

Review

Marker- and genomics-assisted assessments over three decades across Europe reveal substantial genetic diversity and adaptive potential in pedunculate oak (*Quercus robur* L.), informing operational conservation strategies

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Abstract

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This review synthesizes three decades of molecular evidence on the genetic diversity and conservation of pedunculate oak (*Quercus robur* L.) across Europe. A methodological synthesis delineates three phases of marker evolution: Phase I (1993–2003) – isozymes, RAPD, AFLP and early SSRs establishing population-genetic baselines; Phase II (2004–2014) – multi-marker integration and QTL analyses linking marker variation to adaptive traits; and Phase III (2015–2026) – the genomic era with WGS, SNP, ddRADseq and GBS systems enabling high-resolution inference of demography and local adaptation. Genetic diversity of *Q. robur* was assessed using allelic richness, observed and expected heterozygosity, fixation and differentiation indices, chloroplast haplotype diversity and SNP-based genomic metrics, consistently showing high within-population diversity, low but significant among-population differentiation maintained by extensive gene flow and spatially structured adaptive variation shaped by postglacial history and environmental gradients, confirming strong evolutionary and adaptive capacity across Europe. Integrating SSR, SNP and phenotypic evidence reveals robust adaptive potential to drought and water stress. Based on these findings and EUFORGEN guidance, a tiered conservation strategy is proposed: (i) *in situ* preservation of large, interbreeding stands; (ii) provenance-based seed transfer within seed zones; (iii) *ex situ* conservation of marginal populations; and (iv) *circa situm* management in productive landscapes. This synthesis establishes a marker-informed framework linking evolutionary processes to actionable conservation, thereby strengthening the adaptive capacity of *Q. robur* under climate change across Europe.

Keywords

forests, GWAS, high-resolution genomics, landscape genetics, neutral markers, QTL

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Introduction

Pedunculate oak (*Quercus robur* L.) is a keystone broad-leaf species distributed across Europe and Western Asia, where it thrives in diverse habitats ranging from mesic woodlands to xeric environments (EATON et al., 2016). As a foundational species, *Q. robur* plays a pivotal ecological role by supporting biodiversity and contributing to the structure and function of forest ecosystems, while also serving as a vital economic resource for timber production across European countries (LÖF et al., 2015). For instance, LANDEKIĆ et al. (2024) reported that high-quality *Q. robur* logs are of exceptionally high commercial value in Croatia and Slovenia. Similarly, Serbian public forest management enterprises, Vojvodinašume and Srbijašume, list the highest-quality log classes as premium timber resources (JP VOJVODINAŠUME, 2025; JP SRBIJAŠUME, 2025).

Despite their importance, *Q. robur* forests are becoming increasingly vulnerable throughout Europe due to combined effects of human activity, biological threats, and changing climatic conditions. Specifically, many ecosystems of this species have been modified by past human activities, such as habitat fragmentation (DEGEN et al., 2021a), land-use change and management practices (HUNG et al., 2025) and interventions affecting water dynamics in floodplain forests (LENK et al., 2025). Moreover, these forests are under increasing pressure from pathogens and pests, including the non-native species expansion (HOCH et al., 2024; ZLATKOVIĆ et al., 2024). This in conjunction with abiotic threats is causing a phenomenon known as “acute oak decline” (ZLATKOVIĆ et al., 2018). Lastly, species distribution modelling predicts moderate to large range contractions at the southern margin of *Q. robur*’s distribution including Portugal, Spain, France, Italy, parts of the Balkans, Greece, and Turkey, under the intermediate climate scenario SSP2-4.5. Under the more severe scenario SSP5-8.5, projected range contractions extend further north, potentially affecting parts of Germany (DYDERSKI et al., 2025). Consistent with these broader European trends, climate-change projections for Austria, Slovenia, Hungary, Croatia, and Serbia suggest significant declines in habitat suitability for *Q. robur* (SALLMANNSHOFER et al., 2021). These pressures threaten the sustainability of *Q. robur* populations, making the development of effective conservation and management strategies more urgent than ever. As a result, research into the adaptation and resilience of *Q. robur* has tremendously intensified in recent decades. A review of the literature on marker-based assessments of genetic diversity in *Q. robur* shows that *Quercus petraea* (Matt.) Liebl. (sessile oak) is commonly analyzed alongside it, owing to their ecological overlap and frequent but low hybridization between the two species (CURTU et al., 2007; PAKULL et al., 2025). The frequent joint investigation of *Q. robur* and *Q. petraea* in genetic and evolutionary studies is well justified by their ecological, genetic and evolutionary proximity. These two interfertile oak species codominate temperate broadleaf forests across much of Europe, displaying broad sympatric distributions and overlapping ecological niches (JURKŠIENĖ et al., 2020).

Nevertheless, *Q. robur* tends to occupy hydromorphic and flood-prone lowland sites, while *Q. petraea* is more competitive on well-drained, acidic uplands. Their divergent ecological preferences provide a natural framework for testing hypotheses on local adaptation, edaphic tolerance and climate resilience (ANNIGHÖFER et al., 2015).

In Europe, three major oak glacial refugia have been identified, including the Iberian, Italian Peninsula and the Balkans. Among these, the Balkans have been recognized as a key refugium, supporting high levels of genetic diversity, harboring a high diversity of distinct and, in part, unique haplotypes, and acting as a vital source for the recolonization of Central and Eastern Europe following the last glacial period (PETIT et al., 2002). The high genetic, phenotypic, and adaptive variation observed across Europe is likely the result of long-term population persistence combined with substantial long-distance gene flow, interfertility and a high level of outcrossing (CURTU et al., 2007). Across the southeastern European refugial region, *Q. robur* populations exhibited homogeneous genetic diversity, negligible population differentiation, and no detectable genetic structure (TEMUNOVIĆ et al., 2020). At the continental scale however, current genetic and chloroplast haplotype patterns largely reflect postglacial recolonization dynamics. Distinct lineages originating from multiple southern refugia expanded northwards, and the elevated haplotype richness seen in central Europe likely stems from secondary contact between these recolonizing fronts (DEGEN et al., 2021d). Because acorns are typically moved only a few hundred meters by vertebrate dispersers and effective pollen flow commonly falls below 100 m, gene movement since the Holocene has been insufficient to homogenize haplotypes originating from different refugial sources. Consequently, isolation-by-distance and marked spatial genetic structuring have persisted (DEGEN et al., 2021d). Population-level analyses further indicate the presence of several gene-pool clusters, with reduced levels of genetic diversity characterizing the northern, eastern and south-eastern margins of the natural distribution (DEGEN et al., 2022).

Natural hybridization and introgression are frequent in sympatric stands, blurring species boundaries and offering a unique opportunity to study mechanisms of reproductive isolation, gene flow and speciation in long-lived, outcrossing tree species (DUCOUSSO and BORDACS, 2004). Numerous studies have shown that while hybrid individuals occur, reproductive barriers – such as flowering asynchrony or postzygotic selection – maintain species integrity over evolutionary timescales (MARIETTE et al., 2002; SCOTTI-SAIN-TAGNE et al., 2004a; CURTU et al., 2007; NEOPHYTOU et al., 2015). The pedunculate and sessile oaks are a prominent example, as they share similar postglacial recolonization histories, having expanded from partly overlapping refugial areas in southern Europe. Low hybridization rates among four oak species in Romania (*Q. robur*, *Q. petraea*, *Q. pubescens* and *Q. frainetto*) indicate that reproductive barriers remain effective and that species identity is largely maintained (CURTU et al., 2007). Chloroplast DNA studies have revealed slight differences in lineage composition, contrib-

uting to the resolution of European oak phylogeography and the reconstruction of colonization routes (PETIT et al., 2002; COTTRELL et al., 2002). The consistent co-analysis of *Q. robur* and *Q. petraea* has also been instrumental in designing conservation strategies, defining seed transfer zones and informing sustainable forest management practices that preserve adaptive genetic variation in both species (DEGEN et al., 2021b; BURGER et al., 2021). The dual-species approach enhances the resolution of evolutionary and ecological patterns and provides a robust comparative model for the study of gene-environment interactions, hybridization dynamics and the evolutionary consequences of forest management in European oaks (DUCOUSSO and BORDACS, 2004; PAKULL et al., 2025).

More broadly, European oaks represent an evolutionary successful group in which long generation time, extensive standing genetic variation, recurrent hybridization and adaptive introgression have jointly supported persistence and diversification under heterogeneous and constantly changing environments (KREMER and HIPPEL, 2020).

Aim of the study

The aim of this review is to systematically synthesize and critically evaluate three decades of molecular and genomic research on the genetic diversity, population structure, and adaptive potential of *Q. robur* across its European distribution range. More specifically to:

- trace the methodological evolution from early-stage molecular markers (isozymes, random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), etc.) to high-resolution genomic systems (single-nucleotide polymorphism (SNP), double digest restriction-site associated DNA sequencing (ddRADseq) and genotyping-by-sequencing (GBS) and whole genome sequencing (WGS)), capturing both neutral and potentially adaptive variation.
- identify consistent patterns in within- and among-population genetic variation and post-glacial structuring.
- translate these findings into a coherent, operational framework for *in situ*, *ex situ* and *circa situ* conservation under accelerating climate change.

The ultimate purpose of the present paper is to strengthen long-term conservation and adaptive management of *Q. robur* genetic resources in Europe by bridging the gap between molecular research and applied forest management. It integrates findings from population genetics, quantitative trait analyses, and recent genomic studies.

Methodology

This paper is structured as an integrative review that synthesizes three decades of *Q. robur* genetic variation re-

search across Europe, integrating findings from diverse marker systems, spatial scales, adaptation and evolutionary contexts to support future conservation, genetic monitoring and biodiversity-assessment strategies for the species. The process did not involve any new data generation, statistical or correlation analyses, but relied exclusively on published, peer-reviewed scientific literature. Studies were identified through targeted searches in Web of Science, SCOPUS, and institutional databases, using relevant keywords. Search covered the period from 1993 to 2026 and combined taxon-specific, marker-specific and topic-specific terms. The core search logic combined “*Quercus robur*” with terms such as “genetic diversity”, “population structure”, “phylogeography”, “chloroplast DNA”, “microsatellite”, “SSR”, “SNP”, “ddRADseq”, “GBS”, “QTL”, “GWAS”, “adaptive variation”, “provenance”, “forest reproductive material” and “conservation genetics”. Additional references were identified through backward and forward citation checking of key review papers and highly cited empirical studies. All retrieved papers were screened for relevance based on explicit inclusion criteria: (i) the study must provide empirical data on molecular or genomic diversity, (ii) the focal taxon must be *Q. robur* or mixed *Q. robur*–*Q. petraea* stands, and (iii) genetic parameters must be reported or inferable. Studies were excluded when they dealt only with morphology, silviculture, pathology, physiology or species distribution modelling without molecular, genomic or marker-assisted evidence. Publications were also excluded when *Q. robur* was not analyzed at species or population level, when genetic parameters could not be extracted or interpreted, or when the paper represented a general oak review without primary evidence relevant to the synthesis. Studies including *Q. petraea* were retained only when *Q. robur* was explicitly analyzed or when mixed *Q. robur*–*Q. petraea* stands were necessary for interpreting hybridization, introgression, species assignment or shared phylogeographic patterns. Selected publications were organized chronologically and classified according to the type of genetic markers used, resulting in three methodological phases that reflect the evolution of forest genetic research. Phase I (1993–2003) encompassed studies employing isozymes, RAPD, AFLP, and early microsatellites that established baseline information on heterozygosity and gene flow. Phase II (2004–2014) integrated multiple marker systems and introduced QTL mapping to connect neutral genetic variation with adaptive traits, such as phenology and growth. Phase III (2015–2026) represented the genomic era, characterized by high-throughput SNP, ddRADseq and GBS platforms providing fine-scale demographic and adaptive insights. For each retained study, extracted information included year of publication, geographic scope, sampled populations, marker system, analytical approach, reported genetic parameters, main findings and conservation relevance. Marker systems were grouped according to their main inferential function and biological interpretation. Neutral nuclear markers, including isozymes, RAPD, AFLP and SSRs, were considered primarily in relation to neutral diversity assessment, population genetic structure,

fine-scale spatial genetic structure, gene flow, inbreeding and species assignment in mixed *Q. robur*–*Q. petraea* stands. Adaptive or putatively adaptive marker systems, including QTL-linked markers, candidate-gene SNPs, genome-wide SNPs, ddRADseq, GBS and GWAS/GEA-related approaches, were considered in relation to adaptive-trait mapping, genotype–environment associations, local adaptation and climate-resilience inference. Chloroplast and mitochondrial markers were treated separately because they mainly inform phylogeographic lineage tracing, postglacial recolonization routes, seed-mediated dispersal and provenance history. Operational conservation, forest reproductive material (FRM) monitoring and biodiversity informatics applications were then interpreted as cross-cutting outputs supported by these three marker categories. This coding allowed comparison among studies even when marker systems and statistical outputs were not directly equivalent. Each study was manually annotated in a comparative data table (Supplementary S1) capturing marker system, aim, study region, and reported diversity metrics to ensure methodological consistency. Additionally, Supplementary S2 provided a schematic timeline linking methodological advances with the scientific questions they enabled, illustrating how increasing genomic resolution improved inference power through time. A quantitative meta-analysis was not performed because the reviewed studies differed substantially in marker systems, geographic regions and methodological phases, therefore, the focus was rather on convergence of evidence across these aspects. The emphasis was on data comparability across marker systems, regional coverage and ecological representativeness of sampled populations. The analysis also included cross-referencing of methodological protocols to highlight consistency in sampling strategies, allele scoring and data interpretation, thus ensuring reproducibility of the synthesis. We adopted a critical synthesis, to identify robust patterns and derive conservation recommendations applicable across Europe, while distinguishing them from findings that remain method- or region-specific. Ultimately, this approach provided a comprehensive overview of how marker development shaped the understanding of *Q. robur*'s genetic diversity, structure, and conservation relevance across Europe.

ChatGPT 5.5 was used solely for language editing to improve clarity and readability. All AI-assisted edits were critically reviewed and accepted, modified, or rejected by the authors before incorporation. It was not used to generate scientific content, analyze data, interpret results, or formulate conclusions.

From early neutral markers to high-resolution genomics: methodological development in assessing *Quercus robur* genetic diversity across Europe

Supplementary Table S1 presents a chronological synthesis of studies employing different marker systems to investigate the genetics of *Q. robur*. The following is an interpretation of marker systems evolution in relation to the three different phases.

Phase I (1993–2003)

The evolution of marker systems in *Q. robur* research has responded to four intertwined pressures: i) falling genotyping costs with rising throughput, ii) the need to detect ever subtler patterns of structure, iii) adaptation and operational demands for provenance control and conservation, and iv) continuous need to assess and understand diversity beyond morphometric and silvicultural measurements. Isozymes (MÜLLER-STARCK et al., 1993) were the first broadly accessible, co-dominant markers and established baseline heterozygosity and weak subdivision, but their few, modestly polymorphic loci limited power to resolve F_{ST} in the 0.01–0.05 range. Early investigations employing isozymes and RAPDs provided initial insights into hybridization and interspecific gene flow but suffered from low reproducibility and limited polymorphism, restricting their capacity to resolve fine-scale diversity patterns (BACILIERI et al., 1996). RAPD based analyses (YAKOVLEV and KLEINSCHMIT, 2002) saw declining use due to dominant inheritance and reproducibility issues. While AFLPs improved resolution by generating numerous anonymous loci, their dominant inheritance precluded heterozygosity estimation and constrained population-level inference; moreover, although studies in mixed stands detected substantial marker-frequency differences, the absence of species-specific loci limited their diagnostic value (BAKKER et al., 2001; COART et al., 2002).

Phase II (2004–2014)

PCR-based microsatellites (SSRs) for *Q. robur* arrived in 1997 (STEINKELLNER et al., 1997) and KAMPFER et al. (1998), who in particular, introduced 32 highly polymorphic loci, offering codominance, high allelic diversity and Mendelian inheritance; paired with legacy isozymes in 1998 (STREIFF et al., 1998), they revealed fine-scale spatial genetic structure within mixed stands that enzymes alone could not detect. Early SSR applications in elite trees detected high polymorphism and even triploidy (LEFORT et al., 1998). Subsequent studies (BARRENECHE et al., 1998; AVANZI et al., 2025) showed that SSRs provide codominant, highly polymorphic loci suited for estimating allelic richness (A_r), observed (H_o) and expected heterozygosity (H_e) and fixation indices (F_{ST}), revealing both high genetic diversity typical of *Q. robur*'s outcrossing system and pronounced latitudinal structuring with elevated private allelic richness (PAr) in Italian rear edge populations (AVANZI et al., 2025).

As questions shifted from “how diverse?” to “how structured across the genome?”, researchers added AFLPs (MARIETTE et al., 2002): hundreds of anonymous loci delivered broad genomic coverage at low cost when only a handful of SSRs were available. Because AFLPs are dominant, they complemented rather than replaced SSRs. Chloroplast SSRs and haplotypes added a maternal lineage perspective, elucidating postglacial migration patterns and distinguishing between indigenous and introduced gene pools, as demonstrated in German Slavonian oak studies (BURGER and GAILING, 2022). These findings corroborate

the persistence of high nuclear diversity despite historical translocations, with low F_{ST} (0.01–0.02) reflecting extensive gene flow (BURGER et al., 2021). cpDNA surveys also resolved lineage composition and colonization routes (PETIT et al., 2002). Comparative marker studies highlighted that SSRs captured finer scale diversity (higher H_e and A_r), while AFLPs reflected broader differentiation (MARIETTE et al., 2002). Analytical work cautioned that classical indices like G_{st}/D_{st} may underestimate subdivision in highly polymorphic, outcrossing taxa (GREGORIUS et al., 2007). Combined morphological and nuclear SSR data improved species assignment in hybridizing complexes, though genetic clustering alone was often robust (RELLSTAB et al., 2016).

Phase III (2015–2026)

The introduction of SNP genotyping via ddRADseq provided genome wide coverage and finer resolution of subtle differentiation across eastern populations, improving demographic inference and effective population size (N_e) estimation (BLANC JOLIVET, 2020). Genomic resource development through hypomethylated libraries facilitated SNP discovery (LESUR et al., 2015). Compared to SSRs, SNPs reduced scoring error and increased statistical power, particularly for detecting cryptic structuring and adaptive variation. High resolution SNP genotyping (DEGEN et al., 2021b, 2021c, 2021d) enabled detection of allelic diversity ($\nu a=1.472$ – 1.603) and low heterozygosity ($H_o \approx 0.305$ – 0.358) in fragmented eastern populations, captured broad scale spatial autocorrelation up to 1,250 km, and delineated two major gene pools with west–east structuring influenced by postglacial recolonization and introgression from *Q. petraea*. Recent applications include SNP based genotyping by sequencing in semi natural UK woodland (HUNG et al., 2025) and development of 38 near diagnostic SNPs to resolve white oak species assignments (KREMER et al., 2024). Early genome scans integrating AFLPs, SSRs, SNPs and SCARs identified outlier loci under directional selection (SCOTTI SAINTAGNE et al., 2004a). Integrative approaches using isozymes and cpDNA documented cyto nuclear discordance due to historical introgression (CURTU et al., 2011). EST derived SSRs helped distinguish species discriminant markers likely under selection from provenance specific loci shaped by gene flow and local adaptation (NEOPHYTOU et al., 2010).

From 2004 onward, the field pivoted decisively toward trait–genome links: multi-marker genome scans and the first QTL maps (SCOTTI-SAINTAGNE et al., 2004b) identified loci for spring phenology and early growth, while a parallel scan localized genomic regions differentiating *Q. robur* and *Q. petraea* (SAINTAGNE et al., 2004b), foreshadowing how selection can maintain species boundaries despite gene flow. Comparative mapping extended QTL coherence across species (CASASOLI et al., 2006) and stress-response QTL for waterlogging tolerance (PARELLE et al., 2007) tied adaptive physiology to specific genomic intervals. In the same period, chloroplast DNA haplotypes (GAILING et al., 2007) refined lineage and provenance in-

ference: maternally inherited, haploid cpDNA – effectively one quarter of the nuclear effective population size – retains strong phylogeographic signal and traces seed-mediated dispersal even when nuclear structure is weak.

With foundational resources in place, transcript-derived and genomic resources (LESUR et al., 2015) enabled EST-linked markers that anchor variation to genes. Using mature, inexpensive SSR panels, landscape-genetic studies (VRANCKX et al., 2014a, 2014b) quantified pollen flow, inbreeding and fragmentation effects at management-relevant scales, while EST-SSRs (NEOPHYTOU et al., 2015) helped separate anthropogenic seed transfer from adaptive divergence. At range edges, SSRs remained optimal through cross-study comparability, high heterozygosity per locus, and relatively low-cost assay suitable for peripheral, data-poor contexts (DEGEN et al., 2019). Conceptually, the period from 2012 onward consolidated Q_{ST} – F_{ST} and polygenic frameworks, providing formal tests to distinguish selection on quantitative traits from drift and offering a principled bridge between QTL results and population-genetic baselines.

A major enabling step was the publication of the oak reference genome (PLOMION et al., 2018), which placed earlier QTL intervals in precise genomic context, accelerated candidate-gene discovery and facilitated dense SNP assay design. The next leap was statistical and economic: reduced representation sequencing (BLANC-JOLIVET, 2020) and targeted SNP/indel panels (DEGEN et al., 2021b) delivered thousands of low-errors, genome-wide biallelic loci; because power to detect weak structure and infer demography scales with the number of independent loci, SNPs outperformed SSRs for fine structure, N_e estimation and introgression mapping. Whole-genome and landscape-genomic analyses (LEROY et al., 2020a, 2020b) then revealed massive post-glacial gene flow and adaptive introgression in European white oaks, allowing allele–environment associations to be cross-checked against QTL intervals for trait-based inference of local adaptation. High-density GBS and near-diagnostic SNP sets (HUNG et al., 2025) have converted research advances into operational tools – species assignment, provenance matching, and routine monitoring – directly informing seed transfer and conservation planning under climate change. Most recently, whole-genome sequencing (WGS) combined with GWAS enabled the identification of wood quality trait-associated SNPs in *Q. robur*, which can subsequently be incorporated into genomic prediction models to facilitate the early selection of superior genotypes for forest breeding and management (LOBO et al., 2026). Beyond trait prediction, whole-genome and pan-genome analyses provide powerful tools for identifying the genomic basis of local adaptation. By integrating SNPs, structural variants (SVs), and outlier analyses, these approaches can reveal adaptive loci and introgressed genomic regions associated with climatic adaptation that would remain undetected using SNP-based analyses alone (LIANG et al., 2025).

State-of-the-art epigenomic approaches have enabled the study of DNA methylation variation across natural populations by combining whole-genome bisulfite se-

quencing for genome-wide discovery with targeted methylation profiling for population-level analyses (LESUR et al., 2024). Building on these methodological advances, latest epigenomic studies have revealed DNA methylation as an additional regulatory layer contributing to our understanding of phenological variation, developmental regulation and environmental responsiveness in *Q. robur* (SANCHEZ-LUCAS et al., 2025).

The transition from isozymes and RAPDs to SSRs and SNPs did not simply increase technical resolution; it changed the biological questions that could be addressed. Early markers established high within-population diversity and weak differentiation, whereas genomic tools enabled finer inference on introgression, seed-source assignment and adaptive variation.

Consistent patterns in within- and among-population genetic diversity

Q. robur generally exhibits high diversity while differentiation among populations is generally low (ZANETTO et al., 1994; SIEGISMUND and JENSEN, 2001), although regional patterns reflect the interplay of landscape connectivity, introgression and anthropogenic interventions such as seed transfer (Supplementary Table S1). Meta analysis indicates fragmentation and management can significantly affect genetic parameters (VRANCKX et al., 2012), challenging the notion that woody species are inherently resistant to genetic erosion. In western Germany, BURGER et al. (2021) observed weak differentiation between indigenous and Slavonian oaks, aligning with high gene flow reported in the Balkans according to TRUDIĆ et al. (2021a).

In the UK (Wytham Woods), HUNG et al. (2025) found minimal structure at local scales, but detected inbreeding in young plantations contrasting with NEOPHYTOU et al. (2015), who observed higher diversity in younger Upper Rhine stands due to 20th century seed transfers introducing novel variants. On the landscape level, AVANZI et al. (2025) identified a latitudinal diversity gradient in Italy, with southern populations showing distinct genetic profiles and elevated private allelic richness, while ISSR markers differentiated phenological varieties in Russia (CHOKHELI et al., 2016). Nuclear SSRs in South Ural populations detected pronounced differentiation ($F_{ST} = 0.0652$) and genetic drift at range edges (DEGEN et al., 2019) while empirical work at regional scales (e.g., Serbia) confirms low among-population F_{ST} at nuclear loci (KESIĆ et al., 2021). Genomic SNP studies (DEGEN et al., 2021b, 2021c, 2021d) revealed that eastern populations, despite fragmentation and reduced stand sizes, retain comparable allelic richness, but show higher differentiation, reflecting historical isolation and limited contemporary gene flow (i.e., spatial autocorrelation extended up to 1,250 km and two west-east gene pools were delineated with signals of *Q. petraea* introgression). NEOPHYTOU et al. (2010) documented markedly lower diversity in Greece ($H_o = 0.43$ for QrZAG87) and even lower diversity in Bulgaria ($H_o = 0.36$ for QrZAG87),

contrasting with high values in Serbia (TRUDIĆ et al., 2021a). These results suggest possible bottlenecks or reduced gene flow in parts of the southeastern range. YÜCEDAĞ and GAILING (2013) documented weak, but significant cpDNA differentiation ($cpG_{st} = 0.22$ in Turkey) and fitness consequences of inbreeding. Oak populations present a high degree of pollen immigration rates (pollen may travel up to several tens of kilometers; BUSCHBOM et al., 2011), and inbreeding levels are low (VRANCKX et al., 2014a, 2014b; NEOPHYTOU et al., 2015); which explains the low genetic differentiation among populations found in several studies. Recent fine-scale evidence from a mixed, naturally regenerating forest stand in Poland further confirms the importance of local spatial genetic structure in *Q. robur*. SANDURSKA et al. (2024), using nuclear microsatellites, found significant spatial genetic structure in both adult and seedling cohorts, with stronger structure in seedlings than in adults. Notably, the study also showed that pollen immigration can reduce spatial genetic structure in offspring resulting from external pollination, while relatedness among trees may remain significant at distances up to approximately 60 m. These findings are directly relevant for seed harvesting, as they support maintaining sufficient distance among seed trees to avoid excessive relatedness in collected reproductive material. Most neutral genetic variation (>90%) is maintained at the intrapopulation level, reflecting extensive gene flow and large effective population sizes, with only a few percent of diversity partitioned among populations (SIEGISMUND and JENSEN, 2001; VAKKARI et al., 2020). At the continental scale, subtle geographic genetic structure exists, and chloroplast DNA surveys reveal distinct regional haplotypes tracing to separate glacial refugia, and nuclear markers show isolation-by-distance clines rather than sharp genetic breaks (COTTRELL et al., 2002; BLANC-JOLIVET and LIESEBACH, 2015). Despite this neutral homogeneity, common-garden studies have found significant genetic differentiation in adaptive traits (e.g., bud burst phenology, growth rates) among *Q. robur* provenances, often in clinal patterns along climatic gradients (BALIUCKAS and PLIURA, 2003). Such findings imply that, even when neutral markers show low differentiation due to gene flow, quantitative traits can still diverge under local selection, a contrast also observed in related oak species. Populations at the species' range margins and in fragmented habitats tend to show slightly reduced allelic richness and elevated interpopulation divergence due to genetic drift and limited gene flow (VAKKARI et al., 2006; VAKKARI et al., 2020). For example, northern peripheral stands in Finland exhibit higher fixation indices (F_{ST} on the order of 5–7%) and lower heterozygosity compared to more central European populations (VAKKARI et al., 2006; VAKKARI et al., 2020). Nevertheless, even these marginal and isolated populations still retain considerable genetic variability, heterozygosity and genetic diversity comparable to core populations (SANDURSKA et al., 2019). Overall, adaptive differentiation and unique alleles can emerge in response to local environmental conditions (BLANC-JOLIVET and LIESEBACH, 2015; BALIUCKAS and PLIURA, 2003).

Postglacial phylogeographic structure and diversity dynamics of *Quercus robur* in Europe inferred from molecular markers

Continent-wide genomic surveys document massive post-glacial gene flow among European white oaks (LEROY et al., 2020a) and adaptive introgression affecting climate-related variation (LEROY et al., 2020b). BALLIAN et al. (2010) detected 108 alleles across 12 Bosnian populations using four nuclear microsatellites, revealing elevated heterozygosity ($H_o = 0.838\text{--}0.880$) and low fixation indices (mean $F_{is} = 0.273$), suggesting preserved adaptive potential despite fragmentation. Populations closer to presumed glacial refugia in Bosnia and Herzegovina exhibited higher allelic richness and heterozygosity compared with Western Europe, suggesting that refugial proximity contributed to genetic resilience. GÖMÖRY et al. (2001), analyzing 25 populations across Slovakia, Bulgaria and Russia using isozymes, also reported slightly higher heterozygosity in *Q. robur* than *Q. petraea* ($H_e \approx 0.16$ vs. $0.13\text{--}0.15$) and minimal interspecific differentiation, with most allelic variation shared and interspecific components explaining <8% of total gene diversity. These findings collectively underline the importance of conserving large, interbreeding populations to maintain genetic connectivity and adaptive potential across its European range (GÖMÖRY et al., 2001; BALLIAN et al., 2010).

Recent molecular analyses of *Q. robur* populations in Croatia (POPOVIĆ et al., 2023) indicate high among-population structuring and the presence of multiple maternal lineages, identifying Croatia as a major contact zone of post-glacial recolonization routes rather than a genetically eroded range margin (POPOVIĆ et al., 2023). The weak phylogeographic signal in nuclear markers and the generally limited isolation by distance are most consistently explained by extensive pollen-mediated gene flow, which can reduce nuclear differentiation among populations while organellar lineages remain spatially structured.

Molecular phylogeography of *Q. robur* in Europe is currently based on a consistent and robust evidentiary framework that integrates organellar genetic markers with independent palynological evidence, enabling reconstruction of the species' postglacial history at a resolution that is directly relevant for biodiversity research and conservation practice. Continental scale approaches combining chloroplast haplotype mapping with fossil pollen records demonstrate that during the Last Glacial Maximum the distribution of European deciduous oaks was largely confined to three major southern refugial regions, corresponding broadly to western, central and eastern Europe, from which Holocene range expansion proceeded (BREWER et al., 2002; BLANC JOLIVET and LIESEBACH, 2015; LEROY et al., 2020). This expansion was accompanied by the persistence of sub-refugia, haplotype exchange among refugial areas and the formation of secondary refugia during rapid climatic oscillations at the end of the glacial period, resulting in complex but interpretable phylogeographic patterns (PETIT et al., 2002; BREWER et al., 2002; PETIT and HAMPE, 2006). A critical methodological foundation

of these inferences is the experimentally confirmed maternal inheritance of the chloroplast and mitochondrial genomes in *Q. robur*, which renders chloroplast DNA a marker of seed mediated gene flow and thus particularly suitable for reconstructing colonization routes and long term spatial genetic structure (DUMOLIN et al., 1995). Phylogeographic interpretation in European white oaks must nevertheless explicitly account for their interfertility and for the extensive secondary contact and introgression that accompanied postglacial expansions, producing genomes that can be understood as mosaics of regions with differing permeability to gene flow across species boundaries (LEROY et al., 2017; LEROY et al., 2020). This broader evolutionary context is consistent with the view of oaks as a highly successful temperate tree lineage in which gene flow and hybridization do not necessarily erode species integrity but may contribute to adaptive potential under changing environments (KREMER and HIPPE, 2020). In this context, the integration of organellar haplotypes with nuclear microsatellite and SNP markers has become the standard analytical framework for disentangling historical demographic signals from contemporary gene flow, while simultaneously supporting applications that directly contribute to biodiversity knowledge and genetic conservation. Marker assisted DNA fingerprinting enables reliable species identification and geographic origin assignment when supported by appropriate reference datasets, which is particularly important for the traceability of forest reproductive material and for reducing the risk of afforestation using maladapted or non-local provenances (BLANC JOLIVET and LIESEBACH, 2015). More recently, high throughput genotyping by sequencing and targeted SNP approaches have demonstrated that accurate assignment to regional gene pools can be achieved across large spatial scales, namely an accuracy of 93 percent within the eastern distribution range of pedunculate oak, thereby establishing marker assisted phylogeography as an operational tool for seed source selection, verification of declared origin and the planning of conservation strategies aimed at preserving the evolutionary legacy embedded in representative populations (DEGEN et al., 2021b; DEGEN et al., 2022).

Integrating genomic, phenotypic and transcriptomic evidence of diversity to assess *Quercus robur* adaptive potential

The integration of genetic, phenotypic and environmental data highlights the complex interplay shaping *Q. robur*'s drought adaptation. BOGDAN et al. (2017) and TEMUNOVIĆ et al. (2020) provided compelling evidence for local adaptation, though their methodologies diverged. TEMUNOVIĆ et al. (2020) used Genotype-Environment Association (GEA) analyses to link SNP allele frequencies with water availability, while BOGDAN et al. (2017) focused on phenotypic traits like survival and growth under drought. Both studies converge on the conclusion that *Q. robur* populations from drier habitats possess adaptive advantages, yet their approaches emphasize different aspects of adaptation.

Bridging these perspectives, STOJNIC et al. (2019) and VASTAG et al. (2020) concentrated on leaf functional traits to identify those that directly influence water-use efficiency in *Q. robur* seedlings, and can also serve as reliable indicators of this species' drought tolerance. These phenotypic studies complement the genetic insights of TEMUNOVIC et al. (2020) by providing functional traits that can serve as proxies for genetic adaptation in breeding programmes. However, VASTAG et al. (2020) focused on half-sib lines highlights the genetic variability even within closely related populations, suggesting that selection for drought resilience must also consider intra-population diversity. UTKINA and RUBTSOV (2017) review the characteristics of early and late phenological forms of *Q. robur*, focusing on their differences in leaf flushing timing, habitat preferences and responses to environmental factors. The authors discuss the historical context of these phenological forms, their distribution across various regions, and the contrasting views on their habitat preferences. They highlight the late form's superior resistance to frost and insect damage, making it preferable for plantations. The contrasting methodologies across studies, ranging from GEA analyses (TEMUNOVIC et al., 2020) to proteomic and transcriptomic approaches (SPIEB et al., 2012), highlight the need for integrative frameworks. While GEA studies excel at identifying candidate genes for local adaptation, they may overlook the phenotypic expression of these genes under field conditions. Conversely, phenotypic studies like those by BOGDAN et al. (2017) and STOJNIC et al. (2019) provide actionable traits for breeding but may lack the genomic resolution to pinpoint causal mechanisms. This methodological diversity complicates direct comparisons but also enriches the broader understanding of *Q. robur*'s adaptive strategies. For example, Gradient Forests used by MEGER et al. (2024) offer predictive insights into population vulnerability, while multivariate regression trees (MRT) employed by BOGDAN et al. (2017) link specific environmental variables to population differentiation. The integration of these tools could provide a more comprehensive understanding of adaptive variation and its drivers.

Two studies investigated the response of *Q. robur* to drought stress, employing different approaches and time scales. SPIEB et al. (2012) conducted a comprehensive two-year experiment analyzing morphological, physiological, and transcriptomic responses to long-term drought and subsequent rewatering. They found that long-term drought significantly reduced shoot growth and altered the timing and number of leaf flushes. During the early phase of drought, soluble sugars such as glucose and fructose accumulated, while prolonged drought led to an accumulation of more stable osmolytes, such as quercitol and mannitol. Transcriptomic analysis revealed that over 3% of expressed sequence tags (ESTs) were differentially expressed, reflecting activation of defense responses which revealed stronger in the second year. Rewatering resulted in important compensation growth, suggesting that oak exhibits adaptive mechanisms enabling survival and recovery from prolonged drought.

SERGEANT et al. (2011) focused on a single grow-

ing season, aiming to mimic a dry summer. They used a two-dimensional difference gel electrophoresis (2D-DIGE)-based proteomic study alongside morphological and carbohydrate analyses. Reduced growth and altered developmental stage transitions were observed. The proteomic data, along with the complementary transcriptomic data from SPIEB et al. (2012), suggested initial metabolic adaptation to maintain functionality. However, prolonged drought eventually overwhelmed these adaptive mechanisms, leading to a decline in the molecular machinery at the final sampling point. Interestingly, while overall RuBisCo levels decreased, fragments were found to increase, possibly indicating degradation processes under stress. Other proteins involved in carbohydrate metabolism, stress responses, and nutrient storage exhibited significant changes. The study by TRUDIC et al. (2021b), which highlights the role of senescence-related genes such as *wrky53*, *rd22*, and *sag21*, providing critical insights into the genetic mechanisms underlying adaptive drought related stress responses in *Q. robur*, introduces an important nuance to our understanding of the species' adaptability by showing that gene expression patterns vary primarily among phenological groups within a population. This finding emphasizes the complexity of genetic regulation and its interplay with phenological traits.

Recent epigenomic evidence further expands this integrative framework. SANCHEZ-LUCAS et al. (2025), using whole-genome bisulfite sequencing in mature *Q. robur* trees and their progeny, reported distinct seasonal and generational DNA methylation signatures. Seasonal variation was mainly associated with CHH (cytosine-H-H context, where H = A, T or C) methylation dynamics, particularly from spring to summer and autumn, while parent-offspring differences were more pronounced in CG (cytosine-guanine) and CHG (cytosine-H-guanine context, where H = A, T or C) contexts. These findings suggest that epigenetic regulation may contribute to phenology, developmental programming and short-term environmental responsiveness in long-lived oaks.

Genomic mapping of adaptive traits in *Quercus robur*: from QTLs to GWAS

Population-genetic assessments and trait-mapping approaches (QTL mapping and GWAS) address complementary aspects of genetic variation in *Q. robur*. While traditional QTL mapping connects phenotypes to genomic regions, Genome-Wide Association Studies (GWAS) extend this concept to natural populations, leveraging standing variation and population-level linkage disequilibrium to detect loci contributing to trait variation (KORTE and FARLOW, 2013; CORTES et al., 2021). GWAS bridges the gap with population genetics which quantifies how neutral and (putatively) adaptive variation is structured across space and time. When combined, they strengthen inference about local adaptation, help discriminate drift from selection and make genetic monitoring and seed transfer guidelines more trait-informed (SCOTTI-SAINTAGNE et al.,

2004a, 2004b).

QTL mapping in *Q. robur* has identified genomic regions controlling key adaptive traits, most notably spring phenology and early growth (SCOTTI-SAINTAGNE et al., 2004b), tolerance components to waterlogging (PARELLE et al., 2007), and cross-species-informative regions for adaptive traits via comparative mapping (CASASOLI et al., 2006). The availability of a high-quality *Q. robur* reference genome further enables precise localization of QTL, candidate-gene identification and design of targeted genotyping panels (POMION et al., 2018). Theory predicts that quantitative trait divergence (Q_{ST}) should exceed neutral marker divergence (F_{ST}) under spatially heterogeneous selection; conversely, $Q_{ST} \approx F_{ST}$ suggests drift (LE CORRE and KREMER, 2012). In oaks, leveraging common-garden trait data (e.g., budburst timing) against genomic differentiation thus helps validate whether QTL-linked regions participate in adaptation rather than reflect demographic history alone. In parallel, interspecific QTL scans have localized genomic clusters underlying diagnostic morphological differences between *Q. robur* and *Q. petraea*, highlighting polygenic, distributed architectures that can also shape intraspecific patterns (SAINTAGNE et al., 2004; LE CORRE and KREMER, 2012). QTL effect sizes can be small, environment-specific, and pedigree-dependent; replication across sites/years and integration with association mapping are advisable (SCOTTI-SAINTAGNE et al., 2004b; CASASOLI et al., 2006). Given pervasive gene flow, single marker “diagnostics” are unlikely to be robust; polygenic scores anchored in biologically validated QTL are more defensible. Finally, because standing variation is high, but differentiation is low in *Q. robur*, careful modelling of structure and demographic history is essential when inferring selection. QTL studies and population genetics are mutually informative in *Q. robur*: QTLs indicate *what* to monitor (trait-linked regions), while population genetics indicates *where and how* to monitor (sampling frames, demographic baselines). Their integration yields more reliable inferences about adaptation and supplies actionable markers for conservation and management.

The number of QTLs detected, and their individual effects vary considerably, reflecting the complexity of each trait and the differing selective pressures they face. The studies also differ in their experimental designs and the level of replication, influencing the power to detect QTLs and the precision of effect estimations.

Complementing these QTL-based insights, GWAS in *Q. robur* now allows trait–genotype associations to be tested directly in natural populations. For instance, a mixed-model association analysis of ~819 genome-distributed SNPs detected significant marker associations with survival, height, acorn weight, and powdery mildew infection in a juvenile oak cohort (BARRÈS and DESPREZ-LOUSTAU, 2024).

While all mentioned studies contribute significantly to our understanding of *Q. robur* genetics, their combined results underscore the complex interplay between genetic architecture, environmental influence and the specific traits under investigation. Future research should aim to

integrate these findings to improve our understanding of the genetic basis of adaptive traits and strengthen conservation and breeding strategies for this ecologically and economically important species.

From genetic evidence to operational conservation: biodiversity informatics, FRM and forest genetic resources (FGR) monitoring

Biodiversity informatics is considered relevant to this review because molecular and genomic evidence becomes applicable to conservation practice when it is integrated into structured data systems, genetic conservation units, seed-source documentation and long-term monitoring frameworks. For *Q. robur*, platforms such as SilvaGRIS, EUFGIS and the Quercus Portal can be regarded as mechanisms through which dispersed marker-based evidence is translated into operational information for forest genetic resource conservation, provenance evaluation and adaptive forest management. Through these systems, population-genetic knowledge can be documented, compared and spatially interpreted across countries and conservation contexts, thereby supporting more evidence-based decision-making.

The Quercus Portal (accessible at <https://quercusportal.pierroton.inrae.fr/>) serves as a critical tool for advancing research and conservation of oak species, including *Q. robur*. It provides access to genetic, taxonomic, and distribution data, supporting complex cross database queries and linking to the Evoltree eLab system (STIERSCHNEIDER et al., 2016). Regular updates include interactive tools, maps and images, enabling researchers and policymakers to explore genetic diversity and resilience, facilitating informed conservation and management strategies under climate change (TRUDIĆ et al., 2024). Its integration of genomic data underscores its role as a benchmark for digital tools supporting forest biodiversity management (EHRENMANN et al., 2014).

Based on the most recent datasets extracted from the SilvaGRIS information system, 28 European countries participated in the Second Report on the State of the World's Forest Genetic Resources exercise (FAO, 2025a). Of these, 25 countries reported national distribution data for *Q. robur*, referring to areas within national territories where the species occurs naturally and, where applicable, where it has been introduced. Furthermore, 21 countries reported non-molecular characterization of *Q. robur* forest genetic resources, defined as the description and evaluation of populations or provenances based on field observations, provenance trials, or ecological and climatic zonation of the species' distribution range relying on visually observable heritable traits consistently expressed across environments. In addition, 18 countries reported molecular characterization of *Q. robur* genetic resources, based on the use of molecular markers and/or genomic approaches for the description and evaluation of genetic diversity and structure (FAO, 2025b).

In practical terms, these results provide an integrated

assessment of how well *Q. robur* forest genetic resources are documented, understood and managed across Europe, while also highlighting persisting capacity gaps. The widespread availability of national distribution data, reported by 25 of the 28 participating countries, indicates that the spatial occurrence of *Q. robur* is largely mapped at the national scale. Such detailed, up to date and spatially explicit distribution data are essential for species distribution modelling under future climate scenarios and for identifying and locating suitable FRM in support of conservation efforts. This level of information directly supports forest planning, conservation prioritization and restoration activities, enabling the designation of *in situ* conservation units, alignment with protected-area networks and the integration of *Q. robur* into national forest and climate-adaptation strategies. Nevertheless, the absence of such data in a small number of countries points to remaining geographic knowledge gaps that may constrain evidence-based decision-making.

The fact that 21 countries reported non-molecular characterization demonstrates that most European countries possess operational, field-based knowledge on phenotypic and adaptive variation in *Q. robur* populations or provenances. This information underpins practical forestry decisions, particularly regarding the selection of appropriate reproductive material, provenance choice for afforestation and restoration and the matching of planting material to site conditions under current and projected climates. Conversely, countries lacking such characterization face an increased risk of maladaptation due to the use of poorly matched or insufficiently evaluated forest reproductive

material.

By contrast, molecular characterization, reported by only 18 countries, remains less widely implemented. Although not essential for routine silvicultural practice, molecular and genomic data are critical for quantifying genetic diversity, resolving population structure, identifying unique or marginal gene pools and assessing genetic risks associated with fragmentation, introgression or inappropriate gene flow. The uneven availability of molecular data therefore limits the capacity to define long-term genetic conservation priorities, to coordinate transboundary management of shared gene pools, and to design robust climate-adaptive and assisted restoration strategies. At the same time, recent evidence from natural *Q. robur* stands shows that molecular data alone may be insufficient for predicting growth stability, supporting the need to combine genomic information with dendrochronological, phenotypic and ecological monitoring indicators (HALL et al., 2025).

SilvaGRIS data indicate that Europe has established a solid baseline for mapping and phenotypic understanding of *Q. robur* forest genetic resources, but that genetic-level knowledge remains incomplete and unevenly distributed. In practical terms, this means that current management and restoration efforts are generally supported by adequate spatial and field-based information, while the long-term resilience, evolutionary potential and genetic integrity of *Q. robur* populations are not yet consistently addressed. Targeted expansion of molecular characterization, particularly in countries already conducting non-molecular assessments, would therefore substantially strengthen climate-resilient management and conservation of *Q. robur* forest genetic

Table 1. Comparative coverage of *Quercus robur* genetic information across Europe

Information source	Type of genetic/ molecular information	Number of European countries covered	Basis of reporting/ inclusion	Key limitations
SilvaGRIS (FAO, SoW-FGR-2 reporting)	Molecular characterization (use of molecular markers and/or genomic approaches reported at national level)	18	Official country reporting to FAO under the Second Report on the State of the World's Forest Genetic Resources	Heterogeneous depth and marker types; reporting does not guarantee population-level resolution or harmonized datasets
EUFGIS (EUFORGEN framework)	Genetic information linked to Gene Conservation Units (GCUs)	7	Countries that uploaded <i>any</i> genetic diversity data associated with registered <i>Q. robur</i> GCUs	<5% of GCUs genetically characterized; strong spatial and national bias
This study (literature-based critical synthesis)	Marker-based genetic diversity, structure, phylogeography and adaptation (SSR, cpDNA, SNP, AFLP, etc.)	approx. 25 (pan-European coverage)	Peer-reviewed studies included in the integrative review, covering partially Northern, Western, Central, Southern, Eastern and South-Eastern Europe	Uneven sampling intensity; study designs and markers not standardized across countries

resources at both national and European scales.

The studies covered in this review collectively confirm that populations of *Q. robur* in the WB exhibit high genetic diversity, which plays a pivotal role in local adaptation to environmental challenges, particularly with regard to water availability. This genetic resilience is critical for the species' long term survival and its capacity to withstand increasing pressures from climate change. The observed low genetic differentiation between geographically close populations underscores the importance of gene flow in maintaining genetic diversity and adaptive potential. Despite these insights, much remains unknown about the genetic basis of *Q. robur*'s adaptability. Addressing such gaps (Table 1) is essential for advancing both scientific knowledge and practical conservation efforts.

The European Forest Genetic Resources Programme (EUFORGEN) published technical guidelines on how to conserve *Q. robur* and its accompanying sympatric species, *Q. petraea* across European continent based on field work and marker assisted data. Current recommendations suggest that *Q. robur* should be conserved primarily through *in situ* management that maintains large, inter-breeding stands and promotes natural regeneration, since pollen flow is extensive and most nuclear genetic diversity resides within populations. The most acute genetic risks arise from introducing exotic genotypes via plantations and from silvicultural shifts (e.g., abandonment of coppice and widespread conversion to high forest), compounded by biotic threats such as oak mildew and the potential for oak wilt (ALBERTO et al., 2013; MARÇAIS and DESPREZ-LOUSTAU, 2014; JEGER et al., 2018). When artificial regeneration is unavoidable, forest reproductive material must be sourced locally and transferred only within provenance regions, preferably from selected local seed stands with known phenotypic performance and management histories. *Ex situ* measures (e.g., clonal seed orchards based on autochthonous material) are recommended only to secure marginal, high-altitude, or small, range-edge populations and other situations where natural regeneration cannot ensure persistence. A coherent European programme should sample across the species' ecolog-

ical and phenotypic range, explicitly conserve evolutionary processes (including natural hybridization with *Q. petraea*) and retain traditional management systems that have produced locally adapted ecotypes (DUCOUSO and BORDÁCS, 2004). Recent evidence also shows that the genetic quality of *Q. robur* planting material depends more strongly on seed collection practice than on long-term acorn storage. ŻUKOWSKA et al. (2025), using nuclear microsatellites in two Polish seed stands, found that seedlings grown from acorns before and after storage maintained high and comparable genetic diversity. However, collected acorn lots were not fully representative of their source stands, indicating that the number and spatial distribution of mother trees are critical for maintaining effective population size and avoiding excessive relatedness in future planting material.

Based solely on the European Information System on Forest Genetic Resources (EUFGIS), the current evidence indicates a clear quantitative-qualitative imbalance in the conservation reporting of *Q. robur*. The most recent EUFGIS update lists 326 gene conservation unit (GCU) populations of *Q. robur*, demonstrating that *in situ* conservation coverage of the species is now extensive and well established across Europe. However, only 15 datasets associated with these GCUs include genetic information, and these originate from just seven countries. This means that less than 5% of the registered GCU populations are supported by assessed genetic diversity parameters, and that genetic characterization is geographically highly concentrated (EUFGIS, available at <https://eufgis.org/>, accessed on 17 December 2025).

In practical terms, EUFGIS currently provides robust evidence of spatial commitment to dynamic conservation of *Q. robur*, but offers limited insight into the genetic composition, representativeness, and adaptive potential of the conserved populations. The observed increase per country participation over time, visible in Fig. 1, reflects improved engagement with EUFORGEN reporting and the expansion of GCU designation. Nevertheless, the scarcity of genetic datasets implies that most GCUs are managed and reported without a validated genetic baseline, constraining the ability to evaluate population viability under climate change, detect genetic ero-

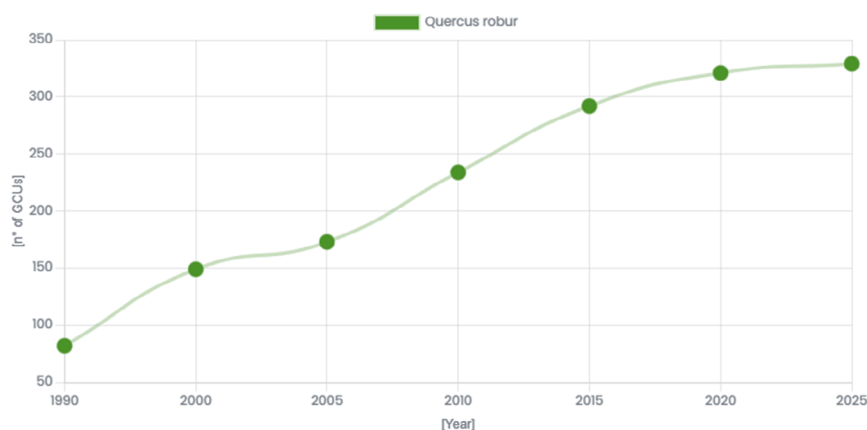


Fig. 1. Temporal evolution of country participation and strategic focus in the dynamic conservation of *Quercus robur* within the EUFGIS framework (1990–2025) (taken from EUFGIS, <https://eufgis.org/> on 17 December 2025).

Table 2. Recommendations for advancing genetic research and climate-smart adaptive management of *Quercus robur* in Europe for three types of stakeholders based on reviewed studies

Stakeholder	Recommendations	Objective	Value	Supporting or directly proposed conservation measure (<i>in situ</i> , <i>ex situ</i> or <i>circa situm</i>)*
Scientific community	GWAS	Identify specific genes and alleles associated with adaptive traits such as drought tolerance and phenological plasticity.	Enables targeted breeding programmes and enhances understanding of genetic resilience to climate change.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	High-resolution population genomics	Conduct whole-genome resequencing across diverse populations to comprehensively analyze adaptive genetic variation.	Provides a detailed genetic basis for conservation and management decisions, supporting ecosystem adaptability.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Functional genomics	Investigate the roles of candidate genes to understand molecular mechanisms driving traits like water-use efficiency and stress tolerance.	Facilitates molecular-level interventions to improve <i>Q. robur</i> resilience in the face of abiotic stresses.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Integrative multi-omics studies	Combine genomic, epigenomic, transcriptomic and phenotypic data with environmental information to establish causal links between genetic and adaptive traits.	Enhances predictive accuracy for climate adaptation strategies and improves conservation planning.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Epigenetic studies	Investigate epigenetic modifications and their role in adaptive traits like drought tolerance and phenological shifts.	Reveals non-Mendelian mechanisms of adaptation, enabling rapid-response strategies for changing environments.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Cross-species comparisons	Conduct studies comparing <i>Q. robur</i> with related species (<i>Q. petraea</i> , <i>Q. cerris</i>) to identify shared and unique adaptive mechanisms.	Broaden conservation strategies by identifying transferable traits and mechanisms across species.	Supporting (<i>in situ</i> , <i>circa situm</i>)
	Long-term monitoring	Continuously monitor <i>Q. robur</i> populations under varying environmental conditions to assess their adaptive capacity	Tracks population health and adaptation trends, providing critical data to mitigate long-term ecosystem stress	Supporting (<i>in situ</i> , <i>circa situm</i>)
	Predictive modeling	Refine predictive models with genomic data to forecast <i>Q. robur</i> 's responses to future environmental changes, supporting proactive management strategies.	Improves proactive conservation efforts, reduces risks of population decline and informs policy development for ecosystem resilience.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Citizen science engagement	Develop community-based programmes for monitoring genetic diversity using accessible tools.	Enhances monitoring coverage, fosters community involvement and raises awareness of conservation challenges.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)

Stakeholder	Recommendations	Objective	Value	Supporting or directly proposed conservation measure (<i>in situ</i> , <i>ex situ</i> or <i>circa situm</i>)*
Forestry practitioners	Conservation of high-diversity populations	Prioritize populations with high genetic diversity and drought tolerance to maintain long-term adaptive capacity in changing climates.	Ensures the survival of ecologically significant populations and promotes sustainable ecosystem services.	Directly proposed (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Incorporate morphological traits in breeding programmes	Use traits like stomatal density and leaf mass per area as indirect criteria to enhance water-use efficiency and drought resistance.	Supports the development of resilient tree stock for forestry, ensuring productivity and stability under climate stress.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Comprehensive monitoring programmes	Track genetic markers and ecophysiological parameters (e.g., photosynthesis, stomatal conductance) to support adaptive reforestation and conservation efforts.	Informs real-time adaptive management strategies, maintaining ecological balance and optimizing forest productivity.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Dynamic conservation and reforestation strategies	Leverage findings from genomic and physiological studies to design reforestation strategies tailored to local and future environmental conditions.	Promotes healthy forest ecosystems while aligning with climate-smart forestry goals and long-term sustainability.	Support directly proposed conservation measures
	Application of predictive tools	Use predictive models integrating genomic and ecological data for effective reforestation planning and population management.	Reduces uncertainty in reforestation efforts, ensuring resource efficiency and strengthening ecosystem resilience to environmental changes.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Assisted gene flow	Facilitate the movement of genetic material between isolated populations to enhance genetic diversity and reduce inbreeding risks.	Promotes genetic connectivity and boosts adaptive potential in fragmented landscapes.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Climate-responsive seed banks	Establish seed banks storing germplasm from genetically diverse populations, prioritizing those most at risk from climate change.	Provides a safeguard against catastrophic losses and supports future reforestation and restoration efforts.	Direct (<i>ex situ</i>)
	Support for genetic monitoring programmes	Establish national and regional programmes for monitoring genetic diversity and adaptation in <i>Q. robur</i> populations.	Provides critical insights into population health and adaptive capacity, ensuring proactive management strategies	Supporting (<i>in situ</i> , <i>circa situm</i>)
	Funding for genome-wide research	Allocate funds for genome-wide association studies and high-resolution population genomics to identify adaptive genetic traits	Drives discovery of adaptive traits, enhancing conservation and breeding programmes to tackle climate challenges.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)

Stakeholder	Recommendations	Objective	Value	Supporting or directly proposed conservation measure (<i>in situ</i> , <i>ex situ</i> or <i>circa situm</i>)*
Policy makers	Incorporation of genetic data in policy frameworks	Embed genetic findings into forestry and conservation policy frameworks to ensure data-driven decision-making.	Ensures that genetic research directly informs practical conservation and forestry decisions.	Supporting (<i>in situ</i> , <i>ex situ</i> , <i>circa situm</i>)
	Promotion of assisted gene flow initiatives	Facilitate the movement of genetic material between fragmented populations to enhance diversity and reduce inbreeding.	Improves genetic resilience in fragmented landscapes, supporting ecosystem stability.	Supporting (<i>in situ</i> , <i>circa situm</i>)
	Development of climate-responsive seed banks	Prioritize the establishment of seed banks containing diverse germplasm to safeguard genetic resources against climate change.	Secures the genetic foundation of <i>Q. robur</i> , enabling adaptive management under climate stress.	Direct (<i>ex situ</i>)
	Encouragement of international collaboration on genetic conservation	Foster international partnerships to exchange knowledge, resources, and strategies for genetic conservation of <i>Q. robur</i> .	Enables knowledge sharing and coordinated efforts, maximizing the impact of conservation initiatives.	Supporting (<i>in situ</i> , <i>circa situm</i>)
	Policy for sustainable use of genetic resources	Create policies ensuring equitable and sustainable utilization of <i>Q. robur</i> genetic resources.	Balances resource use with conservation goals, ensuring long-term sustainability of <i>Q. robur</i> populations.	Supporting (<i>in situ</i> , <i>circa situm</i>)
	Implementation of genomic tools in reforestation policies	Adopt genomic data to inform reforestation efforts, ensuring the use of genetically diverse and climate-resilient planting materials.	Enhances the success of reforestation projects and promotes biodiversity in restored ecosystems.	Supporting (<i>in situ</i> , <i>circa situm</i>)

*Explanation: *In situ* conservation maintains genetic resources within their natural habitats and evolving populations, *ex situ* conserves them outside natural habitats in controlled collections (e.g., seed banks, clonal archives) and *circa situm* safeguards genetic diversity in managed or production landscapes near original localities (e.g., farms, plantations, shelterbelts) where evolutionary processes can still operate under human management (FAO, 2025a).

sion, or prioritize units for assisted gene flow or adaptive management. Consequently, within the EUFGIS framework, *Q. robur* conservation is currently driven primarily by ecological and management criteria, while systematic genetic monitoring remains an exception rather than a standard component of dynamic conservation practice.

While official reporting systems (SilvaGRIS and EUFGIS) demonstrate increasing institutional engagement with *Q. robur* conservation, they currently cover a substantially narrower genetic evidence base than that available in the scientific literature. This review therefore consolidates and systematizes dispersed, multi-decadal genetic knowledge across at least 25 European countries, effectively bridging the gap between research outputs and operational conservation frameworks. Across the different stakeholder groups (Table 2) a range of tools can be applied, each serving distinct objectives and providing specific value for supporting

Q. robur conservation efforts throughout Europe.

Concluding remarks

This review demonstrates that three decades of molecular and genomic research have substantially advanced the understanding of genetic diversity, population structure and adaptive capacity in *Q. robur* across Europe. Despite that regional variation shaped by postglacial dynamics, environmental gradients and anthropogenic pressures, the species consistently exhibits high within-population diversity and low but significant differentiation, reflecting extensive gene flow and strong evolutionary potential. The transition from early neutral markers to high-resolution genomic platforms has enabled increasingly precise inference of demographic history, local adaptation and introgression, while linking genetic variation to relevant ecophysiological traits. The evolutionary success of oaks has relied on the

maintenance of genetic diversity, interpopulation connectivity and adaptive variation; these same processes should therefore remain central to conservation and forest reproductive material policy for *Q. robur* under climate change.

The accumulated evidence presented herein supports a multi-tiered conservation strategy integrating *in situ* preservation of large, interbreeding stands, *ex situ* safeguarding of marginal populations, provenance-based seed transfer and *circa situm* management for long term sustainability of *Q. robur*. Genomic tools now provide actionable guidance for seed sourcing, monitoring, assisted gene flow and climate adaptive reforestation planning. As climate pressures intensify, the integration of genetic data into forest policy, management frameworks and long-term monitoring programmes will be essential for maintaining the adaptive capacity of *Q. robur* and ensuring the resilience of European forest ecosystems.

Continued investment in genomic resources, co-ordinated European collaboration and the alignment of research outputs with operational forestry will further strengthen evidence-based decision-making and will support the sustainable conservation of this keystone species.

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Supplementary material

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