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Contrasting Genomic Signatures of Climate Adaptation and Adaptive Plasticity Across the Distribution Ranges of Sessile Oak and European Beech

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ABSTRACT

The persistence of organisms in changing climates depends on both phenotypic plasticity and adaptation. However, despite extensive research, it remains largely unclear how forest trees will genetically adapt or phenotypically acclimate to future climates. In this study, we investigated the genetic architecture of tree-ring and leaf traits in sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*) and tested for signals of climate adaptation at loci controlling these traits. We combined trait data from common gardens established in the 1990s across the species' European ranges with climatic and genomic data. We conducted genome-wide association (GWA) analyses and tested the effects of temperature and precipitation transfer distances on associated loci. Our GWA analyses revealed a complex, multi-locus genetic architecture underlying functional traits in both species. Sessile oak displayed a greater number of trait associations than European beech and we found indications of pleiotropy, particularly in sessile oak. European beech showed limited plastic and adaptive responses to climate at the genomic level. In contrast, sessile oak showed signals of both adaptive plasticity and climate adaptation, particularly at loci associated with growth responses to extreme droughts and to long-term summer temperature. Our findings suggest that sessile oak possesses a stronger capacity to respond to climate change than European beech. This capacity may facilitate range expansion in sessile oak, while raising concerns about the sustainability of beech in European lowland forests under future climates.

1 | Introduction

Anthropogenic climate change is expected to further increase global temperatures, with projections indicating a rise of 1°C–5.7°C within the next 100 years (Pörtner et al. 2022). This warming is accompanied by shifts in other important environmental pressures, particularly the frequency and intensity of heatwaves and extreme droughts (Hammond et al. 2022). These rapid environmental changes have already impacted the persistence and performance of plant and animal populations across ecosystems (Allen et al. 2010; Anderson and

Song 2020; Urban 2024). For instance, during the summers of 2003, 2018 and 2022, central and western Europe experienced severe droughts and heatwaves that caused premature leaf shedding or scorching and local dieback in dominant tree species such as spruce, silver fir and beech (Hermann et al. 2023; Schuldt et al. 2020). As climate change shifts selection regimes, populations adapted to current climates may experience maladaptation as formerly adaptive traits are no longer beneficial, increasing the risk of local extinction (Anderson and Song 2020; Urban 2015). Because phenotypic traits arise from evolutionary processes and the underlying

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genetic architecture (Bomblies and Peichel 2022; Savolainen et al. 2013), uncovering this architecture is key to understanding how organisms are adapted to their current climate and how they may respond to future changes.

How traits explain population persistence under climate change depends on a combination of phenotypic plasticity and adaptation. Phenotypic plasticity in the strict sense is a genotype's ability to produce different phenotypes in response to environmental variation, for example, within a generation (Nicotra et al. 2010). It is commonly observed, especially in sessile organisms such as plants (Sultan 2000) and its effect depends on whether the phenotype shifts toward (adaptive) or away from (maladaptive) the local optimum (Acasuso-Rivero et al. 2019; Ensing and Eckert 2019; Ghalambor et al. 2007). Adaptive plasticity may buffer populations against climate change, providing time for natural selection to drive adaptation. Trees often exhibit extensive plasticity in key functional traits, that is, physiological, morphological or phenological traits linked to fitness and climate sensitivity (Violle et al. 2007; Fréjaville et al. 2019; Vizcaíno-Palomar et al. 2020). However, plasticity alone may not be sufficient for long-term population persistence and an evolutionary response is likely required. Local adaptation arises from genotype-by-environment interactions and is specifically shaped by the fitness effects of alleles underlying adaptive traits under different selection regimes (Orr 2009; Bomblies and Peichel 2022). Adaptation occurs over multiple generations, as natural selection shifts allele frequencies. Rapid adaptation to climate change is possible (Franks et al. 2007; Bergland et al. 2014); however, it remains uncertain whether long-lived organisms, such as trees, can adapt quickly enough (Jump and Penuelas 2007; Franks et al. 2014; Frank et al. 2017).

The evolutionary response of populations to climate change depends on the genetic architecture (i.e., the composition and organization of genetic variation, including the number and effect sizes of loci and the level of pleiotropy) underlying adaptive traits. The fitness effect of adaptive alleles at major effect loci under natural conditions are well documented in specific species (e.g., three-spined sticklebacks *Gasterosteus aculeatus*, Barret et al. (2008) and thale cress *Arabidopsis thaliana*, Oakley et al. 2014). However, most adaptive traits, including those involved in response to climate, are quantitative with a highly polygenic genetic architecture, that is, controlled by multiple loci with small individual effects (e.g., Bamba et al. 2019; Bomblies and Peichel 2022 and references therein). This potentially makes signatures of selection harder to detect at the genomic level and may overestimate the influence of plasticity in natural populations. Additionally, pleiotropy, where a single locus affects multiple traits, is widespread in plants and may either facilitate or constrain adaptation, depending on trait interactions (Visscher et al. 2017; Watanabe et al. 2019).

Long-lived species with long generation times, typical of many forest trees, rely heavily on phenotypic plasticity to cope with environmental change (Petit and Hampe 2006; Salguero-Gomez et al. 2016). Growth and phenology-related traits, in particular, are highly plastic across a range of tree species (Cooper et al. 2018; Vitasse et al. 2010; Sáenz-Romero et al. 2017; Schmeddes et al. 2024). Despite high plasticity, numerous studies indicate that tree populations are highly vulnerable to climate change,

with increasing evidence of climate-driven declines (Allen et al. 2010; Levesque and Hamann 2022; Schmied et al. 2023) and limited evolutionary change (Dauphin et al. 2021). For example, recent heatwaves and extreme droughts have triggered major dieback across several major European tree species, not only drought-sensitive ones, such as Norway spruce (*Picea abies*, Vitali et al. 2017), Scots pine (*Pinus sylvestris*, Rigling et al. 2018) and European beech (*Fagus sylvatica*, Leuzinger et al. 2005) but also, to a lesser extent, drought-tolerant sessile oak (*Quercus petraea*) and silver fir (*Abies alba*, Schuldt et al. 2020). Overall, the future distribution ranges of temperate forest species remain uncertain (Hartmann et al. 2022), with recent projections suggesting that European beech forests could decline by 20%–50% as a direct consequence of climate change within the next century (Martinez del Castillo et al. 2022).

These observed diebacks have increased interest in forest management strategies aimed at facilitating climate adaptation by moving seeds and planting trees from preadapted populations (assisted gene flow, Aitken and Whitlock 2013). Introducing genotypes from populations presumably adapted to warmer and/or drier conditions may also allow intra- and interspecific introgression of adaptive alleles (Matyas 2021; Leroy et al. 2020). However, most studies on tree responses to climate change have focused on phenotypic variation (e.g., Depardieu et al. 2020; Zas et al. 2020), leaving the genomic aspects less explored. The emerging interdisciplinary field of dendrogenomics, combining dendrochronology with genomic analyses, is yielding valuable insights into the genomics of tree adaptation to climate (Krutovsky 2022 and references therein). Dendrochronology offers a powerful retrospective tool to analyse individual growth responses to climatic variation with annual temporal resolution. Unlike static trait measurements, dendrochronological records capture annual variation and directly quantify responses to extreme events, such as severe droughts, which are essential for tree persistence but often overlooked in ecological genetic analyses like genome-wide association (GWA) studies. For example, studies in conifers have combined genomic and growth data to uncover patterns of demographic history and natural selection (e.g., Martínez-Sancho et al. 2021) and GWA studies have started to identify genes underlying growth responses to climate (Heer et al. 2018; Housset et al. 2018; Trujillo-Moya et al. 2018; Depardieu et al. 2021). In parallel, genotype-environment association (GEA, Rellstab et al. 2015) studies have identified genomic signals consistent with local adaptation in various tree species (e.g., Rellstab, Zoller, et al. 2016; Borrell et al. 2019; Milesi et al. 2019). By combining long-term phenotypic, climatic and genomic data, dendrogenomics offers a powerful framework for understanding the genetic architecture of tree adaptation to climate change.

Using this framework, we focus on sessile oak and European beech, which are two ecologically and economically major tree species in Europe. European beech often dominates European temperate forests, but species composition varies regionally and both sessile oak and European beech cover large environmental gradients and are widely distributed across Europe (Mauri et al. 2022). Sessile oak harbours exceptionally high genetic diversity (Milesi et al. 2024), elevated rates of intra-specific ecological divergence and frequently hybridizes with a propensity for introgression, which may facilitate climate

adaptation, despite extensive gene flow (Kremer 2016; Kremer and Hipp 2019; Leroy et al. 2020). In European beech, GEA studies have identified genomic signals of climate adaptation (Postolache et al. 2021; Pluess et al. 2016; Lazic et al. 2024) and GWA analyses have uncovered genomic regions potentially involved in drought resistance (Pfenninger et al. 2021). However, other research indicates that only certain European beech populations show evidence of adaptation and the response to climate change is hence highly population-specific (Kreyling et al. 2014).

In a previous study, we used tree-ring-derived functional traits related to growth and climate sensitivity in both species, revealing clear species-specific differences in plasticity and adaptation in response to climatic variation (Martínez-Sancho et al. 2025). However, the genetic architecture underlying these fitness-related traits and the role of associated loci for climate adaptation remain unclear. Here, we performed GWA analyses to characterize the genetic architecture and link alleles at candidate loci to key climatic variation. In addition, we used a genotype-by-environment framework to assess whether allelic variation differs in trait-climate reaction norms along climatic transfer distances. This approach allows us to distinguish between phenotypic plasticity and adaptive genetic responses. Specifically, we addressed three questions: (1) What is the genetic architecture of functional traits in sessile oak and European beech? (2) How does the genetic architecture differ between the species? (3) Is there evidence of climate adaptation at loci controlling these functional traits?

2 | Materials and Methods

2.1 | Experimental Design

We used the same experiments and phenotypic data as described in Martínez-Sancho et al. (2025). Briefly, we exploited a network of common gardens of sessile oak (hereafter oak) and European beech (hereafter beech) established in the 1990s (Sáenz-Romero et al. 2017; Robson et al. 2018). For each species, we selected four common gardens across their European range (Figure 1). Oak had a full reciprocal design with nine provenances from the Madsen collection (Madsen 1990) planted in each common garden (Table S1) excluding the Turkish provenance, which had a large proportion of trees putatively belonging to the non-target species *Q. pubescens* from all analyses (see *Genetic data* and Methods S1; Figure S1–S3). The beech network consisted of eleven provenances unevenly distributed across all gardens (Table S1).

2.2 | Phenotypic Data

In fall 2021, 16 individuals, separated into two blocks, were randomly sampled per species, provenance and common garden. Detailed pedigree information is not available for these historical common gardens and individuals can therefore not be assigned to known half-sib families. Consequently, our analyses treat provenance as the unit of origin rather than family structure and sampled trees are assumed to represent a random mixture. To evaluate potential cryptic relatedness among individuals,

genome-wide relatedness was quantified and incorporated into subsequent analyses (see Genome-Wide Association (GWA) Analyses).

We focused on eleven functional traits divided into five categories (Table 1 and Martínez-Sancho et al. 2025): (i) *tree size* including diameter (at breast height, DBH) and height; (ii) *leaf morphology* represented by specific leaf area (SLA); (iii) *tree growth increment* as basal area increments (BAI) for the period 2006–2021; (iv) *long-term growth responses to climate* including the Pearson correlation between tree growth and spring and summer mean temperature and precipitation (sprpre, sumpre, sprtmea, sumtmea); and (v) *short-term growth responses to extreme drought* as defined by Lloret et al. (2011), including three resilience components. These were: resilience (Rs), the ratio of post-drought to pre-drought growth, resistance (Rt), the ratio of growth during the drought to the preceding period and recovery (Rc), the ratio of growth after the drought to that during the drought. Competition was estimated based on the four direct neighbours using the Hegyi index (Canham et al. 2004). Trait values were extracted for each tree to suit GWA analyses. For details see Methods S2.

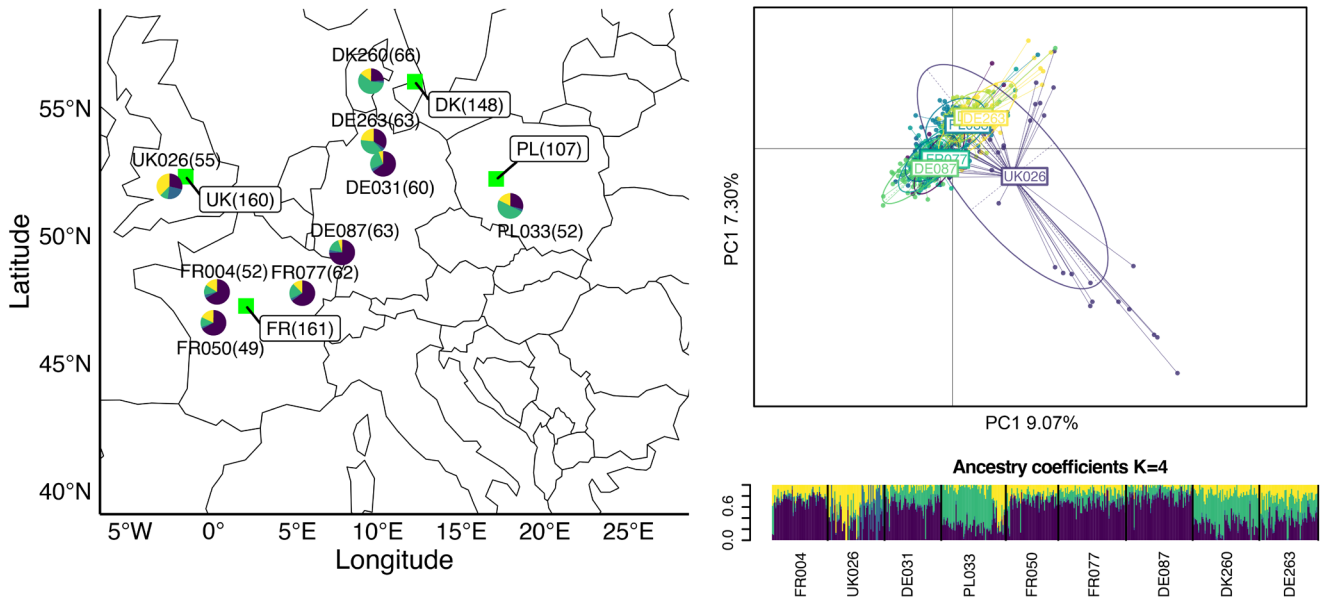
2.3 | Climatic Data

To characterize the climate of provenance origin and common gardens sites, we used CHELSA v2.1 and CHELSAcruts datasets (Karger et al. 2017). Climate data for provenances corresponded to the periods 1961–1990, while data for the common gardens covered 1987–2021. For climate adaptation analyses, we focused on two key ecologically relevant climatic variables: mean annual temperature (Bio1) and total annual precipitation (Bio12) (Figure S5). This selection minimized redundancy, as other bioclimatic variables are derived from these two and are thus highly correlating (Figure S6). From the datasets, we extracted mean annual temperature (hereafter temperature) and mean monthly total precipitation (hereafter precipitation) for both the provenances and the common garden sites over the respective time periods.

2.4 | Genetic Data

From each 576 oak and beech trees, we collected 10–15 leaf buds, or in total for 66 cases across species, cambium samples and dried the samples in silica gel. DNA was extracted from 10 to 30 mg dried tissue using a bead-based plant kit and DNA quantity and quality were assessed using spectrophotometry (Methods S3). ddRAD sequencing followed a modified protocol of Peterson et al. (2012) and was performed at IGA Technology Services (Udine, Italy). Demultiplexed Illumina reads were aligned to the *Q. robur* and *F. sylvatica* reference genomes using BWA-MEM (Li and Durbin 2009). Reads with mapping quality below 4 were excluded (Methods S2). We performed SNP calling using Stacks v2 (Catchen et al. 2013), retaining loci represented in at least 75% of the metapopulation and using a maximum observed heterozygosity of 80%. Individuals with > 10% missing data were excluded and we further filtered oak and beech individuals with individual missingness above 50% and 20% from oak and beech, respectively, as these individuals were clear outliers in their respective

A) Sessile oak



B) European beech

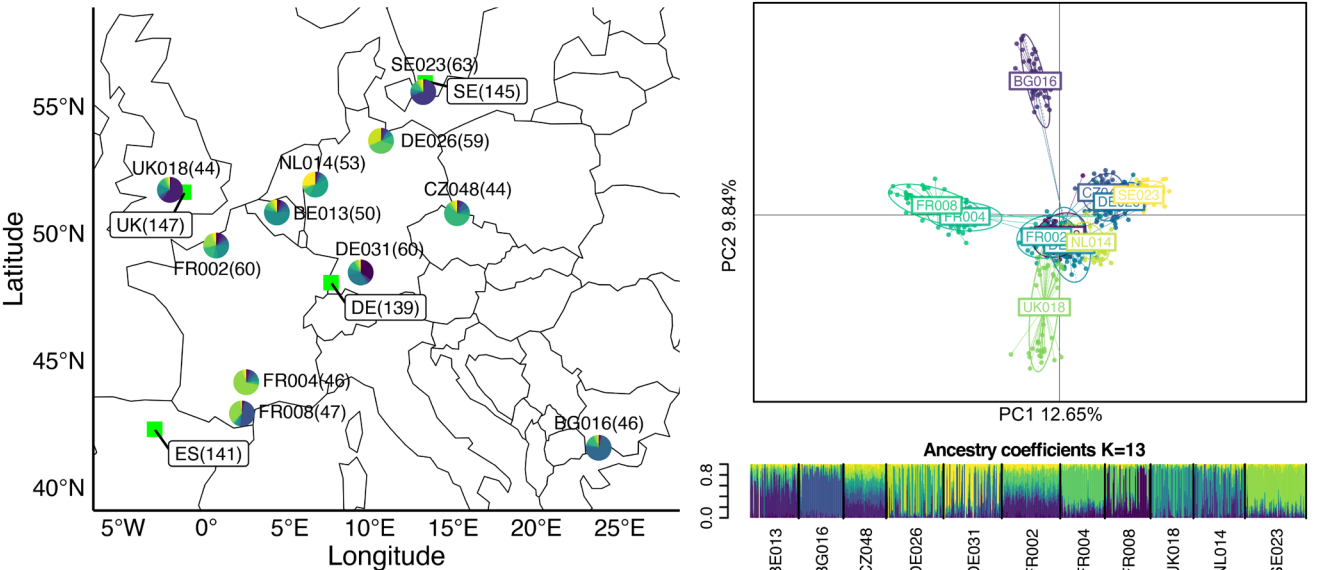


FIGURE 1 | Location of sessile oak (*Quercus petraea*, A) and European beech (*Fagus sylvatica*, B) common gardens (green squares) and provenances (pie charts) including their population genetic structure (pie charts and right panels). Numbers in parentheses represent the total number of samples at each common garden or from each provenance (for details see Table S1). Pie charts show the average ancestry coefficients per population from sNMF. Principal component (PC) and sNMF analyses (pie charts and barplots) are based on the neutral SNP datasets of the respective species. *K* represents the number of ancestral populations; for oak, *K*=4 is shown and for beech *K*=13, the rest of the ancestry coefficients are presented in Figure S4.

datasets. We further applied a 5% minor allele frequency (MAF) filter. For population genetic analyses involving putatively neutral and unlinked genetic variation, we additionally created a 'neutral' SNP set by applying a Hardy-Weinberg equilibrium filter with a *p* value threshold of 0.0001 and thinning SNPs by random selection of one SNP per 1000 bp to avoid loci potentially affected by selection. RADseq provides genome-wide coverage, yet we note that this approach limits our ability to capture the full spectrum of the relevant variation (Lowry et al. 2017). However, RADseq remains an effective tool as shown in plant GWA studies for uncovering the genetic architecture of adaptation (e.g., Lind et al. 2017; Gramlich et al. 2022; Parchman et al. 2012).

Separating *Q. petraea* morphologically from co-occurring white oak species like *Q. pubescens* and *Q. robur* is difficult (Kremer et al. 2002, Rellstab, Bühler, et al. 2016) due to high phenotypic plasticity and extensive hybridization (Rellstab, Bühler, et al. 2016; Reutimann et al. 2020). Therefore, we performed initial population genetic analyses to identify and exclude trees that were not *Q. petraea* or were highly admixed (for details see Methods S1). This resulted in excluding the entire Turkish provenance and individual trees from other provenances from all analyses, yielding a final dataset for oak of 500 individuals (99–142 per common garden; Table S1). Except for the Polish common garden, each provenance had at least 9 individuals per

common garden. These values are similar to the final dataset for beech, which contained 572 individuals, with 139 to 147 per common garden (Table S1).

2.5 | Genetic Diversity and Population Structure

All population genetic and further analyses were performed in R v4.2.0 (R Core Team 2022). Using the neutral SNP set to describe the neutral genetic structure and diversity, we first performed principal component analyses (PCA) using the R package *adegenet* v2.1.10 (Jombart and Ahmed 2011) and estimated ancestry coefficients using the sparse nonnegative matrix factorization (sNMF) clustering algorithm (Frichot et al. 2014) with the R package *LEA* v3.14.0 (Gain and François 2021). For sNMF, we explored models up to $K=10$ and $K=20$ for oak and beech, respectively, using 10 replicates per model and used the cross-entropy value to choose the K value that best fitted the data. We then calculated observed (H_o) and expected heterozygosity (H_e), inbreeding coefficient (F_{IS}), nucleotide diversity without invariant sites (π) and pairwise F_{ST} among provenances, using the R package *hierfstat* v0.5.11 (Goudet 2005). We tested for isolation by distance (IBD) using linearized F_{ST} ($F_{ST}/1-F_{ST}$) and ln-transformed geographic distance (Rousset 1997) with a Mantel test with 1001 permutations using the R package *ecodist* v2.1.3 (Goslee and Urban 2007).

2.6 | Genome-Wide Association (GWA) Analyses

To account for environmentally induced phenotypic variation, we used residuals from trait-based linear mixed effect models in our GWA analyses. In these models, for each trait, residuals were obtained by implementing site and competition as fixed effects and experimental block as a random effect. To identify loci in the genome associated with the functional traits, we used two complementary methods implemented in GEMMA v0.98.5 (Zhou and Stephens 2012): univariate linear mixed effect models (hereafter LMM) and Bayesian sparse linear mixed models (hereafter BSLMM). Relatedness and population structure can increase false positives in GWA analyses (Korte and Farlow 2013). To minimize this effect, we estimated relatedness matrices using the neutral SNP set in GEMMA and included them as a covariates in all GWA models. Moreover, using the neutral SNP set, we performed PCAs and included the PC components as covariates to account for population structure. For LMMs, we explored up to PC19 (i.e., explaining ~85% of the variance) and retained those improving model fit, as diagnosed by QQ-plots and genomic inflation factors (λ). The statistical significance of associations was determined using the Wald test (Wald 1943). Associations were considered statistically significant if they fulfilled either of two criteria: a p -value cutoff based on the Bonferroni correction (0.05/number of tests) and on a suggestive threshold defined as 1/number of tests (Lander and Kruglyak 1995; Guo et al. 2017). These two methods provide alternative stringency levels to account for multiple testing: while Bonferroni correction is highly conservative (assuming all tests being independent, Benjamini and Hochberg 1995; Kaler et al. 2019) the suggestive threshold indicates associations that would reach stronger significance given a larger sample size.

To account for linkage disequilibrium (LD) between significant associations, we estimated correlations between pairwise combinations of the associated SNPs and retained the SNP with the lowest p -value for pairs with Pearson $r^2 > 0.6$, estimated using *vcftools* (Danecek et al. 2011). We ran the BSLMMs four times with 40 million iterations, a burn-in rate of 10 millions and thinning interval of 1. We visually diagnosed model convergence using the trace plots and considered SNPs with a posterior inclusion probability (PIP) above 0.01 as sparse effect loci. To identify putative functional significance, we investigated the significant loci by aligning them with genome annotations from the respective reference genome assemblies using a defined window of ± 200 base pairs around each locus. Potentially pleiotropic associations were visualized in R using the *UpSetR* package (Conway et al. 2017). To examine whether high overlap of significant loci among traits tends to occur between statistically correlated traits, we quantified pairwise Pearson correlations among all traits and compared them to the number of shared significant loci for each trait pair. To test whether identified loci were disproportionately located within gene regions, we overlapped associated loci and all tested SNPs (hereafter background SNPs) with annotated gene models using the *GenomicRanges* v1.48.0 R package (Lawrence et al. 2013) and performed a Fisher's exact test to assess enrichment. We used the hyperparameters from the BSLMMs to further characterize the genetic architecture and report the proportion of phenotypic variance explained by all SNPs (PVE, an approximation of narrow sense heritability), the proportion of phenotypic variance explained by sparse effect loci (i.e., large-effect loci, PGE), the degree of polygenicity (ρ) and the proportion of variants with nonzero effect (π).

2.7 | Genotype-Environment Association (GEA) Analyses

For complementary evidence of climate adaptation, we conducted genotype-environment association (GEA) analyses (Rellstab et al. 2015) using temperature and precipitation of the provenance origins as predictors of allele frequency with latent factor mixed models (LFMM, Frichot and François 2015) using LFMM 2 (Caye et al. 2019) in the R-package *LEA3* v3.14.0 (Gain and François 2021). LFMM accounts for population structure by incorporating latent factors as random factors (inferred from the genotype matrix). We explored latent factors up to $K=9$ for oak and $K=11$ for beech. We performed 10 independent runs of the algorithm per species and evaluated model fit using QQ-plots and λ . The primary goal of these analyses was to identify complementary evidence of adaptation, so we focused on the top 1% significant loci rather than applying an FDR correction. This approach allowed us to focus on loci strongly associated with temperature or precipitation that were also identified in the GWA analyses as potentially important for climate adaptation. We accounted for LD by estimating pairwise LD among loci by identifying pairs of loci in high LD (Pearson $r^2 > 0.6$), similar to the LMM GWA approach described above. Among loci in high LD, we retained only the one with the lowest p value. Lastly, we evaluated whether the loci identified in the LFMM analyses were in high LD with loci identified in GWA using the same LD approach.

TABLE 1 | Summary of the genome-wide association (GWA) analyses. The number of significant loci detected in oak and beech using linear mixed models (LMM) and Bayesian sparse linear mixed models (BSLMM) are listed. For both species, all loci identified as significant in the LMM analyses were also identified as sparse effect loci in the BSLMM analyses. Significance thresholds were $p < 0.05$ after Bonferroni correction or a suggestive threshold of 1/number of tests for LMM and posterior inclusion probability (PIP) > 0.01 for BSLMM. Loci are categorized based on functional groups and traits.

Functional group and trait	Oak		Beech	
	No. SNPs LMM	No. SNPs BSLMM	No. SNPs LMM	No. SNPs BSLMM
Tree size				
DBH: Diameter at breast height	3	37	3	10
Height: Total tree height	6	171	2	35
Leaf morphology				
SLA: Specific leaf area	7	255	2	3
Tree growth increment				
BAI: Basal area increment	3	50	2	3
Long-term growth responses to climate				
Sprpre: Correlation between growth and spring precipitation	1	72	2	21
Sumpre: Correlation between growth and summer precipitation	1	33	0	6
Sprtmea: Correlation between growth and spring temperature	2	88	3	14
Sumtmea: Correlation between growth and summer temperature	3	47	3	2
Short-term growth responses to extreme drought				
Rs: Resilience to extreme drought	5	37	3	18
Rt: Resistance to extreme drought	3	27	1	10
Rc: Recovery after extreme drought	4	29	1	4

2.8 | Genotype-By-Climatic Distance Interactions

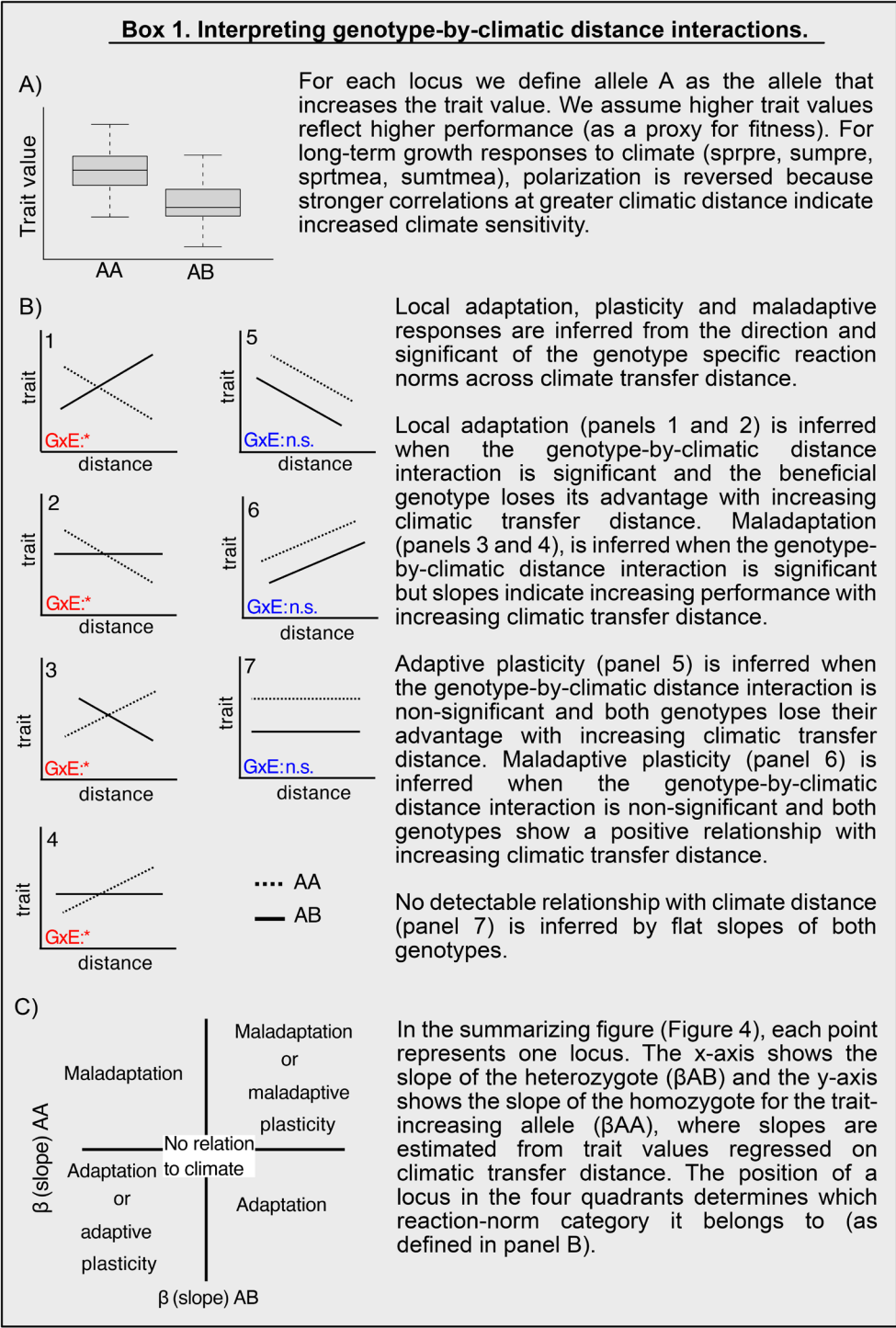
To test whether the loci identified in GWA are involved in climate adaptation, we tested how the effect of alleles associated with the studied phenotypic traits interact with environmental distance (Box 1). If these loci contribute to climate adaptation, beneficial allelic effects should decrease as climatic differences between provenance origin and common garden sites increase. Phenotypic traits and temperature and precipitation values were standardized to a mean of zero and SD of one before the analyses, following De Lisle and Svensson (2017). Climatic transfer distances were calculated as the Euclidean distance in climate space between the original provenance locations and the common garden sites.

For each locus, we tested for adaptive or plastic responses to climate (Box 1). Due to many significant loci having low minor allele frequencies, the number of homozygote individuals carrying the minor allele was too small for reliable estimation of their genotype-by-environment interactions. We therefore excluded minor allele homozygotes and compared major allele homozygotes with heterozygotes for each locus as in Troth et al. (2018) to maintain statistical power. We implemented linear mixed

effects models with genotype, climate transfer distance (temperature or precipitation) and its interaction with genotype as fixed effects. Competition was included as an additional fixed effect while site and block were included as random effects. Due to low sample sizes, we excluded three-way interactions between genotype and temperature and precipitation transfer distances. We assessed significance of the interaction terms using likelihood ratio tests and evaluated comparisons between genotypes using the *emmeans* R package v2.0.1 (Lenth 2017), controlling for multiple testing using the Tukey method.

To enhance interpretability, we polarized the alleles by defining the A allele as increasing trait values, such that AA homozygotes have higher trait values than AB heterozygotes. For long-term climate response traits (sprpre, sumpre, sprtmea and sumtmea, Table 1) polarization was reversed because an adaptive response is expected to be indicated by increased strength of the correlation as climatic distance increases (increased sensitivity to climate). Genotype-by-climatic distance effects and genotype-specific reaction norm patterns were then interpreted in terms of local adaptation, adaptive plasticity, maladaptation, or maladaptive plasticity following the framework summarized in Box 1. We note that SLA cannot

BOX 1 | Conceptual Framework for Classifying Genotype-Specific Reaction Norms in Response to Climatic Transfer Distance. Illustrations of how slopes of the homozygous trait-Increasing genotype (β_{AA}) and the heterozygote (β_{AB}) are interpreted in terms of local adaptation, adaptive plasticity, maladaptation, or maladaptive plasticity are shown in Panel C.



readily be interpreted in terms of adaptation, as the directionality of this trait does not consistently reflect fitness across environments.

3 | Results

3.1 | Genetic Data

For oak, sequencing of 496 individuals resulted in 484,956 SNPs. After bioinformatic processing we retained 13,587 and 6987 high-quality SNPs across 494 individuals, for the full and neutral/unlinked dataset, respectively. Despite removing some individuals, the experimental design remained intact with each provenance represented in each common garden. All SNPs were successfully aligned to the reference genome.

For beech, sequencing of 576 individuals resulted in 297,322 SNPs, of which, after bioinformatic processing, we retained 26,455 and 7548 high-quality SNPs across 572 individuals for the full and neutral/unlinked dataset, respectively. Similar to oak, some individuals were removed without altering the integrity of the experimental design. The beech data included 246 SNPs that were not located in scaffolds anchored to the linkage map of 12 chromosomes of beech; these SNPs were included in the analyses but excluded from the Manhattan plots.

3.2 | Genetic Diversity and Population Structure

Observed (H_o) and expected heterozygosity (H_e) were consistent across both species, with beech showing overall higher diversity than oak (mean H_o , oak: 0.112 ± 0.002 SD; beech: 0.276 ± 0.005 ; mean H_e , oak: 0.112 ± 0.002 ; beech: 0.276 ± 0.006 , Table S2). Nucleotide diversity (π) was high and consistent across species, although higher in beech (mean π , oak: 0.012 ± 0.001 ; beech: 0.027 ± 0.001 , Table S2). Inbreeding coefficients (F_{IS}) indicated low inbreeding in most oak provenances (mean F_{IS} : 0.032 ± 0.006 , Table S2) while beech provenances varied, showing low negative to positive values (mean F_{IS} : -0.001 ± 0.022 , Table S2). Both species exhibited IBD, but the effect was substantially weaker in oak than in beech (Figure S7A, oak: Mantel $r = 0.53$, $p = 0.002$; Figure S7B, beech: Mantel $r = 0.71$, $p = 0.001$). Genome-wide pairwise relatedness matrices indicated generally low relatedness among individuals within provenances, with no evidence for substantial cryptic family structure (Figure S8). Only 6 out of 161,596 pairwise comparisons in beech exceeded a relatedness of 0.25 (half-sibs) and none out of 121,771 comparisons in oak exceeded this threshold.

Cross-entropy analyses of ancestry coefficients indicated that, for oak, $K=4$ best explains the variation in the data (Figures S9A, S4A). In oak, UK provenance trees formed a distinct genetic cluster, evident in both the ancestry assignment and the PCA (Figure 1A). Moreover, provenances of Poland (PL033), Denmark (DK260) and Germany (DE263) mostly consisted of another genetic cluster. For beech, a larger number of genetic clusters was indicated, with $K=13$ best explaining the data (Figures S9B, S4B). Overall, beech exhibited more pronounced genetic structure between provenances than oak, also supported by the PCA (Figure 1). The three southernmost

provenances (FR004, FR008 and BG016) and partly the UK provenance (UK018) appeared distinct from other beech provenances. However, only the two southernmost French provenances (FR004 and FR008) separated along PC1 (12.65%) while the Bulgarian provenance (BG016) and some trees of the UK provenance (UK018) separated on PC2 (9.84%) (Figure 1B).

3.3 | Genome-Wide Association (GWA) Analyses

For LMMs in oak, inclusion of PC components (estimated using the neutral SNP set to capture underlying population structure) caused a deflation of the QQ plots and they were therefore not included in the final models for each trait. Across LMM analyses, λ values ranged from 0.97 to 1.07 (Figures S10, S11), which, together with the QQ plots, indicated adequate control for population structure and relatedness. After pruning for LD, we retained multiple significant loci for each trait (example in Figure 2; all others in Figures S11, S12; total numbers in Table 1). We identified a total of 38 and 846 SNPs significantly associated with the functional traits using the LMM and BSLMM approaches, respectively. Both models yielded the highest number of associated SNPs in traits such as SLA, height, and sprtmea. Notably, all loci identified with the LMM approach were also identified with BSLMM. MAFs were variable; for example, MAFs for height ranged from 0.051 to 0.350 and for BAI from 0.073 to 0.299. Approximately 78% of the loci identified using BSLMM (618 of 797 SNPs) were located within genes, which was similar to the proportion of genic SNPs in the background dataset (76%, 9457 of 12,463 SNPs), and Fischer's exact test found no significant enrichment ($p = 0.305$, odds ratio = 1.10, 95% CI = 0.92–1.31). Also, among the loci identified in both LMM and BSLMM, the majority were located within genes, suggesting functional relevance (Table S3). Moreover, several SNPs were associated with multiple traits, particularly within functional groups (Figure 3). Locus overlap among traits was sparse overall and not primarily among highly correlated traits (Figure 3; Figures S13, S14).

Beech exhibited a substantially stronger population structure than oak and therefore, we included multiple PC components to control for population structure in several cases (Table S3). Across all analyses, we recovered λ values ranging from 0.97 to 1.05 (Figures S10, S15), which together with the QQ plots indicated that in most cases we had sufficiently accounted for population structure and relatedness. For beech, the LMM and BSLMM identified 22 and 126 SNPs, respectively, as significantly associated with the functional traits (example in Figure 2, all others in Figures S15, S16; total numbers in Table 1). Across both models, traits such as height, Rs and sprpre showed the highest number of associations. Importantly, all SNPs identified through LMM were also identified using the BSLMM approach, indicative of the robustness of the modelling approaches. MAFs varied across traits, for example, MAFs ranged from 0.058 to 0.285 for height and was 0.065 for BAI. Of the SNPs identified with BSLMM, 42% (50 of 119 SNPs) were located within genes compared to 47.1% (12,408 of 26,336 SNPs) of background SNPs; Fischer's exact test found no significant enrichment ($p = 0.271$, odds ratio = 0.81, 95% CI = 0.55–1.19). Additionally, some SNPs were associated with multiple traits that mostly showed high correlations with each other (Figure 3; Figures S13, S14).

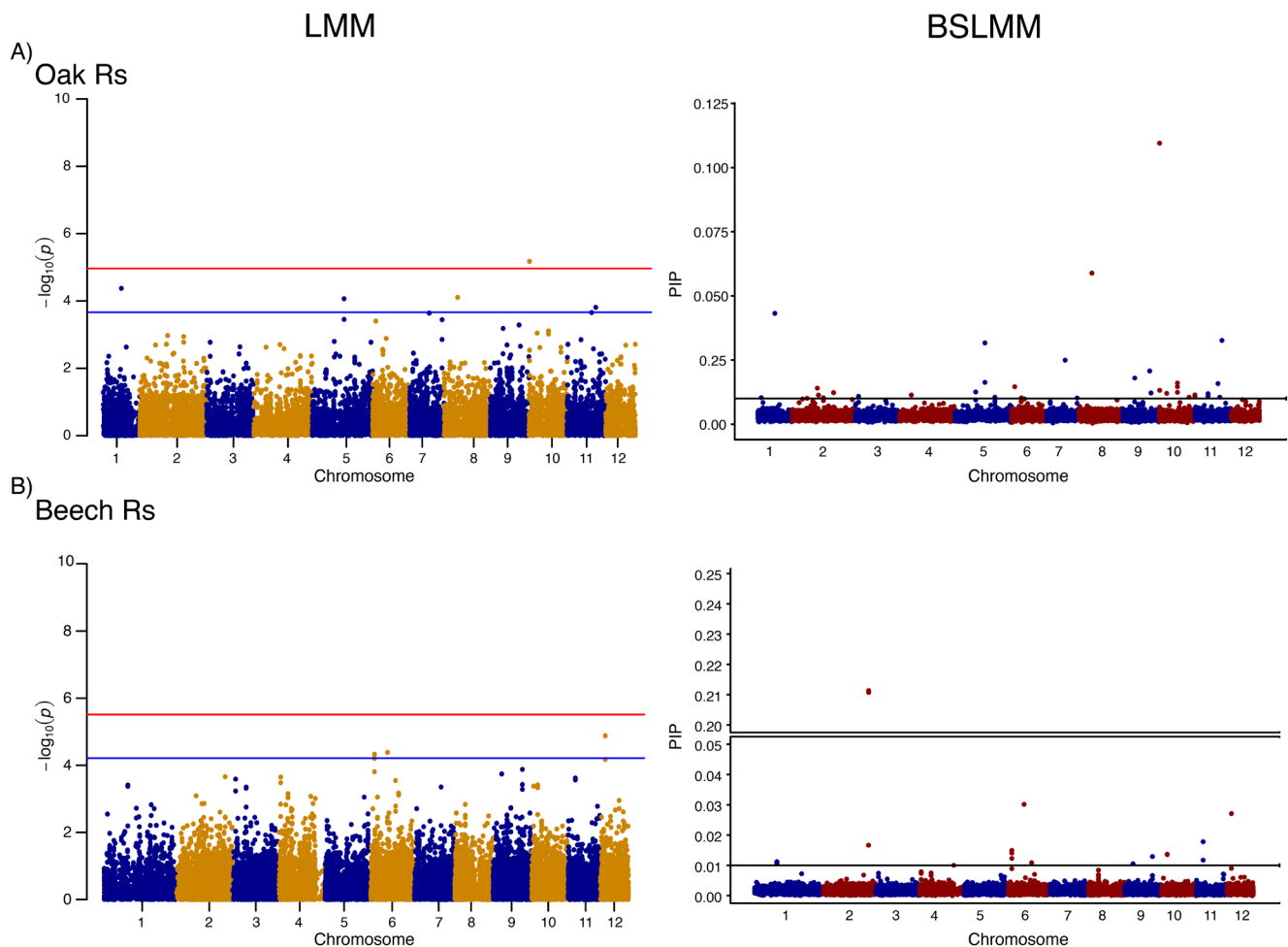


FIGURE 2 | Manhattan plots for the genome-wide association (GWA) analyses for resistance to extreme drought (Rs) in (A) oak and (B) beech. Left and right panels show the linear mixed models (LMM) and Bayesian sparse linear mixed models (BSLMM) Manhattan plots, respectively. For LMM, the blue and red horizontal lines indicate significance thresholds at the suggestive and Bonferroni levels, respectively. The horizontal grey line in BSLMM denotes the posterior inclusion probability (PIP) > 0.01 threshold for statistical significance. Note that only Rs is presented here, GWA results for the rest of the traits are presented in Figures S10, S11, S14, S15.

3.4 | Genetic Architecture

BSLMM revealed modest but variable genetic contributions across traits in both species, with estimated PVE values (proportion of phenotypic variance explained by all SNPs) spanning nearly an order of magnitude (Table 2). Genetic contributions to tree size traits were relatively low. In both species, PVE was lowest for DBH and slightly higher for height, while species differences were small relative to uncertainty (Table 2). Estimates of π (proportion of SNPs with nonzero effect) in tree size traits were consistently low, while ρ (degree of polygenicity) showed moderate estimates but wide credible intervals, limiting strong inference on the extent of polygenicity. For oak, leaf morphology exhibited stronger inferred genetic control than the tree size traits. Here, specific leaf area (SLA) showed the highest PVE among all traits; however, it had lower values in beech (Table 2). As for other traits, estimates of π were low and ρ was moderate with broad credible intervals. Tree growth increment (BAI) showed intermediate levels of genetic contribution. Oak exhibited higher PVE than beech, while estimates of π , ρ and PGE were characterized by substantial uncertainty in both species.

Long-term growth responses to climate showed generally low to moderate genetic contributions. PVE values were low for precipitation-related traits in both species, while temperature responses showed slightly higher values for spring temperature in beech. Across all climate response traits, estimates of π remained low and ρ had wide credible intervals. Short-term growth response to extreme drought (resilience, resistance and recovery) showed consistently low PVE values and high uncertainty. Estimates of π were near zero and ρ showed moderate values with wide credible intervals. Overall, BSLMM results indicate that genetic contributions vary substantially among traits, with leaf morphology and growth-related traits generally showing higher PVE than climate- and drought-response traits.

3.5 | Genotype-Environment Association (GEA) Analyses

Using latent factor mixed models (LFMM), we identified 16 SNPs associated with temperature in oak after correcting for linkage disequilibrium (LD). These loci were scattered across

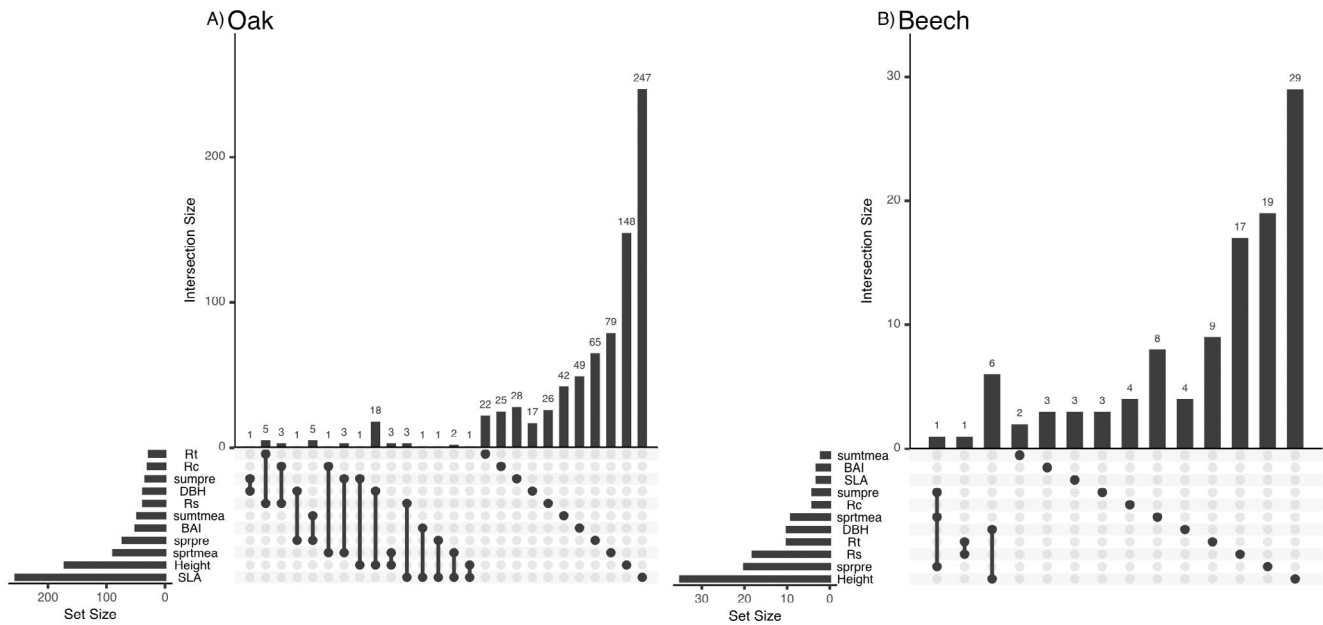


FIGURE 3 | Assessment of pleiotropy in the genome-wide association (GWA) analyses. UpSet plots illustrating the overlap of significant genetic loci across phenotypic traits in (A) sessile oak and (B) European beech. The left bar plots represent the total number of significant loci for each trait (for details, see Table 1), while the upper bar plots show the number of loci shared between different combinations of traits. Black dots connected by lines indicate the specific trait combinations contributing to each intersection. All loci identified in the linear mixed models (LMM) were also recovered by the Bayesian sparse linear mixed models (BSLMM) in both species, the plots display the combined set of significant loci, with LMM hits representing a subset of the BSLMM loci.

the genome (Figure S17A). Similarly, 21 loci were associated with precipitation, also widely spread across the genome (Figure S17B). Notably, 8 of the temperature-associated loci were in high LD with SNPs previously identified in the GWA analyses for specific traits, including specific leaf area (SLA) (2), basal area increment (BAI) (1), the correlation between growth and spring precipitation (sprpre) (3) and recovery after drought (Rc) (2) (Table S4). Additionally, one precipitation-associated locus was in high LD with a locus identified in the GWA analyses for SLA. For beech, the LFMM analyses identified 43 loci associated with temperature after LD pruning, distributed across the genome and 41 loci associated with precipitation, with a notable peak on chromosome 6 (Figure S17C,D). Interestingly, only one of these loci was in high LD with a locus identified in the GWA, specifically associated with the correlation between growth and spring temperature sprtmea (Table S4).

3.6 | Genotype-By-Climatic Distance Interactions

For resilience to extreme drought (Rs), oak loci predominantly exhibited negative slopes under both temperature and precipitation transfer distances, with a larger number of loci with significant interactions with precipitation (Figure 4). In contrast, beech showed weaker responses; most loci were clustered around slopes of zero. The presence of loci where genotype AA (homozygote for the allele associated with increasing the trait value) had a negative slope ($\beta_{AA} < 0$) and genotype AB showed a slope near zero ($\beta_{AB} = 0$) suggests that the negative effects of climatic transfer distance were stronger in AA homozygotes compared to heterozygotes. For resistance to extreme drought (Rt), genotype-by-environment interactions were generally weak under both

temperature and precipitation transfer distances in both species, with only a few significant GWA loci identified (Figure 4B). Most slopes estimated by genotype-by-climate distance relationship were clustered around slopes of zero, suggesting limited genetic and plastic responses to both environmental variables. For recovery after extreme drought (Rc), very few GWA loci were identified for beech, while for oak, nearly all loci exhibited significant negative slopes under temperature transfer distances, with only one significant genotype-by-environment interaction (Figure 4C). For precipitation transfer distances, although the slopes were still negative, the majority of slopes estimated for most loci were clustered around zero (Figure 4C).

For both DBH and height in oak, most loci associated with temperature transfer distances showed positive slopes for both genotypes, clustering in the upper right quadrant (Figure S18A,B). Beech showed the same trend, though loci were more concentrated around slopes of zero. Most of the loci for DBH showed no significant genotype-by-environment interactions, whereas a greater number of loci for height displayed significant interactions in both species. For precipitation transfer distances, no strong directionality of trends was observed and both species showed limited response to climatic variation.

For SLA, oak exhibited a pronounced but diverse relationship with temperature transfer distance (Figure S18C). A large number of loci showed significant genotype-by-environment interactions, but most loci were either clustered around slopes of zero or displayed a combination of responses. Similarly, no clear trend emerged for beech. For precipitation transfer distance, the majority of loci in oak revealed signals of plasticity (Figure S18C), with many significant genotype-by-environment interactions

TABLE 2 | Summary (median and range) of genetic parameter estimates from the Bayesian sparse linear mixed models (BSLMM) for sessile oak and European beech. Parameters include pi (proportion of SNPs with nonzero effects), rho (degree of polygenicity), PVE (proportion of phenotypic variance explained by all SNPs, an approximation of narrow sense heritability) and PGE (proportion of genetic variance explained by sparse-effect, i.e., large-effect loci).

	Sessile oak				European beech			
	pi	rho	PVE	PGE	pi	rho	PVE	PGE
Tree size								
DBH:	0.001 (0, 0.02)	0.427 (0.02, 0.967)	0.084 (0.004, 0.274)	0.264 (0, 0.94)	0.001 (0, 0.01)	0.549 (0.029, 0.98)	0.111 (0.009, 0.272)	0.423 (0, 0.972)
Diameter at breast height								
Height: Total tree height	0.002 (0, 0.02)	0.524 (0.037, 0.969)	0.166 (0.016, 0.381)	0.449 (0, 0.964)	0.001 (0, 0.009)	0.483 (0.032, 0.961)	0.177 (0.053, 0.327)	0.378 (0, 0.955)
Leaf morphology								
SLA:	0.003 (0, 0.021)	0.521 (0.034, 0.97)	0.208 (0.026, 0.452)	0.452 (0, 0.967)	0.001 (0, 0.01)	0.588 (0.035, 0.985)	0.041 (0.001, 0.206)	0.442 (0, 0.973)
Specific leaf area								
Tree growth increment								
BAI:	0.001 (0, 0.019)	0.536 (0.052, 0.963)	0.191 (0.031, 0.402)	0.392 (0, 0.946)	0 (0, 0.01)	0.58 (0.03, 0.988)	0.023 (0.001, 0.12)	0.378 (0, 0.966)
Basal area increment								
Long-term growth responses to climate								
Sprpre:	0.002 (0, 0.021)	0.532 (0.031, 0.977)	0.084 (0.004, 0.282)	0.42 (0, 0.969)	0.001 (0, 0.01)	0.485 (0.024, 0.974)	0.108 (0.005, 0.344)	0.347 (0, 0.961)
Correlation between growth and spring precipitation								
Sumpre:	0.001 (0, 0.02)	0.552 (0.03, 0.982)	0.05 (0.002, 0.209)	0.404 (0, 0.969)	0 (0, 0.01)	0.548 (0.027, 0.985)	0.033 (0.001, 0.176)	0.358 (0, 0.965)
Correlation between growth and summer precipitation								

(Continues)

TABLE 2 | (Continued)

	Sessile oak					European beech				
	pi	rho	PVE	PGE		pi	rho	PVE	PGE	
Sprtna: Correlation between growth and spring temperature	0.002 (0, 0.018)	0.601 (0.042, 0.982)	0.089 (0.004, 0.297)	0.515 (0, 0.977)		0.001 (0, 0.011)	0.418 (0.019, 0.962)	0.2 (0.015, 0.569)	0.304 (0, 0.95)	
Sumtna: Correlation between growth and summer temperature	0.002 (0, 0.02)	0.569 (0.034, 0.982)	0.064 (0.003, 0.224)	0.45 (0, 0.974)		0 (0, 0.009)	0.636 (0.043, 0.986)	0.089 (0.003, 0.361)	0.523 (0, 0.976)	
Short-term growth responses to extreme drought										
Rs: Resilience to extreme drought	0.001 (0, 0.02)	0.574 (0.034, 0.982)	0.067 (0.003, 0.223)	0.433 (0, 0.969)		0.001 (0, 0.01)	0.525 (0.027, 0.983)	0.066 (0.003, 0.229)	0.368 (0, 0.963)	
Rt: Resistance to extreme drought	0.001 (0, 0.02)	0.554 (0.031, 0.982)	0.053 (0.002, 0.209)	0.405 (0, 0.967)		0.001 (0, 0.01)	0.467 (0.023, 0.973)	0.077 (0.004, 0.246)	0.316 (0, 0.956)	
Rc: Recovery after extreme drought	0.001 (0, 0.019)	0.532 (0.028, 0.98)	0.057 (0.002, 0.214)	0.364 (0, 0.963)		0 (0, 0.01)	0.585 (0.033, 0.985)	0.036 (0.001, 0.143)	0.401 (0, 0.968)	

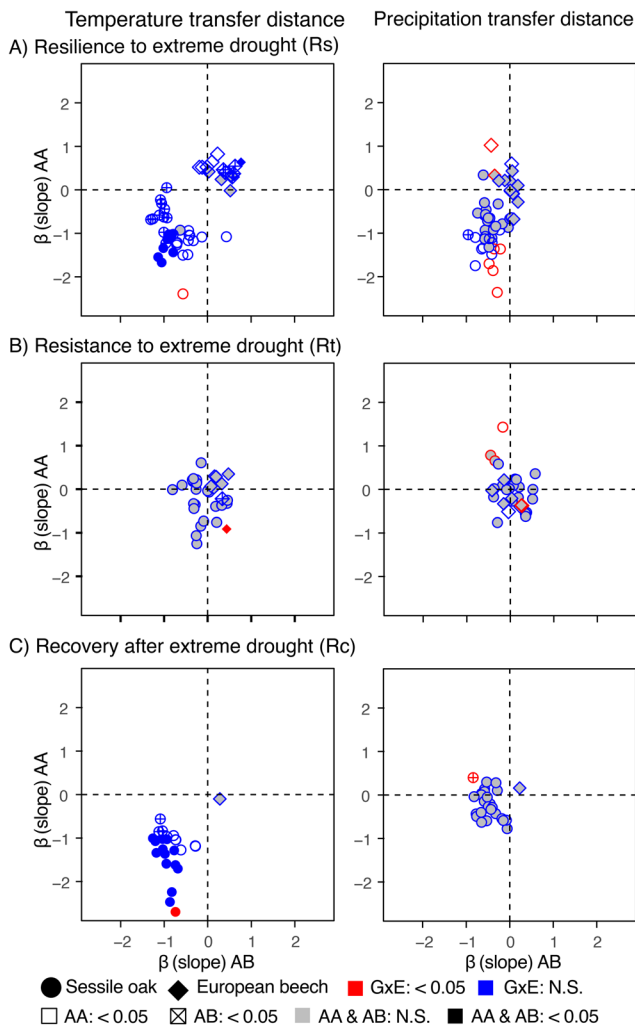


FIGURE 4 | Genotype-by-climatic transfer distance interactions for short-term responses to extreme drought. Left columns show responses to temperature transfer distance and the right columns show responses to precipitation transfer distance. (A) resilience to extreme drought (Rs), (B) resistance to extreme drought (Rt) and (C) recovery after extreme drought (Rc). The y-axes represent the effect size (slope) of the homozygous genotype that increases the trait value, while the x-axes represent the effect size of the heterozygous genotype. Red and blue colours indicate significant and non-significant genotype-by-environment interactions ($p < 0.05$), respectively. Hollow and cross symbols represent AA and AB significance, respectively. Grey symbols indicate that neither genotype is significant and filled indicate that both are significant. For the interpretation of these plots in terms of adaptation and plasticity, see Box 1.

and significant positive slopes for both genotypes. As with temperature transfer distance, beech displayed limited responses to precipitation transfer distance, with loci clustered around a slope of zero. Note that with our analysis, results for SLA can only be interpreted in terms of plasticity, but not adaptation, since SLA cannot be polarized for higher or lower fitness. The BAI loci showed no clear direction in response to temperature transfer distance in both species. However, for precipitation transfer distance, a primarily plastic response was identified in oak, with negative slopes for the AA genotypes but two loci with a significant genotype-by-environment interaction (Figure S18D).

Finally, long-term climate response traits (sprpre, sumpre, sprtmea, and sumtmea) showed no consistent directional responses to climate transfer distances (Figure S18E–H), with most loci clustering around zero slopes, with a combination of maladaptive and adaptive plastic responses. Notably, adaptively plastic responses were identified in sumtmea in oak.

4 | Discussion

We combined phenotypic and climatic data from sessile oak and European beech provenances, grown across widely distributed common gardens in Europe, with genomic data to investigate the genetic architecture of functional traits and its relevance for future climate scenarios. Our previous study (Martínez-Sancho et al. 2025), using the same sampling design without genomic data, observed striking species-specific patterns: oak showed signals of both climate adaptation and phenotypic plasticity, while beech exhibited fewer adaptive signals and a stronger reliance on phenotypic plasticity. In the present study, we expanded upon those findings by integrating landscape genomic analyses with different GWA models to characterize trait genetic architecture and test for genomic evidence of climate adaptation. Our results indicate that growth and climate-growth response traits in both species are influenced by multiple loci, consistent with expectations for complex polygenic genetic architectures. Consistent with Martínez-Sancho et al. (2025), we found contrasting responses to climate. Oak displayed clear genomic signals of climate adaptation and adaptive plasticity, as evidenced by genotype-by-climatic transfer distance relationship for both short-term drought response traits (resilience, resistance and recovery to extreme drought) and long-term responses to summer temperature. In contrast, beech generally showed a weak or absent relationship with climatic distance of genotypes at loci associated with the same traits. These findings highlight how species-specific genetic architectures underlying functional traits can reveal distinct patterns or even strategies for coping with climate change. They also raise further concerns about the future vulnerability of beech under ongoing climate change.

4.1 | Genetic Architecture of Functional Traits

Across both species, we found evidence for complex genetic architectures underlying the studied functional traits, with contributions distributed across multiple loci. However, oak consistently showed more significant genotype–phenotype associations than beech (Table 1). For example, in oak, BSLMM analyses identified dozens to hundreds of loci for traits like DBH, height and SLA. In contrast, beech showed substantially fewer associations across traits, with some (e.g., BAI and SLA) yielding three or fewer SNPs. The strongest species contrasts in the number of detected associations emerged for traits linked to climate, where oak exhibited notably more loci linked to long-term growth responses to summer temperature and short-term resilience to extreme drought. We also found indications of potentially pleiotropic loci, particularly among functionally related traits (Figure 3). Consistent with this, overlap of associated loci tended to occur among traits, especially in oaks. This pattern indicates that traits share a substantial fraction of their underlying loci, reflecting a shared genetic architecture rather than

independent sets of causal variants. However, distinguishing true pleiotropy from correlated responses remains challenging and future work is needed to clarify the causal relationships among traits and shared loci. High degrees of pleiotropy may also influence evolvability, as opposing selection acting across traits may impose evolutionary constraints and trade-offs (Paaby and Rockman 2013). However, pleiotropy does not necessarily constrain adaptation, when allelic effects are aligned across traits, it can actually facilitate adaptive responses to environmental change (Hämälä et al. 2020; Whiting et al. 2024). The overall pattern of multi-locus genetic contributions aligns with findings across various forest tree species where traits, such as growth and phenology are typically controlled by numerous loci of small to moderate effect (e.g., Lind et al. 2017; Sork et al. 2013; González-Martínez et al. 2007). Notably, all loci identified by LMM were also recovered by BSLMM, supporting the robustness of these associations and suggesting they are unlikely to be false positives (Lind et al. 2017; Martin et al. 2021). In both oak and beech, many BSLMM-identified loci were located within annotated gene regions. However, we found no significant enrichment of associated SNPs of genic regions compared to all RADseq SNPs. Although many annotations are predicted or general, the comparable genic distribution of associated and background SNPs across both species suggests the signals are unlikely to be artifactual. Rather, they likely reflect a biologically meaningful genetic architecture, with causal variants potentially located both within and outside annotated genes. Nevertheless, we note that our inferences using RADseq can only describe broad patterns of genetic architecture rather than exhaustively identify causal variants. Further insights may come from fine-mapping or integration with expression data to resolve the genomic context of key loci.

The difference in the number of associations between oak and beech likely reflects differences in genetic control and polygenicity. However, it may also reflect differences in the detectability of these associations, as highly polygenic architectures dominated by many small-effect loci are inherently more difficult to resolve with our current resolution (see also Lazic et al. 2024). However, additional factors likely contribute to these interspecific differences. For example, differences in genetic diversity and population structure can affect GWA power, particularly for detecting small-effect loci underlying polygenic traits (Korte and Farlow 2013; Visscher et al. 2017; Price et al. 2010). In our case, beech showed higher heterozygosity and nucleotide diversity than oak, aligning with, for example, Meger et al. (2021), but contrasting with Milesi et al. (2024), where oak exhibited higher genetic diversity than beech. While higher genetic diversity can enhance evolutionary potential, it can also introduce noise, obscuring signals of trait-associated loci. The stronger IBD and pronounced population structure found in beech (Figure 1; Figure S7) necessitated more covariates in LMMs, eventually reducing statistical power. In contrast, oak's extensive long-range gene flow and frequent introgression within the genus (Kremer and Hipp 2019; Leroy et al. 2020) resulted in lower population structure, likely improving power to detect with small-effect loci.

The BSLMM hyperparameters are consistent with complex, multi-locus genetic architectures in both species, while also highlighting substantial uncertainty in the precise degree of polygenicity (Table 2). Such wide credible intervals for BSLMM

hyperparameters are commonly observed and reflect the limited identifiability of genetic architecture parameters in moderately sized datasets rather than a lack of biological signal (Gramlich et al. 2022; Šarančić et al. 2025; Ferrão et al. 2024; Dowell and Mason 2023). In oak, traits such as DBH, SLA and components of drought resilience showed low to moderate heritability (as expressed by PVE) and a contribution from sparse-effect (i.e., large-effect) loci. This was indicated by moderate estimates of PGE and rho, although wide credible intervals limit strong inference regarding the relative contribution of large-effect loci. In contrast, beech showed lower heritability for several traits (especially SLA and BAI) and no clear evidence for strong contributions of sparse-effect loci, with polygenicity estimates remaining uncertain. Similar patterns of genetic architecture characterized by many small-effect loci have been observed in other species. For example, leaf morphology and climate response traits in *Populus trichocarpa* showed highly polygenic architecture (Chhetri et al. 2019), while growth responses to climate in *Pinus strobus* are controlled by numerous small-effect loci (Housset et al. 2018). These findings are consistent with the theory that fitness-related traits often evolve under weak selection acting on many loci (Bomblies and Peichel 2022; Savolainen et al. 2013). Our findings contribute to the growing evidence that functional traits in long-lived trees often involve complex, multi-locus genetic architectures, consistent with polygenic models (Lind et al. 2018; de Miguel et al. 2022).

4.2 | Contrasting Patterns of Oak and Beech in Adaptation to Climate

Genotype-by-climate-distance interaction analyses revealed clear contrasts between the two studied species (Figure 4; Figure S18). Oak showed stronger genomic responses to climatic transfer distances. For key traits such as resilience to extreme drought (Rs), many loci displayed significant genotype-by-climate interactions with negative slopes (Figure 4), indicating local adaptation (Savolainen et al. 2013; Kawecki and Ebert 2004), where beneficial alleles confer fitness advantages under home climatic conditions, but lose effectiveness with increasing climatic distance. In contrast, beech showed limited genomic responses, with most loci clustering around slopes of zero, indicating comparatively weak detectable genomic responses and limited phenotypic plasticity in relation to climate transfer distances. Precipitation transfer distance had a pronounced effect on Rs in oak, suggesting precipitation as a key driver of adaptive drought responses. Similarly, for the other extreme drought-related traits (i.e., resistance (Rt) and recovery (Rc)), oak showed stronger genomic responses and greater adaptive plasticity than beech, as indicated by steeper reaction norm slopes across loci. GEA analyses further supported this pattern, identifying temperature-associated loci in oak in high LD with GWA loci for resilience (Rc), basal area growth increment (BAI) and specific leaf area (SLA). In beech, only one such locus was detected. These contrasting responses are consistent with prior findings of higher drought sensitivity and lower adaptive capacity in beech, particularly at its southern range edge (Zimmermann et al. 2015; Hackett-Pain et al. 2016; Dorado-Liñán et al. 2019). As drought events intensify, this limited responsiveness raises concerns about beech's long-term persistence and adaptive potential, especially at its trailing edge.

Species contrasts extended across multiple traits (Figure S18). For DBH and height, we found signs of maladaptive plasticity and maladaptation in both species, with stronger effects in oak. However, these findings rely on the assumption that higher growth (i.e., higher trait values) corresponds to higher fitness. While this is often a reasonable proxy (Younginger et al. 2017), it might not apply across species, traits, or environments. For example, populations from range-edge or from extreme latitudes and elevations often show reduced growth when transplanted to contrasting conditions. This reduced growth may reflect local adaptation to shorter growing seasons, frost risk, or hydraulic limitations, rather than lower fitness (Savolainen et al. 2007; Alberto et al. 2013; Vitasse et al. 2014). Such populations may prioritize survival or resource conservation over biomass accumulation. Therefore, while growth is frequently linked to reproductive output, reduced growth in foreign environments may represent adaptive responses to home-site constraints rather than maladaptation.

A similar trend was observed for long-term climate sensitivity traits: oak showed signs of adaptive plasticity, while beech responses were generally weak or absent. For SLA, oak displayed numerous loci with complex genotype-by-environment interactions in response to both temperature and precipitation transfer distances, while beech again showed minimal genomic and plastic responses. These patterns align with observation in other species, where leaf morphological traits such as SLA are typically highly polygenic and highly plastic (Gunn et al. 1999). Although SLA often exhibits clinal variation, it is not a consistent proxy for fitness. For example, plants from drier environments commonly have lower SLA values (Wright et al. 2004), likely reflecting its association with water-use efficiency (Cunningham et al. 1999). Thus, while the observed SLA variation observed here matches ecological expectations, its adaptive relevance is context-dependent and shaped by both plasticity and local environmental constraints.

Our findings align with broader patterns in tree ecology and evolutionary genetics. Previous studies highlight high genetic diversity, elevated gene flow and extensive adaptive introgression in oak, factors which, combined with strong selection pressure, likely facilitate the evolution of local adaptation (Kremer and Hipp 2019; Leroy et al. 2020; Torres-Ruiz et al. 2019). Genotype-environment association (GEA) analyses have detected signals of local adaptation to precipitation gradients in both *Q. petraea* (Rellstab, Zoller, et al. 2016) and in related oak species such as *Q. robur* (Temunović et al. 2020; Rellstab, Zoller, et al. 2016), *Q. pubescens* (Rellstab, Zoller, et al. 2016), *Q. rugosa* (Martins et al. 2018), *Q. longinix* (Sun et al. 2024) and *Q. suber* (Pina-Martins et al. 2019). Moreover, recent temporal genomic studies demonstrated directional allele frequency shifts in *Q. petraea* at climate-associated loci over the last three centuries supporting their capacity for adaptation to environmental change (Saleh et al. 2022). Our results are also consistent with phenotypic studies reporting higher drought tolerance in oak compared to beech (Zimmermann et al. 2015). In contrast, the weak adaptive genomic signals detected in beech do not fully align with previous studies. Several report phenotypic and genomic evidence of local adaptation in beech, particularly at range edges and for loci associated with phenological traits (e.g., Kreyling et al. 2014; Meger et al. 2021; Schmeddes et al. 2024). This suggests that

adaptive responses in beech may be more spatially localized or trait specific. For example, Lazic et al. (2024) found limited evidence of local adaptation or genomic association for phenology in common garden and reciprocal transplant experiments, yet reported highly polygenic and localized signals. Including additional traits such as phenology or cold tolerance and performing population-specific analyses, may help uncover more nuanced signatures of adaptation or adaptive plasticity in beech.

4.3 | Dendrogenomics Reveals the Complex Genetic Architecture of Growth and Climate Responses

Pioneering studies (Housset et al. 2018; Heer et al. 2018) applied GWA analyses to dendrochronological traits by association of SNPs with tree-ring-derived phenotypes like basal area increment (BAI) or resilience components to drought. Specifically, Heer et al. (2018) identified genomic regions in *A. alba* associated with drought-related growth decline and recovery, implicating loci in hormonal signalling and abiotic stress response pathways. Subsequent research expanded on these studies. For example, Depardieu et al. (2021), applied GWA analyses to tree-ring traits in *Picea glauca* common gardens and identified associations with both anatomical traits (e.g., early and latewood density) and functional climate sensitivity traits derived from growth chronologies.

Together with more recent work combining dendrochronology with genomic data in *A. alba* (Coşgun et al. 2025), these findings support predominantly a polygenic model underlying climate responsive growth in trees. Collectively, these studies show that integrating tree-ring based phenotypes with genomic data is a powerful approach for detecting loci linked to adaptation and climate resilience in trees. Building on this, our study integrates tree-ring derived functional traits from long-established common gardens with genomic and climate data to further elucidate the genetic basis of climate responsive growth in trees.

4.4 | Implications and Outlook

We revealed the genetic architectures and contrasting climate responses of oak and beech across their distribution ranges. In oak, our findings highlight the importance of maintaining or facilitating gene flow across climate gradients and conserving genetically diverse populations to promote adaptive capacity and long-term persistence (Aitken and Bemmels 2016; Aitken and Whitlock 2013). Similar conservation strategies have been explored in other forest species such as *Betula nana* (Borrell et al. 2019) or *P. abies* (Milesi et al. 2019). In contrast, the absence of clear adaptive signals in beech suggests that the natural or assisted movement of genotypes from warmer, drier regions may not confer adaptive benefits at target sites. Although European beech exhibits high heterozygosity and nucleotide diversity, which reflects substantial standing genetic variation, our results indicate that functional traits are controlled by a multi-locus genetic architecture with weak and inconsistent climate associations, which is expected to limit the speed of adaptive responses. Therefore, our outcomes point to a compounded vulnerability to climate change, supporting projections

of range contraction under future climatic scenarios (Martínez del Castillo et al. 2022). Oak, by comparison, appears to possess greater potential to respond through both adaptation and phenotypic plasticity. For beech, conservation strategies should focus on safeguarding local genetic diversity, especially in range-edge populations, which might harbour crucial variation for future resilience. Our results underscore the need for species-specific management approaches and provide a genomic framework for climate-informed forest conservation and assisted gene flow.

To translate these insights into actionable forest management strategies, several steps are critical. First, functional validation of candidate loci, especially those associated with drought resilience, is essential, as shown for root traits in oak (Le Provost et al. 2022). Second, expanding the scope of analyses to include more populations, especially at ecological margins and incorporating higher-resolution genomic data (e.g., whole-genome sequencing or targeted capture) could reveal additional signals of local adaptation. These signals may be particularly evident when analyses are extended to include fitness-related traits beyond growth, such as survival. Finally, our study reinforces the value of dendro-genomic approaches for uncovering the molecular basis and adaptive relevance of climate responses in forest trees (Heer et al. 2018; Housset et al. 2018; Krutovsky 2022). These approaches enable the analysis of integrative, individual-based traits with high temporal resolution. By explicitly linking allelic effects to climatic distances, we captured nuanced genomic and phenotypic responses to climatic variation. This integrative perspective offers valuable insights into the selective forces shaping functional traits under changing conditions, particularly the roles of extreme drought events and long-term temperature and precipitation regimes and provides a foundation for predicting how long-lived tree species can persist and adapt in the face of rapid climate change.

Author Contributions

Patrick Fonti, Elisabet Martínez-Sancho, Yann Vitasse and Christian Rellstab acquired funding. Aksel Pålsson, Elisabet Martínez-Sancho, Yann Vitasse and Christian Rellstab developed the concept of the study. Patrick Fonti and Yann Vitasse contributed to the sampling. Elisabet Martínez-Sancho processed tree-ring data and prepared the traits. René Graf performed laboratory work. Aksel Pålsson analysed the data, with support from Christian Rellstab. Aksel Pålsson wrote the manuscript, with input from all co-authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Raw ddRAD sequencing data have been deposited in the European Nucleotide Archive under the project accession PRJEB113073/ERP193499. “ddRAD sequencing of sessile oak and European beech for climate adaptation analyses”. Phenotypic data and genomic variant files are deposited in the Dryad Digital Repository under: <https://doi.org/10.5061/dryad.fqz612k71>. R code supporting data processing and analyses is available from the GitHub repository: <https://github.com/akselpaallsson>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Methods S1.** Exclusion of non-target species and highly admixed individuals in oak. **Methods S2.** Phenotypic data. **Methods S3.** Genetic data. **Figure S1:** (A) Cross-entropy and (B) ancestry coefficients, estimated using the sNMF algorithm, for sessile oak. Turkish provenance (TU277) included. **Figure S2:** PCA of the neutral genetic data of sessile oak with the Turkish provenance (TU277) included. **Figure S3:** Cross-entropy and ancestry coefficients, estimated using the sNMF algorithm, for sessile oak. Turkish provenance (TU277) excluded. **Figure S4:** Ancestry coefficients estimated using the sNMF algorithm. (A) Sessile oak and (B) European beech. **Figure S5:** Mean annual temperature (Bio1) and total annual precipitation (Bio12) at the origin of the provenances, calculated using data from the CHELSA datasets for the period 1961–1990. **Figure S6:** Correlation matrices (Pearson correlation coefficients) of the 19 bioclimatic variables (bioclims) at the provenance locations of (A) sessile oak and (B) European beech. **Figure S7:** Pairwise F_{ST} comparisons between provenances and isolation by distance (IBD) for (A) sessile oak and (B) European beech. Mantel tests were performed on linearized F_{ST} values and ln-transformed geographic distances. **Figure S8:** Relatedness matrices for (A) sessile oak and (B) European beech, estimated using the neutral SNP dataset. **Figure S9:** Cross-entropy values of the sNMF analysis for (A) sessile oak and (B) European beech. **Figure S10:** GWA results for the most parsimonious linear mixed models (LMMs) for sessile oak and European beech for the trait Rs. **Figure S11:** GWA results for the most parsimonious linear mixed models (LMMs) for sessile oak. **Figure S12:** GWA results from the Bayesian sparse linear mixed models (BSLMM) for sessile oak. **Figure S13:** Pairwise Pearson correlation coefficients between the functional traits measured across the provenances in (A) sessile oak and (B) European beech. **Figure S14:** Relationship between pairwise phenotypic trait correlations (Pearson r) and the number of shared loci among traits in (A) sessile oak and (B) European beech. Each point represents a pair of traits. **Figure S15:** GWA results for the most parsimonious linear mixed models (LMMs) for European beech. **Figure S16:** GWA results from the Bayesian sparse linear mixed models (BSLMM) for European beech. **Figure S17:** Manhattan plots of the LFMM results in sessile oak (A, B) and European beech (C, D) in relation with temperature (A, C) and precipitation (BD). **Figure S18:** Genotype-by-environment interactions for focal traits in response to temperature and precipitation transfer distances in sessile oak and European beech (circles and diamonds, respectively). **Table S1:** Geographic origin of sessile oak and European beech provenances and number of individuals per provenance and common garden after bioinformatic processing and excluding non-target species and highly admixed individuals (see Methods S1). **Table S2:** Genetic diversity in sessile oak and European beech provenances. **Table S3:** Results of the LMM GWA analyses for sessile oak and European beech. **Table S4:** Loci in high LD identified by both LFMM and GWA (LMM and BSLMM combined) analyses.