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Making use of oak genomes

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Abstract

This review summarizes the contributions of genomics to our understanding of oak evolution and management, both past and ongoing. Far from being exhaustive given the large number of publications following the publication of the genomes, this review emphasizes work conducted in the decade following publication of the first two complete oak genome assemblies, and major findings and achievements regarding (1) oak evolutionary history, (2) speciation and introgression, and tools for (3) tree breeding and (4) management and conservation of native forests. While reviewing recent advances, the review also looks to the future by highlighting the research opportunities offered by genomics in conjunction with other developments in ecology and genetics.

Keywords

Quercus, phylogeny, hybridization, introgression, speciation, breeding, selection, conservation

Oaks have been an evolutionary and ecological success in forests of the northern hemisphere due in large part to four properties: high rates of macroevolutionary transitions, high genetic diversity within and among species, rapid migration and rates of adaptation, and oaks' propensity to form syngameons, in which species are interconnected by hybridization and introgression (Kremer & Hipp, 2020). Publication a decade ago of two draft oak genomes (Plomion *et al.*, 2016;

Sork *et al.*, 2016a) and then the first oak reference genome (Plomion *et al.*, 2018) has had a substantial impact on our understanding of oak evolution, ecology, and biology. Since these first oak genome publications, reference genomes have been published for numerous species across seven of the eight oak sections (all except for section Ponticae sensu Denk *et al.*, 2017). These genomes exhibit high synteny (see synteny plots in, e.g., Ai *et al.*, 2022; Zhou *et al.*, 2022a; Kapoor *et al.*, 2023; Larson *et al.*, 2025; Aközbek *et al.*, 2026), enabling comparative analysis across the roughly 56 million years of oak evolution. While genomes are only one source of data, they are particularly integrative.

The availability of reference genomes has spurred significant advances in evolutionary genetics and insights in applied fields such as genetic improvement and the management of natural populations. In this introductory chapter, we provide our perspectives on ways in which oak genomes have been used to understand (1) oak evolutionary history and (2) speciation and introgression and to create tools for (3) tree breeding and (4) management and conservation of native forests. We focus particularly on work over the decade that has followed publication of the first two draft genomes. We do not aim to exhaustively review the vast number of publications that have followed the release of these genomes. Instead, we highlight the main findings and the potential applications that can be expected in the near future. This review thus builds upon previous reviews that have tracked the evolution of research on the genetics of the genus *Quercus* in response to the development of genetic markers and genomics (Kremer *et al.*, 2007, 2012; Gailing *et al.*, 2021)

1 Oak evolutionary history: phylogeny

Early work on the oak phylogeny demonstrated that the DNA markers regions used most widely for angiosperm phylogenetics—the chloroplast, nuclear ribosomal DNA, and collections of a few low-copy nuclear genes—failed to resolve fine-scale phylogenetic relationships in oaks (reviewed in Hipp, 2015, 2024 ch. 5; Kremer & Hipp, 2020). The challenge of low locus sampling was initially addressed using amplified fragment length polymorphisms (AFLPs; Pearse & Hipp, 2009), a method of obtaining genome-wide sampling of SNP variation at restriction sites and length (indel) variation between restriction sites. These data made limited use of the genome but sufficed to resolve species-level relationships within the genus, albeit with some uncertainty. The first truly genomic datasets used restriction-site associated DNA sequencing (RAD-seq) (Hipp *et al.*, 2014) to sequence regions of the genome flanking *Pst*I restriction sites across all chromosomes, though not completely randomly, as *Pst*I is CpNpG-methylation sensitive. These studies are reviewed in another chapter in this volume (Hipp et al., present volume [UPDATE CITATION IN PROOFS]) and so are not detailed here.

New genomic data—including genome skimming, reduced-representation genomic sequencing, and target capture—in the past 5 years have contributed to major advances in our understanding of the sources of phylogenetic discordance in the oak genome. The challenge of phylogenetic inference in oaks has long been attributed primarily to introgression (Hipp, 2015; McVay *et al.*, 2017; Crowl *et al.*, 2020). In the past few years, however, new theoretical work points to the strong effect of longevity on phylogenetic discordance by incomplete lineage sorting (ILS) alone, and an associated empirical study demonstrates that the exclusively woody Fagales, which includes the oaks, demonstrate this susceptibility relative to their sister clade, the Cucurbitales, which comprises a mix of woody and herbaceous species, including numerous annuals (Smith *et al.*, 2026). Analysis of genome resequencing data for *Quercus alba* and related white oaks aligned to a high-quality reference genome for *Q. alba* suggests that as much as 58% of variable SNPs within *Q. alba* are variable among close relatives, and a portion of this variation may be ancestral variation shared among numerous species (Larson *et al.*, 2025). These studies raise new questions of how much of the observed complications in oak phylogenetics is in fact due to hybridization, how much is due simply to the long generation time and large effective population sizes of woody plants generally.

A few new studies help resolve this question. A Fagaceae phylogeny based on 2,124 nuclear loci from 90 species documents extensive cytonuclear discord: the nuclear genome shows strong differentiation among lineages, whereas the plastid genome shows strong segregation of the family across continents, including ancient gene flow events between genera: the North American genera *Notholithocarpus* and *Chrysolepis* fall within an exclusively American plastome clade with the American oaks and the Eurasian white oaks; and the Eurasian oak clades (sections *Ilex*, *Cerris*, and *Cyclobalanopsis*) fall with the Eurasian genera *Lithocarpus*, *Castanopsis*, and *Castanea* (Zhou *et al.*, 2022b). Decomposition analysis of the contributions of ILS, gene flow, and gene-tree estimation error explained 39% of gene tree variation across internal nodes of the phylogeny; estimation error accounted for 21% of variation, while ILS and gene flow explained 9.8% and 7.8% of the variation, respectively (Shen *et al.*, 2025). A parallel study found that observed levels of cytonuclear discordance could not be explained by ILS alone, at least at deeper nodes of the phylogeny, most strikingly between *Quercus* species and co-occurring genera related to *Quercus* (Liu *et al.*, 2025). Estimation error explained the smallest proportion of among-gene-tree variation (0.6–3.6%), with ILS and gene flow explaining 3.3% and 6.6% respectively in a dataset of 98 orthologs for 431 taxa (ca. 70% *Quercus*), and 19% and 5.2% respectively in a dataset of 2,821 orthologs for 89 taxa (ca. 60% *Quercus*). In both datasets pared down to only oaks (*Quercus*), ILS was ca. 2–3 times more important than gene flow in explaining variation among gene trees.

These results suggest that introgression has been a part of Fagaceae evolution since the birth of the family. However, ILS also plays a crucial role, and a larger one in at least some contexts, raising the question of the degree to which species-specific alleles matter to the existence of oak species. The problems of phylogenetic inference in oaks likely converge on the challenges of phylogenetic inference in all woody plants in this way (Buck *et al.*, 2023; Sanderson *et al.*, 2023; Zhu *et al.*, 2024; Xu *et al.*, 2025), but the prevalence of ancient introgression that transgresses even generic boundaries is particularly striking in *Quercus*. The advent of widespread genomic data will aid in this work but also complicate it, as homology assessment and variant-calling can be highly influenced by which genomes are used as a reference (Mohn *et al.*, 2026).

These advances in our understanding of oak phylogeny run along in parallel with new fossil data (e.g., Liu *et al.*, 2020; Sadowski *et al.*, 2020; Denk & Bouchal, 2021; Vieira *et al.*, 2023) and new approaches to jointly modeling climatic niche evolution, trait evolution, lineage diversification, and biogeography (e.g., Denk *et al.*, 2023; Folk *et al.*, 2023; Yang *et al.*, 2023; Martín-Sánchez *et al.*, 2024; Althaus *et al.*, 2025). We are excited about the novel insights into the importance of introgression, convergence, and niche conservatism in the oak diversification promised by integrating these sources of data into a synthetic picture of oak macroevolution.

2 Introgression and speciation

2.1 Gene flow within oak syngameons

Oaks hybridize while remaining distinct morphologically, ecologically, and genomically (Trelease, 1917; Palmer, 1948; Muller, 1952; Tucker, 1961; Hardin, 1975; Whittemore & Schaal, 1991; Kremer & Hipp, 2020; Lazic *et al.*, 2021; Rauschendorfer *et al.*, 2022), often over the course of hundreds of generations of interbreeding (Stebbins *et al.*, 1947; Howard *et al.*, 1997; Wu *et al.*, 2024). Moreover, many oaks grow in multispecies communities (Cavender-Bares *et al.*, 2018; Cannon *et al.*, 2024) where numerous species can hybridize and share genes by introgression (e.g., Ribicoff *et al.*, 2025). As a consequence, oaks form “syngameons” (Lotsy, 1917; Grant, 1971; Hardin, 1975; Cannon & Petit, 2020), systems of multiple species that introgress while remaining distinct as species . Oaks are not unique in this regard: syngameons are well studied in clades across the Tree of Life, including numerous tree genera (Johnson *et al.*, 2015; Sun *et al.*, 2018; Cannon & Lerdau, 2019; Cannon, 2021; Buck *et al.*, 2023; Whittemore & Miller, 2023; Touchette *et al.*, 2024; Guo *et al.*, 2025; Qin *et al.*), corals (Ladner & Palumbi, 2012; Mao, 2020), humans (Schaefer *et al.*, 2021; Zeberg *et al.*, 2024), and beetles and butterflies (Boecklen, 2017).

Oaks stand out, however: for introgression within oak syngameons is documented between species separated by as many as 40 million years, and the persisting high diversity of oak communities has long raised questions as to how oaks remain distinct in sympatry (Hardin, 1975). It was early on hypothesized that hybridization was controlled in oaks in part by demography, and in part by ecology. From the demographic side, it was argued that hybrids would be highest when there was high asymmetry between species; pollen swamping is an expected outcome when a solitary individual of a given species is surrounded by members of a cross-compatible species (Lepais *et al.*, 2009, 2013; Lagache *et al.*, 2014; Klein *et al.*, 2017). From the ecological side, it was hypothesized that selection against genetically admixed individuals may play a key role in the maintenance of oak species (Stebbins *et al.*, 1947; Van Valen, 1976), with introgression favored in intermediate or disturbed habitats (Anderson, 1948; Muller, 1952).

Recent genomic data provide modest insights into these factors. Four studies show a range-marginal effect on introgression, which may be either ecological or demographic. Parker et al. (2025a) show high introgression between the eastern North American *Q. bicolor* and *Q. lyrata* near the edge of the range of *Q. bicolor*. Ribicoff et al. (2025), also studying the eastern North American white oaks, found that proximity to the margin of a species' range was the only significant predictor of introgression / hybridity. The third study, by Nagamitsu et al. (2020) demonstrates introgression from a predominantly coastal species (*Q. dentata*) into coastal ecotypes of a predominantly inland species (*Q. mongolica* var. *crispula*). The fourth study highlighted increased introgression at the northern margin of the *Q. petraea* and *Q. robur* geographic range, facilitating the colonization of *Q. petraea* (Beatty *et al.*, 2016). All four of these studies could be explained by demography (gene flow into the rarer species due to pollen competition) or selection (individuals of a species near the margin of its range performing better because they are introgressed with adaptive alleles from the more abundant species).

Other studies point more explicitly to a potential role of ecology in maintaining species boundaries. Reutimann et al. (2023) showed a correlation between among-site variation in habitat diversity and among-site variation in overall introgression levels in communities of European white oaks. The study does not include demographic imbalance as a covariate, but it nonetheless suggests that ecological diversity may promote introgression. In a follow-up study, Zimmerman et al. (2025) argued that hybrids tend to occupy the habitat of one parental species rather than intermediate habitat, based on a binning of individuals into hybrid classes based on inferred admixture thresholds, though their supplementary analyses suggest a nearly linear relationship between predicted admixture and environment; thus it remains unclear how important ecological selection is to the maintenance of species boundaries in this system. Wu et al. (2024), studying two sympatric red oaks, demonstrate a range of admixture levels in the wild, correlated with traits suspected to relate to habitat specialization; a higher proportion of hybrids in *ex situ* collections compared to the mature trees of the wild populations, suggesting ecological selection against hybrids in the wild; and higher-than-expected genetic differentiation at several candidate loci for habitat specialization.

More excitingly, population genetic studies over the past two decades have demonstrated two microevolutionary outcomes of introgression. First, introgression can facilitate colonization and succession. Hybridization followed by repeated unidirectional backcrossing from a late-successional donor species to an early-successional recipient species accelerates the migration of the former (Petit *et al.*, 2003). Second, introgression can enhance adaptation. While some early studies provided molecular evidence for adaptive introgression based on SSRs or AFLPs (Howard *et al.*, 1997; Dodd & Afzal-Rafii, 2004; Lind-Riehl *et al.*, 2014; Khodwekar & Gailing, 2017), stronger evidence has come from a few recent genomic studies. In a study of genomic variation across a wide range in *Q. robur* and *Q. petraea*, Leroy et al. (2020) uncovered *Q. robur* alleles at higher frequencies in high-elevation and cool or wet *Q. petraea* populations. The loci implicated control stomata, which regulate the movement of carbon dioxide, oxygen, and water vapor into and out of the tree: these are genes that likely influence how efficiently a plant can use moisture. Kim et al. (2018) and O'Donnell et al. (2021; 2023) document gene flow from California scrub white oaks (particularly *Q. berberidifolia*) into a southern California endemic (*Q. engelmannii*). Gene flow is strongly asymmetrical, ancient, and potentially associated with the latter's initial adaptation to the southern Californian Mediterranean-type climate. Fu et al. (2022) demonstrated adaptive introgression of potential *cis*-regulatory elements between *Q. variabilis* and *Q. acutissima*. Introgressed regions were judged to be adaptive based on replicated patterns of introgression in different pairs of populations for those same two species, connecting population pairs with similar environmental conditions; presence in low-recombination regions; and conservation of expression patterns in more widely introgressed regions.

One of the themes of recent rangewide genomic studies is the geographic heterogeneity of introgression: widespread species appear to exchange alleles with a variety of more restricted species in different areas of their range. Thus Ren et al. (2025) working on *Q. aquifolioides* in China, Degen et al. (2021) on *Q. robur* in Europe, and Ribicoff et al. (2025) on *Q. macrocarpa* in eastern North America all find that the genetic diversity of the species they investigate is due at least in part to the fact that the species encounter and introgress with different species in different areas of their range. This phenomenon echoes the long-observed pattern of localized organellar DNA sharing between oak species (Whittemore & Schaal, 1991; Dumolin-Lapegue *et al.*, 1999; Petit & Excoffier, 2009) and points to the importance of introgression in oak genetic diversity. More studies like these are needed to understand how important introgression is to ecotypic (and most likely adaptive) variation across oak species.

It remains to be seen what the combination of experimental studies and genome sequencing will tell us about the balance between selection against introgressants; barriers to reproduction operating before acorn establishment; and adaptive introgression. Partial reproductive isolation between oaks (Rushton, 1993; Yacine & Bouras, 1997; Boavida *et al.*, 2001; Abadie *et al.*, 2012; Lepais *et al.*, 2013) coexists with introgression (references above), as is the case in other plant genera, in which unfit F_1s can nonetheless give rise to fully fertile, introgressed offspring within just a few generations (Grant, 1966; Cannon & Scher, 2017). We predict that this balance will vary across the oak Tree of Life, with strong ecological barriers dominating in some circumstances, intrinsic barriers—prior to competition in natural populations—in others. Genomic data will be essential to showing what genes govern these processes, which ones define species, and which ones are shared among species.

2.2 Speciation and species boundaries

An early oak researcher, Dr. L. D. Gale, wrote that "if the oaks could intermix in their native forests and the resulting hybrids continue to stock the ground, what inextricable confusion must follow. Instead of 75 species of oaks on the North American continent, as now enumerated, we should have millions" (Gale, 1856, p. 77; note that his mention of 75 species in North America is lower than the current estimate of 91, much lower if we include the ca. 160 species of Mexico). While Dr. Gale's skepticism about taxonomic stability in the face of natural hybridization was high even for his time, the reality of oak species, even with molecular data, has been uncertain. Early studies using isozymes failed to recover distinctions between species (Manos & Fairbrothers, 1987; Guttman & Weigt, 1989), and several studies using a handful of microsatellite loci failed to reliably classify individuals into well-known ecologically and morphologically distinctive species (Aldrich *et al.*, 2003; Craft & Ashley, 2006; Moran *et al.*, 2012). It was thus unclear based on early molecular data whether the genetic cluster species concept (Mallet, 1995), which is widely employed in systematics, could be applied reliably to oaks.

Genome-wide data demonstrated that oak species are in fact fairly well behaved; they are, as Coyne and Orr (2004) argued, not actually the "worst case scenario" they have long been thought to be. Most studies of oaks that use large numbers of microsatellites (e.g., Muir *et al.*, 2000), AFLPs (e.g., Kashani & Dodd, 2002; Hipp & Weber, 2008), hand-picked SNP sets (e.g., Guichoux *et al.*, 2011; Hipp *et al.*, 2019), or large numbers of SNPs from genome resequencing or RAD-seq (e.g., Cavender-Bares *et al.*, 2015; Ortego *et al.*, 2018) rebut Gale's assertion that natural hybridization would lead to "inextricable confusion": there is gene flow between species, but individuals within oak species generally cluster using genomic data (Lazic *et al.*, 2021). In a study of 151 SNP-based datasets, four of them from white oaks, oak species exhibit 76% monophyly, higher than the 70% average across all datasets (Huang *et al.*, 2026). This aligns with Rieseberg et al.'s (2006) analysis of phenotypic and crossing studies in plants to suggest that traditional oak species are neither significantly better nor significantly worse than most genera in their correlation to genomic clusters. Moreover, data from at least one study suggests that distantly related oak species may differentiate at common regions of the genome, due either to parallel selection or conserved genome structure that favors divergence at some regions more strongly than others (Shi *et al.*, 2024). While there appear not to be single regions of the genome that universally distinguish oak species (Hipp *et al.*, 2020, Fig. 4), taxonomy may be governed by nonrandom, clustered, or predictable regions of the genome.

While many of the studies of adaptive gene flow and syngameon dynamics cited in the previous section are from heavily-studied, widespread species of Europe and North America, we expect that some of the most exciting insights are to be gained in less-studied groups, particularly in highly diverse areas of Mexico and China (Valencia-Avalos, 2020). Morales-Saldaña et al. (2022, 2024), for example, investigated the white oaks of the northern Mexican mountains using microsatellites and then a Hyb-Seq probe kit developed for *Quercus*. They distinguished numerous lineages traditionally assigned to a single, widespread species, *Quercus laeta*. Their work demonstrates that this single species in fact comprises several species of a widespread Mexican white oak syngameon, and it highlights areas of introgression.

3 Contributions of genomics to oak breeding

3.1 Conventional oak breeding

Activities in oak breeding and genetic improvement have been limited in comparison to other forest trees due to biological constraints including delayed reproductive maturity, irregular fruiting, and the recalcitrant nature of acorns, which rapidly lose viability over the course of a year or more of storage (Bonnet-Masimbert, 1984; Connor, 2004). Furthermore, oak forests are renewed mainly by natural regeneration, and oak planting is scarcely used even in intensively managed oak forests, limiting the use of genetically improved reproductive material in operational forestry (Jarret, 2004; Johnson *et al.*, 2019). Finally, due to oaks' longevity and changing uses of their wood, breeding goals related to the economic value of oak trees (mainly growth, wood quality and stem form) may vary over decades (Kleinschmit *et al.*, 1975; Savill & Kanowski, 1993; Steiner, 1993). However, compared to conifers in intense breeding programs, deciduous species possess biological peculiarities that fostered early genetic improvement initiatives. First, deciduous species—oaks in particular—can be more easily propagated through vegetative reproduction (sprouting, cuttings or in vitro culture). Second, in the 1930s, naturally-occurring triploid poplars were found to exhibit exceptional growth (Müntzing, 1936; Nilsson-Ehle, 1936). This discovery led to the first selection methods in broad-leaved tree species, which involved vegetatively propagating the triploid trees found in the forest. During the 1940s, Johnsson found within a large sample size that 0.41% of oak trees were triploids (Johnsson, 1946). Triploid oaks, like the triploid poplars, were unusually large (Butorina, 1993), inspiring oak genetic improvement through identification and propagation of natural triploids (Lefort & Douglas, 1999). Although oak breeding inspired by triploidy may seem anecdotal today (Raebild *et al.*, 2024), easy detection of triploids by genomic methods made them easier than ever to discover (Dzialuk *et al.*, 2007; Gathercole *et al.*, 2026). The deployment of triploids by vegetative reproduction has not received much attention for plantation although propagation methods of oaks have been much improved by biotechnological means (Vieitez *et al.*, 2012). Finally, by the end of the 1900s, breeding strategies of oaks followed the steps of other forest tree improvement programs, based on recurrent selection methods, starting with phenotypic selection in natural stands of elite trees, followed by progeny testing of these trees, and establishing seed orchards for the deployment of improved stock (White *et al.*, 2007). Such programs have mainly been implemented for widely distributed species with high economical value: *Q. rubra* (Alexander & Woeste, 2016; Woeste *et al.*, 2021), *Q. alba* (Abbott *et al.*, 2024), *Q. petraea, Q. robur* (Kleinschmit, 1998; Hubert & Savill, 1999; Savill *et al.*, 2004), *Q. suber* (Eriksson *et al.*, 2017; Sampaio *et al.*, 2021), and *Q. acutissima* (Cheon *et al.*, 2009; Na *et al.*, 2015). Because of their delayed flowering period, late trait expression, and the technical constraints in performing controlled crosses, oak breeding programs are behind those of fast-growing species and are, at best, in the final stages of the first generation. However technological advances in genomics have offered prospects to overcome these barriers, some of which have been explored recently.

3.2 Genomics-assisted oak breeding

Some of the biological constraints to oak breeding have been addressed during the last decades by two innovative methods that resulted from genomic advances: Breeding Without Breeding (BWB; El-Kassaby & Lstiburek, 2009), and Genomic Selection (GS; Meuwissen *et al.*, 2001). By reconstructing kinship relationships through parentage analysis (using microsatellites or SNPs) directly within natural stands, BWB simplifies and accelerates genetic selection procedures, which are traditionally carried out in progenies produced by controlled crosses. BWB eliminates one of the most time-consuming and cumbersome steps in breeding oaks by bypassing the phase of controlled crosses, while still maintaining control over mating combinations, thereby enabling the estimation of genetic parameters essential for conducting breeding programs. While the BWB approach has not yet been implemented at large scales in oak breeding populations, it has made it possible to segregate open pollinated matings into large size full sib families, facilitating the construction of genetic maps and QTL detection (Bakker, 2001; Konar *et al.*, 2017).

The second potential contribution of genomics to oak breeding stems from the improvement of genetic evaluation provided by the genomic prediction of breeding values through Genomic Selection (GS). In traditional tree breeding programs, breeding values of trees for traits of interest are estimated using their phenotypic values and those of all their related sibs as predictors (Grattapaglia *et al.*, 2018). By capturing genome associations between genome wide SNPs and genes controlling the attributes of interest, genomic prediction not only improves the estimation of breeding values, but allows to implement selection at a juvenile stage when the trait itself is not yet expressed (El-Kassaby *et al*, 2024). Hence breeding cycles can be significantly shortened and oak improvement accelerated. In comparison to conventional estimation of breeding values, genomic prediction is more efficient when traits show low heritability and are highly polygenic (McGaugh *et al.*, 2021), both of which are often the case in oaks (reviewed in Gailing *et al.*, 2021).

Genomic Selection to estimate breeding values has recently been tested in *Quercus robur* for improving wood related traits (Lobo *et al.*, 2026) and resistance to diseases (Carleial *et al.*, 2026).

3.3 Genetic improvement *in situ*

Conventional oak genetic improvement programs are conducted in designed experiments, such as progeny tests and seed orchards, that require time and labor demanding activities to be established. Such programs produce improved reproductive material (seedlings or cuttings) that can only be used for plantations, while most oak forests are renewed by natural regeneration. By contrast, in highly valuable oak forests managed under even aged regimes, stands are progressively thinned until they reach the point to be renewed. At this stage, seed trees are phenotypically selected that will ultimately mate by open pollination and produce the next generation of the stand. Genomics offers the possibility to replace phenotypic selection with genetic selection as an alternative means of genetic improvement. The proposed method is inspired by BWB and GS principles transferred to natural stands and proceeds in two steps. First, genetic relatedness between all trees is estimated using molecular genetics prior to the seed cut. Once all pairwise genetic relationships are established, they will be used to predict the breeding value of each tree as in conventional breeding populations (progeny tests). Second, breeding values can even be improved by GS, provided genotyping is sufficiently dense. Breeding values can then be used by the forester to screen the stand and select on genetic grounds the best progenitors for the next generation. These methods have been explored in *Quercus petraea* and *Quercus robur* (Alexandre *et al.*, 2020b,a) but are challenged by technical limits to predict breeding values *in situ*. While genetic relationships between all pairs of trees within a natural stand could be reconstructed with a dense sampling of SNPs (more than 15,000), the limited variation of relatedness may severely constraint the statistical estimation of genetic parameters (heritability) or breeding values (Lesur *et al.*, 2018; Alexandre *et al.*, 2020a). Mature oak stands exhibit low mean relatedness and reduced variation of pairwise relatedness due to random mating and extensive pollen flow (Klápště *et al.*, 2021). Much larger sampling designs would be needed to overcome such constraints. These results were, however, obtained in only one case study, and the method deserves to be explored in a larger context before concluding on the operational implementation of BWB and GS *in natura*.

3.4 Population selection and seed sourcing

Most oak species are not undergoing genetic improvement programs *per se*, using the breeding machinery that we have just reviewed. For these species, extant forests are the source of reproductive material, which has led to the installation of provenance testing for seed sourcing in many parts of the world (Kremer *et al.*, 1993 and references therein). As in other long lived tree species, comparisons of oak populations from different origins showed prevalent local adaptation, with populations closer to test sites expressing higher fitness than others in oak species of America (Kriebel *et al.*, 1976; Cavender-Bares & Ramírez-Valiente, 2017; Lindback *et al.*, 2023; Thomas *et al.*, 2024; Rea *et al.*, 2024, 2026; Ostrowsky *et al.*, 2026), Europe (Sáenz-Romero *et al.*, 2017; George *et al.*, 2020), and, with a few exceptions, the Mediterranean regions (Ramírez-Valiente *et al.*, 2022). Discovery of local adaptation has contributed to delineating seed zones (a.k.a provenance regions in the European context) and making recommendations for seed sourcing. Today, spatial and geographic patterns of differentiation detected in common gardens have shifted provenance decisions by considering transfer of reproductive material (assisted gene flow) to cope with climate change (Bert *et al.*, 2020; Matyas, 2021). Phenotypic evaluation of populations conducted in common garden was further enriched by genomic and environmental scans (landscape genomics), which make it possible to identify genetic imprints of environmental drivers (either biotic or abiotic) on adaptive traits (Sork *et al.*, 2016b; Tischenko *et al.*, 2024). Landscape genomics together with phenotypic evaluation in common gardens allowed therefore to enlarge seed delineation at a larger geographic scale. Finally, seed sourcing can further be refined by assessing genomic offset of populations. Genomic offset combines genomic and environmental information and aims at estimating for a given population the genomic distance between current and future environment at loci of adaptive significance (Rellstab *et al.*, 2016; Yuan *et al.*, 2023; Buck *et al.*, 2026). Prediction of future response of populations based on genomic offset can be validated by assessing in provenance tests the same distance but directly at the phenotypic level, e.g. at fitness related traits (Rellstab *et al.*, 2021).

4 Management and conservation of native forests

We have just recalled contributions of genomics to our understanding of evolutionary history, introgression, and genetic improvement of oaks (*Quercus*). These fields of research represent a broad spectrum of genomic applications and point the way toward further applications that will benefit from recent advances in genomics, but also in phenomics and environmental sciences in general. Databases containing genomic, phenomic, and environmental information have expanded considerably in recent years. Access to reference genomes within each botanical sections of the genus *Quercus* make is possible to assay a substantially larger range of genomic diversity, including not only SNPs but also structural genomic variants, both neutral and adaptive (Gailing *et al.*, 2021; Lazic *et al.*, 2021). Advanced image-based phenotyping, air-borne lidar technology, and high throughput phenotypic platforms make it possible to capture adaptive traits (growth, phenology, disease resistance) of single trees for large populations in natural or controlled environments (Bian *et al.*, 2022). Finally, highly accurate and finely resolved past and future climatic data are now accessible in large databases, enabling investigations of ongoing and future response of trees to environmental change (Karger *et al.*, 2017). The increase in scalability and resolution due to the continuous and concomitant enrichment of genomic, phenotypic and environmental data has significantly enhanced our ability to assess and study the evolution of natural and experimental oak populations. For the time being, the future of oaks has mainly been addressed through modeling approaches based on climatic and growth data. Across the Northern hemisphere, Species Distribution Models (SDM) predict contractions of oak ranges in warm-dry margins of the distribution (Gomez-Mendoza & Arriaga, 2007; Ramirez-Preciada *et al.*, 2019; Sun *et al.*, 2020; Vila-Vicosa *et al.*, 2020), while expansions are foreseen at the northern limits (McKenney *et al.*, 2007; Axer *et al.*, 2021; Tang *et al.*, 2023). In North America and Europe, SDM models predict retraction of conifers and transition from conifers towards broadleaf (oak) dominated forests at northern latitudes. Similarly, growth models predict increase productivity at higher latitudes due to CO_2 fertilization and longer growing season, while reduced growth will dominate in the south due to more frequent drought stresses (Hanewinkel *et al.*, 2013; Reich *et al.*, 2015). These distributions and growth projections are however only environmental-phenotypic constructions and can be altered by evolutionary processes tailored by such life history traits as long generation time, high gene flow, and large standing genetic variation. These projections call also for research initiatives in three areas where genomics may contribute to the sustainability of oak forests: adaptation to climate change, conservation and management of genetic resources (Backs & Ashley, 2021; Tischenko *et al.*, 2024).

4.1 Adaptation to climate change

The response of oak trees to ongoing and future climate change is a key concern for managers and a major focus of research that can be tackled using genomic tools (Zhang *et al.*, 2025). Adaptive potential is ideally estimated from the genetic variance in fitness (reproductive success), but this variance is difficult to assess in long lived species such as trees (Hendry *et al.*, 2018; Walsh, 2022). Alternatively, the genetic diversity of traits related to fitness may stand as a proxy of the adaptive potential, and if this information is lacking, genomic diversity may be the ultimate resource (Hoezel *et al.*, 2019; Lazic *et al.*, 2021). In *Q. petraea* and *Q. robur*, for example, the genetic variance of fitness was estimated and, when compared with estimates from other plants and animals, was among the highest values observed so far (Alexandre *et al.*, 2020b). More to the point, genetic variance in fiteness traits also correlated with the high values of genomic diversity estimated in a rangewide collection of *Q. petraea* populations (Milesi *et al.*, 2024). The adaptive potential of *Q. petraea* is also supported by the very high levels of genetic diversity found throughout their natural distribution (Milesi *et al.*, 2024). Conducting parentage analysis and estimating genomic relatedness in oak stands should make it possible to get access to the genetic variance of fitness and provide insights into their adaptive potential. Furthermore, when there is adaptive potential, adaptive evolution can be enhanced by human mediated assisted selection based on breeding values estimated *in situ* for adaptive traits. Using semi-automated phenotyping of these traits together with genomic based kinship analysis would make is possible to implement genetic selection along the life cycle of oaks as the climate changes (Lstiburek *et al.*, 2023).

Retrospectively, adaptive trajectories of oak populations can be tracked by monitoring temporal genomic changes during periods of significant climate changes, thereby providing evidence of adaptive potential. Genome wide SNP variations were observed in age structured cohorts of *Q. petraea* that have experienced the transition between the Little Ice Age and the onset of the Anthropocene warming (Saleh *et al.*, 2022). Alternatively, adaptive responses at the genome level have been more often explored in oaks by substituting space for time, and assessing genomic variation between present populations that have grown under different climates, using landscape genomics (Sork *et al.*, 2013; Fetter *et al.*, 2017). In a series of studies on North American (Sork *et al.*, 2016b; Martins *et al.*, 2018; Gugger *et al.*, 2021; Ortego *et al.*, 2023), European (Rellstab *et al.*, 2016; Pina-Martins *et al.*, 2019; Meger *et al.*, 2024), and Asian (Du *et al.*, 2020; Gao *et al.*, 2021; Feng & Du, 2022; Yuan *et al.*, 2023) oak species, highly polygenic signatures were correlated with climatic variation among populations, characterized by small frequencies differences widely distributed in the genome. Oaks may provide unique case studies to compare temporal and spatial adaptive responses to past and present climatic changes. Temporal evolutionary changes can be explored using either living trees of different ages that have experienced recent or contemporary climate changes, or ancient DNA of subfossil and archeological remains that may make it possible to extend genetic monitoring back to the Bronze Age (Kremer, 2024; Wagner *et al.*, 2024). Coupled with current landscape genomics and genome-wide association studies in provenance tests, ancient and contemporary genome and phenome reconstruction will enlighten evolutionary adaptive responses to climate change.

4.2 Conservation

Conservation genetics is primarily concerned with species whose survival is threatened by their current demographic status. In a review on this topic focusing on oaks, Backs and Ashley (2021) reported 124 species that were of concern, including 112 species falling into the IUCN “threatened” category (Carrero *et al.*, 2020), and an additional 12 vulnerable species due to lack of recruitment and regeneration recorded in the USA (Backs & Ashley, 2021). Decisions regarding species conservation are often based at least in part on a descriptive analysis of the level and distribution of genetic diversity (Rossetto *et al.*, 2021). Unfortunately, of the 124 species listed by Backs and Ashley, at the time of their publication, only 16 have undergone diversity surveys that could guide sampling for *ex situ* or *in situ* conservation, and information from closely-related species is generally a poor predictor of the intensity of *ex situ* conservation required to conserve genetic diversity (Hoban *et al.*, 2020). Information is most available for North American species (e.g., *Q. lobata*, *Q. dumosa*, *Q. engelmannii*, *Q. hinckleyi*, *Q. tomentella*) and Asian species (e.g., *Q. arbutifolia*, *Q. bambusifolia*) and one North African species (*Q. afares*) (Backs & Ashley, 2021 and references therein).

For the remaining species, landscape genomics, which integrates environmental and genomic data, may help refine the sampling of conservation units by identifying the main environmental factors shaping the distribution of genetic diversity. Conservation genomic approaches can, for example, inform seed provenance decisions, and help make informed decisions among species conservation, ecosystem preservation, and status quo conservation approaches (Mead *et al.*, 2024). Additionally, integrating data on species life history, geographic range, and ecological extent, combined with simulations, shows high potential to inform conservation action even in the absence of molecular genetic data (Hoban *et al.*, 2018; Hoban, 2019; Bruns *et al.*, 2022; Rosenberger *et al.*, 2022), though the imperfect correlation between genetic diversity and both population size and range size points to the importance of ongoing empirical study (Spence *et al.*, 2021). Conservation actions can also be enhanced by additional results extracted from genomic inventories conducted at the landscape level, when multiple oak species co-habit. For example, admixture estimates will indicate whether interspecific gene flow was or is active and deserves to be maintained or restored, to sustain syngameon cohesion or reinforce the evolutionary potential of the population (Wu *et al.*, 2024). Finally, the genomic information provided by the inventory may clarify taxonomic classification and phylogenetic uncertainty, facilitating cross species comparisons before defining conservation priorities among species. Altogether, genomic based diversity inventories, admixture assessments, taxonomic and phylogenetic clarification will contribute to identify evolutionary significant units that are selected for preserving the evolutionary potential of the species (Hoezel, 2023).

4.3 Sustainable genetic resource management

As we have noted, significant changes in oak distributions (expansions, contractions) are expected in response to climate change, including artificial extensions by plantations promoted by several countries to increase carbon sequestration. Furthermore, exposure to hazards, extreme events, diseases and insects outbreaks are also expected to increase (Grünig *et al.*, 2026). To anticipate these disturbances, many countries have launched monitoring projects, starting with biodiversity and forest health before implementing adaptive management strategies (Tkacz *et al.*, 2013; Feng *et al.*, 2016; Michel *et al.*, 2024). More recently, genetic monitoring initiatives have been implemented, which are designed as an early warning system of profound changes in structure and demography, loss of viability and decline (Konnert *et al.*, 2011; Gal-Babicz *et al.*, 2026). Genetic and genomic monitoring consist in a forward time assessment of temporal changes of metrics regarding neutral and adaptive diversity, population structure, mating system, reproduction. These metrics are continuously upgraded with advancements in genomics and discoveries of genes controlling adaptive traits (Gal-Babicz *et al.*, 2026). Genetic monitoring has been implemented in the two continental wide distributed oaks species in Europe (*Q. petraea* and *Q. robur*) and are currently being extended to other oak species. Complementary to the genetic monitoring, a dynamic conservation network of genetic resources of oak species has been put in place as a subset of the monitoring network (Aravanopoulos *et al.*, 2015; Lefèvre *et al.*, 2020). In this context, conservation does not focus on endangered species, but rather on widely distributed species, with the aim of maintaining their diversity across their entire range, as some of these conservation units may serve as seed sources for plantations.

Predicted changes of oak distributions will lead to more frequent and widespread regeneration of oak forests, whether through natural or artificial means. Renewal of oak stands is a critical phase when genetic information is redistributed enhancing opportunities for genetic changes. With regard to natural regeneration, extensive research has previously been conducted on forest tree mating and reproduction systems using conventional methods of kinship analysis and gene flow studies based on genetic fingerprinting (Ashley, 2021 and references therein). The combined use of genomic and environmental data will provide insights into the ecological determinants of gene flow, the distribution of reproductive success among the seed trees, and the level of hybridization and introgression in mixed oak stands feeding nature-based solutions for regenerating oak stands (Tischenko *et al.*, 2024). Ultimately, as mentioned earlier, monitoring of reproductive success and genomic relatedness of seed trees will make it possible to estimate the genetic variance of fitness, and the evolutionary potential of the stand that is renewed by natural regeneration. With regard to renewal through planting, research combining landscape genomics with population differentiation in common gardens will help to identify the best seed sources and, if necessary, determine whether to use assisted gene flow. Genomic tools will also make it possible to track the flow of seeds by developing traceability methods based on molecular fingerprints (Tischenko *et al.*, 2024). In the long term, knowing the origin of the seeds used for plantation will make it possible to assess retrospectively the success of the transfer.

Prospects

Understanding and conserving oaks at the level of populations, communities, and species will require continued interdisciplinary research and action. Genomics will play an important role in this, as genomes integrate uniquely across these levels of inquiry and analysis. In the years to come, we are particularly excited about the prospects for genomic contributions in several areas, including:

Pangenomes to investigate the effects of genome architecture on divergence and introgression. Pangenomes reduce reference-mapping bias, help catalog structural variants and gene duplications, and make it easier to distinguish accessory from core genome regions (Tellini *et al.*, 2025; Edwards *et al.*, 2025). Recent comparative oak genome studies (cited above) demonstrate that while there is high synteny among oak genomes, structural variants are common both within and among oak species. One pangenome has been published to date in oaks (Liang *et al.*, 2025), and this along with recent studies in other woody plant species (e.g., Liu *et al.*, 2024; Li *et al.*, 2025) point to the high potential for pangenomes to contribute to our understanding of how speciation, introgression, and lineage diversification are shaped by genome structural variants, particularly the interaction between intraspecific structural variants and introgression in influencing local adaptation.

Genomic approaches combined with common garden studies to understand the underpinnings of climate adaptation and to make conservation recommendations. Linkage maps and genome resequencing in common gardens has been essential to understanding of the traits that underlie local adaptation (e.g., Bartholomé *et al.*, 2020; Gailing *et al.*, 2021 sect. 4.3). Combining landscape genomics with genome-sequenced reciprocal transplant experiments can help quantify rates of adaptation to ongoing environmental change as well as the risk individual populations face, and also identify appropriate populations for seed sourcing (e.g., Browne *et al.*, 2019; Gugger *et al.*, 2021; Mead *et al.*, 2024; Parker *et al.*, 2025b). We consider this particularly important to addressing the question of how important introgression may be to the future success of oaks, as we have few studies documenting the fitness effects of introgressed alleles along replicated gradients or in experimental settings (Leroy *et al.*, 2020).

Identifying parallel patterns in gene flow and divergence across species and clades. Oaks have been successful in part because they have evolved parallel solutions to similar ecological problems, most dramatically in the Americas (Cavender-Bares, 2019; Althaus *et al.*, 2026) and also in Eurasia as well as between Eurasia and the Americas (Alonso-Forn *et al.*, 2020; Denk *et al.*, 2023). We do not know, however, to what degree the parallel evolution of different oak lineages in common environments may be due to genomic features conserved or introgressed among lineages, nor the nature of selection shaping these parallelisms (though see Shi *et al.*, 2024). Complicating matters is the role of shared ancestral polymorphisms in shaping genetic diversity within oak species (e.g., Larson *et al.*, 2025). Comparative genomics, combined with experimental ecological studies, will give us increasing insight into how the evolutionary heritage of oaks and evolutionary novelties within lineages intersect to shape the genus we know today and its trajectory.

Understanding genetic resilience to extreme events. Climate change, and the more frequent occurrence of extreme events expose trees to evolutionary challenges, to which oaks can respond with resilience (Grünig *et al.*, 2026). Despite increased mortality rates reported in several studies, resilience can be triggered by the maintenance of reproductive and recruitment capabilities benefiting from the large genetic diversity sustained in oak stands (George *et al.*, 2022). The interactions between demographic mechanisms (fertility, competition) and evolutionary mechanisms (gene flow, hybridization, juvenile selection) during recruitment that may lead to greater resilience deserve to be explored through studies in genetics and ecology benefiting from genomic resources (Kremer *et al.*, 2025 and references therein).

Ultimately, we cannot see how microevolution and macroevolution can be separated from one another: phylogeny within a syngameon is entangled with gene flow among species and sorting of alleles into species; and local adaptation, selection, and genetic variation within species are shaped by the suite of historically and currently co-occurring species with which they might be exchanging genes and the evolutionary history that produced today's species, populations, and biotic communities. While oaks are susceptible to the same challenges to reconciling macroevolutionary and microevolutionary processes that affect clades across the Tree of Life (Rolland *et al.*, 2023; Schluter, 2024), the difficulty is compounded by distinguishing within-species variation from among-species variation that is shared by introgression. Thus oaks evolve "on two fronts": both within species and through introgression within the syngameon (Burger, 1975).

We see empirical work on the implications of oak syngameon dynamics for future adaptation as a key contribution to genomics in the coming decade. In an oak syngameon, what do we lose when we lose a species? To what degree do we lose unique alleles, and to what degree do those alleles escape into other species? Interdisciplinary studies drawing on genomics will be crucial to addressing these and related questions.

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