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▶ **To cite this version:**

Lisa Tischenko, Nathalie Isabel, Lyne Touchette, Éric Normandeau, Brian Boyle, et al.. Genomic structure and environmental adaptation in northern red oak: Foundations for climate-resilient forestry. Forest Ecology and Management, 2026, 616, pp.123879. ⟨10.1016/j.foreco.2026.123879⟩. ⟨hal-05661374⟩

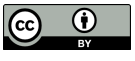
HAL Id: hal-05661374

https://hal.inrae.fr/hal-05661374v1

Submitted on 18 Jun 2026

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Forest Ecology and Management 616 (2026) 123879

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Genomic structure and environmental adaptation in northern red oak: Foundations for climate-resilient forestry

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ARTICLE INFO

Keywords:
Quercus rubra
Genetic diversity
Population genomics
Resilience and adaptation
Forest management
Climate change

ABSTRACT

Understanding genomic variation and adaptation of widespread tree species across their range is useful for predicting responses to environmental change and guiding sustainable forest management. *Quercus rubra* (Northern red oak) is a dominant hardwood species in eastern North America. Yet, its genomic diversity and adaptive structure remain poorly characterized. Using genotyping-by-sequencing (GBS), we generated 20,847 single nucleotide polymorphisms (SNPs) from 843 individuals sampled across 72 populations spanning the species' native range. Population and landscape genomic analyses revealed a broadly homogenous pattern of genetic variation, with weak but significant population structure, predominantly shaped by neutral processes, including postglacial demographic history and extensive historical gene flow. To detect signatures of local adaptation, we combined F_{ST}-based outlier detection with genotype–environment association (GEA) approaches. Across four genome scan methods, 142 SNPs were identified by at least two analytical approaches. Although temperature-related variables, particularly extreme minimum temperature (EMT), and moisture indices (MSP, SHM) showed significant associations with allele frequency variation, climate explained only a small fraction of total genomic variance. These results indicate that adaptive signals in *Q. rubra* are detectable but weak, consistent with polygenic adaptation involving small allele-frequency shifts. Together, our findings suggest that *Q. rubra* likely combines a polygenic genomic background with high within-population genetic diversity and inferred phenotypic plasticity rather than strict local adaptation to cope with environmental changes. This study provides a genomic foundation for *Q. rubra* and creates resources to support conservation planning, breeding programs, and the development of genomic traceability tools for provenance verification.

1. Introduction

Climate change is increasingly challenging the resilience of forest tree species (Anderegg et al., 2019), driven by more frequent and severe natural disturbances (e.g., insect and disease outbreaks, droughts, wildfires). These pressures are already driving climatic maladaptation,

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https://doi.org/10.1016/j.foreco.2026.123879
Received 6 February 2026; Received in revised form 24 April 2026; Accepted 5 May 2026
Available online 16 May 2026
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whereby local populations become mismatched with their environment, contributing to widespread forest decline observed in many regions worldwide (Allen et al., 2010; Hammond et al., 2022). Because climate change is proceeding faster than the adaptive capacity of many forest trees, local population persistence will depend not only on natural selection but also on proactive management strategies that anticipate future climatic conditions. Accordingly, to adequately prepare forests for future climate and safeguard biodiversity and ecosystem services, forest management will require adaptive strategies based on genomics information coupled with common garden, including the consideration of challenging species, which are often understudied and more difficult to manage (e.g., non-commercial species of ecological importance such as *Taxus baccata*; Mayol et al., 2020, endangered species *Quercus* spp.; Backs and Ashley, 2021, and species threatened by pathogens or insects such as *Fraxinus* spp; Huff et al., 2022).

Forest trees have long generation times and limited dispersal, making *in situ* adaptation dependent on standing genetic variation (Aitken et al., 2024). Provenance trials have provided invaluable information on how genetic variation shapes clinal and ecotypic patterns in phenotypic traits involved in local adaptation (Matyas, 1994; Sork et al., 2013). They are powerful tests to identify resilient genotypes, as they compare populations in a common environment and reveal differences in survival, growth, or reproductive success shaped by their source populations (de Villemereuil et al., 2016; Matyas, 1994). However, common garden experiments are often time-consuming (e.g., long establishment phases, repeated measurements over years) and not available for all species. In this context, over the past decades, genomic resources have expanded substantially, making this approach an increasingly important or complementary tool for assisting forest managers to identify and deploy resilient genotypes, populations, or species, thereby supporting genomic-informed planning of conservation, reforestation, and breeding programs (Cortés et al., 2020; Isabel et al., 2020). Despite genomic advancements, practical applications in forest management remain challenging (Heuertz et al., 2023). Genomic information can support adaptive forest management strategies such as assisted migration, where climate-adapted individuals are moved within or beyond their species' ranges to match future environmental conditions (Chen et al., 2022), and genomic selection, which uses markers associated with adaptive traits (e.g., drought tolerance, growth, or pest resistance) to identify and select trees with the highest potential for survival and reproduction (Lebedev et al., 2020).

While these approaches are already successfully applied in conifer breeding programs (Laverdière et al., 2022; Lenz et al., 2020; Mahony et al., 2020; Sáenz-Romero et al., 2020), growing evidence shows that many conifers in Canada are already experiencing drought stress, increased mortality, and regeneration failures (Brecka et al., 2020; Urli et al., 2013). These observations emphasize the need to take action by further integrating genomic-informed strategies and expanding research to broadleaf species such as oaks (George et al., 2020; Ufimov et al., 2025), thereby extending population genomic approaches beyond a narrow focus on a limited set of commercial species to not only support productivity, but also promote sustainable and healthy forests (Isabel et al., 2020).

Oaks (*Quercus* spp.) are diverse and widespread, and their high genetic variation and frequent hybridization have supported their long-term persistence, making them relevant models for adaptation studies and climate-informed forest management (Hipp et al., 2020; Kremer and Hipp, 2020; Plomion et al., 2018; Lang et al., 2021). Within this genus, northern red oak (*Quercus rubra* L., section Lobatae) is an ecologically important species and a valuable commercial timber. It occurs across eastern North America, from the Canadian Maritimes westward to Minnesota and south to Arkansas, Alabama, and Georgia, thriving under diverse climatic and soil conditions (Sander, 1990). Increasingly, *Q. rubra* is recognized as a strategic species for forest management and urban greening under climate change, a role noted since its introduction to Europe in the late 17th century as an ornamental tree and later becoming an important species for wood production (Houba, 1887; Nagel, 2015). Its drought tolerance and adaptability make it a candidate for enhancing forest resilience as conifers decline due to drought, pests, and diseases (Aubin et al., 2018). It also provides key ecosystem services, including production of highly valuable timber (Nicolescu et al., 2020), wildlife habitat (Anderson et al., 1999; Tallamy and Shropshire, 2009), nutrient cycling, and carbon storage (Hansen, 2000; Stoler and Relyea, 2011). Promoting its use in forests, agroforestry, and urban landscapes can diversify forestry, support non-timber products, and mitigate urban biodiversity loss as ash, elm, and beech succumb to invasive pests and pathogens such as emerald ash borer, Dutch elm disease, and beech bark disease (Bauer and Volpe, 2017; Iverson et al., 2016).

Despite its wide distribution and economic importance, *Q. rubra* remains understudied at the genomic level, particularly in the northern portion of its range, including Canadian natural stands, which are critical for understanding adaptive limits and guiding assisted migration or reforestation strategies under climate change. Few molecular studies have described the geographic distribution of its genetic diversity, and existing work varies in marker types and sampling strategies (Borkowski et al., 2017; Magni et al., 2005; Sork et al., 1993). Regional genetic structure has been documented, notably in the northern range margin, including mainland, peninsular, and island populations (Götz et al., 2022), as well as along the steep environmental gradient of the Lake Superior coast (Gómez Quijano et al., 2024). While introduced populations in Europe have been compared with their North American sources (Merceron et al., 2017; Pettenkofer et al., 2020, 2019), a comprehensive genomic perspective across the species' native range is still lacking, representing a critical knowledge gap for informed forest management and conservation planning.

The recent release of the first high-quality reference genome assembly for *Q. rubra* (Kapoor et al., 2023) represents a major advance in international efforts to develop genomic resources for this non-model species (Formenti et al., 2022). This resource enables the identification of genomic markers, such as single-nucleotide polymorphisms (SNPs) linked to adaptation, shedding light on the mechanisms shaping the species' response to environmental challenges.

Characterizing both neutral and adaptive components of genetic variation is essential to understanding and conserving the evolutionary potential of forest species (Aitken et al., 2008). Neutral markers reflect demographic processes (e.g., gene flow, genetic drift, and historical population structure) shaped by postglacial recolonization and major biogeographical features (e.g., glacial refugia and major landscape barriers) following the Last Glacial Maximum (LGM; Avise, 2009). Eastern North America studies showed that genetic diversity does not necessarily decrease with latitude (Lumibao et al., 2017; Nadeau et al., 2015; Schumacher et al., 2022), contrasting with the classical "southern richness-northern purity" pattern observed in Europe that suggested the presence of southern refugia (Petit et al., 2003). In *Q. rubra*, chloroplast DNA (cpDNA) haplotype distributions suggest weak phylogeographic structure and widespread haplotypes, a pattern consistent with persistence in multiple cryptic northern refugia during the LGM and rapid postglacial recolonization (Magni et al., 2005). Such historical and biogeographical context is essential for understanding current population structure and interpreting signals of local adaptation.

Adaptive genetic variation, on the other hand, underlies local adaptation and can be detected using common garden experiments, genome-wide association studies (GWAS), and genotype–environment association (GEA) analyses (Hoban et al., 2016; Sork et al., 2013). In *Q rubra*, provenance trials and common garden experiments provide evidence for local adaptation in key traits such as growth, phenology, and tolerance to drought and cold (Daubree and Kremer, 1993; Deneke, 1974; Kriebel, 1993; Merceron, 2016; Schlarbaum and Bagley, 1981). The emergence of landscape genomics, which integrates genomic, spatial, and environmental data, has provided a powerful framework to study local adaptation while accounting for neutral genetic structure

(Rellstab et al., 2015; Sork et al., 2013). GEA methods have been successfully applied in broadleaf and conifer species (Goessen et al., 2025; Nadeau et al., 2016), allowing genome-wide analyses of thousands of SNPs and revealing that climatic drivers of adaptation vary widely among taxa. For example, in American chestnut (*Castanea dentata*), precipitation-related variables and their interaction with summer temperature dominate adaptive signals, reflecting adaptation to high evaporative demand rather than extreme cold (Sandercock et al., 2024). In contrast, species with more northerly distributions, such as lodgepole pine (*Pinus contorta*), red spruce (*Picea rubens*), and yellow birch (*Betula alleghaniensis*), show adaptive patterns primarily associated with winter temperature and cold tolerance (Capblancq et al., 2023; Yu et al., 2022; Cummins, 2025). These contrasts highlight how species' biogeographical ranges and climatic limits shape the genomic basis of local adaptation.

Before genomic tools can be effectively applied to conservation and breeding in *Q. rubra*, it is essential to establish a clear picture of its genetic diversity and structure across its native range. Firstly, the species' genetic variation must be characterized at a genome-wide scale to understand how populations are structured and how this structure relates to environmental gradients or hybridization with congeners. Secondly, such genomic insights will serve as a foundation for developing informed conservation strategies and breeding programs adapted to future environmental conditions. By carefully managing seed resources and responsibly implementing assisted migration and genomic selection strategies (Lazic et al., 2021; Lobo et al., 2025), we can enhance the resilience of northern red oak populations, mitigate the effects of climate change, and contribute to the long-term sustainability of Canadian forests while supporting both natural and urban ecosystem services (see Tischenko et al., 2024).

In this study, we investigated range-wide genomic variation in *Q. rubra* using SNPs generated by genotyping-by-sequencing (GBS) to address key knowledge gaps across its native distribution. We hypothesized that *Q. rubra* exhibits weak to moderate genetic structure, with most genetic diversity occurring within populations (Kremer and Petit, 1993), as observed in other widely distributed forest tree species in eastern North America (e.g., *Pinus strobus,* Nadeau et al., 2015; *Juglans cinerea*, Schumacher et al., 2022; *Fraxinus pensylvanica*, Huff et al., 2022). Such patterns reflect high gene flow and historical demographic processes that generate continuous genetic variation rather than sharply defined clusters (Jaramillo-Correa et al., 2009). Consistent with this expectation, weak genetic differentiation across the natural range of *Q. rubra* has been reported in previous studies using different marker types (Borkowski et al., 2017; Merceron et al., 2017). Our second hypothesis was that, despite the overall weak genetic structure of *Q. rubra*, part of its genomic variation reflects local adaptation to environmental gradients. Given its broad native range and evidence of genetic variation pattern from common garden studies (e.g., growth, phenology, drought and cold tolerance; Deneke, 1974; Kriebel, 1993; Schlarbaum and Bagley, 1981), we expected adaptive variation to be primarily associated with temperature-related gradients, including cold conditions, as reported in other widely distributed temperate forest tree species (Capblancq et al., 2023; Nadeau et al., 2016; Yu et al., 2022; Cummins, 2025).

2. Materials and methods

2.1. Sampling design

We collected leaf samples from 1632 accessions across 168 locations within northern red oak's natural distribution during 2019–2023 (see supplementary Table S1 for the complete collection of samples of the study). The first 617 leaf samples came from a collection gathered by the Canadian Forest Service (CFS; the Laurentian Forestry Centre in Quebec City, QC, as well as the Atlantic Forestry Center in Fredericton, NB), including material from multiple Canadian provinces (Quebec, Ontario, Manitoba, New Brunswick, Nova Scotia, Prince Edward Island) and states in the USA (Maine, New Hampshire, New York, Pennsylvania, Ohio, Virginia, West Virginia, and North Carolina). An additional 159 samples were obtained from a provenance trial set up by the Ministère des Ressources naturelles et des Forêts du Québec (MRNFQ), covering additional sites in Quebec and Ontario, as well as Indiana, Minnesota, Wisconsin, New York, Vermont, Pennsylvania, and Ohio. Further 600 DNA samples were obtained from French and German provenance trials, encompassing sites originating from both Canada (Ontario) and the USA, including Nebraska, Georgia, Illinois, Indiana, Iowa, Maryland, Massachusetts, Michigan, Minnesota, New Jersey, North Carolina, Pennsylvania, Vermont, West Virginia, and Wisconsin, and are treated as representing their source populations in downstream genetic analyses. The remaining 256 samples were provided by various North American collaborators, including governmental agencies and academic institutions (see Acknowledgements section). To minimize biases associated with unequal sample sizes and to ensure robust estimates of genetic parameters, population sizes were adjusted by regrouping samples based on precipitation and temperature distribution maps (See Supplement File 2: Fig. S1a-b). Each population sample was ensured to contain at least five individuals, while larger populations were limited to a maximum of 30 accessions. However, six populations (YL, Arkansas, n = 2; SY, Pennsylvania, n = 2; WY, Ohio, n = 2; MI, Minnesota, n = 3; ME, Quebec, n = 3; PA, West Virginia, n = 3) had fewer than five individuals, but we chose to keep them as they were collected from underrepresented areas within the species' distribution (Fig. 1). Additional 326 samples from other species in the oak section Lobatae, phylogenetically closely related to or confirmed to hybridize with *Q. rubra*, were obtained from arboreta or seed orchards established in the USA and Canada (see supplementary Table S1, column Species_field). The collected leaf samples were dried on silica gel and stored at ambient temperature. The natural population samples were later integrated into a broader genotyping dataset that also included material from parallel studies, such as urban populations and other oak species, resulting in a combined variant call format (VCF) file described below (see Section 2.2.2 Genotyping and SNP calling).

2.2. DNA extraction, genotyping, and SNP calling

2.2.1. DNA extraction

Using 96-well plates, each collected sample, containing approximately 10–20 mg of dried leaf tissue, was added individually to a well along with a 3 mm diameter metal bead and then ground twice for 30 s in a mixer mill MM 400 at 30 Hz (grinding was repeated if necessary).

Quercus spp. are known to store large amounts of phenolics and polysaccharides within their leaf tissue, making genomic DNA extraction difficult (Csaikl et al., 1998). To overcome this issue, we used a modified cetyltrimethylammonium bromide (CTAB) protocol (Doyle et al., 1987), with all steps performed at room temperature unless stated otherwise. To each ground sample, 573 µl of Carlson lysis buffer (CTAB 2%, NaCl 1.4 M, EDTA 20 mM, Tris–HCl 100 mM, 1% PEG 6000), 12 µl Proteinase K, 12 µl β-mercaptoethanol, and 3 µl RNase A (100 mg/mL) were added. Samples were bead-milled twice in extraction buffer for 15 s at 25 Hz to ensure thorough mixing, and then incubated for 1 h at 65°C. The samples were then extracted twice; a first extraction with 500 µl of a phenol:chloroform:isoamylalcohol 25:24:1 mixture, followed by vortexing (10 s) and centrifugation at 6300 x g for 10 min after which the aqueous layer was transferred to a clean tube. A second extraction was done with 500 µl of chloroform:isoamylalcohol 24:1 mixture with vortexing (10 s) and centrifugation (6300 x g, 10 min). Subsequently, DNA was precipitated by adding 0.6–0.7 volumes of cold 100% isopropanol, gently mixed, and centrifuged at 6300 x g for 20 min. DNA pellets were washed with 500 µl of 70% ethanol and centrifuged at 6300 x g for 20 min. DNA was dried at room temperature and resuspended in 100 µl of preheated EB buffer (10 mM Tris-Cl, pH 8.5) at 65°C. When necessary to improve purity, DNA was re-precipitated by adding 0.1 vol

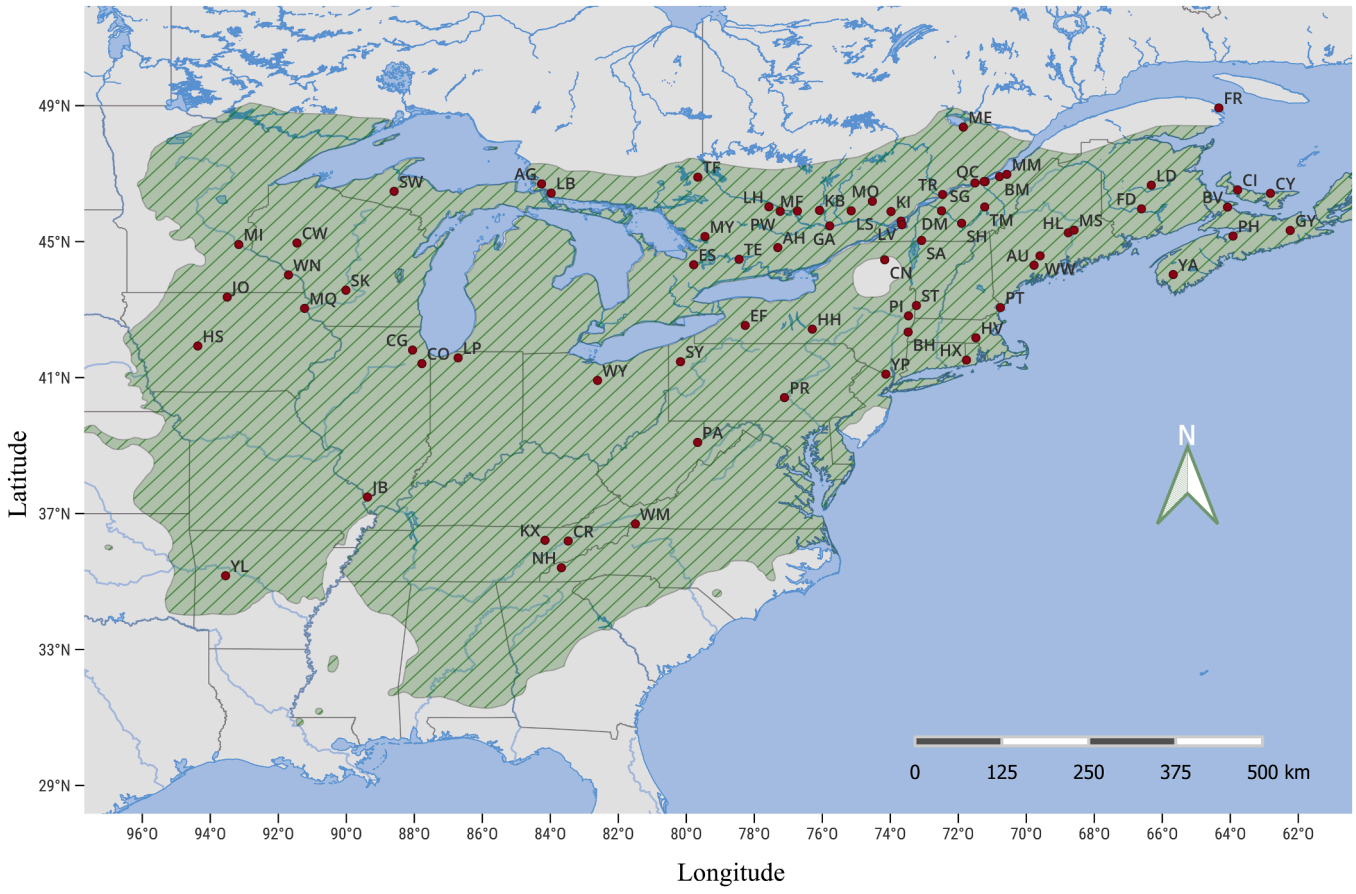


Fig. 1. Geographic distribution of *Quercus rubra* populations used in genotyping-by-sequencing (GBS) based analyses. Each red dot represents a sampling site. The dashed green area indicates the species' natural distribution range (Little, 1971).

of 3 M sodium acetate and 2 volumes of cold isopropanol, followed by the same washing and resuspension steps. DNA quality and quantity were evaluated using NanoDrop 8000 Spectrophotometer and Qubit 2.0 Fluorometer respectively. Two extraction batches were performed, one in 2022 and another in 2023.

2.2.2. Genotyping and SNP calling

Library preparations for our Illumina triple digest GBS (3D-GBS,de Ronne et al., 2023) method were conducted at the Plateforme d'Analyses Génomiques of the Institut de Biologie Intégrative et des Systèmes (IBIS, Université Laval, Québec, Canada) using a modified procedure of the one previously described by Poland et al., (2012). The modifications consisted of: (i) using three restriction enzymes *(PstI*, *NsiI*, and *MspI)* instead of the original *PstI/MspI* enzyme combination; (ii) performing a size selection step with Blue Pippin (SAGE Sciences), with elution times set between 50 and 70 min on a 2% gel before PCR amplification. Plate barcodes were added according to the procedure described by Colston-Nepali et al. (2019). The libraries were sequenced on an Illumina NovaSeq 6000 platform at the Centre d'expertise et des services Génome Québec in Montréal, Canada, generating paired-end reads, with 100 bp for the first batch and 80 bp for the second and third batches, in FastQ format. Sequencing was carried out in three separate batches (April 2023, February 2024, and March 2024) because not all samples were available at the start of 2023, and a supply issue with the *NsiI* enzyme necessitated the generation of a third batch. Out of the 1632 collected *Q. rubra* individuals, 1065 were successfully sequenced (see supplementary Table S1, column sequencing_success).

Data preparation, genotyping, and filtration were conducted using STACKS v2.66 and stacks_workflow v2.66 (https://github.com/enormandeau/stacks_workflow) (more details are provided in Supplement File 1: Method S1). Raw reads were cleaned from adapter sequences with Cutadapt version 4.6, demultiplexed with *process_radtags* v2.66, and aligned to the published *Q. rubra* reference genome v.2.1 (Kapoor et al., 2023). The initial VCF file contained 2290 samples and 543,785 SNPs, with an average genotype coverage of 48.51 and an overall missing genotype rate of 20.42%. A schematic overview of all filtering steps and dataset reductions is provided in Supplement File 2 (Fig. S2). After quality filtering, the dataset was reduced to 2176 samples, 140,682 SNPs, with an average coverage of 63.94, and a missing genotype rate of 7.33%.

Three different subsets were generated from the final VCF file corresponding to: (i) natural *Q. rubra* populations, (ii) urban *Q. rubra* populations, and (iii) other oak species. For the present study, only the subset corresponding to natural populations was retained (n = 1065 individuals). Quality filtering was subsequently re-applied to this subset (Supplement File 1: Method S1) to remove SNPs that became invariant or rare following subsettting, resulting in a dataset of 1044 individuals and 93,105 SNPs.

2.2.3. Batch effect removal and further data filtration

Based on Principal Component Analysis (PCA), we identified SNP loci that could drive a possible batch effect (see Method S2 in Supplement File 1: and Fig. S3 in Supplement File 2). Consequently, we removed 3175 loci that contributed the most to genomic variations depicted by PCA-axis 2 according to "loadings" over 0.005 (see Supplement File 2: Fig. S4) and, more specifically, found that the variations seemed to have been caused by differences between the two extraction batches (see Supplement File 2: Fig. S3).

After the removal of batch effect, PCA revealed that 35 individuals clustered separately from the main group of samples (see Supplement

File 2: Fig. S3). Because oak species often occur in sympatry and exhibit substantial variation in leaf morphology due to hybridization, morphological identification alone may be unreliable. To assess whether these PCA outliers reflected taxonomic misassignment or admixture with closely related species, we used an additional subset of the VCF file (see Supplement File 2: Fig. S2) including *Q. rubra* and nine closely related species of the same section (i.e. *Q. ellipsoidallis, Q. palustris, Q. coccinea, Q. velutina, Q. shumardii, Q. marilandica, Q. imbricaria, Q. illicifolia* and *Q. pagoda*, see Supplement File 2: Fig. S5).

Population structure analyses were then performed using sNMF implemented in the R package LEA v3.10.2 (Frichot and François, 2015). These analyses showed that the 35 PCA outlier individuals did not cluster with *Q. rubra* but instead grouped with other *Quercus* species. This pattern is consistent with misassignment or admixture with closely related species (see Supplement File 2: Fig. S6). Removal of these individuals further reduced the dataset to 1009 individuals.

Finally, stringent filtering steps were applied prior any population-level analysis. In brief, SNPs were filtered by minor allele frequency (MAF) > 0.025, and potential duplicate samples were removed using the function *gl.report.replicates()* from the dartR package v2.9.9.5 (Gruber et al., 2018). Duplicate samples were defined using a minimum genotype similarity threshold of 99%, such that pairs of individuals sharing at least 99% of loci were considered duplicates. (see Supplement File 2: Fig. S7). MAF filtering (> 0.025) reduced the number of SNPs from 89,930 to 20,847. Subsequent removal of 20 duplicate individuals reduced the sample size from 1009 to 989. To avoid population over-representation, sample sizes for three populations from Quebec, Canada (MT, QC, and GA) were capped at a maximum of 30 individuals per population, resulting in the removal of 146 individuals. Therefore, the final dataset comprised 843 individuals and 20,847 SNPs (see Supplement File 2: Fig. S2).

2.3. Population genomic structure

2.3.1. Genetic structure in Q. rubra

Different approaches were used to assess population genetic structure and identify genetic lineages (clusters) within *Q. rubra* natural distribution range. First, PCA was performed with the *glPCA()* function to visualize population structure using the R package *adegenet* v2.1.10 (Jombart and Ahmed, 2011) and retaining 5 PCs. Then, to assess neutral population structure, we used a complementary genetic clustering approach, the sparse non-negative matrix factorization (sNMF; Frichot et al., 2014) implemented in the R package *LEA* v3.10.2 (Frichot and François, 2015) as the computationally fastest alternative to the model-based STRUCTURE program (Pritchard et al., 2000). Our sNMF analyses were performed using default parameters for $K = 1$–10, with 20 repetitions, 10,000 iterations, and the value of the regularization parameter set to 100. The optimal number of K was selected when the cross-entropy criterion exhibited the lowest value or where the cross-entropy criterion began to plateau (Gugger et al., 2021). Maps of individual admixture proportions were generated in QGIS v3.28 (Moyroud and Portet, 2018) using pie charts.

2.3.2. Spatial autocorrelation analysis

To identify spatial patterns of genetic structuring while accounting for the geographic distribution of sampling locations, we conducted a spatial Principal Component Analysis (sPCA) using a Delaunay triangulation network. sPCA jointly maximizes genetic variance and spatial autocorrelation, allowing the detection of spatial genetic structure, particularly in continuously distributed species (Jombart et al., 2008). We ran sPCA using *spca()* and visualized the variance against spatial autocorrelation (Moran's Index) with *screeplot()*, with both functions provided by the adegenet (Jombart, 2008) R package v2.1.10. Positive eigenvalues indicate the presence of global structure, while negative eigenvalues indicate local structure. To test for significance of global and local structure, we performed a Monte Carlo simulation using 999 permutations as described by Jombart et al. (2008). When the structure was significant, we geographically mapped and interpolated the individual scores of the first principal component of the sPCA.

To test for isolation-by-distance (IBD), we performed a Mantel test with 999 permutations between all pairs of *Q. rubra* populations using the *gl.ibd()* function of the dartR package v2.9.9.5 (Gruber et al., 2018). This assessed the relationship between geographic and genetic distances among sampling populations, using geographical distance (km) and transformed pairwise F_{ST} (i.e., $F_{ST}/(1 - F_{ST})$), respectively (Rousset, 1997).

2.4. Population genomic statistics

Genetic diversity statistics per population were estimated using the *gl.report.heterozygosity()* function from the dartR v2.9.9.5 package (Gruber et al., 2018). We calculated observed heterozygosity (H_o), unbiased expected heterozygosity (uH_e), and inbreeding coefficient (F_{IS}). For F_{IS}, 95% confidence intervals were calculated on 1000 locus-based bootstrap replicates were used to assess statistical significance. Pairwise F_{ST} was estimated between each population according to Weir and Cockerham (1984) using the function *gl.pop.fst()* from the dartR package v2.9.9.5 (Gruber et al., 2018); their value significance was tested using 1000 bootstrap replications.

2.5. Genome-wide selection scans/landscape genomics (GEA)

To detect loci potentially influenced by natural selection, we performed two complementary F_{ST} outlier detections: OutFLANK v.0.2 (Whitlock and Lotterhos, 2015) and BayeScan 2.1 (Foll and Gaggiotti, 2008). BayeScan uses a Bayesian framework to identify candidate loci under selection by analyzing allele frequency differences among populations through a multinomial-Dirichlet model. Analyses were run with prior odds of neutrality set to 1000. The Markov Chain Monte Carlo (MCMC) parameters included a total of 100,000 sampled iterations, a thinning interval of 10, 20 pilot runs of 5000 iterations each, and a burn-in period of 50,000 iterations. The internal *q-value* estimation implemented in BayeScan was used to assess significance, and loci with a posterior false discovery rate (FDR) *q-value* < 0.05 were considered outliers.

OutFLANK infers the neutral distribution of F_{ST} using a maximum-likelihood approach, excluding loci likely to be under strong spatially diversifying selection. Outlier detection was performed using the *gl.outflank()* function from the dartR package v2.9.9.5 (Gruber et al., 2018) with the following recommended parameters: left and right trimming fractions set to 0.05, a minimum heterozygosity threshold of 0.1, and an FDR *q-value* cutoff based on the Benjamini–Hochberg procedure (Benjamini and Hochberg, 1995) of 0.05 to detect outlier loci. To visualize the chromosomal distribution of SNPs and highlight those identified as outliers by both approaches, we generated a Manhattan plot. This plot displays the *q-values* of all SNPs across the 12 oak chromosomes, with a horizontal line indicating the FDR-based significance threshold used to define outliers.

While F_{ST}-based approaches identify loci showing unusual levels of population differentiation potentially due to selection, they do not directly consider environmental gradients that may drive local adaptation. To complement these F_{ST}-based methods and explicitly test for environmental associations, we performed a genotype–environment association (GEA) analysis, which is comparable to a conventional GWAS but, instead of the phenotypic data, climate or other (bio) geographical data are used.

Environmental data for each population were extracted from the ClimateNA v7.50 database (Wang et al., 2016) using the ClimateNAr R package v3.0.0 for data extraction (https://climatena.ca), based on sampling coordinates (latitude and longitude). A total of 25 annual climatic variables, representing 1961–1990 climate normals, were obtained (Supplementary Table S2). Among these variables, only the mean

annual solar radiation (MAR) was excluded due to missing data. To avoid multicollinearity, we assessed pairwise correlations using the *pairs.panels()* function from the psych R package v2.5.6 (Revelle, 2025), and retained variables with correlations < 0.7 (Supplement File 2: Fig. S8), prioritizing those variables most relevant to our study. Using *vif()* from the usdm R package v2.1–7 (Naimi, 2023), we also removed variables that had a variance inflation factor (VIF) ≥ 10. This resulted in the selection of four variables: MSP (May to September Precipitation), SHM (Summer Heat-Moisture Index), EMT (Extreme minimum temperature over 30 years), and RH (Relative Humidity). These variables represent the cold temperature gradient (EMT) and complementary moisture and precipitation gradients (MSP, SHM, RH), capturing the main axes of environmental variation relevant to *Q. rubra* adaptation, consistent with climate drivers previously identified in this species (Kapoor et al., 2023; Gómez Quijano et al., 2024). These variables were standardized for subsequent analyses by subtracting the mean and dividing by the standard deviation. To account for spatial autocorrelation, we computed geographic distances among populations and generated a distance-based Moran's eigenvector map (dbMEM) using the adespatial v0.3–23 R package (Dray et al., 2025) and then applied forward selection to retain the dbMEM variables that significantly explained genetic variation.

One GEA was performed using a Latent Factor Mixed Model 2.0 (LFMM2) analysis (Caye et al., 2019) implemented in the LEA package v3.10.2 (Gain and François, 2021). This univariate approach detects associations between genetic variation and environmental variables while accounting for population structure in the linear model. Because LFMM does not tolerate missing data, we used an imputed SNP dataset (see Supplement File 1: Method S1). Analyses were conducted separately for each of the four variables using the *lfmm2()* function, specifying $K = 3$ latent factors to control for population structure (see results Section 3.1. Population genomic structure and diversity). *P*-values were then computed using the *lfmm2.test()* function, which adjusts for confounding effects, such as population structure, by applying a genomic control procedure based on the genomic inflation factor (GIF). A visual examination of histograms of adjusted *p*-values was performed to assess the confounding effect of the population structure as recommended in the LFMM manual (Supplement file 2: Fig. S9 a-b). Finally, we applied the FDR correction (Storey and Tibshirani, 2003) using the *qvalue()* function from the qvalue R package v2.30.0 (Storey, 2022) and retained SNPs with *q*-values < 0.05 as candidate genetic variants potentially under selection.

Two redundancy analysis (RDA)-based approaches were additionally used. RDA is a constrained ordination method that models the linear relationships among the climatic variables and genomic variation (Capblancq et al., 2018; Capblancq and Forester, 2021). First, a partial RDA (pRDA) was performed to decompose the genetic variance attributable to climate, geography, and neutral population structure, respectively. Following the approach described by Capblancq and Forester (2021), allele frequencies at the population-level were used as the response matrix. The neutral genetic structure was modeled using the first three principal components (PCs) from a PCA of the imputed genomic data, excluding the outlier loci identified in the environmental RDA to avoid the effect of adaptation. The geographic structure was represented by the significant axes of a distance-based Moran's eigenvector map (dbMEM), which were selected via forward selection. We first ran a full model that included climate, geography, and neutral genetic structure, and then conducted three partial RDAs to isolate the pure contribution of each component by conditioning on the other two. This frameword for variance decomposition allowed us to quantify the relative influence of climate, geography, and structure on genetic variation across populations.

An RDA genome-wide scan was performed to identify candidate loci potentially associated with environmental variation, using the same imputed dataset as for the LFMM analysis. Climatic predictors consisted of the four bioclimatic variables described above. Candidate SNPs were initially identified without conditioning on neutral population structure, as correcting for neutral structure can reduce the power to detect loci under selection, particularly when adaptive and demographic processes are spatially confounded (Capblancq et al., 2023; Capblancq and Forester, 2021; Savolainen et al., 2013). Outlier loci were identified using the *rdadapt()* function, provided as a custom script in the RDA tutorial of Capblancq and Forester (2021) and not distributed within an R package. This function detects SNPs with extreme loadings on significant constrained axes, and we applied a 5% FDR threshold to identify candidate loci. For comparison, a partial RDA was also performed on the first three PCs of the neutral genetic variation to assess the robustness of climate-associated signals (Supplement File 2: Fig. S10). All RDA and pRDA models were implemented using the *rda()* function from the vegan v2.6–4 R package (Oksanen et al., 2025), and the significance of predictors and ordination axes was assessed using the *anova.cca()*, function with 999 permutations.

To ensure reliability, only SNPs detected as outliers by at least two methods (RDA, LFMM, Bayescan, OutFLANK) were retained for subsequent identification of overlapping or nearby genes. Genes overlapping with SNP outliers were identified using the *findOverlaps()* function from the R package GenomicRanges v1.50.2 (Lawrence et al., 2013). For each outlier SNP, a $\pm$ 5 kb window around the SNP position was considered, based on the *Q. rubra* reference genome annotations from the GFF3 file available on TreeGenesDB (https://treegenesdb.org/organism/Quercus-rubra, last accessed October 08, 2025). Functional information for each gene, including precomputed best BLAST hits to model species and GO terms were retrieved from the Qrubra_687_v2.1.annotation_info.txt file provided on the same website.

3. Results

The final dataset for natural *Q. rubra* populations comprised 20,847 SNPs, 843 samples, and 72 populations after quality controls (see supplementary Table S3 for the final dataset of *Q. rubra* samples included in downstream genetic analyses).

3.1. Population genomic structure and diversity

Significant global genetic structure was detected in the sPCA analysis as indicated by large positive eigenvalues ($p = 0.001$; Supplement File 2: Fig. S11a-d), whereas no significant local genetic structure was found ($p = 1$; see Supplement File 2: Fig. S11a-d). The first global component captured a broad spatial trend, with populations from the southwestern and northeastern parts of the range showing marked genetic differentiation (Fig. 2a–b).

Three populations ES (Essa, Ontario, Canada), SG (Saint-Augustin, Quebec, Canada), and BV (Baie Verte, New Brunswick, Canada), emerged as distinct genetic clusters in the sNMF analysis, each forming a separate group and inflating the optimal number of ancestral clusters ($K = 6$; Supplement File 2: Fig. S12a–b). In the PCA, SG and BV appeared slightly outside the main cloud of points along the PC1-PC2 axis and a fourth population (JB, Jonesboro, Illinois, USA) also showed peripheral placement but was not identified as an outlier by sNMF. However, when visualizing PC2-PC3, ES, SG, and BV were clearly separated from the rest of the populations, whereas JB clustered closely with the main genetic continuum (Supplement File 2: Fig. S13a-b). Given their consistent divergence across methods and disproportionate influence on clustering, ES, SG, and BV were excluded from subsequent analyses to better resolve the core population structure. Their removal revealed a more coherent genetic gradient among the remaining populations (Fig. 3a), resulting in a final dataset of 802 genotypes used for all downstream analyses.

Most individuals formed a nearly continuous distribution along the first principal component (PC1, 0.57% of variance), reflecting broad-scale population structure. PC1 values varied gradually across the geographic range, with western populations (e.g., JB, Illinois; SK, Wisconsin; HS, Iowa; YL, Arkansas, all in USA) generally exhibiting lower

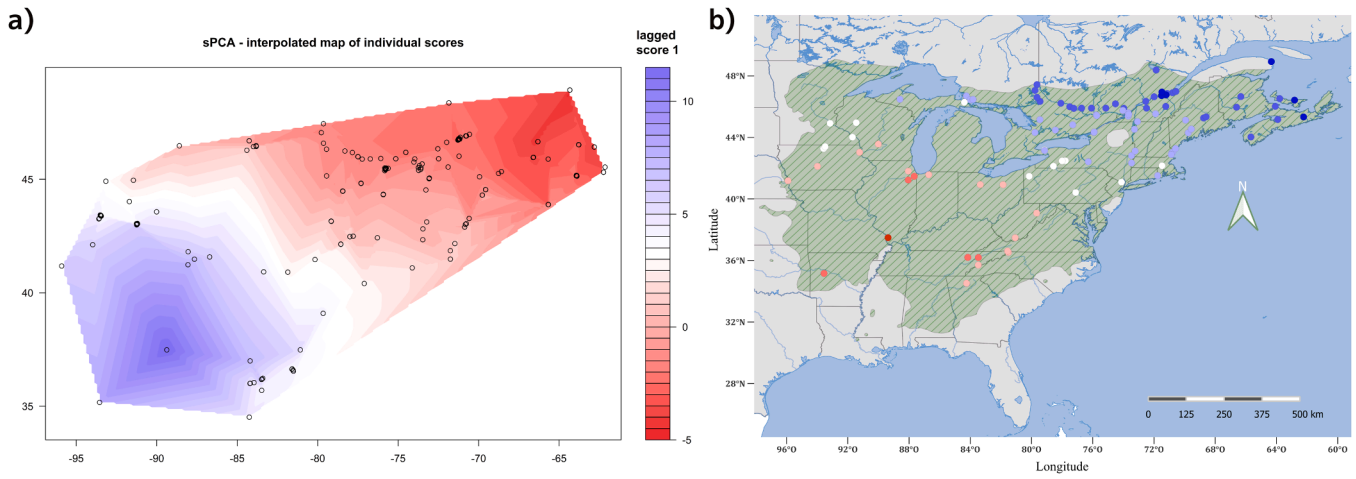


Fig. 2. Global genetic structure in *Q. rubra*. Values of the first principal component (PC1) for *Q. rubra* natural populations showing significant global structure in the spatial principal component analysis (sPCA) (see Supplement File 2 Figure S8a-d). a) Interpolated lagged values. b) PC1 values mapped onto the geographic distribution. The dashed green area indicates the species' natural distribution range (Little, 1971).

values and northeastern populations (e.g., CY and CI, Prince Edouard Island; GY, Nova Scotia; FD, New Brunswick; FR, Quebec, all in Canada) higher values. Several populations from the central southern part of the range (e.g., CR, KX, both within Tennessee, USA) were positioned closer to western populations along PC1, consistent with a broad west-–to–northeast spatial gradient in genetic variation (Fig. 3a).

The refined sNMF analysis (excluding the three outlier populations, see above) identified three main ancestral clusters (K = 3), supported by the lowest cross-entropy value (Supplement File 2: Fig. S14). At higher values of *K*, groups became increasingly admixed and less biologically interpretable (Supplement File 2: Fig. S15a-c). The individual ancestry coefficients (Fig. 3c) reveal a continuous genetic structure, with varying degrees of admixture across the range (Supplementary Table S4). The geographic distribution of cluster membership (Fig. 3b) reflects the spatial pattern observed along PC1**:** the yellow cluster predominates in the southwestern populations, the blue cluster dominates in the northeastern populations, and the pink cluster is concentrated in intermediate regions, possibly reflecting admixture or transitional genetic backgrounds. For clarity, these three main genetic clusters will hereafter be referred to as the South-west (yellow), Central (pink), and North-east (blue) clusters, based on their geographic predominance. The Mantel test revealed a significant pattern of IBD (Supplement File 2: Fig. S16) with a moderate effect ($r = 0.23$, $p = 0.003$).

Genetic diversity was relatively homogeneous among populations of *Q. rubra* (Fig. 4a-b, see supplementary Table S5). Unbiased expected heterozygosity (uH_e) ranged from 0.114 in YL (Arkansas, USA) to 0.168 in QC (Quebec, Canada), with a mean value of 0.157. Observed heterozygosity (H_o) ranged from 0.112 in YL (Arkansas, USA) to 0.160 in KX (Tennessee, USA), with a mean of 0.134. No significant trends in H_o were detected with latitude or longitude ($p > 0.5$), whereas uH_e showed a weak but significant positive relationship with latitude ($R^2 = 0.088$, $p = 0.013$), but not with longitude ($p = 0.26$). In all populations, uH_e was consistently higher than H_o.

The inbreeding coefficient (F_{IS}) ranged from 0.005 in KX (Tennessee, USA) to 0.158 in PH (Nova Scotia, Canada), with a mean of 0.116 (Fig. 4c, see Supplementary Table S5). F_{IS} showed a weak but significant positive relationship with latitude ($R^2 = 0.14$, $p = 0.0018$), but not with longitude ($p = 0.41$). Most populations showed a significant deficit of heterozygotes. In some populations where confidence intervals overlapped zero, the lack of statistical significance likely reflects limited sample sizes rather than true biological differences among populations. Inbreeding coefficients were particularly elevated in the Maritime provinces (Nova Scotia, Prince Edward Island, and Gaspésie in eastern Quebec) of Canada and were statistically significant in all populations except for CY (Prince Edward Island; Fig. 4c, see Supplementary Table S5).

Pairwise F_{ST} values ranged from 0.001 to 0.205 (see Supplementary Table S6 and Supplement File 2: Fig. S17), with an average of 0.038, indicating low to moderate genetic differentiation among populations. The most differentiated populations are YL (Arkansas, USA) and ME (Quebec, Canada) ($F_{ST} = 0.205$), while the least differentiated pairs are CR–KX (both within Tennessee, USA) ($F_{ST} = 0.001$) and TF-AH (both within Ontario, Canada) ($F_{ST} = 0.001$). Overall, YL (Arkansas, USA) shows the highest differentiation relative to all other populations, with F_{ST} values ranging from 0.093 to 0.205 (see Supplementary Table S6 and Supplement File 2: Fig. S17). This population is geographically distant from the other sampled populations, with a substantial sampling gap, and is represented by only two individuals, which may influence estimates of genetic differentiation.

3.2. *Genomic signature of selection and adaptation to climate*

The RDA results showed that the full model integrating climate, geographic, and neutral population genetic structure variables explained 32% of the total variation in population allele frequencies (Table 1). Among these, partial RDAs (pRDAs) revealed neutral genetic structure (ancestry) as the strongest unique predictor, accounting for 36% of the explained variance (adjusted $R^2 = 0.092$; $p = 0.001$) after controlling for climate and geography. Climatic variables uniquely explained 18% of the explained variance (adjusted $R^2 = 0.010$; $p = 0.017$) after controlling for geography and ancestry, suggesting a small but significant role of environment. Geographic variables uniquely explained 29% of the explained variance (adjusted $R^2 = 0.022$; $p = 0.004$) after controlling for climate and ancestry, indicating a detectable spatial genetic pattern. A substantial proportion of the explained variance (17**%**) was confounded among the three predictor sets and could not be uniquely attributed to any of them.

The unconstrained RDA identified two major axes of genetic variation, with RDA1 and RDA2 explaining 50.2% and 18.2% of the constrained variance, respectively (Fig. 5a). RDA1 was primarily associated with extreme minimum temperature over 30 years (EMT, 0.85) and May to September precipitation (MSP, 0.56). RDA2 was mainly associated, with summer heat moisture index (SHM; −0.89) showing the strongest loading, closely followed by May to September precipitation (MSP; 0.80).

Using a 5% FDR threshold, RDA detected the largest number of candidates, with 1487 outliers, followed by BayeScan (Supplement File 2: Fig. S18b) with 682 SNPs. OutFLANK identified 17 candidates

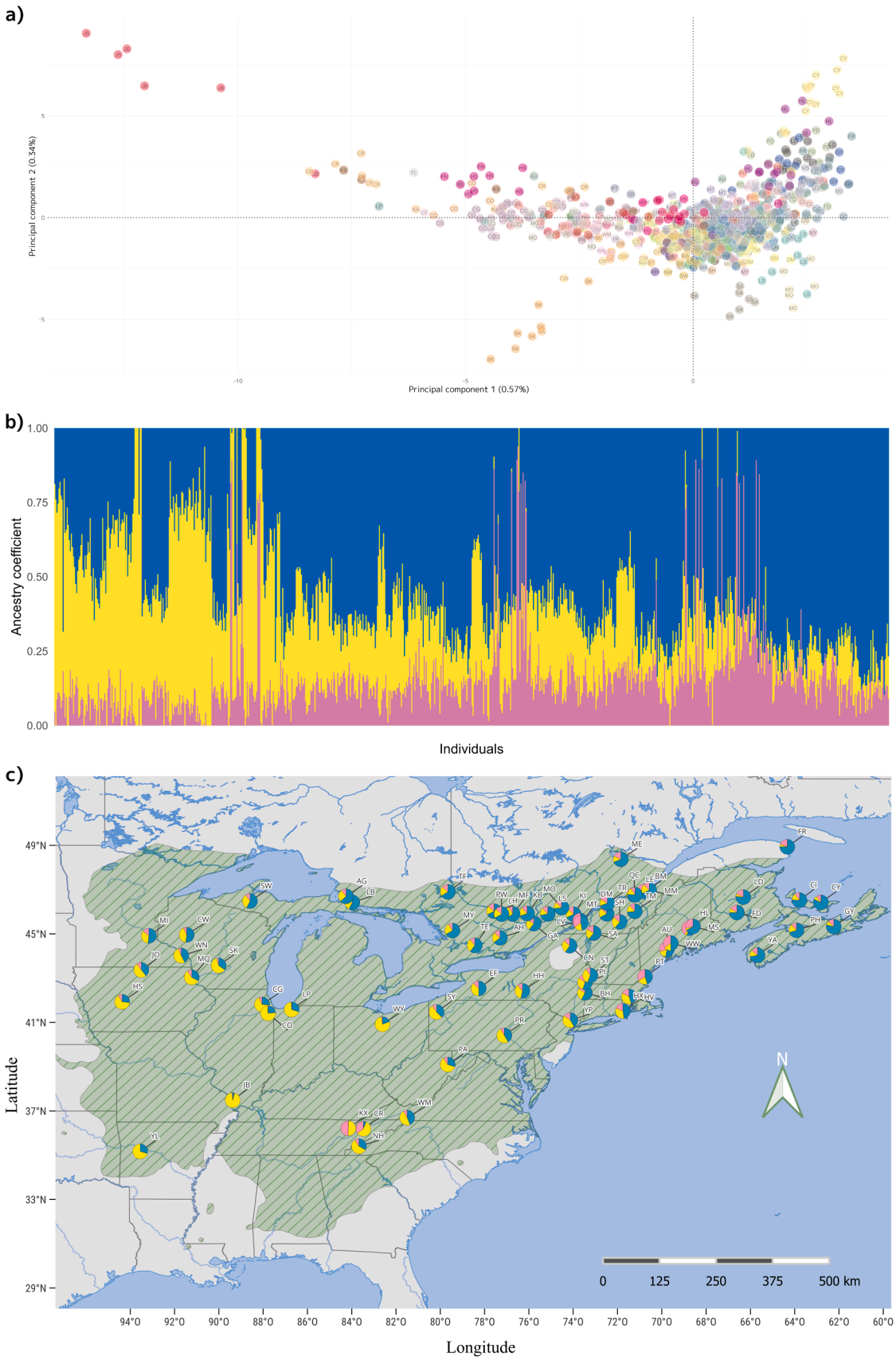


Fig. 3. Geographic distribution of genetic variation across *Q. rubra* natural populations. a) PCA of the first two PCs with collectively less than 1% explained variation. b) Individual assignment plot to each genetic cluster for $K = 3$, sorted from west to east. c) Map showing the geographic distribution of these 69 populations. Pie charts represent the average proportion of individuals assigned to each of the three genetic clusters within each population. The dashed green area indicates the species' natural distribution range (Little, 1971).

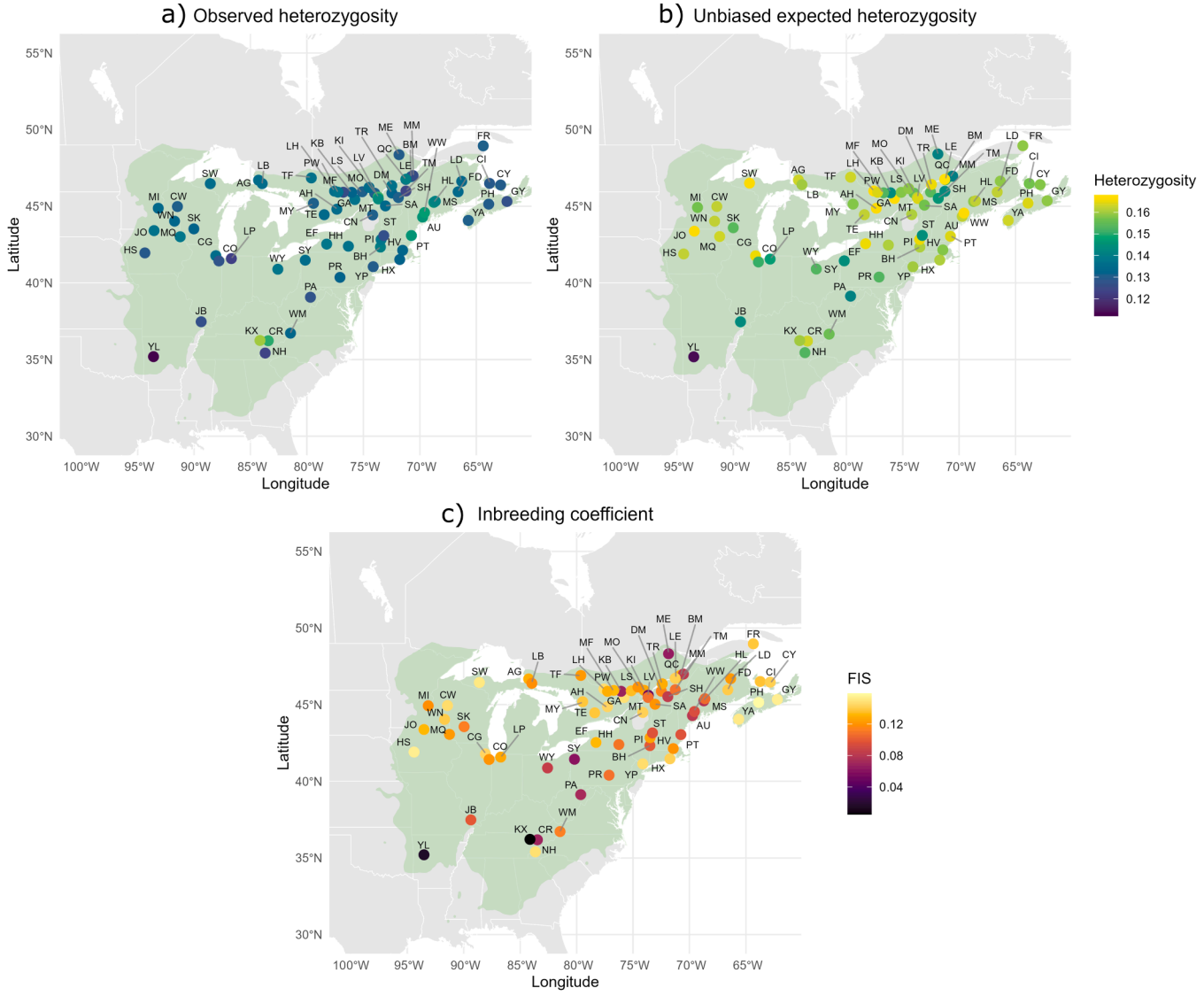


Fig. 4. Geographic distribution of genetic diversity in *Q. rubra*. a) observed (H_o) and b) unbiased expected heterozygosities (uH_e) and c) inbreeding coefficient (F_{IS}) across its natural range. . The green area indicates the species' natural distribution range (Little, 1971).

Table 1
Partitioning of genomic variation in *Q. rubra* using partial redundancy analysis (pRDA) among climate, neutral population structure, and geographic variables. Statistical significance of each component was assessed using one-way ANOVA (permutation = 999). Asterisks show significance levels. *F* = allele frequency, geog. = geography, clim. = climate, and anc. = ancestry.

RDA Model	Inertia	Adjusted R^2	*p* (>*F*)	*F*	Proportion of explainable variance	Proportion of total variance
Full model: *F* ~ *clim.* + *anc.* + *geog.*	56.402	0.160	0.001***	1.994	1.00	0.32
Climate: *F* ~ *clim.* | (*geog.* + *anc.*)	10.195	0.010	0.017*	1.172	0.18	0.06
Geography: *F* ~ *geog.* | (*clim.* + *anc.*)	16.565	0.022	0.004	1.269	0.29	0.09
Ancestry: *F* ~ *anc.* | (*clim.* + *geog.*)	20.36	0.092	0.001***	3.120	0.36	0.12
Confounded climate/geography/ancestry	9.282				0.17	0.05
Total unexplained	119.647					0.68
Total variance	176.049					1.00

Notes: *p < 0.05, **p < 0.01, ***p < 0.001

(Supplement File 2: Fig. S18a), while LFMM (Supplement File 2: Fig. S19) detected the fewest, with only 9 (Supplementary Table S7).

Only one SNP (see SNP 720362:64:- in Tables S7) was detected by all four genome scan methods (Fig. 5b) but was not located in a gene. However, a total of 142 SNPs were identified by at least two approaches, with the majority (118 SNPs) overlapping between RDA and BayeScan (Fig. 5b).

The LFMM analysis identified nine SNPs associated with the

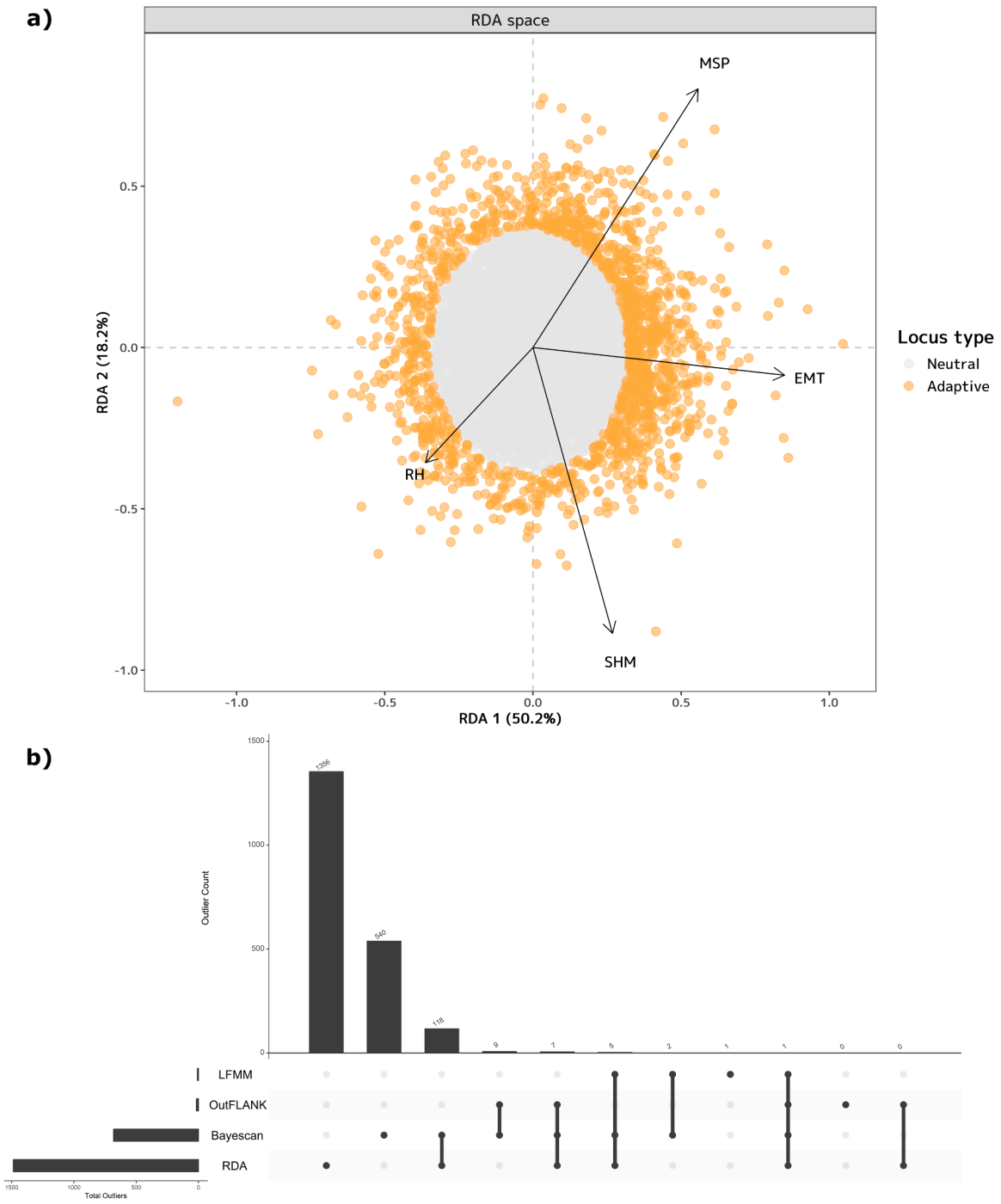


Fig. 5. Landscape genomic analyses in *Q. rubra*. a) Redundancy analysis (RDA) of SNP–environment associations (without correction for neutral population structure). Orange points represent adaptive loci, grey points represent putatively neutral loci, and arrows indicate environmental variables. Locus scores were scaled (×20) to improve visualization relative to environmental vectors. b) UpSet plot showing the overlap among outlier SNPs detected by the four approaches used in this study (RDA, LFMM, Outflank, and Bayescan). The horizontal bars indicate the total number of outliers detected by each method, while the vertical bars represent the number of SNPs shared among specific combinations of methods.

environmental variables EMT and SHM (see Supplement File 2: Fig. S19a-b and supplementary Table S7). Eight SNPs were associated with EMT, and three SNPs were associated with SHM, with two loci associated with more than one environmental variable. SHM-associated SNPs were found on chromosomes 2, 7, and 9, while EMT-associated SNPs were located on chromosomes 2, 3, 7, 11, and 12, with three SNPs associated with chromosome 9. Two of these SNPs were also detected by BayeScan, and none were detected by OutFLANK. One of the SNPs detected by BayeScan was located 3065 kb downstream of a gene (SNP 610876:15:-; Table S7-S8).

Out of the 142 SNPs identified by the GEA analysis, 74 were located in or near genes, corresponding to candidate genes associated with 12 biological processes (BP), 31 molecular functions (MF), and 6 cellular components (CC), with individual genes often linked to multiple processes (supplementary Table S8). Among molecular functions, binding- and enzyme-related activities were most frequent, particularly ATP binding, protein binding, and kinase/phosphatase activities. Biological processes were dominated by protein phosphorylation, metabolic and

transport-related processes, while cellular components were mainly associated with membranes, the cytoplasm, and the cell wall.

4. Discussion

Relatively few studies have investigated environmental association in North American oak species to date. In *Q. rubra*, two prior SNP-analyses are available, with Gómez Quijano et al. (2024) focusing on a regional scale in the Great Lakes area and Kapoor et al. (2023) examining a broader transect from the southern Appalachian region to Ontario. By adopting a range-wide sampling design, our study more broadly assesses how demographic history and climate jointly shape genetic variation in this species. Our objectives were to describe the population structure and identify signatures of local adaptation in *Q. rubra* by using 20,847 SNPs to characterize genomic variation across 69 populations spanning the native distribution. Our results revealed a continuous southwest–northeast genetic structure with generally low to moderate differentiation among populations, indicating that neutral processes such as historical gene flow and postglacial demographic history explain most of the observed genomic variation. Climate and geography contributed smaller but significant effects, suggesting a subtle but detectable role of natural selection in shaping allele frequencies. Despite the predominance of neutral variation, genome scans identified 142 candidate loci detected by at least two methods, primarily associated with temperature and moisture-related climate variables, indicating a weak polygenic signal of local adaptation. Overall, these results suggest that current genetic structure in *Q. rubra* is primarily driven by neutral processes, while adaptive genetic variation appears polygenic and thus subtle and potentially complemented by phenotypic plasticity and high within-population genetic diversity, suggesting that resilience across the species' broad environmental range may arise from the synergistic contributions of plasticity and genetic standing variation. In this context, our findings provide a comprehensive genomic framework for informing conservation and management measures in both natural and urban environments.

4.1. Genome-wide genetic structure reflects demographic history and connectivity

The geographic distribution of genetic variation in *Q. rubra* indicates that historical gene flow and postglacial recolonization following the LGM have resulted in a largely continuous spatial gradient of genomic composition. Unlike European oaks, which recolonized from a few isolated southern refugia and retain strong chloroplast differentiation (Petit et al., 2003), North American oaks, appear to have persisted closer to the former glacial margin during the LGM (Williams, 2003). Even in Europe, nuclear markers indicate oaks maintain relatively high genetic diversity at northern latitudes despite evidence for southern refugia (Lumibao et al., 2017; Milesi et al., 2024). In comparison, *Q. rubra* appears even more homogeneous, likely reflecting multiple scattered refugia, continuous populations, and the absence of major east–west mountain barriers (Jaramillo-Correa et al., 2009). This pattern has also been confirmed at a continental scale across multiple North American tree species (Gougherty, 2022), including oaks (e.g. *Q. alba,* Lumibao et al., 2017; *Q. macrocarpa*, Zacharias et al. in preparation). Subsequent postglacial expansion over relatively short distances likely promoted lineage mixing and minimized bottlenecks, resulting in the homogenized yet diverse genetic landscape observed today.

Consistent with this historical context, weak genetic differentiation across the natural range of *Q. rubra* has previously been reported using microsatellite markers (Borkowski et al., 2017) and a smaller set of SNPs (Merceron et al., 2017), consistent with our large SNP dataset generated using GBS approach. Regional RAD-Seq studies, such as Gómez Quijano et al., (2024) in the Great Lakes, reported a global F_{ST} of 0.028, comparable to our overall mean F_{ST} of 0.038. PCA, sNMF and sPCA analyses reveal widespread admixture and a southwest–northeast gradient, reflecting extensive historical gene flow typical of wind-pollinated oaks (Kremer and Hipp, 2020). Other widespread North American broadleaf species with large populations and high gene flow also show weak structure (e.g. *Juglans cinerea*, $F_{ST} = 0.045$; Hoban et al., 2010, *Fraxinus pensylvanica*, $F_{ST} = 0.0057$; Huff et al., 2022). These values align with a multi-species assessment which reporting range-wide F_{ST} values below 0.1 across 20 species northeastern tree species (Royer-Tardif et al., 2021), suggesting that genetic variation in *Q. rubra* is shaped by similar processes at local and continental scales.

Genetic diversity was broadly homogeneous with high within-population heterozygosity and no strong latitudinal decline. Consistent with other widely distributed oak species (Craft and Ashley, 2010; Oyama et al., 2020; Xiong et al., 2020) as well as more range-restricted taxa (Ashley et al., 2018; Backs, 2015; Backs and Ashley, 2016). This likely reflects shared life-history traits that maintain large effective population sizes, including long lifespan and extensive pollen-mediated gene flow. Longevity allows the accumulation of somatic mutations contributing to standing genetic variation (Plomion et al., 2018) while pollen dispersal and interspecific hybridization further promote genetic diversity across populations (Kremer and Hipp, 2020).

Although one southern Appalachians population shows strong membership to a discrete (pink) cluster, this cluster is not consistently represented in intervening populations. Clustering results at $K = 3$ should therefore be interpreted cautiously, as model-based algorithms assume a fixed number of genetic groups and can be less robust under low differentiation or unbalanced sampling (Wang, 2022). The observed differentiation may reflect geographic, connectivity, or landscape barriers, rather than a distinct historical lineage. Chloroplast DNA studies reported rare haplotypes in the southern Appalachians (Magni et al., 2005; Neophytou et al., 2025), suggesting a relict character of these marginal populations, with landscape barriers limiting genetic exchange with the core of the distribution. However, sampling in this region was limited, and additional populations would be needed to better assess genetic variation in the southern range.

Elevated heterozygosity and admixture may partly reflect past interspecific hybridization, a widespread phenomenon in oaks that leaves persistent genomic signatures (Degen et al., 2021). In the central and southern of the range, *Q. rubra* co-occurs with several sympatric species, including *Q. coccinea*, *Q. velutina* or *Q. marilandica* (see Supplement File 2 Fig. S20), creating opportunities for historical hybridizations, that have documented in multiple studies, particularly in regions of geographic overlap (Cannon et al., 2024; Cannon and Petit, 2020; Hipp et al., 2019; Khodwekar and Gailing, 2017; Moran et al., 2012; Sullivan et al., 2016). Several populations assigned to the central cluster were sampled near or within urban areas. Although classified as "natural", they may be influenced by anthropogenic activities, including planting from diverse seed sources, potentially introducing atypical genetic signals or inflating heterozygosity.

Interestingly, northeastern Maritime provinces (Nova Scotia, Prince Edward Island, and eastern Quebec) exhibit high FIS values together with high uH_E, suggesting reduced gene flow or fine-scale substructure rather genetic impoverishment. Geographic isolation, habitat fragmentation, and limited dispersal (e.g., pollen and seed) along the coast and on islands likely reduced gene flow while opportunities for interspecific hybridization are minimal, as *Q. rubra* is largely allopatric in this region (see Supplement File 2 Fig. S17).

For this study, we decided to include six populations with fewer than five individuals because they are located in underrepresented areas of the species' range (YL, Arkansas, n = 2; SY, Pennsylvania, n = 2; WY, Ohio, n = 2; MI, Minnesota, n = 3; ME, Quebec, n = 3; PA, West Virginia, n = 3). However, the F_{ST} estimates and diversity indices for these populations should be interpreted with caution, as small sample sizes can skew estimates of allele frequencies. Furthermore, three populations (ES, SG, and BV) were excluded from subsequent analyses due to their consistent outliers in the PCA and sNMF methods. Since they were grouped with species of the section Lobatae within *Q. rubra* in the joint

PCA (Supplement File 2: Fig. S6), their divergence may instead reflect a strong family structure or hybridization with closely related species not included in our dataset. Further investigations could be conducted to understand the origin of their divergence.

Despite this genetic continuity at large scale, more recent local adaptation could have influenced the selection of specific loci. To explore this possibility, we conducted genome-environment association analyses to identify loci potentially involved in local adaptation across the natural range of *Q. rubra*.

4.2. Climate-associated genomic variation despite extensive gene flow

Variance partitioning showed that neutral genetic structure explains the largest portion of the variation, outweighing the contributions of both spatial and climatic factors. This pattern is expected given that most loci across the genome are likely neutral, with only a small fraction contributing to climate-driven adaptation (Forester et al., 2018). Accordingly, although climate-associated loci were detected, evidence for local adaptation remains weak, climate variables explained only ~1% (adjusted $R^2 = 0.010$) of the total genetic variation, and only 142 SNPs were identified by at least two independent methods. Nevertheless, despite the dominance of neutral variation, genome scan analyses using multiple methods including RDA, LFMM, OutFLANK, and BayeScan, identified subsets of loci associated with climatic variables, particularly extreme minimum temperature over 30 years (EMT), May to September Precipitations (MSP), and Summer Heat-Moisture Index (SHM).

The homogenizing effect of long-distance gene flow, which is known to be strong in oaks due to anemophilous pollen (Kremer and Hipp, 2020), can theoretically reduce the genomic signal of local adaptation by diluting alleles under selection. However, in our study, despite low population differentiation, we detected loci significantly associated with environmental variables. This suggests that local natural selection can be enough to counteract the homogenizing effects of gene flow and leave a detectable genomic signature, consistent with previous findings in oaks (Gómez Quijano et al., 2024; Sork, 2015). Adaptive divergence in long-lived forest trees is often polygenic, such that phenotypic differentiation may arise from subtle allele frequency shifts at many loci, resulting in weak signals at individual loci (Kremer and Le Corre, 2012). This decoupling between trait differentiation and genome-wide structure has been reported in both oaks and poplars, where strong divergence in adaptive traits is observed despite limited differentiation at neutral markers (Gómez Quijano et al., 2024; Porth et al., 2015). Reports of clinal variation in phenotypic traits found in *Q. rubra* historical provenance trials are consistent with this observation. Variation in budburst timing exhibited a longitudinal trend, with populations from the eastern part of the range generally flushing earlier than western populations, while leaf coloration showed a latitudinal gradient, with high-latitude populations exhibiting earlier autumn coloration and low-latitude populations coloring later (Deneke, 1974; Kriebel, 1993; Kriebel et al., 1976; Schlarbaum and Bagley, 1981). Although growth traits did not follow a clear latitudinal or longitudinal gradient, northern populations (from the Mississippi River to western Maine) generally grew faster than other populations, and populations from western (Kriebel, 1993; Kriebel et al., 1988; Schlarbaum and Bagley, 1981), drier parts of the range (e.g., Iowa, Kansas, Missouri) had higher drought tolerance and survival (Deneke, 1974; Kriebel et al., 1976). These results indicate that, despite low overall population differentiation, functional traits related to adaptation vary predictably with environmental gradients, consistent with the genomic signals detected in our study.

4.3. Cold-temperature gradients and candidate genes underlying adaptation

In general, both temperature and precipitation are important drivers of adaptation, but temperature generally leaves a stronger genomic signature in most studied trees (Gugger et al., 2021; Martins et al., 2018; Nadeau et al., 2016; Yu et al., 2022). To our knowledge, only two other studies have investigated climate association in *Q. rubra,* but they were conducted at different scales (Gómez Quijano et al., 2024; Kapoor et al., 2023). Their findings are consistent with our results, as they also reported associations with cold temperatures as a primary driver, along with precipitations. We found no overlapping candidate loci between studies, but all three reports detected associations on chromosome 9, suggesting that this chromosome may harbour regions involved in cold adaptation, even if the exact genomic positions differ. Differences among detected outliers are expected because F_{ST}-based outlier methods (e.g., BayeScan, OutFLANK) identify loci with unusually high F_{ST}, which are candidates for divergent selection among populations, whereas GEA methods (e.g., LFMM, RDA) detect loci whose allele frequencies covary with environmental gradients (Lotterhos and Whitlock, 2015). Moreover, multivariate approaches such as RDA can capture subtle multilocus signals of weak selection, while univariate methods such as LFMM test each SNP independently and are less sensitive to weak selective effects (Forester et al., 2018). In this study, we focused on outliers identified in common across analyses, but loci detected only in a single method may also represent candidates under weaker selection (Forester et al., 2018; Lotterhos and Whitlock, 2015).

Several of our candidate SNPs were located near genes with known homologues involved in abiotic stress responses. For instance, SNP 388841:45:+ was located 1307 bp downstream of *Qurub.05G015800*, a gene homologous to Late Embryogenesis Abundant (LEA), which protects cells from abiotic stress (e.g., drought, cold, and salinity) and contributes to plant growth and development in model plant species (Lan et al., 2013; Zhou et al., 2023). Two additional SNPs, 914908:29:- and 306698:57:-, were located near *Qurub.11G223800* (4379 bp downstream) and *Qurub.04G068500* (2291 bp downstream), respectively, both homologous to pectinesterase/pectinesterase-inhibitor (PME/PMEI) genes involved in cell-wall remodeling during abiotic stress (Coculo and Lionetti, 2022). We detected SNP 914114:70:+ positioned 1539 bp upstream of *Qurub.11G220800*, homologous to RHD SIX-LIKE 1, a transcription factor in the jasmonate (JA) signaling pathway involved in root hair development and defense responses (Han et al., 2022), and another SNP 547998:74:- which overlaps *Qurub.06G225900*, homologous to an F-box family protein involved in hormonal signaling, flowering, secondary metabolism, circadian rhythms, and responses to both abiotic and biotic stresses (Zhang et al., 2019).

Other candidate genes were found in Abscisic Acid (ABA)-mediated signaling pathways. Several of them are implicated in drought stress, including SNP 570891:22:- overlapped the PP2C homolog *Qurub.07G046800*, while SNPs 414257:31:+ (*Qurub.05G105200*) and 672046:79:+ (*Qurub.08G171600*) overlapped protein kinase homologs, and SNP 610876:15:- was 3065 bp downstream of *Qurub.07G190800*, also a protein kinase homolog (Lim et al., 2015; Singh et al., 2015). Additionally, SNP 814713:62:+ , located 4360 bp downstream of *Qurub.10G115600*, was associated with a protein kinase homologous to *Arabidopsis* At1g18390. Interestingly, a SNP in the genotype-phenotype association study of Housset et al., (2018) identified this same *Arabidopsis* homolog in *Pinus strobus*, where it was associated with drought tolerance. We also detected SNP 865100:70:-, located 1410 bp downstream of *Qurub.11G064600*, homologous to LRR-RLK genes, which are central to development and responses to abiotic and biotic stresses (Liu et al., 2017), and SNP 771499:12:+ , located 1085 bp upstream of *Qurub.10G000100*, homologous to a respiratory burst oxidase homolog (RBOH), an NADPH oxidase mediating Reactive Oxygen Species (ROS) signaling in early stress responses (Wang et al., 2018). Finally, SNP 865027:24:-, located 250 bp upstream of *Qurub.11G064500*, homologous to Glycine-Rich RNA-Binding Protein (GRP7; At2g21660), may influence ABA-mediated abiotic stress responses by promoting stomatal closure under cold stress, enhancing cold tolerance, while favoring stomatal opening under dehydration or salt stress, reducing tolerance, and also contributing to pathogen defense (Kim et al., 2008).

The majority of the candidate genes identified in our study are associated with broad abiotic stress response pathways, including ABA signaling, cell-wall remodeling, and ROS signaling, rather than highly specialized environment-specific functions. This suggest that *Q. rubra* may rely on a largely generalist stress-response strategy, with weak selection acting on a limited key loci embedded in a broader polygenic adaptive background (Ghalambor et al., 2007; Kremer et al., 2025).

4.4. Phenotypic plasticity as a potential explanation for weak genomic signals

The weak genomic signal identified in this study, together with the broad abiotic stress response functions of candidate genes discussed in Section 4.3, suggests that the adaptive strategy of *Q. rubra* likely combines three complementary components: a polygenic adaptive background, weak selection acting on a limited number of stress-tolerance loci, and phenotypic plasticity. This combination could explain how *Q. rubra* persists across diverse environmental conditions despite limited genetic differentiation among populations, suggesting that this species relies more on plasticity and high within-population genetic diversity rather than on strong environment-specific local adaptation to cope with environmental changes.

Evidence for high phenotypic plasticity in *Q. rubra* comes from studies in both introduced and native range. In Germany, where the species was introduced over 300 years ago, provenance trials including seed sources from the native range (Georgia, Tennessee, Indiana, USA, and Ontario, Canada), as well as introduced stands from Germany, reported high phenotypic plasticity in vessel traits and variable trade-offs between growth and resistance to extreme events (Kormann et al., 2024b, 2024a). These findings are consistent with observations in the species' natural range, where Leites et al., (2019) detected only weak clines in growth potential explaining less than 20% of the variance and reported that most phenotypic variation occurs within populations. Together, these findings suggest that, even when local adaptation signals are weak, differences in performance strategies and plastic responses may still occur. In eastern North American oaks ecophysiological evidence indicates that they display diverse plastic responses to drought, reflecting contrasting functional strategies rather than strong local genetic adaptation; however, these responses may only partially mitigate increasing drought stress (Novick et al., 2022). While phenotypic traits were not measured in this study, the weak climate-associated genomic signal observed alongside high levels of within-population genetic diversity mirrors patterns documented in German provenance trials. Together, these findings highlight the potential role of plasticity and standing genetic variation in mediating responses to environmental gradients in red oak. This interpretation is consistent with reports of stronger phenotypic plasticity in broadleaf species than in conifers, where natural selection is more frequently expressed as clinal or ecotypic differentiation (Sáenz-Romero et al., 2019), and has also been documented in other oak species such as *Q. petraea* (Sáenz-Romero et al., 2017).

The polygenic basis of adaptation raises the question of whether genetic and plastic effects are oriented in the same direction along climatic gradients. In trees, positive covariation of plastic and genetic effects (cogradient) has been documented in oaks and eucalyptus, where both sources of variation contribute synergistically to the overall adaptive response (Kremer et al., 2014, 2025). Whether such cogradient variation occurs in *Q. rubra* remains to be formally tested, as common garden experiments combining phenotypic and genomic data would be required to formally partition genetic and plastic effects (Albecker et al., 2025). If confirmed, it would further support the hypothesis that plasticity and genetic adaptation contribute synergistically, reinforcing the species' capacity to respond to environmental gradients. Furthermore, populations combining high levels of standing genetic variation and polygenic architecture of fitness are expected to show rapid adaptive responses to new selection pressures (Kremer et al., 2025; Kremer and Le Corre, 2012), suggesting that *Q. rubra* retains considerable evolutionary potential despite weak signals of local adaptation at individual loci. These findings have direct implications for seed sourcing and assisted migration. Empirical evidence suggests that tree species' range expansions generally lag behind shifting environmental conditions, especially at northern range limits, implying that natural migration may be insufficient to track ongoing climate warming (Sittaro et al., 2017). For example, in a broad-scale common-garden experiment conducted in Michigan, *Q. rubra* populations originating from the southern part of the species range (e.g., Virginia, Illinois, Indiana, Pennsylvania) showed a phenological mismatch with local climate, resulting in frost damage and, presumably, reduced fitness (Lindback et al., 2023). In contrast, at a smaller geographic scale, central Minnesota populations translocated into northern Minnesota exhibited higher survival, greater growth, and better phenological matching with the extended growing season (Etterson et al., 2020).

These contrasting outcomes suggest that while assisted migration may be feasible, it requires careful of seed source selection and consideration of the spatial scale of transfer. The combination of phenotypic plasticity, polygenic adaptation, and weak genetic clinal patterns observed in this species indicates that strictly localized seed sourcing may not always be necessary. Instead, the capacity of *Q. rubra* to respond plastically to a variety of environments supports the use of broader seed transfer frameworks, provided that decisions are informed by both neutral and adaptive genetic variation. This is consistent with the weak clinal patterns reported from provenance trials and aligns with similar findings in *Q. petraea* (Girard et al., 2022; Sáenz-Romero et al., 2017). Nevertheless, plasticity alone may be insufficient to buffer maladaptation under extreme climatic conditions, particularly at range margins. In such contexts, seed transfer strategies should be carefully evaluated using genome-wide data in combination with experimental trials, while maintaining high within-population genetic diversity to preserve long-term adaptive potential. Our study, therefore, provides one of the first range-wide genomic baselines for *Q. rubra,* offering a valuable foundation for such management decisions.

5. Conclusion

This study provides a comprehensive range-wide genomic characterization of *Q. rubra* based on 20,847 SNPs across 69 of its natural populations. Our results show that neutral processes (e.g., postglacial recolonization, historical gene flow, and extensive pollen dispersal) are the primary drivers of genetic structure, resulting in a largely continuous genetic landscape with a broad southwest-to-northeast gradient and overall low population differentiation. Despite the preponderance of neutral variation, weak but statistically detectable climate-associated genomic signals were identified, with adaptive differentiation primarily associated with cold temperature extremes and moisture-related climatic factors. Importantly, this weak adaptive signal does not indicate an absence of adaptation but rather supports an integrated adaptive strategy combining phenotypic plasticity, polygenic background adaptation, and weak selection acting on a limited number of stress-tolerance loci.

From a conservation perspective, the overall weak genetic structure suggests that a network of regularly distributed conservation units may be sufficient across much of the core range, while additional efforts should focus on more differentiated regions (e.g., southern Appalachians). This framework supports the use of complementary *in situ* and *ex situ* conservation strategies, particularly for populations at the species' trailing edge, where *ex situ* conservation may represent a key tool to safeguard genetic resources under ongoing climate change.

Finally, the genome-wide dataset generated here could form a valuable baseline for the development of genetic traceability tools and future integrative studies. In particular, combining genomic data with biotic interactions, soil factors, and experimental trials will be essential for fully characterizing the adaptive landscape of *Q. rubra* and for

translating findings into effective forest management strategies.

Funding

This work was supported by the Génome Québec Genomics Integration Program (2022–2025), 'Genomics-Informed Forest Certification and Wood Traceability Tools and Protocols' to I. Porth and N. Isabel and funded by the Government of Canada's Genomics Research and Development Initiative (GRDI), the 2 Billion Trees (2BT) program, and The Wood ID Project: Cataloguing Canadian trees to help tackle illegal logging.

CRediT authorship contribution statement

Charalambos Neophytou: Writing – review & editing, Resources. **Martin Williams:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Mirko Liesebach:** Writing – review & editing, Resources. **Simon Jansen:** Writing – review & editing, Resources. **Lyne Touchette:** Writing – review & editing, Resources, Investigation, Data curation. **Ilga Porth:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Nathalie Isabel:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Brian Boyle:** Resources, Methodology. **Éric Normandeau:** Writing – review & editing, Data curation. **André Rainville:** Resources. **John J. MacKay:** Writing – review & editing, Resources. **Antoine Kremer:** Writing – review & editing, Resources. **Lisa Tischenko:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT (Open AI) to improve readability and language of the manuscript, and for some R coding. The authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank E. Dussault, J.-F. Légaré, P. Labrie, C. Bourdon, V. Seigner, S. Lapierre, X. Archambault, and P.-A. Grenier for assistance with field sampling, and M. Lamothe and B. van der Meer for their support in DNA extraction protocol development and laboratory work (all from Natural Resources Canada, NRCan). We are also grateful to A. Roe, A. Wardlaw, C. Carscadden, I. DeMerchant, D. McPhee, S. Pilon, K. Burgess, M. Spearing, M-.C. Gros-Louis, A. Toussignant, B. Hamel, B. Marquis, D. Rhodes, and C. Zimmerman (NRCan) for their help with field sampling; I. DeMerchant additionally contributed to the preparation of Fig. S1a and S1b. We also thank C. Delisle (Kahnawake Environment Protection Office), K. Sandvall (Forest Gene Conservation Association), Peter N. (NSDOLF), M. Jamieson, and M. Harris (Island Nature Trust) for assistance with field sampling and local access to samples. We are also grateful to P. Bibeau, F. Audet, Y. Isabelle, and J. Fontaine for their generous volunteer support during tree sampling.

Thanks to G. Morin (Institut de Biologie Intégrative et des Systèmes), who prepared the samples for Genotyping. We thank P. Tanguay (NRCan) for facilitating contacts that helped us obtain additional samples from regions in the United States not covered in our initial dataset. We also thank S. Hardy (Enracinart) for facilitating access to additional trees, and to R. Kenyon and D. Voyer for kindly granting access to their tree.

We are grateful to C. D. Nelson (USDA Forest Service), O. Gailing (University of Göttingen), D. Lazik (Thünen Institute), K. McLaughlin (New York State Department of Environmental Conservation), A. Russell (Rhode Island Department of Environmental Management, Division of Agriculture and Forestry), G. LeMay (Maine Forest Service, Department of Agriculture, Conservation & Forestry), M. A. Ony (University of Tennessee), and D. Sigouin (Parks Canada) for their substantial contributions to field sampling efforts. We also acknowledge the teams involved in these collections, including E. Dionne and A. Karter (Maine Forest Service team), W. E. Klingeman (University of Tennessee team), and members of the New York State Department of Environmental Conservation team coordinated by K. McLaughlin, including J.J. Kathe, J. Capito, M. Dolan, Jack, Tristan, and Erin.

We also acknowledge our U.S. collaborators A. Hipp (Morton Arboretum), I. Scadden (Western Gulf Forest Tree Improvement Program) and C. Ding (Texas A&M) for oak sample provision (Cherrybark oak from Texas, Arkansas, Louisiana, and Mississippi; Shumard oak sourced from Texas, Dallas-Fort Worth area, and those planted at the Morton Arboretum). We also thank M. Lobdell and the staff of the Morton Arboretum for their support. We further thank G. Otis-Prud'homme for facilitating access to the Québec *Quercus rubra* provenance trials (Ministère des Ressources naturelles et des Forêts du Québec).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123879.

Data availability

Data will be made available on request.

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