **f**: bark; **g**: isolated individual of *Q.*

petraea on trachytic volcanic outcrops in a mixed forest with *Fagus sylvatica* at very low altitude in the Tolfa mountains – central Italy; **h**: *Q. petraea* subsp. *austrotyrrhenica* Brullo, Guarino & Siracusa with a shrubby understorey dominated by *Ilex aquifolium* in the Madonie mountains—Sicily; *Q. petraea* subsp. *austrotyrrhenica* leaf and fruit (photo: **a–g** R. Di Pietro; **h–i** L. Gianguzzi)

in the sampling design to compare and delve deeper into differences within the *Q. petraea* group. As the aim of this research was not to carry out a complete morphological-molecular revision of *Quercus petraea* in Europe, but rather to shed light on some long-debated critical taxa present within the collective group, only a relative low number of “diagnostic” populations were considered. A biogeographical/taxonomical criterion was used to select the collection sites. Specifically, *Q. banatus* and *Q. petraea* subsp. *austrotyrrhenica* specimens were collected in the *locus classicus* of these taxa, i.e. Oravița, in the Banat region of Romania (Kučera 2018) and the Madonie Mountains in Sicily (Brullo et al. 1999), respectively (Table 1).

Three out of the four Serbian collection sites (i.e. Mount Suvor, Mount Tara, and Mount Kopanik) were located on serpentine substrates and were selected as they were reported in Flora of Serbia and other scientific contributions as mainly hosting populations of *Q. dalechampii* auct. non

Ten (Cvijeticanin 1999; Stevanovic 2012). Of the two populations collected at the northern Italian site of the Euganean Hills (IT19), one was always reported by local authors as belonging to *Q. dalechampii* auct. non Ten. (provisionally as *Q. petraea* L. subsp. *polycarpa* (Schur) Soó in a recent contribution), while the other (IT20) belongs to *Q. petraea* subsp. *petraea* (see Masin and Tietto 2005; Proietti et al. 2021; Masin et al. 2025). All the other collection sites are known to host only natural populations of *Q. petraea* subsp. *petraea*. The geographic coordinates and the lithological characteristics of the collection sites are reported in Table 1 while the climatic parameters were produced in ClimateChart.net (Zepner et al. 2021) and are shown in Fig. S1.

Sampling was performed on adult trees at the end of summer when acorns were also present to maximise species identification. To avoid capturing family structures, the individuals collected were chosen to be at least 30 m apart. The oak specimens collected were identified provisionally

Table 1 Populations of *Quercus* species analysed in this study at ten nuclear microsatellite markers. The identity number (ID pop.) includes the ISO code of the country where the sample was collected. Taxa marked with an asterisk (*) are those belonging to the *Q. petraea* s.l. group. The name *Q. dalechampii* refers to *Q. dalechampii* auct. non Ten. Geographic coordinates refer to the WGS84 system

ID pop.	Country	Locality	Geology	Taxon	No. of samples	Latitude	Longitude	Altitude (m a.s.l.)
AT02	Austria	Pfaffenberg	Mesozoic dolomite	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	48.2611	16.3056	386
CZ31	The Czech Rep.	Brno-Kohoutovice	Metamorphic rocks	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	49.2842	16.7974	548
ES43	Spain	Las Machorras	Cretaceous Limestone	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	43.1189	−3.5808	823
FR08	France	Donzère Ovest Ligne L.G.V.	Mesozoic limestone	<i>Q. petraea</i> subsp. <i>petraea</i> *	10	44.4475	4.7067	96
HR06	Croatia	Mt. Psunj	Metamorphic rocks	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	45.3223	17.3459	402
IT20	Italy	Euganean Hills	Trachy-Rhyolite	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	45.3173	11.6878	441
IT46	Italy	Mt. Cimini (Vitorchiano)	Ignimbriti	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	42.4316	12.1871	737
IT47	Italy	Tolfa	Trachytes	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	42.1470	11.9407	392
RS36	Serbia	Vrdnik	Lacustrine sediments	<i>Q. petraea</i> subsp. <i>petraea</i> *	20	45.1296	19.8062	280
IT16	Italy	Pomieri, Geraci Siculo	Quartzitic sandstone	<i>Q. petraea</i> subsp. <i>austrotyrrhenica</i> *	20	37.8583	14.0581	1324
IT17	Italy	San Luca (Aspromonte)	Gneiss	<i>Q. petraea</i> subsp. <i>austrotyrrhenica</i> *	20	38.1286	15.9796	1397
RO33	Romania	Oravița	Gneiss/mudstones/marls	<i>Q. banatus</i> *	20	45.0434	21.7449	506
IT19	Italy	Euganean Hills	Trachy-Rhyolite	<i>Q. dalechampii</i> *	20	45.3431	11.7617	41
RS37	Serbia	Mt. Tara	Serpentine	<i>Q. dalechampii</i> *	10	43.9032	19.4838	1197
RS38	Serbia	Mt. Suvobor	Serpentine	<i>Q. dalechampii</i> *	20	44.1168	20.1588	740
RS67	Serbia	Mt. Kopaonik	Serpentine	<i>Q. dalechampii</i> *	14	43.2653	20.7437	1080
CZ30	The Czech Rep.	Pavlov Hills	Limestone	<i>Q. pubescens</i> subsp. <i>pubescens</i>	20	48.8477	16.6932	221
IT22	Italy	Ome	Marly-Limestone	<i>Q. pubescens</i> subsp. <i>pubescens</i>	20	45.4314	10.6282	81
IT89	Italy	Fosso Cardone/Catarozzolo	Limestone/Conglomerates	<i>Q. pubescens</i> subsp. <i>pubescens</i>	20	40.1181	16.2214	561
RS35	Serbia	Grgurevci	Serpentine	<i>Q. pubescens</i> subsp. <i>pubescens</i>	20	45.1417	19.6640	420
RS193	Serbia	Mt. Tara	Serpentine	<i>Q. pubescens</i> subsp. <i>pubescens</i>	10	43.9032	19.4838	1197
CZ32	The Czech Rep.	Lednice (distr. Břeclav)	Quatern. Alluvial deposits	<i>Q. robur</i> subsp. <i>robur</i>	20	48.7526	16.8152	188
ES41	Spain	Leioa	Quatern. Alluvial deposits	<i>Q. robur</i> subsp. <i>robur</i>	20	43.3253	−2.9708	34
IT14	Italy	Insugherata Nat. Reserve	Quatern. sands and tuffs	<i>Q. robur</i> subsp. <i>robur</i>	20	42.0073	12.3901	117

in the field, at the time of sampling, based on the information gathered from taxonomic, floristic and phytosociological scientific papers published on those areas, as well as the collectors' expert knowledge. It was ascertained a priori that only one taxon belonging to the collective group of *Q. petraea* s.l. was reported in the sites of collections in the taxonomic and phytosociological literature. A second identification stage was also carried out in the

laboratory using diagnostic keys from floras published at the European, national, and local levels (Amaral Franco 1990; Schwartz 1993; Brullo et al. 1999; Stevanović 2012; Pignatti et al. 2017–2019). However, it should be noted that all the taxa currently included in the *Q. petraea* collective group are identified based on non-univocal diagnostic morphological traits which overlap widely between different taxa.

The plant material collected from each tree (including twigs, leaves, buds, flowers, and fruits) was preserved as herbarium voucher specimens in the Herbarium Universitatis Aeserniae (IS) [Table S1; Thiers 2025 (continuously updated)]. The nomenclature of the investigated taxa follows IPNI (2025). Regarding the name *Q. dalechampii* Ten. (accepted as separate species in POWO 2025), Di Pietro et al. (2012) highlighted the confusion surrounding its application and proposed a lectotype (herbarium NAP) referring to a specimen belonging to the *Q. pubescens* collective group characterized by hairy leaves and twigs. Tenore's species was misidentified and mis-applied by most of central and eastern European botanists who identified an oak species characterized by glabrous leaves and twigs under *Q. dalechampii* Ten. This species belongs to the *Q. petraea* collective group (see discussion paragraph). Accordingly, throughout the text, we report "*Quercus dalechampii* auct. non Ten." according to the recommendation 50D.1 of the *Shenzhen Code* (Turland et al. 2018). This indicates that, in this paper, the name "*Q. dalechampii* auct. non Ten." refers to a taxon belonging to the *Q. petraea* collective group. The maps in the manuscript were created using QGIS software version 3.20 (QGIS.org 2025).

Nuclear microsatellite marker analyses

DNA extraction, amplification, and sequencing

The microsatellite [simple sequence repeat (SSR)] marker analyses were performed on the entire dataset of 24 populations. Twenty trees for each population, except for population RS193 (10 trees), FR08 (10 trees), RS37 (10 trees), and RS67 (14 trees), were investigated. Genomic DNA was extracted from dried leaves (about 20 mg per individual), with two different DNA extraction kits, the Qiagen DNeasy™ Plant Kit (Qiagen, Hilden, Germany) and the EchoLUTION Plant DNA Kit BioEcho (Cologne, Germany), following the manufacturer's instructions. The samples were genotyped at 12 Expressed Sequence Tag-Simple Sequence Repeats (EST-SSRs), which were selected based on the level of polymorphism and according to other studies on European white oaks (Lepais et al. 2009; Guichoux et al. 2011a, b; Neophytou et al. 2010; Curtu et al. 2015; Antonecchia et al. 2015; Di Pietro et al. 2021). All the microsatellite markers used were originally developed and rigorously tested on *Q. petraea* and *Q. robur* populations by Durand et al. (2010). The set of EST-SSR markers includes: PIE239, PIE227, PIE223, PIE215, PIE020, PIE152, PIE243, PIE242, PIE267, PIE102, PIE258, PIE271 (Table S2). Three different multiplex reactions were used to combine the primer pairs for nuclear EST-SSRs: Mu1 (PIE239, PIE227, PIE223, PIE215), Mu2 (PIE020, PIE152, PIE243, PIE242),

Mu3 (PIE267, PIE102, PIE258, PIE271). Uniform PCR procedures were followed for all taxa and the 12 markers. A touchdown PCR program was selected and performed in a Biometra Thermocycler TOptical Gradient 96 (Biometra, Goettingen, Germany). The PCR protocol started with denaturation at 95 °C for 15 min, followed by 10 cycles of 1 min denaturation at 94 °C, annealing at 60 °C (−1 °C per cycle) for 1 min, and extension at 72 °C for 1 min. The second step consisted of 25 cycles of 1 min denaturation at 94 °C, 1 min annealing at 50 °C and 1 min extension at 72 °C, followed by a final extension step at 72 °C for 20 min. To determine the EST-SSR sizes, capillary electrophoresis was run on an ABI3130XL genetic analyser (Applied Biosystems, USA). The GeneScan 500 ROX internal size standard was used. To analyse fragment sizes and for genotyping, GeneMapper v4.0 (Applied Biosystems) was used. Peaks automatically detected by the software were checked for consistency and, if necessary, corrected manually. Allele calling and binning, the process that converts raw allele lengths into allele classes with a size expressed by an integer (Idury and Cardon 1997), was performed by visual assignment. To rule out systematic genotyping errors, analyses were repeated for dubious results through re-extraction, re-amplification, and re-genotyping across all loci to estimate the technical error rate associated with allele scoring and binning. As two markers, PIE239 and PIE258, did not amplify properly and the binning showed a significant overlap in bin boundaries, the genetic analyses were performed on the remaining 10 microsatellite loci (Table S3).

Genetic diversity and differentiation

The number of alleles (K_L) and polymorphic information content (PIC) per locus were calculated using Cervus v. 3.0.7 (Marshall et al. 1998). The list of observed alleles and the mean number of alleles per locus were obtained with GenAlEx v. 6.5 (Peakall and Smouse 2012). Null allele occurrence was assessed using MicroChecker v. 2.3.4 (Van Oosterhout et al. 2004) and their frequencies were estimated using the expectation–maximization algorithm (Dempster et al. 1977) implemented in FREENA (Chapuis and Estoup 2006). The number of private alleles (N_p) was calculated using GenAlEx v. 6.5. Allelic richness (A_r after rarefaction to 18 allele copies), observed (H_o) and expected (H_e) heterozygosity, along with Wright's indices (Wright 1969), including the fixation index (F_{IS}) for each population and pairwise F_{ST} , were calculated using SPAGeDI v.1.5.d (Hardy and Vekemans 2002). The significance of the F-statistic was tested with 1000 permutations. Pairwise F_{ST} values between populations were estimated following Weir and Cockerham (1984) and subsequently visualized with the R package hierfstat (Goudet 2005).

Genetic structure analysis

The genetic structure of the 24 *Quercus* populations (sixteen of *Q. petraea* s.l., five of *Q. pubescens* subsp. *pubescens*, and three of *Q. robur* subsp. *robur*) was assessed using the Bayesian clustering algorithm implemented in the STRUCTURE 2.3.4 software package (Pritchard et al. 2000). Since a strong signal from *Q. pubescens* subsp. *pubescens* and *Q. robur* subsp. *robur* could obscure subtle genetic structure within the *Q. petraea* collective group, a separate STRUCTURE analysis was performed on the 16 *Q. petraea* s.l. populations to detect finer-scale differentiation and highlight possible variation in the genetic structure when this taxonomic group was analyzed in isolation from other oaks. The admixture model with correlated allele frequencies and no prior information on the geographical location of the samples or their taxonomical classification was selected. Twenty replications were run for each value of K, considering values, from K=1 to K=10, with a burn-in length of 50,000 iterations and a run length of 100,000 iterations. The optimal number of clusters (K) was determined using StructureSelector (Li and Liu 2018), following the Puechmille (2016) method, which accounts for uneven sampling. Bar plots of the STRUCTURE assignment results at the different K values were created in R (version 4.3.3; R Core Team 2025), using the tidyverse (Wickham et al. 2019) and ggplot2 (Wickham 2016) packages. The membership coefficient (Q) represents the proportion of assignment of the sample to a genetic cluster, while the qi defines the proportion of membership of a population to the cluster i. Samples with $Q \geq 0.90$ were considered pure members of a single cluster. For graphical purposes, the populations in some figures [Principal Coordinate Analysis (PCoA), Principal Component Analysis (PCA), and Discriminant Analysis of Principal Components (DAPC) related to EST-SSR data] were coloured using the results of the STRUCTURE analysis performed on the full dataset of 24 *Quercus* populations. Specifically, each population was assigned the colour of the cluster to which it showed the highest membership coefficient (considering the clusters identified at the optimal K).

Genetic relationships among taxa and populations

A rooted tree was constructed using the UPGMA method (unweighted pair group method with arithmetic mean) based on Nei's minimum genetic distance (Nei 1973), as implemented in the Populations software v. 1.2.32 (Langella 1999) to identify genetic relationships among the 24 *Quercus* populations, both from a taxonomic and geographical perspective. Bootstrapping was carried out with 1000 replicates over loci, using the grouped population option. The resulting UPGMA tree was visualized in MEGA V11.0.13

(Tamura et al. 2021). A Principal Coordinate Analysis (PCoA) was performed on pairwise genetic distances calculated as the number of allelic differences between individuals, using the diss.dist function in the R package poppr (Kamvar et al. 2014). Additionally, a Principal Component Analysis (PCA) was carried out on individual tree-level data from all the 24 *Quercus* populations and from the 16 *Q. petraea* s.l. populations. A Discriminant Analysis of Principal Components (DAPC) was also conducted on individual tree-level data from the 16 *Q. petraea* s.l. populations, serving as cross-checks for the clustering patterns. Specifically, PCA displayed the biggest total variance, while DAPC minimized the genetic variance within populations and maximised that among populations, enabling the weak population genetic structure to be graphically displayed (Jombart et al. 2010; Gioia et al. 2019; Budde et al. 2023). Both PCA and DAPC were performed using the R software with the dudi.pca function implemented in the R package ade4 (Dray and Dufour 2007) and the dapc function in the R package adegenet (Jombart and Ahmed 2011; Jombart and Collins 2015), respectively.

Morphometric analyses of leaves, twigs, and fruits

The morphological traits of the leaves, twigs, and acorns exclusively of the 16 *Quercus petraea* s.l. populations were analysed (Tables S4–S7). For the morphological leaf trait analysis, nine leaves were selected and analysed for each of the 294 trees, for a total of 2642 leaves considered (four leaves from IT47 were damaged). The leaves were scanned using an Epson GT-15,000 scanner (300 dpi resolution) with the abaxial surface facing upwards. Fourteen leaf traits were assessed on the scanned leaves, following Kremer et al. (2002). The basal shape of the leaf lamina (BS) was determined using Kremer's index (Kremer et al. 2002). Additionally, the number of lobes was counted only in the half of the leaf (NLH). ImageJ (Rasband 1997–2007) was used to measure the dimensional parameters, which included: area (Area), perimeter (Per), lamina length (LL), petiole length (PL), lamina and petiole length (LL+PL), lobe width (LW), corresponding sinus width (SW), and height of the widest point from the base of the leaf (WP). Due to the frequent dependence of leaf size-related traits on environmental or seasonal variations, some “derived traits” were also considered following Kremer et al. (2002) and Rellstab et al. (2016). These “derived traits” include lobe depth ratio (LDR), petiole ratio (Pr), lamina shape or obversity (Ob), lobe width ratio (LWR), and number of lobes in the left half of the leaf (NLH). Boxplots were generated for each morphometric variable to visualize the distribution of values among populations. A Principal Component Analysis (PCA) was performed on the correlation matrix of the traits not

dependent on leaf size (LDR, Pr, Ob, LWR, NLH), using a subset containing the averaged leaf trait values per tree (294 trees). These analyses were performed using the R packages (ggplot2, tibble, tidyr, dplyr, multcompView, ggsignif, grid, coorplot, car, openxlsx, psych), in R version 4.3.3 (Hothorn et al. 2008; Wickham 2016; Fox and Weisberg 2019; Ahlmann-Eltze and Patil 2021; Müller and Wickham 2024; Wickham et al. 2023, 2024; Wei and Simko 2024; Revelle 2024). Linear Discriminant analysis (LDA) was carried out, using PAST 5.3 (Hammer et al. 2001), on four groups, represented by the four *Quercus petraea* s.l. taxa (*Q. banatus*, *Q. dalechampii*, *Q. petraea* subsp. *petraea*, and *Q. petraea* subsp. *austrotyrrhenica*). Group assignment (minimal Mahalanobis distance to the group mean) was cross validated using the jackknifing procedure. In the morphometric analyses (boxplots, PCA, and LDA), the *Q. petraea* s.l. populations were analyzed by grouping them according to both taxonomic groups and genetic clusters. In the first case (taxonomic groups), the populations were distributed within four groups based on their original taxonomic classification (i.e. nine populations of *Q. petraea* subsp. *petraea*, four of *Q. dalechampii*, two of *Q. petraea* subsp. *austrotyrrhenica*, and one of *Q. banatus*). In the second case (genetic groups), the populations were distributed based on the genetic structure analysis performed on the overall data set including 24 populations.

The pubescence of the twigs and leaves was assessed for all available samples, totalling 279 trees (in the HR06, IT17, IT47, and RS37 populations some twigs were damaged). Both the abundance and the type of trichomes were analysed following a grading system applied on a standard area of 1 mm², according to Fortini et al. (2009). Abundance of trichomes was evaluated on twigs (TT), petiole (TP), main vein (TV), and leaf blade (TB). Furthermore, the presence of the four trichomes types, represented by stellate (StH), fasciculate (FH), solitary, and bifurcate trichomes, was examined on the leaf blade of the herbarium vouchers. The abundance of lenticels on the twigs was also considered using a scale ranging from 0 (absent) to 2 (abundant), as described by Fortini et al. (2013). Pubescence traits were analysed using PAST 5.3 (Hammer et al. 2001) employing a UPGMA clustering based on the Gower's (1971) distance method considering either the eight trichomes exclusively or the combination of leaf ("derived traits") and trichome variables (LDR, LWR, NLH, Ob, Pr, TT, TP, TV, TB, TB, StH, TB FH, TB Solitary, TB bifurcate). The pubescence traits and lenticels' abundance were analysed using descriptive methods.

Since acorns were not available for all the sampled trees, the morphological traits of the fruits were only measured on 129 trees, following the protocol proposed by Fortini et al. (2015). The following traits were considered:

four dimensional traits [cupule length (CL), cupule width (CW), acorn length (AL), and acorn width (AW)], three transformed traits (CW/CL, CL/AL, and AL/AW), and five ordinal traits [regularity of cupule edge (RCE), cupule scale shape (SS), type of cupule edge (TCE), presence of a dark spot on the gibbosity of the cupule, and cupule internal hairiness (CIH)]. Due to the varying number of acorns available for each population, the morphological traits of the fruits were reported as the result of descriptive analyses only.

Results

Results from the nuclear microsatellite marker analyses

A total of 444 samples were genotyped at 10 EST-SSR markers. The informativeness of the individual markers is summarized in Table S8. Null alleles were not detected. Private alleles (N_p) were recorded in 14 out of the 24 populations. The frequency of private alleles in the populations ranged from 0.025 to 0.100 (see Table S9). Genetic diversity measures computed over the populations showed that allelic richness (A_r) ranged from 5.11 in IT20 to 6.63 in RS193. The highest allelic richness values were observed in *Q. pubescens* subsp. *pubescens* populations (mean A_r = 6.19). Observed heterozygosity (H_o) ranged from 0.523 in ES41 to 0.800 in RO33 and expected heterozygosity (H_e) ranged from 0.704 in IT20 to 0.781 in RO33. Positive fixation index (F_{IS}) values were recorded for 17 populations; however, only in five of these, F_{IS} values were statistically significant (see Table 2). No significant trends in genetic variation linked to the geographical gradients were detected.

As expected, pairwise population differentiation (F_{ST}) revealed high genetic differentiation among populations belonging to different taxonomic groups. For example, there were notable differences between the three oak macrospecies *Q. petraea* s.l., *Q. pubescens* subsp. *pubescens*, and *Q. robur* subsp. *robur*. The extent of genetic differentiation between pairs of populations is shown in the heatmap in Fig. S2 (see also Table S10). Focusing only on the 16 *Q. petraea* s.l. populations, the highest significant F_{ST} value was recorded between IT46 and RS38 populations (F_{ST} =0.123832, p -value<0.001), while the lowest (F_{ST} =0.0108213, p -value=0.024) was recorded between HR06 and RO33 populations.

According to the estimators implemented in StructureSelector (Li and Liu 2018) and following Puechmaille (2016), the most likely number of genetic clusters for the full dataset of 24 *Quercus* populations was six ($K=6$) (see Fig. S3a). These six clusters are represented by different colours in Fig. 3, where, in addition, results for $K=3$, 4, and 5 are also

Table 2 Genetic diversity indices in the 24 *Quercus* populations analysed. Taxa marked with an asterisk (*) belong to the *Q. petraea* group

ID pop.	No. of samples	Taxon	Missing genotypes %	N_p	A_r (K=18)	H_o	H_e	F_{is}	p value (F_{is})
AT02	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.0 (0.0%)	1	5.71	0.745	0.719	-0.037	0.288
CZ31	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.2 (1.0%)	0	5.95	0.786	0.756	-0.041	0.241
ES43	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.3 (1.5%)	6	5.14	0.625	0.704	0.115	0.007**
FR08	10	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.1 (1.0%)	2	6.07	0.699	0.779	0.108	0.037 *
HR06	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.5 (2.5%)	2	6.02	0.760	0.767	0.009	0.803
IT20	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.0 (0.0%)	0	5.11	0.675	0.704	0.041	0.306
IT46	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.3 (1.5%)	1	5.36	0.690	0.721	0.044	0.254
IT47	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.2 (1.0%)	2	6.04	0.734	0.755	0.029	0.411
RS36	20	<i>Q. petraea</i> subsp. <i>petraea</i> *	0.0 (0.0%)	0	6.01	0.765	0.767	0.002	0.974
Mean (S.D.) - (<i>Q. petraea</i> subsp. <i>petraea</i> *)			5.71 (0.40)	0.720 (0.05)	0.741 (0.03)	0.030 (0.06)			
IT16	20	<i>Q. petraea</i> subsp. <i>austrotyrrhenica</i> *	0.3 (1.5%)	0	5.46	0.669	0.765	0.128	0.000 ***
IT17	20	<i>Q. petraea</i> subsp. <i>austrotyrrhenica</i> *	0.5 (2.5%)	0	5.12	0.681	0.714	0.048	0.230
Mean (S.D.) - (<i>Q. petraea</i> subsp. <i>austrotyrrhenica</i> *)			5.29 (0.24)	0.675 (0.01)	0.739 (0.04)	0.088 (0.06)			
RO33	20	<i>Q. banatus</i> *	0.0 (0.0%)	2	5.94	0.800	0.781	-0.024	0.477
IT19	20	<i>Q. dalechampii</i> *	0.1 (0.5%)	3	5.62	0.658	0.716	0.083	0.015*
RS37	10	<i>Q. dalechampii</i> *	0.0 (0.0%)	0	6.10	0.720	0.755	0.048	0.339
RS38	20	<i>Q. dalechampii</i> *	0.0 (0.0%)	1	5.49	0.745	0.739	-0.009	0.836
RS67	14	<i>Q. dalechampii</i> *	0.0 (0.0%)	1	5.18	0.750	0.731	-0.027	0.587
Mean (S.D.) - (<i>Q. dalechampii</i> *)			5.60 (0.38)	0.718 (0.04)	0.735 (0.02)	0.024 (0.05)			
CZ30	20	<i>Q. pubescens</i> subsp. <i>pubescens</i>	0.0 (0.0%)	0	6.59	0.745	0.760	0.020	0.537
IT22	20	<i>Q. pubescens</i> subsp. <i>pubescens</i>	0.1 (0.5%)	0	6.04	0.673	0.739	0.091	0.009**
IT89	20	<i>Q. pubescens</i> subsp. <i>pubescens</i>	0.6 (3.0%)	0	5.37	0.664	0.719	0.078	0.059
RS35	20	<i>Q. pubescens</i> subsp. <i>pubescens</i>	0.1 (0.5%)	7	6.30	0.779	0.763	-0.023	0.484
RS193	10	<i>Q. pubescens</i> subsp. <i>pubescens</i>	0.0 (0.0%)	1	6.63	0.730	0.774	0.060	0.189
Mean (S.D.) - (<i>Q. pubescens</i> subsp. <i>pubescens</i>)			6.19 (0.51)	0.718 (0.05)	0.751 (0.02)	0.045 (0.05)			
CZ32	20	<i>Q. robur</i> subsp. <i>robur</i>	0.1 (0.5%)	2	5.62	0.734	0.733	-0.002	0.968
ES41	20	<i>Q. robur</i> subsp. <i>robur</i>	3.1 (15.5%)	1	5.47	0.523	0.718	0.279	0.000
IT14	20	<i>Q. robur</i> subsp. <i>robur</i>	0.0 (0.0%)	0	5.72	0.705	0.723	0.025	0.455
Mean (S.D.) - (<i>Q. robur</i>)				5.60 (0.13)	0.654 (0.11)	0.725 (0.01)	0.101 (0.16)		

N_p , private alleles; A_r , allelic richness (rarefied to 18 gene copies); H_o , observed heterozygosity; H_e , expected heterozygosity; F_{is} , fixation index; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

presented. Examining the bar plot for $K=6$, it reveals that clusters 1 (light blue) and 3 (violet) are exclusively composed of *Q. pubescens* subsp. *pubescens* and *Q. robur* subsp. *robur* populations, respectively. In contrast, populations belonging to the *Q. petraea* group exhibit a variable proportion of membership in the remaining four clusters: cluster 2 (orange), cluster 4 (green), cluster 5 (magenta), and cluster 6 (pink). Structure analysis provided different information based on the various K values up to the optimal $K=6$. At $K=3$, populations clustered into three main groups, corresponding to the three macrospecies: *Q. pubescens* subsp. *pubescens*, *Q. robur* subsp. *robur*, and *Q. petraea* s.l. (the

qi values for each of the 24 populations to the three clusters are referred in Table S11). At $K=4$, the *Q. pubescens* subsp. *pubescens* and *Q. robur* subsp. *robur* clusters remained stable. Within the *Q. petraea* s.l. group, a distinct gene pool (shown in green) emerged, primarily characterizing populations from southern Italy and the Balkans. At $K=5$, *Q. petraea* s.l. populations in the northern part of the sampling area revealed a new gene pool (magenta), that was distinct from the populations in southern Italy and the Balkans. Meanwhile, the orange cluster identified at $K=4$ remained in three populations only: Tolfa (IT47) and Cimini mountains (IT46) in central Italy and Mount Kopaonik (RS67)

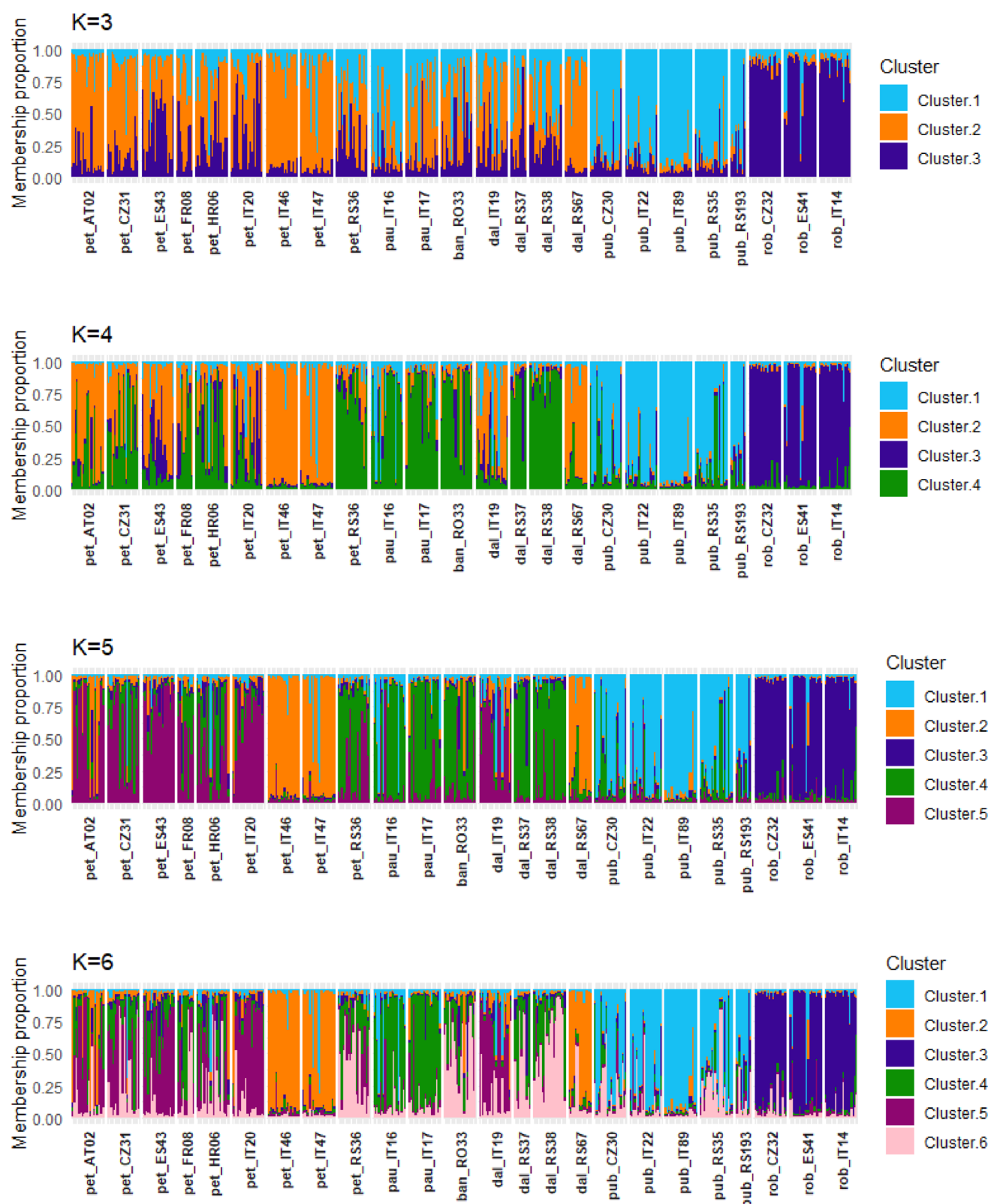


Fig. 3 Bar plot showing the STRUCTURE assignment results for K values ranging from K=3 (top) to K=6 (bottom), based on 10 microsatellite loci and 24 *Quercus* populations. Different colours represent different genetic clusters, while each vertical bar represents an individual with the respective membership coefficients (Q). The different populations are separated

by white vertical lines. Population labels consist of a three-letter abbreviation of the taxon name (ban: *Quercus banatus*, dal: *Q. dalechampii*, pau: *Q. petraea* subsp. *austrorhena*, pet: *Q. petraea* subsp. *petraea*, pub: *Q. pubescens* subsp. *pubescens*, rob: *Q. robur* subsp. *robur*). This is followed by a four-character code identifying the population

in southwestern Serbia. Further differentiation occurred at $K=6$, with a sixth cluster (pink) emerging and separating some of the Balkan populations from the two southern Italian populations (IT16 and IT17) with which they had been associated at $K=4$ and $K=5$.

Table S12 summarizes the proportion of membership (q_i) for each of the 24 *Quercus* populations in the six clusters and Fig. 4 displays this information graphically.

This pattern of genetic structure was largely confirmed when the genetic structure analysis was repeated on the 16 *Q. petraea* s.l. populations only (i.e. excluding the *Q. pubescens* and *Q. robur* populations). However, according to the estimators implemented in StructureSelector (Li and Liu 2018) and following Puechmaille (2016), the most likely number of genetic clusters, for the subset of 16 *Q. petraea* populations, was five ($K=5$) (see Fig. S3b). This indicates the presence of an additional (fifth) genetic cluster compared to that obtained for *Q. petraea* s.l. when the subset of 24 populations also including *Q. pubescens* subsp. *pubescens* and *Q. robur* subsp. *robur* was analyzed. These five genetic clusters are shown in different colours in

Fig. S4, together with the barplots for $K=3$ and $K=4$. The $K=3$ and $K=4$ groupings matched those emerged from the analysis on the entire set of 24 *Quercus* populations. The optimal $K=5$ revealed an additional gene pool (light blue; Fig. S5) regarding the *Q. petraea* s.l. populations located in the north-western side of the sampled area. The proportion of membership (q_i) of each of the 16 *Q. petraea* s.l. populations to the five clusters is summarized in Table S13. However, as this analysis substantially confirmed the genetic structure observed in the full dataset of 24 *Quercus* populations, only the clustering obtained from this 24 populations genetic structure analysis was considered throughout the text.

The UPGMA tree which was based on the Nei's minimum genetic distance among the 24 *Quercus* populations (see Fig. 5), mirrored the clusters that were detected by the genetic structure analysis. With strong support from bootstrapping ($BS=100\%$), the *Q. robur* subsp. *robur* populations formed a distinct group (C), as did the *Q. pubescens* subsp. *pubescens* populations (group B; $BS=83\%$). Bootstrap values within the *Q. petraea* group (A) are lower

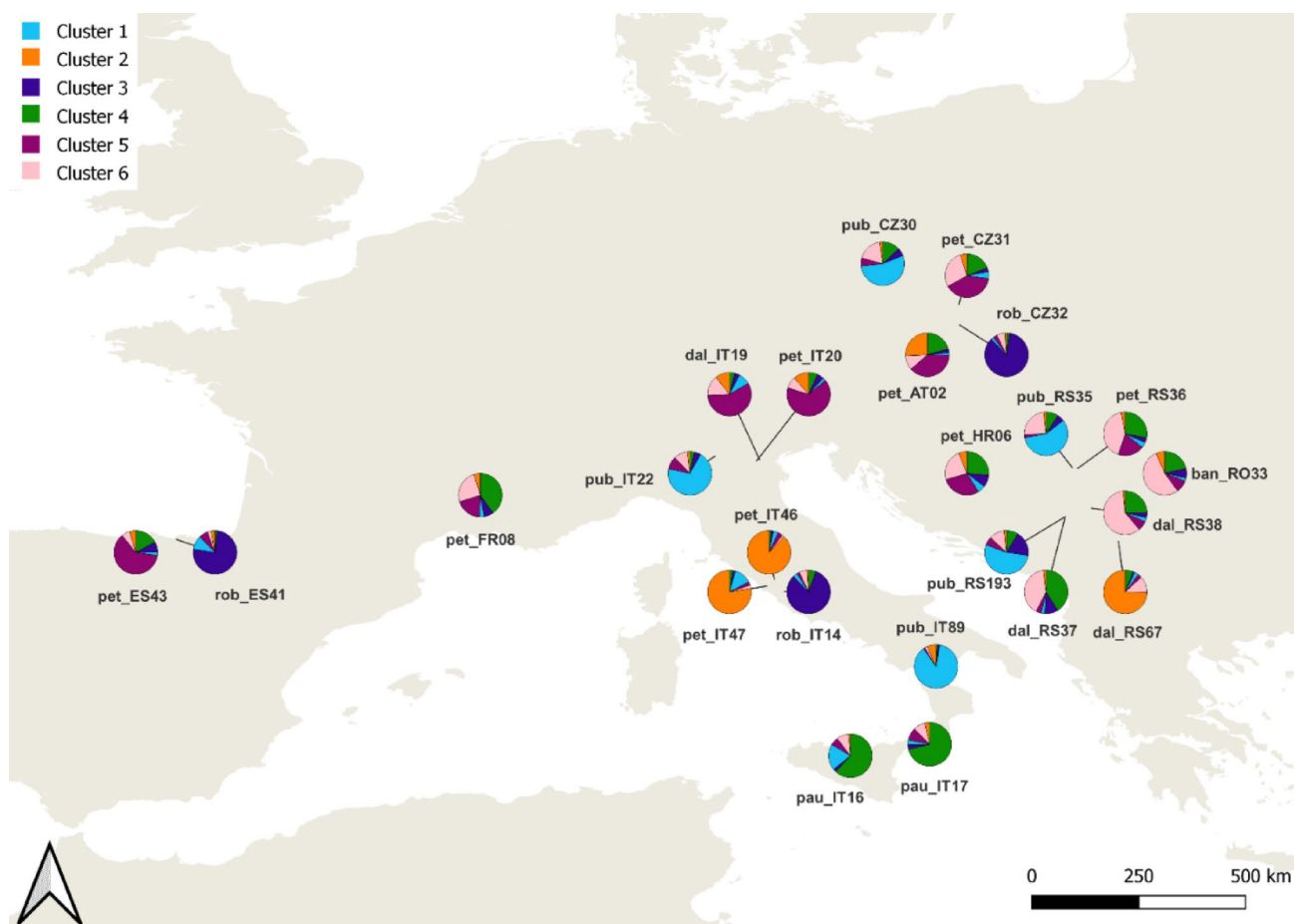
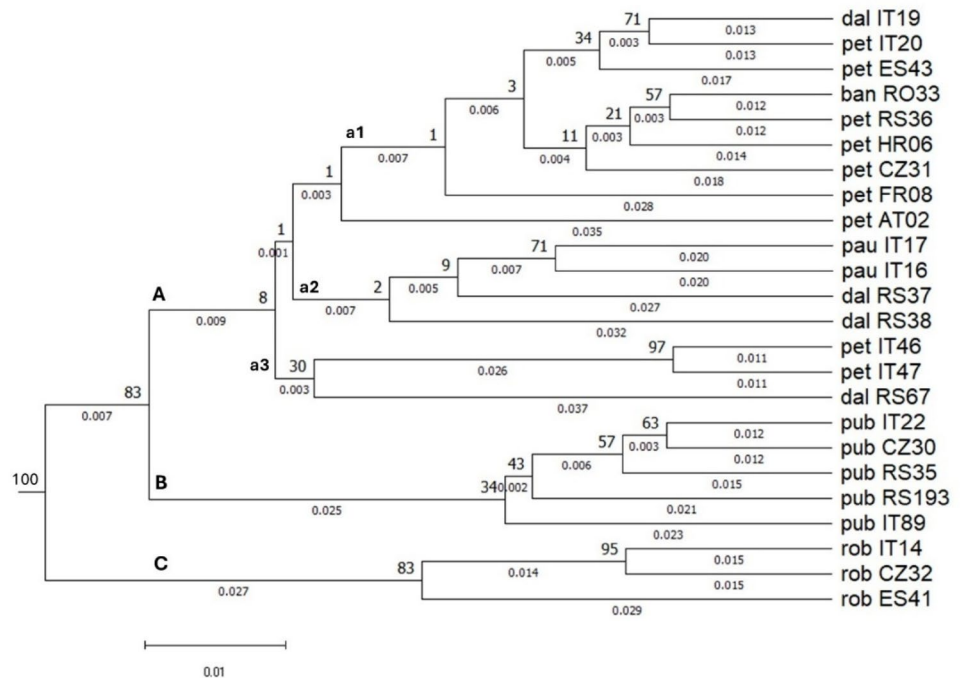


Fig. 4 Distribution map of the 24 *Quercus* populations analysed at 10 microsatellite loci, displaying the results of the Bayesian cluster analysis for $K=6$. Each pie chart represents one population. The colours

inside the pie charts represent the proportion of membership (q_i) values assigned to the six genetic clusters inferred by STRUCTURE. The name of the populations follows the same coding as in Fig. 3

Fig. 5 UPGMA tree based on Nei's minimum genetic distance (1973) of the 24 *Quercus* populations. The horizontal branches represent evolutionary changes measured in genetic divergence (the number shown below each branch). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches. The letters on the branches refer to the identified clusters (A=*Q. petraea* collective group; B=*Q. pubescens* subsp. *pubescens*; C=*Q. robur* subsp. *robur*). The population names follow the same coding system as in Fig. 3



(BS<10%), highlighting three possible sub-clusters: a1, populations from the northern part of the study area (from northern Spain in the west to Romania in the east and from central Italy in the south to the Czech Republic in the north; a2, populations from southern Italy (IT16 and IT17) and western Serbia (RS36 and RS38); a3, populations from central Italy (IT46 and IT47) and central Serbia (RS67).

The grouping pattern observed in the cluster analysis matched the PCoA scatterplot performed on pairwise genetic distances which were calculated as the number of allelic differences between individuals (Fig. 6). In the PCoA1 vs. PCoA2 plot, the genetic distances between all the samples of the 24 populations revealed a clear separation along the first axis (explaining 8.9% of the overall genetic variation), separating the individuals of the three *Q. robur* subsp. *robur* populations from those of the other taxa populations. This axis also revealed subtle divergence between IT46, IT47, and RS67 and the remaining *Q. petraea* collective group populations. The distribution of the populations along the second axis (7.8% of the overall genetic variation) showed the differentiation between the *Q. petraea* collective group populations and the *Q. pubescens* subsp. *pubescens* populations (PCoA1 vs. PCoA3 scatterplot is provided in Fig. S6).

The population genetic structure revealed by the Bayesian clustering and the UPGMA tree was also supported by the PCA scatterplot (Fig. S7), which showed a clear separation between the three main taxonomic groups (*Q. petraea* s.l., *Q. pubescens* subsp. *pubescens*, and *Q. robur* subsp. *robur*) and a less clear separation between the four subgroups belonging to *Q. petraea* s.l. It emerges that the population

the *Q. petraea* subsp. *austrotyrrhenica* population (IT16) was found to have an affinity with the *Q. pubescens* group populations, as already observed in the PCoA scatterplot. The PCA conducted only on the trees belonging to the 16 *Q. petraea* s.l. populations (Fig. S8) reveals a comparable separation among the four subgroups. The DAPC analysis, performed exclusively on individuals belonging to the *Q. petraea* collective group, clearly differentiates populations IT46, IT47, and RS67 from other *Q. petraea* s.l. populations (see Fig. S9).

Results from the morphometric analyses

The summary results obtained for the complete set of morphological leaf trait measurements from the 16 *Q. petraea* s.l. populations are shown in Table S14.

The boxplots for the leaf morphological traits show that the populations of *Q. petraea* subsp. *petraea* from central Italy (IT46 and IT47) and that of *Q. dalechampii* from Mt. Kopaonik (RS67), belonging to the genetic cluster 2 (Figs. 3 and 4), exhibit the highest mean values and greatest variation for all leaf size traits (Area, Per, LL, PL, LL+PL, LW, WP). Conversely, the lowest values for these traits were observed in the populations of *Q. petraea* subsp. *petraea* from France (FR08) and *Q. petraea* subsp. *austrotyrrhenica* from Sicily (IT16), which belong to genetic cluster 4. Populations in the northern part of the sampling area and in the Balkans (clusters 5 and 6) did not show significant differences between them: instead, they displayed intermediate mean values and moderate variation (see Figs. S10–S11).

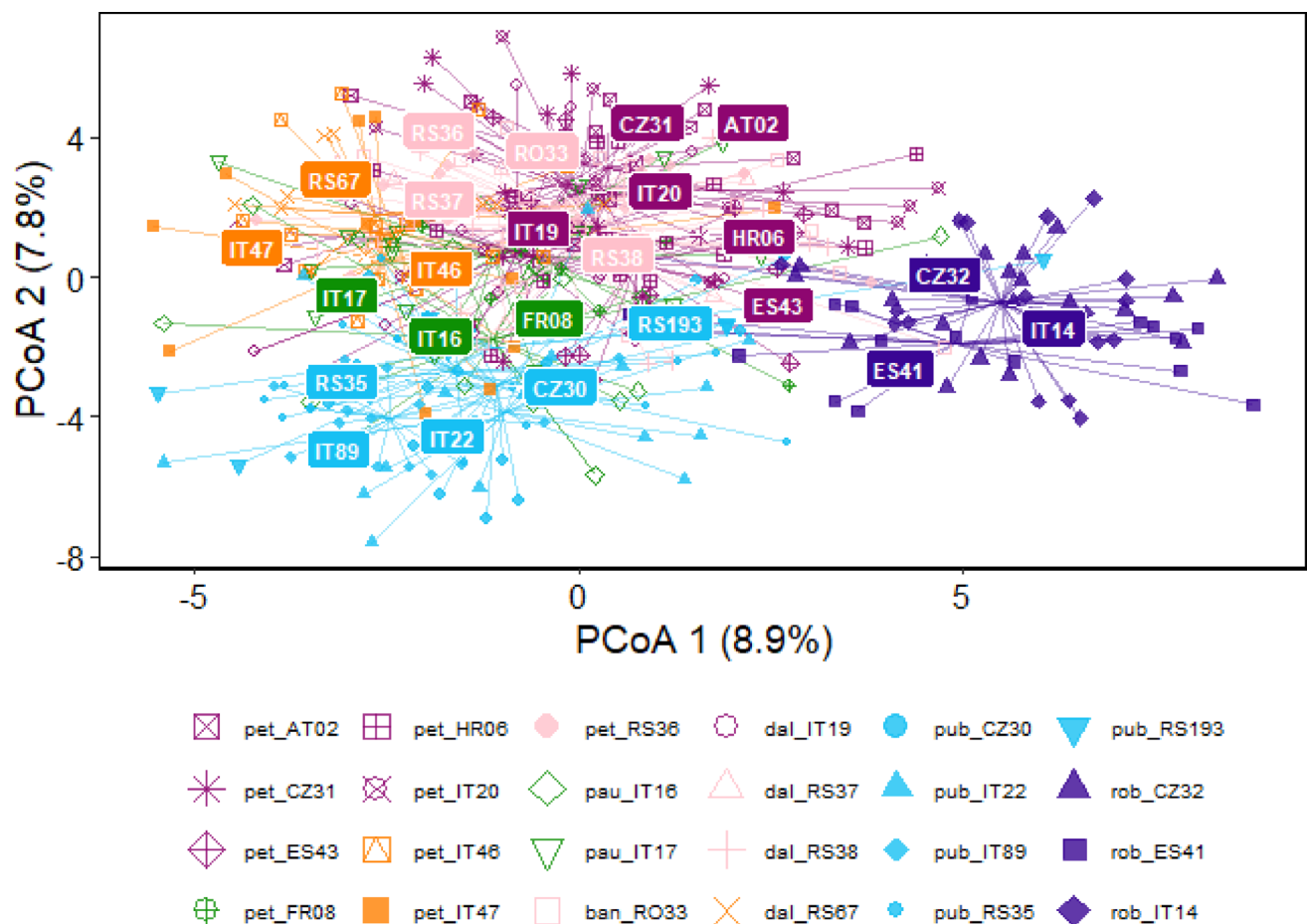


Fig. 6 Two-dimensional Principal Coordinate Analysis (PCoA) scatterplot of the 444 samples belonging to the 24 *Quercus* populations analysed at 10 microsatellite loci. Axis 1 and axis 2 explain 8.9% and 7.8% of the total variance, respectively. The populations are coloured

In the PCA performed on the correlation matrix of the average values per tree (294 trees) for five morphological leaf traits (LDR, LWR, Ob, Pr, and NLH), the first three principal components accounted for 42.22%, 18.26%, and 17.3% of the total variance, respectively (Fig. 7 and Figs. S12–S14). The PC1–PC2 scatterplot did not reveal distinct groupings, suggesting limited morphological differentiation across populations. However, a subtle pattern emerged that aligned roughly with the gene pools identified through the genetic structure analysis (see the “Results from the nuclear microsatellite marker analyses” paragraph). Populations IT46, IT47, and RS67 (cluster 2) were mostly located on the left side (quadrants II and III). Those belonging to cluster 4 from southern Italy (IT16 and IT17) were mostly spread across the right side (quadrants I and IV). Those from the northern part of the sampling area and the Balkans (cluster 5 and 6) occurred across all the quadrants in the central part of the scatterplot. Among the variables, Ob and NLH were most influential in separating populations IT46, IT47, and RS67 from those in the northern part

according to the colour assigned to the cluster in which they exhibit the highest percentage of membership (see Table S12). The population names follow the same coding system as in Fig. 3

of the sampling area. Conversely, Pr, LWR, and LDR were more effective in distinguishing populations from southern Italy and the Balkan Peninsula. Similar patterns of populations separation were evident in the PC1–PC3 scatterplot (Figs. S12, S14).

Discriminant analysis failed to clearly separate *Q. petraea* subsp. *petraea* from *Q. dalechampii* and *Q. banatus*. The individuals belonging to these three presumed taxa appear to blend together in the centre of the graph, forming no distinct grouping. Only the individuals of *Q. petraea* subsp. *austrotyrrhenica* showed partial asymmetric dispersion, evident on the right-hand side of the graph (Fig. 8 and Figs. S15–S17). The jackknifed confusion matrix showed an overall “correct” classification rate of 49.32%, with 8 out of 20 *Q. banatus* individuals, 28 out of 64 *Q. dalechampii* individuals, 84 out of 160 *Q. petraea* subsp. *petraea* individuals, and 25 out of 40 *Q. petraea* subsp. *austrotyrrhenica* individuals correctly classified (Table S15).

Analysis of twig and leaf pubescence, considering both trichome abundance and type, did not reveal a clear

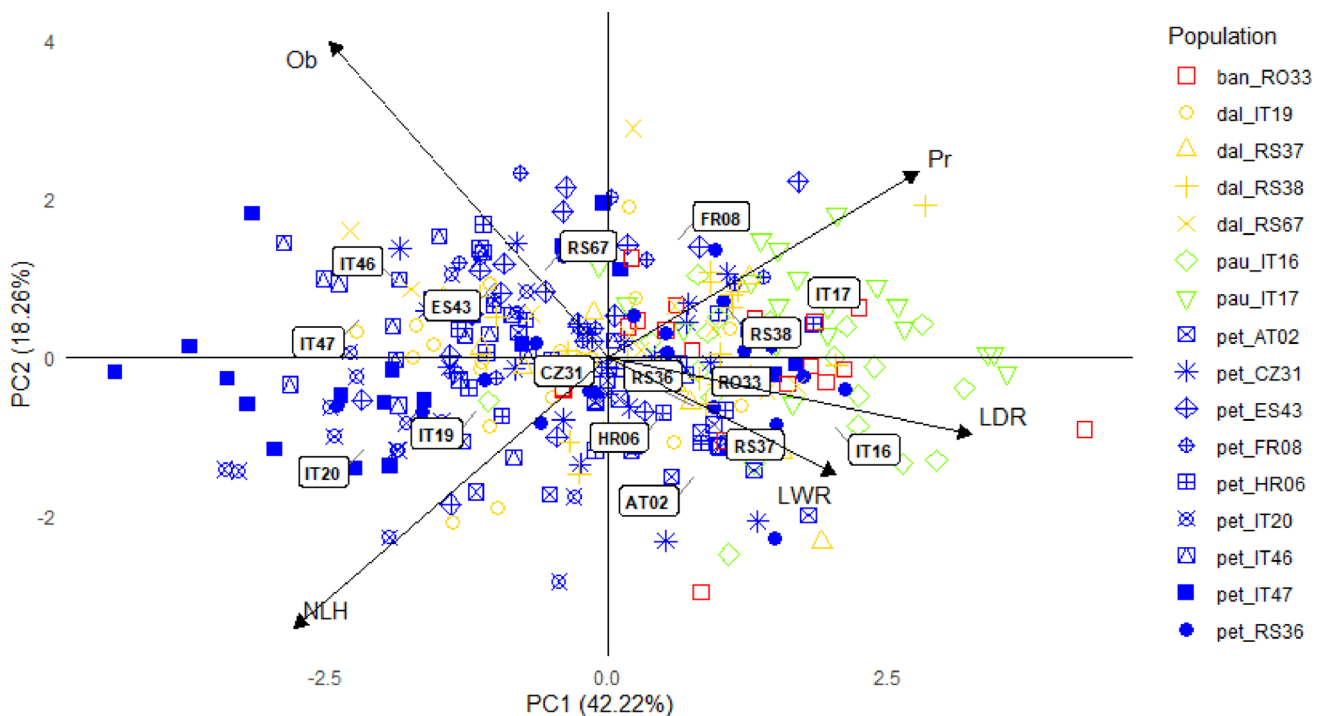


Fig. 7 PCA biplot of 294 samples from 16 *Quercus petraea* s.l. populations, based on five leaf morphological traits (LDR: lobe depth ratio; LWR: lobe width ratio; NLH: number of lobes in the left half of the leaf; Ob: oversity; Pr: petiole ratio). The plot shows principal component axes 1 and 2 (PC1 vs. PC2) which together explain 60.48% of the

total morphological variance. The populations are coloured with the colour assigned to the taxon (*Q. banatus*: red; *Q. dalechampii*: gold; *Q. petraea* subsp. *austrotyrrhenica*: green; *Q. petraea* subsp. *petraea*: blue). The names of the populations follow the same coding system as in Fig. 3

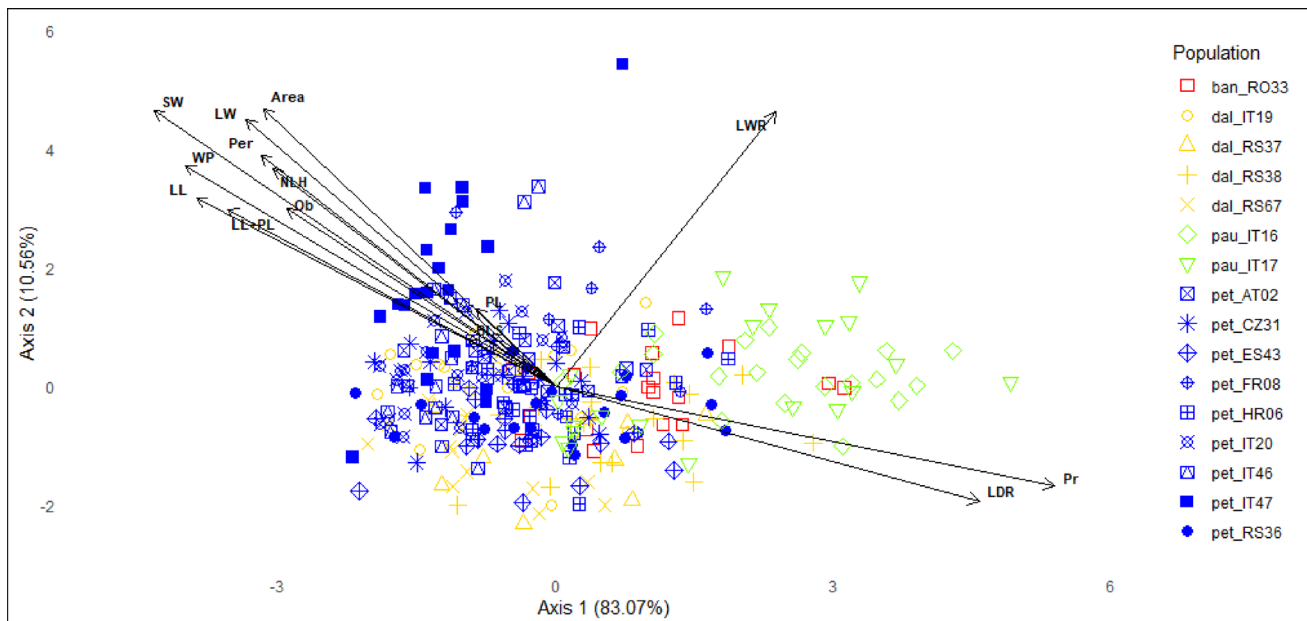


Fig. 8 Linear discriminant analysis (LDA) on discriminant axes 1 and 2 of four *Quercus petraea* s.l. taxa (*Q. banatus*, *Q. dalechampii*, *Q. petraea* subsp. *petraea*, and *Q. petraea* subsp. *austrotyrrhenica*) based on morphometric characters. Points represent trees coloured by original group assignment. The populations are coloured with the

colour assigned to the taxon (*Q. banatus*: red; *Q. dalechampii*: gold; *Q. petraea* subsp. *austrotyrrhenica*: green; *Q. petraea* subsp. *petraea*: blue). The names of the populations follow the same coding system as in Fig. 3

differentiation among the 16 *Quercus petraea* s.l. populations. However, the UPGMA tree based on the Gower's (1971) distance for the 279 *Q. petraea* s.l. trees, using eight trichomes variables, showed that some trees from the FR08 and IT47 populations, and one tree from RS37 population formed a distinct group (Fig. S18). Similar results were obtained in the UPGMA tree based on the Gower distance (Gower 1971) of the 279 trees of *Q. petraea* s.l. built using the combined leaf and trichome variables (Fig. S19). Detailed analysis of the trichome types revealed that fasciculate trichomes were prevalent in these trees and that they were more abundant than in other populations. The abundance of lenticels was quite low for these trees compared to the others (Fig. S20a, b). Descriptive analyses were conducted to identify differences between populations based on acorn traits. These analyses revealed that most fruits in the analysed populations exhibited a pyriform scale shape, often with a red or brown spot on the gibbosity of the cupule. While these observations lack statistical support due to the unavailability of fruit from all trees and populations, the available data suggest that triangular scale shapes were exclusively observed in certain individuals within the IT16, IT17, FR08, and RS37 populations. Furthermore, FR08 and RS37 were the only two populations with exclusively black spots on the gibbosity of the cupule (Fig. S21a, b).

Discussion

The genetic and morphological characteristics of 16 *Quercus petraea* s.l. populations were studied to identify diversity trends that could help to clarify biogeographical and taxonomic questions concerning the *Q. petraea* collective group. Incorporating populations of two potentially hybridising European white oak species, *Q. pubescens* subsp. *pubescens* and *Q. robur* subsp. *robur*, enabled us to assess the degree of purity of the *Q. petraea* collective group populations and highlight their phylogeographic relationships. While only 23.87% of the samples from the full set of 24 *Quercus* populations could be considered genetically "pure", with membership coefficients (Q values) ≥ 0.90 (see Table S16), very few individuals had a gene pool that differed from the collective taxonomic group to which they were originally assigned and even fewer showed similar memberships to multiple species clusters (putative hybrids). Most populations were genetically homogeneous, with a high proportion of membership to a single cluster (Table S12). Therefore, although our sampling revealed signs of hybridization/introgression, a phenomenon that is in any case widely documented in the *Quercus* genus (Rushton 1993; Curtu et al. 2007), it can be considered robust and well-targeted.

Phylogeographic structure of *Quercus petraea* s.l. populations

The *Quercus petraea* subsp. *petraea* population from the Cantabrian region of north-west Spain (ES43) showed the highest number of private alleles (six) (Table S19). This is not surprising as this population is isolated in the dataset and is geographically distant from its nearest neighbour (West-Provence in South-Eastern France), as well as from all the other populations.

According to the floristic literature (Masin and Tietto 2005) in the Euganean Hills (a group of hills of volcanic origin in north-eastern Italy, formed by volcanic cones or lava flows, rising 30 to 600 m above the Po-Venetian Plain), are home to two morphotypes of *Q. petraea*: *Q. petraea* s. str. and *Q. dalechampii* auct. non Ten. Accordingly, our field collections included both morphotypes which were classified as follows: *Q. petraea* subsp. *petraea* (IT20) and *Q. dalechampii* auct. non Ten. (IT19). However, a study of the morphological traits of these two populations based on geometric morphometric analyses (Proietti et al. 2021) found no morphological differences that would justify separating them at the species level. Genetic and new morphological analyses carried out in this study support this finding. Nevertheless, the presence of private alleles only in population IT19, which is hypothesised in the literature to be a thermophilic variant of *Quercus petraea* s. str., and population IT20 (*Quercus petraea* s. str.), which exhibits the lowest values of allelic richness in the entire dataset, suggests that genetic diversification is underway between these two *Quercus petraea* variants from the Euganean Hills. The Euganean Hills are in fact a well-known conservation site for thermophilic flora in northern Italy, as documented by palaeoecological and topoclimatic evidence (Kaltenrieder et al. 2009, 2010; Samartin et al. 2016; Gubler et al. 2018).

In line with the genetic findings of this study, the investigated *Q. petraea* s.l. populations exhibited relatively uniform levels of genetic diversity, which is consistent with the outcomes of other studies on the same taxonomic group (Streiff et al. 1998; Jurkšienė et al. 2020; Eusemann and Liesebach 2021). Both allelic richness and heterozygosity values fell within a rather narrow range of variability when the different populations investigated were compared (Table 2). Borovics and Mátyás (2013) highlighted a decline in allelic numbers and heterozygosity in Hungarian *Q. petraea* populations located in warmer and drier areas. Consequently, a loss of genetic diversity could be expected for the sessile oak populations of Sicily and southern Italy, which are geographically isolated within the Mediterranean Basin and characterized by a substantial decrease in summer rainfall. However, these two populations exhibited heterozygosity and allelic richness values like those of the

other populations investigated. Their location at relatively high altitudes (the sub-montane and lower montane belt) probably compensates for the decrease in summer precipitation through other physical factors (e.g. lower average temperatures, higher air humidity, and greater cloud cover). This ensured that the populations' demographics did not become too restricted over time, thereby preventing loss of genetic diversity due to genetic drift.

Analysis of genetic structure revealed striking similarities between the two *Q. petraea* subsp. *petraea* populations from central Italy (IT46 and IT47) and the *Q. dalechampii* auct. non Ten. population from central Serbia (RS67). These populations are characterized by the same exclusive gene pool. This is an unexpected result from a phylogeographical perspective that is difficult to explain with the current data, so several hypotheses could be put forward. One is that of possible common ancestry, as also seems to indicate the progression of the structure bar-plots from $K=3$ to $K=6$ (Fig. 3; and from $K=3$ to $K=5$ in Fig. S4). In fact, these populations grow in areas with unusual environmental characteristics. The Tolfa and the Cimini mountains are well-known conservation sites for the Italian forest vegetation. Located within the extensive volcanic region on the Tyrrhenian side of central Italy, these mountains are home to Italy's three largest volcanic lakes (Bolsena, Bracciano, and Vico) which have mitigated the negative effects of the Pleistocene climatic upheavals. This has enabled mesophilous forest areas to survive not only during the coldest periods of the Quaternary but also the driest (Follieri et al. 1989; Magri et al. 2015). Several beech heterotopic relict forests are found at altitudes ranging between 160 and 500 m a.s.l. in this area (Anzalone 1961; Di Pietro et al. 2010) whereas almost all the beech forests on the Italian Peninsula are found above 1000 m. Therefore, it is possible that a kind of "ancestral" *Q. petraea* gene pool has been preserved in the Tolfa and Cimini mountains, while being progressively lost in all surrounding areas.

The RS67 population inhabits the south-western slopes of the Kopaonik Mountains in Serbia, where they merge with the deep and long canyon valley of the Ibar River. Together with the other gorges and canyons of the central Balkans this area is characterized by a high richness and diversity of vascular plant species. These include many species belonging to Mediterranean and sub-Mediterranean chorological elements, as well as a significant number of Tertiary relicts (Mišić 1984; Karadžić 2018; Kovačević 2025; Ilić et al. 2022; Sekulić et al. 2021, 2023). The refugial characteristics of these habitats can be attributed to favourable conditions, such as the temperate humid ravine climate which gives rise to a great diversity of microhabitats. Furthermore, relatively weak and localized glaciation during Pleistocene climate fluctuations (Bognar et al. 1991; Kovačević 2025;

Milivojević et al. 2008) provided suitable environmental conditions for various taxa or genetic lines to survive long-term. Due to geographic isolation and limited gene flow from neighbouring populations, these taxa or genetic lines were able to maintain their genetic specificity over a long period of time.

The genetic separation of the Tolfa-Cimini-Kopaonik group is also evident in the cluster analysis (Fig. 5). Here, these populations are nested within the "a3" subcluster, although the bootstrap support (30%) is insufficient to hypothesize a separation of this subcluster at the taxonomic level.

The Tolfa-Cimini-Kopaonik subcluster highlights this Apennine-Balkan connection, which is confirmed by the occurrence of other clusters when the results of the genetic structure analysis for $K=5$ are observed. However, this is not new from a forest phylogeographic perspective, as it has also been evidenced in forest types other than oak forests (Piotti et al. 2017; Cosgün et al. 2025). Previous studies based on cpDNA markers (Fortini et al. 2024; Di Pietro et al. 2024) have also highlighted this trans-Adriatic link for white oaks, reflecting a well-known phylogeographical connection that has been found for several other genera too (Kuzmanović et al. 2017; Janković et al. 2019; Radosavljević et al. 2022). The Balkans and the Apennine Peninsula were connected for extended periods during the cold phases of the Quaternary period, when the Adriatic Sea dried up considerably, enabling plant species to cross it in both directions. A great deal of genetic, floristic, biogeographical, and phytosociological research attests to the close Apennine-Balkan relationship involving all the vegetation types and altitudinal belts (Rivas-Martínez et al. 2004). Even within the *Quercus* genus, the distribution ranges of species such as *Q. cerris*, *Q. frainetto*, *Q. trojana*, *Q. ithaburensis* subsp. *macrolepis*, along with their associated communities, provide sufficient evidence of this relationship (Horvat et al. 1974; Simeone et al. 2018; Di Pietro et al. 2020c). Interestingly, however, for $K=6$, the optimal K according to Puechmaille (2016), the Apennine-Balkan cluster differentiates further, demonstrating increased autonomy of the Balkan populations of *Q. petraea* s.l. This result is more in line with the actual biogeographical framework of south-east Europe. While the importance of the Apennine-Balkan territorial connections remains, the distribution map of genetic clusters (Fig. 4) should be also viewed as the consequence of territorial disjunctions that separated the two peninsulas for very long periods throughout the Quaternary, likely leading to partially divergent genetic evolution. Moreover, it was somewhat expected that a certain degree of Balkan genetic autonomy will be evident in a phylogeographical perspective, even in oak forests context. Within the Apennine-Balkan province, the Balkans occupy a significantly larger

area than the Apennines, compared to which they are much more bioclimatically and environmentally diverse (Španiel and Rešetnik 2022). Furthermore, the Balkans represent the geologically oldest unit and during the Tertiary and Pleistocene they have maintained a close mainland connection with adjacent biogeographic provinces, whereas the Apennine Peninsula has almost always been surrounded by the sea (Meulenkamp and Sissingh 2003).

The presence of a third genetic cluster, which we have defined as “northern”, spanning the entire northern part of the study area from northern Spain to Croatia via northern Italy, Austria, and the Czech Republic, was somewhat unexpected. This is the first time that studies of the nuclear DNA of white oaks in Europe, particularly *Q. petraea*, have revealed a distinction between dominant gene pools in northern and central Europe and those in southern Europe. The geographical demarcation line separating these two genetic groups appears to run through the Po River Valley in Italy and continuing into Eastern Europe via the Sava River valley and on the Danube lowland. In our study, the northern gene pool still prevails in the Austrian and the Czech Republic populations while the south-eastern gene pool prevails in the Romanian population. It would be interesting to discover how the Hungarian populations of *Q. petraea* fit into this context, i.e. whether they are genetically closer to those in the Czech Republic and Austria, or in the Balkans. The same applies to the sessile oak populations of the southern Carpathians. Interestingly, when only the 16 *Q. petraea* s.l. populations were considered, this “northern gene pool” was further subdivided with a new gene pool occurring particularly in the populations of northern Spain, southern France, and Austria (see Figs. S4, S5). This suggests that this genetic cluster may have originated (or been preserved) in the Iberian Peninsula during the cold periods of the Quaternary before migrating eastwards during the postglacial period. This broad west-east migratory route was however one of the possible options already proposed by Petit et al. (2002a, b) and supported by other authors (Hewitt 1999; Olalde et al. 2002). However, it was certainly not the only hypothesis; others proposed shorter-range migratory options linked to the presence of refuge sites in the Balkan area, leading to northwards and westwards stages of postglacial recolonization (Dumolin-Lapègue et al. 1997).

The main clusters identified by the genetic structure analysis were consistent with the groups recognized in the UPGMA dendrogram. However, the low genetic distances represented by bootstrap values and short branches did not provide strong statistical support for many terminal clades or internal nodes. This highlights and confirms the low degree of genetic differentiation within the so called “collective groups” of European white oaks (especially within the *Q. pubescens* and *Q. petraea* complexes) (Franjić et al.

2006; Enescu et al. 2013; Di Pietro et al. 2020, 2021). Similarly, at the plastid level, it was found that the entire group of western Eurasian white oaks have preserved a poorly differentiated DNA, characterized by unfixed genetic diversity and a high number of haplotypes, mostly separated by single mutations (Fortini et al. 2024).

What evidence is there for diversification at the species level within the *Q. petraea* s.l. populations being considered?

One of the recurring taxonomic problems with European white oaks is determining whether additional taxa (species or subspecies) belonging to the *Q. petraea* collective group exist alongside *Q. petraea* (Matt.) Liebl. subsp. *petraea*. Several of these taxa are often considered to be synonyms with each other and include *Q. dalechampii* Ten., *Q. polycarpa* Schur, *Q. petraea* subsp. *polycarpa* (Schur) Soó, *Q. banatus* Kučera, *Q. aurea* Wierzb. They have already been reported in the floras and checklists of several European countries, including the Czech Republic, Hungary, Italy, Slovakia, Romania, Slovenia, Ukraine, and almost all the Balkan countries. These taxa are generally described as being more thermophilic and xerophilic than the typical *Q. petraea* and, according to local or regional floras, they should exhibit identifiable diagnostic morphological traits. However, the aforementioned floras do not always agree on a consistent set of morphological traits to be considered diagnostic and sometimes deviate significantly from the original description of the species.

One aim of this study was to clarify this critical taxonomic issue by collecting and analysing some of these “taxonomically critical” populations that local and national taxonomic literature attributes to taxa other than *Q. petraea* subsp. *petraea*. While the four different gene pools identified in the *Q. petraea* s.l. samples supported a phylogeographical differentiation among the populations investigated, they did not confirm the taxonomic value of the aforementioned critical species. The taxonomic composition of the four groups identified by the structure analysis strictly concerning the *Q. petraea* collective group is sufficient for this purpose. Cluster 2 consisted of populations of *Q. petraea* from central Italy together with a population of *Q. dalechampii* auct. non Ten. from Serbia; cluster 4 consisted of populations of *Q. petraea* subsp. *austrotyrrhenica* from southern Italy and a population of *Q. petraea* subsp. *petraea* from France; cluster 5 consisted of populations of *Q. dalechampii* auct. non Ten. and *Q. petraea* subsp. *petraea* from central Europe; and cluster 6 consisted of populations of *Q. banatus*, *Q. dalechampii* auct. non Ten., and *Q. petraea* subsp. *petraea* from the Balkan Peninsula. Our results revealed that the analysed *Q. dalechampii* auct. non Ten. populations

(from both the Balkans and northern Italy) did not differ significantly from the *Q. petraea* s. str. populations from other areas. However, it should be noted that all the populations of the *Q. petraea* complex included in this study, were found to be genetically distinct from the *Q. robur* subsp. *robur* and *Q. pubescens* subsp. *pubescens* populations included in the comparison dataset, regardless of origin and taxonomic classification. While the morphological differences between *Q. petraea* s.l. and *Q. robur* subsp. *robur* are well identifiable and obvious, the same cannot be said with equal certainty when comparing *Q. petraea* s.l. and *Q. pubescens* subsp. *pubescens*, which are much more similar both genetically and morphologically (Fortini et al. 2015; Leroy et al. 2017; Šijačić-Nikolić et al. 2023). Nevertheless, in our case at least, the high bootstrap value in the cluster analyses and the almost complete lack of interspecific overlap in the PCoA scatterplot (Fig. 6) leaves no doubts as to the genetic separation between these two species. This clear and statistically significant genetic separation between the *Q. petraea*, *Q. pubescens*, and *Q. robur* populations highlights once again that the genus *Quercus* acts as an aggregate of circumscribed taxa rather than as a single, undivided syngameon (Hipp et al. 2020), at least at the level of macrospecies (i.e. well-established and universally accepted species within white oak taxonomical frameworks). This provides further evidence that, despite interspecific gene flow, the genetic integrity of oak species tends to be largely preserved even between closely related sympatric species (Lepais et al. 2013; Gailing and Curtu 2014; Reutiman et al. 2020; Šijačić-Nikolić et al. 2023).

While the analysis of morphological traits yielded some interesting results, it failed to meet expectations regarding the possibility of associating the patterns of morphological and genetic variability with the varied taxonomic and nomenclatural frameworks proposed in floras and checklists. This is consistent with a recent geometric morphometric study of leaf morphology, in which a low degree of differentiation was found when analysing several European populations of *Q. petraea* collected across wide longitudinal and latitudinal gradients (Fortini et al. 2025). According to the Middle-European concept, most of the names currently included in the central and eastern European group of *Q. petraea* (e.g. *Q. aurea* Wirb., *Q. polycarpa* Shur, *Q. banatus* Kučera) are in fact synonyms of *Q. dalechampii* auct. non Ten. This concept refers to Schwarz's (1936–39) interpretation of *Q. dalechampii* Ten., namely an oak species with glabrous leaves and twigs and therefore belonging to the collective group of *Q. petraea*. Schwarz also used this interpretation in his treatment of the *Quercus* genus in Flora Europaea (Schwarz 1993), and it was followed by several authors in various countries, including Savalescu (1952), Jordanov (1936–79), Matyas (1970), Pignatti (1982),

Didukh et al. (2004) etc. However, Schwarz interpretation contrasted with that proposed by Camus (1936–54), who associated *Q. dalechampii* Ten. (in the form of *Q. lanuginosa* subsp. *dalechampii*) to the collective group of pubescent oaks. This was also followed by other authors (Hayek 1970; Brullo et al. 1999; Bock and Tison 2012; Pignatti et al. 2017–2019). Following Di Pietro et al.'s (2012) lectotypification of *Q. dalechampii* Ten., which established that this species belongs to the *Q. pubescens* collective group, several authors have attempted to find an alternative name for the sessile oak populations of central and eastern Europe that were previously assigned to *Q. dalechampii* Ten. However, there is currently no agreement among taxonomists on the hierarchical rank to be assigned to this taxon (see Bartolucci et al. 2018; Kaplan et al. 2022). There is also disagreement on whether it should be considered a species (Govaerts and Frodin 1998; Matula 2008; Stevanović 2012; Nikolić 2015-ongoing), a subspecies (Raab-Straube and von Raus 2013; Dimopoulos et al. 2013) or if this taxon deserves a taxonomic rank at all, or if it should simply be considered a synonym of *Q. petraea* s. str. (Menitsky 1968; Jalas and Suominen 1976; Christensen 1997). In addition to the genetic results of this study not providing evidence for treating *Q. dalechampii* auct. non Ten. as a separate taxon, the morphological analyses also do not seem to provide a decisive support for this treatment. The only morphological traits that seem to correspond to the genetic clusters are the leaf dimensional ones. The largest values of these traits are associated with the *Q. petraea* s.l. communities that we have defined as “ancestral”, namely those found in the volcanic area of central Italy and Mount Kopaonik in Serbia. We are aware that using leaf and acorn size variables for classification hypotheses can be problematic due to significant variations that could occur from one year to the next, particularly due to the inconsistency of seasonal parameters linked to the macro- and meso-climate. Nevertheless, from a taxonomic perspective, this dimensional parameter does not distinguish between a population currently assigned to *Q. petraea* subsp. *petraea* (central Italy) and those assigned to *Q. dalechampii* auct. non Ten. (Mount Kopaonik). Conversely, the morphological traits that are diagnostic of *Q. dalechampii* auct. non Ten. (e.g. the depth of the leaf lobe sinus which is identified here as LDR) appear to be more closely associated with a group of *Q. petraea* subsp. *austrotyrrhenica* specimens (Fig. 7 and Figs. S10, S11). However, this morphological trait was found to be uniformly distributed among the different populations of *Q. petraea* subsp. *petraea*, *Q. dalechampii*, and *Q. banatus* and distributed about randomly among individuals within the same population. The same uniform distribution among different populations is observable for the gibbosity of the acorn cupule trait. In short, these “diagnostic” traits, as well as most of

the morphological traits considered in this study, do not exhibit sufficient discriminatory power to distinguish clusters of sessile oak that can be attributed to *Q. dalechampii* auct. non Ten., or its synonyms (e.g. *Q. banatus*), nor can they distinguish other taxa that may be included in the *Q. petraea* collective group (e.g. *Q. polycarpa*). These findings suggest that variability observed in the morphological traits of *Q. dalechampii* auct. non Ten. individuals fall within the overall variability range of *Q. petraea*. Consequently, it has been proved inappropriate to use the name *Q. dalechampii* (*sensu* eastern European authors), to refer to the populations in this geographical area (the Balkan Peninsula and northern Italy), since no robust morphological characteristics have been identified to distinguish this taxon from *Q. petraea*. We did not collect populations of the putative *Q. dalechampii* in Austria and the Czech Republic but only populations identified as *Q. petraea* subsp. *petraea* by the expert knowledge of collectors and the taxonomic and phytosociological literature. While reports of *Q. dalechampii* are very rare for Austria (Schwarz 1936–39), several contributions to the literature on the Czech Republic explicitly refer to the presence of multiple species of the *Q. petraea* group in this country (Magic 1975, 2006; Koblížek 1993; Požgaj 1999, 2001; Matula 2008). However, these contributions also report the presence of many hybrid individuals within the *Q. petraea* s.l. populations. For this reason, as has already been highlighted for the *Q. pubescens* complex (Di Pietro et al. 2016; Pietro et al. 2020b), it is possible that with randomized sampling based on a large sample size per population, the morphological differences between the different putative species of the *Q. petraea* complex within a forest community could manifest as a continuous pattern. Indeed, the most recent large-scale synthesis on the flora and vegetation of the Czech Republic (Chytrý 2013; Kaplan et al. 2022) remains much more cautious about taxonomic attributions within the *Q. petraea* species complex. To avoid taxonomic inconsistencies (at least about the name *Q. dalechampii*) and in line with the ICN rules, the name *Q. dalechampii* Ten. should only be applied to oak populations belonging to the *Q. pubescens* collective group and excluded from those belonging to the *Q. petraea* group (Di Pietro et al. 2012). Accordingly, Kučera (2018; 2019) proposed substituting the name *Q. dalechampii* Ten. with *Q. banatus* Kučera for the Balkan populations of this species. However, the genetic and morphological variability observed in the unique *Q. banatus* population (RO33) does not seem to support its classification at the species level, as it is not significantly different from the pattern of variation observed within the *Q. petraea* collective group. While this statement may be considered premature, as we have only considered one population of *Q. banatus* (from Banat region of western Romania), it is also true, that our population of *Q. banatus* from Oravița

cannot be considered the same as any others that may occur in south-east Europe. This population was in fact, collected in the *locus classicus* of the species (“woods surrounding Oravița” is the locality indicated in the label of the lectotype of the species), and therefore it is the only population that meets the basic nomenclature requirements to be associated with the name *Q. banatus*.

All the results discussed so far seem to support a simpler taxonomic and nomenclatural arrangement of the European white oaks. This could indicate genetic discontinuity at the macro-species level, with little or no diversification within the single collective groups (e.g., *Q. petraea*, *Q. pubescens*...). However, it is possible that some genetic or morphological discontinuity could be found at a regional scale following extremely detailed genetic and morphometric investigations involving a very large sample size at a strictly local level. If so, the question will be how to classify such “local” systematic evidence within taxonomic-nomenclature frameworks that normally operate at a national or supranational level.

All things considered, the most plausible taxonomic-nomenclatural interpretation of our results, with regard to the populations under investigation, would be to recognize only one taxon at the species level: *Q. petraea* (Matt.) Liebl. All other oak names associated with one or the other population, would be classified as synonyms and included in the intraspecific variability of *Q. petraea*. While this approach is consistent with previous studies on the *Q. pubescens* collective group in Italy (Fortini et al. 2015; Di Pietro et al. 2016; Pietro et al. 2020a, b, 2021), it is partially inconsistent with recent studies on white oaks in the Caucasus and Crimea. These studies hypothesised further taxonomic splitting within the “roburoid” group of European white oaks based on morphological and molecular data (see Semerikova et al. 2023, 2024).

The populations of Sicily (IT16) and Calabria (IT17), which are currently considered a subspecies of *Q. petraea* endemic to southern Italy (i.e. *Q. petraea* subsp. *austrotyrrhenica*) show a high degree of genetic similarity. This was highlighted by the structure analysis and confirmed by cluster analysis and PCoA (Figs. 3, 4, 5 and 6), as well as by the morphometric analysis to some extent. Nevertheless, it does not appear that there are sufficient genetic or morphological differences to distinguish a separate subspecies from the nominal *Q. petraea* subspecies. For population IT16 from Sicily, however, the presence of putative hybrids with *Q. pubescens* was hypothesised and observable in Table S12 ($q_i=0.194$ for cluster 1, $q_i=0.619$ for cluster 4), which was supported morphologically by the presence of fasciculate trichomes on the abaxial leaf surface and triangular acorn scales in some trees. Combining both the genetic and the morphometric results revealed

that populations with a significant contribution from the *Q. pubescens* subsp. *pubescens* gene pool, exhibited lower average values for size-dependent leaf morphological traits and reduced leaf obversity compared to populations with a typical *Q. petraea* gene pool. The box plots clearly show that both IT16 and FR08 (southern France) exhibit very low values for the dependent leaf size traits as well as high LDR (lobe depth ratio) and LWR (lobe width ratio) which indicates pronounced leaf lobes. These morphological characteristics are more commonly associated with *Q. pubescens* subsp. *pubescens* than with *Q. petraea* s.l. The higher presence of putative hybrids in the *Q. petraea* populations in Sicily (very close to the southernmost limit of *Q. petraea* in Europe) and, to a slightly lesser extent, in southern France can be explained by the fact that *Q. petraea* forests, in both regions, are relict enclaves within landscapes predominately characterized by *Q. pubescens* forests (see Braun-Blanquet 1952; Brullo et al. 2001, 2009). As these are peripheral populations, it is crucial to constantly monitor the erosion of their spatial dimension, as this phenomenon is directly connected to the impoverishment of the gene pool and the triggering of progressive genetic drift (Nei et al. 1975; Asins and Carbonell 1987; Millar and Westfal 1992; Schoen and Brown 1993). However, increased events of hybridization between *Q. petraea* and *Q. pubescens* populations in the future, could be viewed as a natural adaptation process of the Mediterranean deciduous oak forest to climate change. The ability of mesophilous species, such as *Q. petraea*, to adapt to climate change could be enhanced by the introgression from more drought-tolerant species, such as *Q. pubescens* (Pütz et al. 2024). According to Früchtenicht et al. (2018) the genus *Quercus* could even benefit from global warming, potentially expanding its European range from 11% to 28–40% by 2100, at the expense of more microthermic tree species. While *Q. petraea* will probably not play a leading role in the Mediterranean where a strong contraction is expected, an expansion in Northern Europe is conceivable (Ülker and Tavşanoğlu 2026).

Conclusions

Analysing the genetic and morphological variability of the *Quercus petraea* collective group across a wide area of central and southern Europe revealed some trends of diversity among taxa and geographical regions. Correspondence between genetic and morphological traits was observed (at least partially) in only a few populations, whereas a significant overlap was evident throughout the entire dataset. Neither genetic nor morphological evidence supported a differentiation of *Q. dalechampii* auct. non Ten. or *Q. banatus* from those currently assigned to *Q. petraea*

s. str. Interestingly, but in our opinion the evidence is still too weak, there is also some indication that the populations of Sicily and Calabria (S. Italy) could be considered as an autonomous subspecies (*Q. petraea* subsp. *austrorhena*). In contrast, all the *Q. petraea* s.l. populations were clearly distinct from *Q. pubescens* subsp. *pubescens* and *Q. robur* subsp. *robur* populations which were included in the dataset as outgroups for comparison.

From a phylogeographical perspective, genetic variation among populations revealed hints of biogeographical structure comprising four major groups. One group was thought to retain signs of an ancestral gene pool; one group was mainly found in the Balkans; one group was spread in southern Italy; and one group was mainly found in western and central Europe. This interpretation is consistent with the paleogeographical and paleoecological reconstructions of environmental changes that characterized the European continent during the Pleistocene ice ages and the subsequent Holocene.

Some relict populations of sessile oak in southern Italy, Sicily, and southern France were found to have undergone episodes of hybridization or introgression with *Q. pubescens*, a process that could play a key role in preserving *in situ* tree biodiversity in the context of current of global warming. Conserving the largest possible collection of alleles for dominant oak species will be crucial for developing consistent conservation strategies for entire oak forest ecosystems in the near future.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no conflict of interest.

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