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Population genetic insights for climate-adaptive oak management: Results from a large-scale study of Turkey oak populations

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ABSTRACT

Human-assisted translocation of oak reproductive material as part of climate-adaptive oak management has long been a key consideration in Central Europe. In this study, we conducted population genetic analysis of 32 Turkey oak (*Quercus cerris* L.) populations from Central and Southeast Europe, using ddRAD-seq genotyping, to support forestry adaptation measures. Our results revealed multiple genetic groups within the sampled range, suggesting that long-distance transfers of reproductive material could lead to the admixture of genetically distinct groups. We also detected a diversity cline, with genetic diversity increasing from the southwest and southeast toward the northwest. The highest diversity was observed in the Carpathian Basin, which is the most continental part of the sampled range and includes many populations near the species' drought limit. In this region, the surplus of genetic diversity may play a crucial role in local adaptation. Our findings further suggest that transferring reproductive material from Southeast Europe to the Carpathian Basin should be approached with caution, as this direction runs counter to the observed diversity gradient. Furthermore, loci under selection and their genotype-environment associations indicate that Turkey oak is primarily challenged by temperature fluctuations and extremes, rather than by water availability, as previously observed in co-occurring sessile oak (*Q. petraea* (Matt.) Liebl.). These results provide valuable support for a detailed assessment of Turkey oak's adaptive capacity, improving the efficiency of provenance selection for climate-adaptive forest management.

1. Introduction

Genetic diversity, adaptability, and resilience are key considerations when sourcing forest reproductive material (Alfaro et al., 2014; Konnert et al., 2015). Selecting appropriate provenances of reproductive material and developing suitable methods for their deployment are essential for enhancing the long-term adaptability of future forests under changing climatic conditions (Aitken and Bemmels, 2016; Bower et al., 2024; Williams and Dumroese, 2013). Achieving this requires precise knowledge of the genetic characteristics of the target species. Oaks (*Quercus* L.) are among the most affected genera by these issues in the Northern Hemisphere, due to their high ecological and economic importance and their widespread representation in forested landscapes.

Oak-dominated forests are key components of temperate ecosystems across the Northern Hemisphere, spanning Eurasia to North America (Menitsky, 2005). In addition to their high ecological value, oak forests also play a significant role in the forestry and wood industry sectors, particularly in Europe, China, and the USA (Rogers et al., 1993; Spiecker, 2021; Wang et al., 2023). Currently, due to their economic importance, most oak forests are under some form of forest and/or conservation management. As oaks generally exhibit high genetic diversity, which constitutes a strong basis for their adaptability under climate change, native oak species may serve as key elements in the local-scale climate adaptation of forestry (Kremer and Hipp, 2020; Schroeder et al., 2021).

Assisted migration is a promising, though long-debated, forestry adaptation strategy that could also be applied to oaks (Aitken and Bemmels, 2016; Pedlar et al., 2012; Xu and Prescott, 2024). It aims to mitigate the negative effects of climate change by increasing the local genetic diversity of tree populations through introducing reproductive material from conspecific populations that grow in site conditions similar to those projected for the target area (Szamosvári et al., 2025).

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The selection of appropriate provenance regions can be guided by the results of provenance trials and climate modelling (Benito-Garzón and Fernández-Manjarrés, 2015; Park and Rodgers, 2023). In addition, the recent development of genomic techniques may significantly enhance the effectiveness of assisted migration in practice (Chen et al., 2022). However, as a more cautious approach, the population genetic attributes of the target species across its range should also be considered. This is important not only to avoid selecting source populations with low genetic diversity, but also to enable the projection and monitoring of genetic changes expected in recipient populations where non-autochthonous genotypes will be introduced.

In this paper, we present the results of a large-scale population genetic survey of Turkey oak (*Quercus cerris* L.) across Central and Southeast Europe. Turkey oak is a Pontic-Sub-Mediterranean species belonging to the section *Cerris*. Its native range extends from southeastern France and the Italian Peninsula, across the Balkans, to Asia Minor (Menitsky, 2005). It reaches the northern edge of its range within the Carpathian Basin in Central Europe (Caudullo et al., 2022). Turkey oak is one of the most abundant oak species in this region, forming large stands that are typically mixed with other oaks and hardwood species (Menitsky, 2005). This species exhibits high phenotypic (Janković, 1956; V. Mátyás, 1970) and genetic diversity (Bagnoli et al., 2016; Özer, 2014), which may be a key factor in its capacity to adapt to climate change.

Given these favorable characteristics, Turkey oak is a promising candidate for forestry adaptation programs in the region, including assisted migration measures (Šimková et al., 2023). In this study, we investigated how the genetic attributes of populations vary geographically, how environmental factors drive local selection and adaptation, and how this variation may inform strategies for moving reproductive material from southern regions toward the Carpathian Basin. Our results highlighted that the biogeography of a species can substantially shape the genetic diversity of current populations. Therefore, long-distance transfers of reproductive material for adaptation purposes should take the species' population genetic attributes into account, to ensure effectiveness and avoid harming natural diversity. Moreover, based on the geographic patterns of diversity, it is not always straightforward whether northern populations require assisted gene flow from southern populations to increase their genetic diversity.

2. Methods

2.1. Selection of the study species

Turkey oak was selected as the study species based on its favorable traits relevant to climate change adaptation and genetic investigations. In the Central European region, particularly in Hungary, prolonged summer droughts are projected to be the most important limiting factors for forests in the future (Hlásny et al., 2014; Lindner et al., 2010; C. Mátyás et al., 2018). As Turkey oak exhibits greater drought tolerance compared to other native oak species, such as pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.), it may emerge as a key species in the context of climate change adaptation. Moreover, in addition to its high abundance, climate-based projections also indicate a substantial range expansion of this species in Central Europe during the 21st century (Illés and Móricz, 2022; Thurm et al., 2018).

Another important factor in choosing this species was the lack of gene flow from other native oak species. Since the closest relatives of Turkey oak in the study regions are white oaks from the section *Quercus*, there is no gene flow between Turkey oak and other oak species. Consequently, interspecific gene flow did not influence the diversity measures of the sampled populations. In addition, randomly introgressed adaptive alleles from related species were unlikely to confound the detection of genomic signals of local adaptation.

In this context, Turkey oak provided a unique opportunity to study population-level genetic diversity and its spatial patterns in a wind-pollinated tree species with large effective population sizes, while excluding the confounding effects of interspecific gene flow.

2.2. Genetic dataset

For the genetic analyses, we used our recently published dataset of 32 Turkey oak populations (Fig. 1.; Lados et al., 2025) sampled across the Balkan Peninsula and the Carpathian Basin. This dataset was developed to assess the species' genetic variability and population structure within the study regions, supporting climate change risk evaluation and decision-making related to climate change and reproductive material sourcing for forestry adaptation.

Here, we provide only a brief overview of the sampling design and genotyping methods, as detailed information is available in the original data paper.

Our sampling objective was to represent the local genetic diversity and site conditions of Turkey oak in the study area. Before sampling, we conducted an extensive literature review to explore site and climatic conditions, as well as forest association types, typical of Turkey oak in different parts of the sampled range.

In addition, as a recent study (Bagnoli et al., 2016) revealed the genetic structure of populations based on chloroplast markers, we also considered the spatial distribution of these genetic groups when selecting stands, aiming to include representatives of each group found in the study area.

Since our primary aim was to capture local genetic diversity, we only selected stands that had regenerated naturally from their own seeds and/or stump shoots. To ensure the stands we sampled reflected realistic forest conditions, we selected sites under regular forest management, except for population RO2, which was a wood pasture containing monumental remnants of the original vegetation.

As a result, 32 Turkey oak populations were sampled, evenly covering the study region (Table 1). All the selected stands were mature and were often mixed with other native oak species, such as *Quercus frainetto* Ten., *Quercus petraea*, and *Quercus pubescens* Willd. In each stand, 10 individuals were sampled (except for population BH2, where 11 individuals were sampled). Fresh leaves were collected for DNA extraction, and diameter at breast height (DBH), tree height, and GPS coordinates were recorded. In addition, soil and tree-ring samples were also collected; however, in this study, only genetic data were analyzed.

Genotyping of the 321 sampled individuals was performed using the double-digest restriction-site associated DNA sequencing (ddRAD-seq) method. This approach enables the detection of a high number of single nucleotide polymorphisms (SNPs) across the genome in non-model organisms, such as many forest tree species, without well-characterized reference genomes (Peterson et al., 2012). By reducing genome complexity in a reproducible manner, ddRAD-seq provides a balance between marker density and sequencing effort, making it particularly suitable for population genomic analyses across large geographic scales (Konar et al., 2017; Ulaszewski et al., 2021). The resulting genome-wide SNP dataset allows robust inference of population structure, genetic diversity, and loci potentially under selection.

SNPs were called using the ref_map pipeline in Stacks v2.62 (Catchen et al., 2013; Rochette et al., 2019), with the Turkey oak (dhQueCerr2.1, NCBI BioProject ID: PRJEB69237) and cork oak 2.0 (Usié et al., 2023) reference genomes. In this study, we used the SNP dataset mapped to the Turkey oak genome, which contained 229,026 raw SNP loci.

The published dataset was designed to be useful for multiple uses. Hence, only a loose filtering was applied during the generation of the dataset. Therefore, to prepare this raw data for our population genetic analyses, we applied an additional filtering step with more stringent filtering thresholds using the populations module from Stacks. First, the original '.ped' and '.map' files were converted to VCF format using PLINK v1.90b7.2 (Purcell et al., 2007). This VCF file was then processed with the 'populations' module, where only the first SNP per locus was retained to reduce linkage among SNP markers. Subsequently, loci with

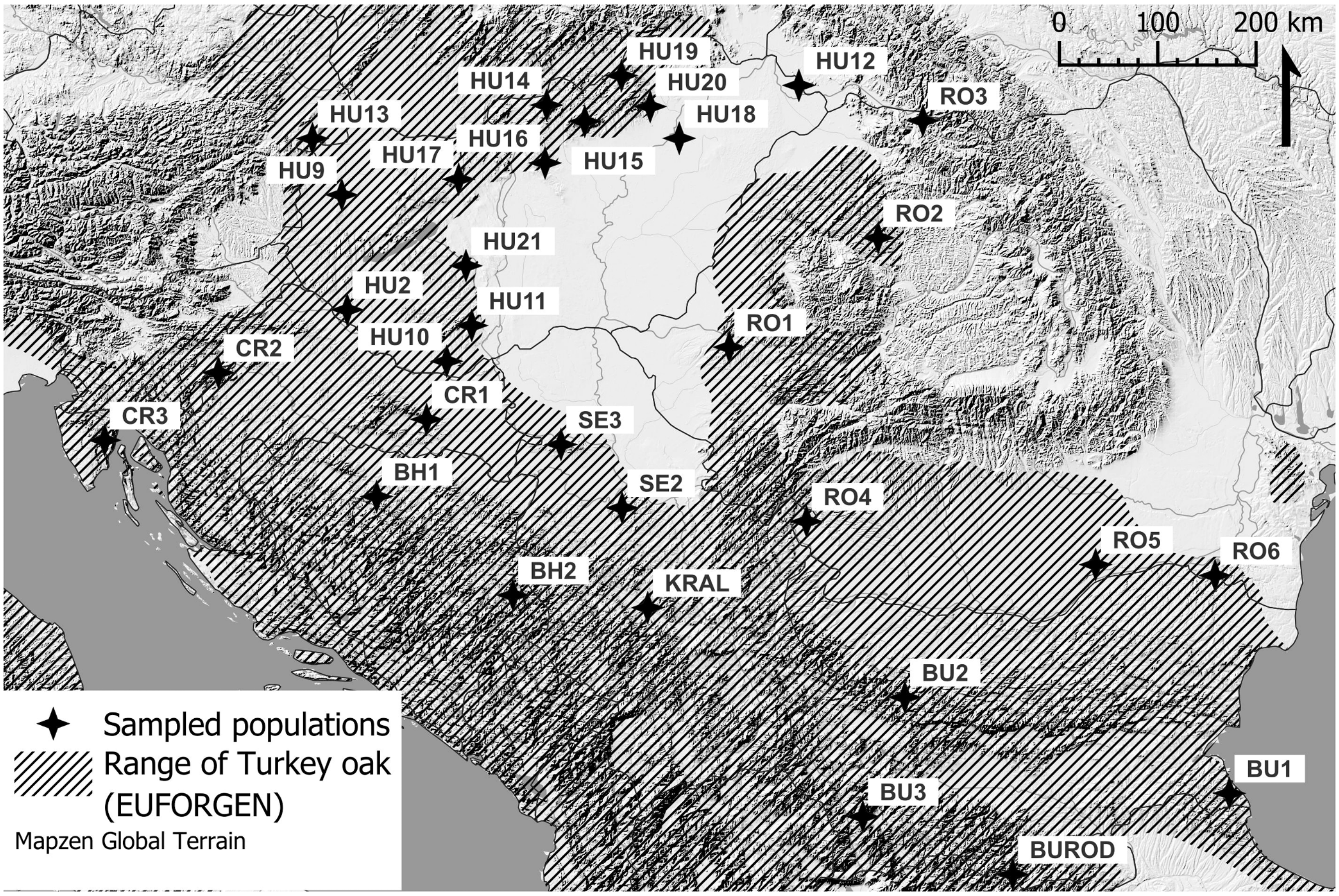

Fig. 1. Geographic map of sampled Turkey oak populations.

more than 5 % missing data and/or a minor allele frequency (MAF) below 5 % were removed. After filtering, 17,172 SNP loci were retained for the population genetic analyses.

2.3. Population genetic analyses

Basic population genetic indices were calculated on the filtered dataset for each sampled population in R v4.4.2 (R Core Team, 2024). First, per-locus values of observed heterozygosity (H_o), gene diversity (H_s), and the inbreeding coefficient (F_{is}) were calculated for each population using the 'basic.stats' function from the 'hierfstat' v0.5–11 package (Goudet and Jombart, 2022), and then averaged across loci. In addition, mean allelic richness per population (Ar) was calculated using the 'allelic.richness' function from the 'poppr' v2.9.6 package (Kamvar et al., 2014), and the Shannon diversity index (H') was computed using a custom R script. Moreover, the mean nucleotide diversity (π) per population was extracted from the 'populations.sumstats.summary.tsv' output of the Stacks 'populations' program after it had been run on the filtered dataset without applying further filters.

To characterize the distribution of within-population values of H_o, H_s, Ar, and F_{is}, these indices were visualized as boxplots using the Python library 'seaborn' v0.13.2 (Waskom, 2021). In addition, ordinary kriging was performed on all diversity indices to illustrate the spatial distribution of genetic diversity across the species' range. Kriging interpolation was restricted to the portion of the range covered by the sampling network. These calculations were conducted using the 'variogram', 'fit. variogram', and 'krige' functions from the 'gstat' v2.1–3 package (Pebesma, 2004). The 'Sph' (spherical) model was used to fit the variogram for all indices, except for the inbreeding coefficient (F_{is}), for which the 'Mat' (Matern) model was applied. The resulting raster layers were then imported into QGIS v3.3 to create diversity maps of the sampled geographic area.

Variance among individuals from different populations was first assessed using principal component analysis (PCA), performed in PLINK. The resulting principal components were visualized on scatterplots along the PC1-PC2 and PC2-PC3 axes using the 'ggplot2' v3.5.1 package (Wickham, 2016). Subsequently, a cluster analysis was carried out using the TESS3 program implemented in the 'tess3r' v1.1.0 package (Caye et al., 2018) to estimate the most probable number of genetic clusters and individual ancestry proportions. Clustering was performed with the 'tess3' function, testing K values from 1 to 10, with 10 replicates for each K (parameters: K = 1:10, ploidy = 2, lambda = 1, rep = 100, method = "projected.ls", max.iteration = 500, mask = 0.1, algo.copy = TRUE, keep = "best"). The optimal number of clusters (K) was determined based on the cross-validation cross-entropy score provided by the same function. Individual ancestry proportions were visualized as bar plots grouped by population using the 'pophelper' v2.3.1 package (Francis, 2017).

A rough estimate of the geographical extent of genetic groups within the sampled part of the distribution range was obtained through spatial interpolation. This interpolation was performed with the 'ggtess3Q' function (applying the kriging model FieldsKrigModel(10)) based on the ancestry matrix corresponding to the best K value and the GPS coordinates of sampled individuals. The resulting interpolated map of genetic groups was visualized in QGIS, accompanied by pie charts showing the proportion of genetic groups within each population (equivalent to the bar chart described above).

Genetic variance was partitioned further and tested for significance at different hierarchical levels using an analysis of molecular variance (AMOVA), implemented via the 'poppr.amova' function in the 'poppr' package. In addition, genetic differentiation between populations and

Table 1
Overview of the 32 sampling locations in the Carpathian Basin and Balkan Peninsula.

Pop ID[a]	N[b]	Country	Geographic region	Latitude (WGS84)	Longitude (WGS84)	Elevation m a.s.l
BH1	10	Bosnia and Herzegovina	Dinaric Alps	44.7289	17.4163	371
BH2	11	Bosnia and Herzegovina	Dinaric Alps	43.8712	19.0725	1075
BU1	10	Bulgaria	Strandzha Mts.	42.1100	27.7700	210
BU2	10	Bulgaria	Balkan Mts.	42.9700	23.8300	600
BU3	10	Bulgaria	Pirin Mts.	41.9002	23.3199	1007
BUROD	10	Bulgaria	Rhodope Mts.	41.3754	25.1401	462
CR1	10	Croatia	Papuk Mts.	45.3920	18.0236	195
CR2	10	Croatia	Žumberak Mts.	45.7890	15.4961	743
CR3	10	Croatia	Istrian Peninsula	45.2133	14.1148	39
HU10	10	Hungary	Villány Mts.	45.8855	18.2678	347
HU11	10	Hungary	Baranya Hills	46.1872	18.5713	277
HU12	10	Hungary	Great Hungarian Plain	48.1706	22.5433	98
HU13	10	Hungary	Sopron Hills	47.7375	16.6374	194
HU14	10	Hungary	Cserhát Mts.	48.0104	19.4807	301
HU15	10	Hungary	Mátra Mts.	47.8788	19.9439	627
HU16	10	Hungary	Gödöllő Hills.	47.5379	19.4622	200
HU17	10	Hungary	Vértes Mts.	47.4045	18.4130	236
HU18	10	Hungary	Great Hungarian Plain	47.7398	21.0909	113
HU19	10	Hungary	Borsod Hills.	48.2488	20.3897	211
HU2	10	Hungary	Zala Hills	46.3200	17.0600	220
HU20	10	Hungary	Bükk Mts.	47.9988	20.7385	209
HU21	10	Hungary	Tolna Hills	46.6875	18.5013	176
HU9	10	Hungary	Kemeneshát	47.2758	16.9937	165
RO1	10	Romania	Lippa Hills	46.0050	21.6993	294
RO2	10	Romania	Cluj-Napoca Hills	46.9199	23.5064	476
RO3	10	Romania	Maramureş Basin	47.8837	24.0488	480
RO4	10	Romania	Romanian Plain	44.5142	22.6360	54
RO5	10	Romania	Romanian Plain	44.1385	26.1466	99
RO6	10	Romania	Oltenia Plateau	44.0435	27.5961	160
KRAL	10	Serbia	Kotlenik Mts.	43.7619	20.7082	307
SE2	10	Serbia	Low Šumadija Region	44.6318	20.3973	278
SE3	10	Serbia	Fruška Gora	45.1769	19.6553	186

[a] Population ID
[b] Number of samples collected

genetic groups was assessed by calculating a pairwise F_{st} matrix with corresponding p-values using the Arlequin v3.5.2.2 program (Excoffier and Lischer, 2010), and the results were visualized as a heatmap using the 'ggplot2' package. For the cluster-level heatmap, a UPGMA tree was also added to the plot to illustrate relationships among clusters. This tree was generated with 1000 bootstrap resampling using the 'aboot' function of the 'poppr' package.

In addition to the analyses of genetic differentiation, SNP loci putatively under selection were also investigated. To identify outlier SNPs, we applied two complementary approaches, as different statistical frameworks for outlier detection often yield only partially overlapping sets of candidate loci. Therefore, combining the results of multiple methods can provide more statistically robust outliers.

Because markers in high linkage disequilibrium (LD) can strongly influence outlier detection, an additional LD filtering step was applied to the dataset using PLINK, with the option –indep-pairwise 10 5 0.2. Furthermore, population RO3 and individuals QCER-HU2–1, QCER-HU2–2, QCER-HU2–12, QC-HU12–5, and QC-HU12–6 were removed prior to these analyses, as they appeared as outliers in the population structure analyses. These outliers may reflect sequencing errors or other factors that could bias outlier detection. After this additional filtering, a total of 306 individuals from 31 populations and 9850 SNP loci were retained for outlier analyses.

The first approach used was PCAdapt (Privé et al., 2020), a widely employed method for detecting SNPs under selection. The approach first performs a PCA on the centered and scaled genotype matrix. It then calculates Mahalanobis distances for all SNP loci based on the selected number of principal components. These distances integrate the Z-scores of each SNP across the retained PCs into a single multivariate statistic. The resulting Mahalanobis distances approximately follow a chi-squared distribution, allowing for the calculation of p-values for each SNP locus. PCAdapt was run with $K = 2$ principal components, as determined by inspection of the PCA eigenvalues obtained from a preliminary PCAdapt run with $K = 20$. To correct for multiple testing, p-values were converted to q-values using the 'qvalue' package (Storey et al., 2024) and SNP loci with q-values < 0.01 were identified as outliers.

The second method applied was OutFLANK (Whitlock and Lotterhos, 2014), which identifies outlier SNPs using a fundamentally different strategy. Unlike PCAdapt, OutFLANK detects outliers based on extreme F_{st} values relative to a neutral F_{st} distribution. This neutral distribution is estimated using a likelihood-based approach on a trimmed set of loci with balanced F_{st} values. Outlier loci are then identified based on q-values calculated from the inferred neutral distribution. OutFLANK was run with the following parameters: RightTrimFraction $= 0.08$, LeftTrimFraction $= 0.35$, Hmin $= 0.1$, and qthreshold $= 0.01$.

In the next step, RAD loci containing outlier SNPs common to both approaches were extracted from the consensus sequences assembled by the Stacks program. These loci were then annotated using the NCBI BLASTN and BLASTX services (https://www.ncbi.nlm.nih.gov/) with default parameters.

To investigate potential associations between selective loci and environmental factors, a genotype–environment association analysis was performed using only the outlier SNPs shared by both methods. Environmental predictors were obtained from the WorldClim v2.1 (Fick and Hijmans, 2017) bioclimatic variables (1970–2000) at 30 arc-second resolution and supplemented with ENVIREM variables calculated from the WorldClim dataset using the "envirem" package (Title and Bemmels, 2018). To reduce multicollinearity among predictors, variables were summarized using PCA, conducted separately for temperature- and precipitation-related variables. Based on the eigenvalue distributions, the first three principal components from each set were retained as predictors (tempPC1, tempPC2, tempPC3, precPC1, precPC2, precPC3).

The association test was performed using the Latent Factor Mixed Model (LFMM) approach implemented in the LEA package (Frichot and

François, 2015). LFMM performs univariate regression analyses while accounting for hidden population structure through the inclusion of K latent factors. In our analysis, the number of latent factors (K) was determined based on the number of five genetic clusters identified by the TESS3 clustering. Because population RO3 (which constituted Cluster1) was excluded from the dataset, K was set to 4 rather than 5 (the number of genetic clusters in the original TESS3 analysis). LFMM was run by using 100 independent runs for each K value, with 10 000 iterations of the Gibbs sampling algorithm and 5000 cycles of burn-in period. GIF-adjusted *p*-values were obtained using the 'lfmm.pvalues' function. Multiple testing was then controlled using the Benjamini–Hochberg procedure, and loci with FDR-adjusted p-values < 0.05 were considered significant.

3. Results

Genetic diversity indices exhibited balanced values in population means, with no large-scale deviations in the calculated values (Table 2). The largest standard deviation was 3.51 %, observed in the allelic richness. The ratio of observed heterozygote loci (H_o) was around 17–19 %, which was slightly lower than the expected values calculated as H_s (19–21 %). This slight deviation was also evident in the low but positive values of the inbreeding coefficient, which were significantly non-zero, as supported by the confidence intervals. Mean allelic richness varies between 1.628 and 1.776, which means biallelic loci had each two alleles on average in 63–78 % of cases within the population. Mean nucleotide diversity was 0.203 with a minimum of 0.189 in the population RO3 and a maximum of 0.213 in HU11. The smallest standard deviation was in the Shannon diversity index (0.002), where the minimum, maximum are 0.343 and 0.349, respectively, and a mean value of 0.347.

Distribution of locus-level diversity indicated small differences between populations for almost all indices (Fig. 2.). The only exception was the allelic richness (Fig. 2c), where some populations (BU1, BU3, BUROD, CR2, CR3, RO3, RO6) exhibited significantly lower per locus values (these populations comprised individuals with a larger number of fixed loci). However, the median value of allelic richness for these populations did not differ from the other populations, except for the population RO3, where the median value was lower. In the case of the observed heterozygosity and population gene diversity, per locus values were balanced between populations, with similar distribution (Fig. 2a-b). However, populations HU11, HU14, HU15, and HU17 had higher median values, indicating the presence of a larger number of heterozygous loci. As for the inbreeding coefficient, per locus values fluctuated around zero, which was the expected distribution in case of Hardy-Weinberg equilibrium (Fig. 2d). In most cases, however, the distribution of values was slightly shifted towards a positive direction despite the median converging to zero.

Sampled populations showed characteristic patterns of genetic diversity across the sampled part of the distribution range (Fig. 3.). Although different indices had different scales and variation between population diversity levels, the geographic pattern of diversity was similar to each other (see Fig. 3a,b,d-f). Namely, there were gradients in diversity, with the level of genetic diversity increasing from southeast and southwest to northwest. According to the observed heterozygosity (Fig. 3a), gene diversity (Fig. 3b), allelic richness (Fig. 3d), nucleotide

Table 2

Per population and overall mean of population genetic indices calculated for the sampled Turkey oak populations, where POPID is the population identifier, *n* the number of individuals sampled in a given population, H_o is the observed heterozygosity, H_s is the within-population gene diversity (Nei, 1987), *Ar* is the allelic richness, π ***is*** the nucleotide diversity, *H'* is the Shannon diversity index, F_{is} is the inbreeding coefficient, $F_{is\_CI\_95}$ is the 95 % confidence interval for the inbreeding coefficient.

POPID	*n*	H_o	H_s	*Ar*	π	*H'*	F_{is}	$F_{is\_CI\_95}$
BH1	10	0.190	0.207	1.734	0.206	0.349	0.083	0.076–0.090
BH2	11	0.177	0.198	1.726	0.197	0.345	0.108	0.102–0.115
BU1	10	0.179	0.193	1.671	0.192	0.346	0.074	0.067–0.081
BU2	10	0.185	0.206	1.749	0.205	0.347	0.106	0.099–0.112
BU3	10	0.175	0.192	1.674	0.191	0.344	0.091	0.083–0.098
BUROD	10	0.170	0.191	1.689	0.190	0.343	0.110	0.102–0.117
CR1	10	0.179	0.204	1.756	0.203	0.345	0.125	0.119–0.132
CR2	10	0.174	0.194	1.697	0.193	0.344	0.104	0.096–0.111
CR3	10	0.172	0.193	1.669	0.192	0.344	0.108	0.101–0.115
HU10	10	0.188	0.211	1.776	0.210	0.348	0.108	0.101–0.114
HU11	10	0.189	0.214	1.776	0.213	0.349	0.115	0.108–0.122
HU12	10	0.187	0.210	1.747	0.209	0.348	0.111	0.103–0.119
HU13	10	0.189	0.210	1.748	0.209	0.349	0.097	0.090–0.104
HU14	10	0.190	0.213	1.771	0.212	0.349	0.108	0.101–0.114
HU15	10	0.189	0.211	1.766	0.209	0.349	0.101	0.095–0.108
HU16	10	0.184	0.208	1.761	0.207	0.347	0.119	0.112–0.126
HU17	10	0.191	0.212	1.770	0.211	0.349	0.099	0.092–0.106
HU18	10	0.186	0.208	1.766	0.207	0.348	0.106	0.100–0.113
HU19	10	0.189	0.211	1.764	0.209	0.348	0.105	0.098–0.112
HU2	10	0.192	0.211	1.741	0.210	0.349	0.087	0.080–0.094
HU20	10	0.187	0.209	1.749	0.208	0.348	0.108	0.102–0.116
HU21	10	0.186	0.207	1.757	0.206	0.348	0.102	0.095–0.109
HU9	10	0.189	0.207	1.733	0.206	0.348	0.089	0.082–0.096
KRAL	10	0.175	0.198	1.727	0.197	0.345	0.117	0.110–0.124
RO1	10	0.184	0.204	1.739	0.203	0.347	0.096	0.090–0.103
RO2	10	0.180	0.201	1.730	0.200	0.346	0.106	0.099–0.113
RO3	10	0.179	0.190	1.628	0.189	0.346	0.055	0.048–0.062
RO4	10	0.182	0.205	1.746	0.203	0.347	0.109	0.102–0.116
RO5	10	0.178	0.199	1.721	0.198	0.345	0.103	0.096–0.110
RO6	10	0.177	0.197	1.707	0.196	0.345	0.101	0.093–0.108
SE2	10	0.177	0.200	1.741	0.199	0.345	0.114	0.107–0.121
SE3	10	0.181	0.202	1.745	0.201	0.346	0.104	0.097–0.112
Overall								
Mean		0.183	0.204	1.734	0.203	0.347	0.102	0.095–0.109
Min		0.170	0.190	1.628	0.189	0.343	0.055	0.048–0.062
Max		0.192	0.214	1.776	0.213	0.349	0.125	0.119–0.132
Sd		0.006	0.007	0.035	0.007	0.002	0.013	0.0135–0.0134

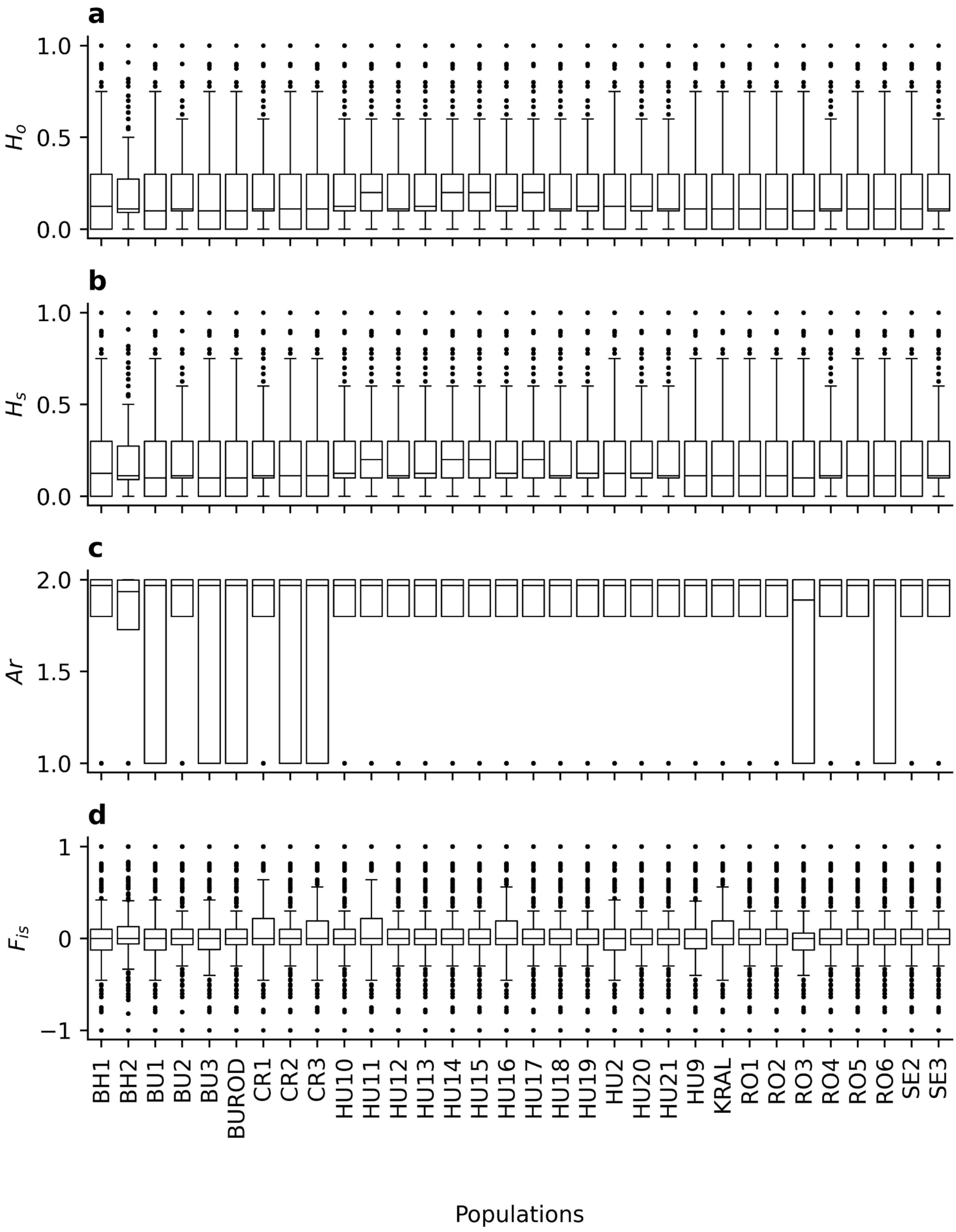

Fig. 2. Within population distribution of per locus observed heterozygosity (a), gene diversity (b), allelic richness (c), and the inbreeding coefficient (d) calculated for the sampled Turkey oak populations.

diversity (Fig. 3e), and Shannon diversity index (Fig. 3f), populations sampled in the central-western part of the Carpathian Basin exhibited the highest genetic diversity, whereas populations in southwestern Croatia and southeastern Bulgaria exhibited the lowest values. In addition, according to the pattern of allelic richness, there was another diversity hotspot extending to the Romanian Plain and northwestern Bulgaria. In the case of the inbreeding coefficient, there was no strong geographic pattern; the level of this index was relatively balanced across parts of the sampled regions.

However, there was also an outlier population, the RO3, which stood out from the general gradient of diversity. Namely, the RO3 population sampled in northwest Romania exhibited the lowest values in several diversity indices (H_s, *Ar,* and π), despite all the neighboring populations having higher values. In addition, this population also had the lowest value of the inbreeding coefficient, indicating a surplus of heterozygote loci relative to the other populations. Nevertheless, the lowest values of the allelic richness and nucleotide diversity suggested a higher number of fixed loci in this population (see also Fig. 2c).

Individual-level principal component analyses (PCA) revealed variation between populations or groups of populations. Along the first principal component axis, which accounts for 4.99 % of the total variance, populations were separated into two overlapping groups, with an admixture zone constituted by populations of the central part of the Carpathian Basin (sampled in Hungary, Serbia, and Romania; Fig. 4a). The order of populations through the main groups followed a general west-east geographic gradient. While there was no clear differentiation along the first axis, individuals of the RO3 population were distinctly separated from the main groups along the second axis, showing a high

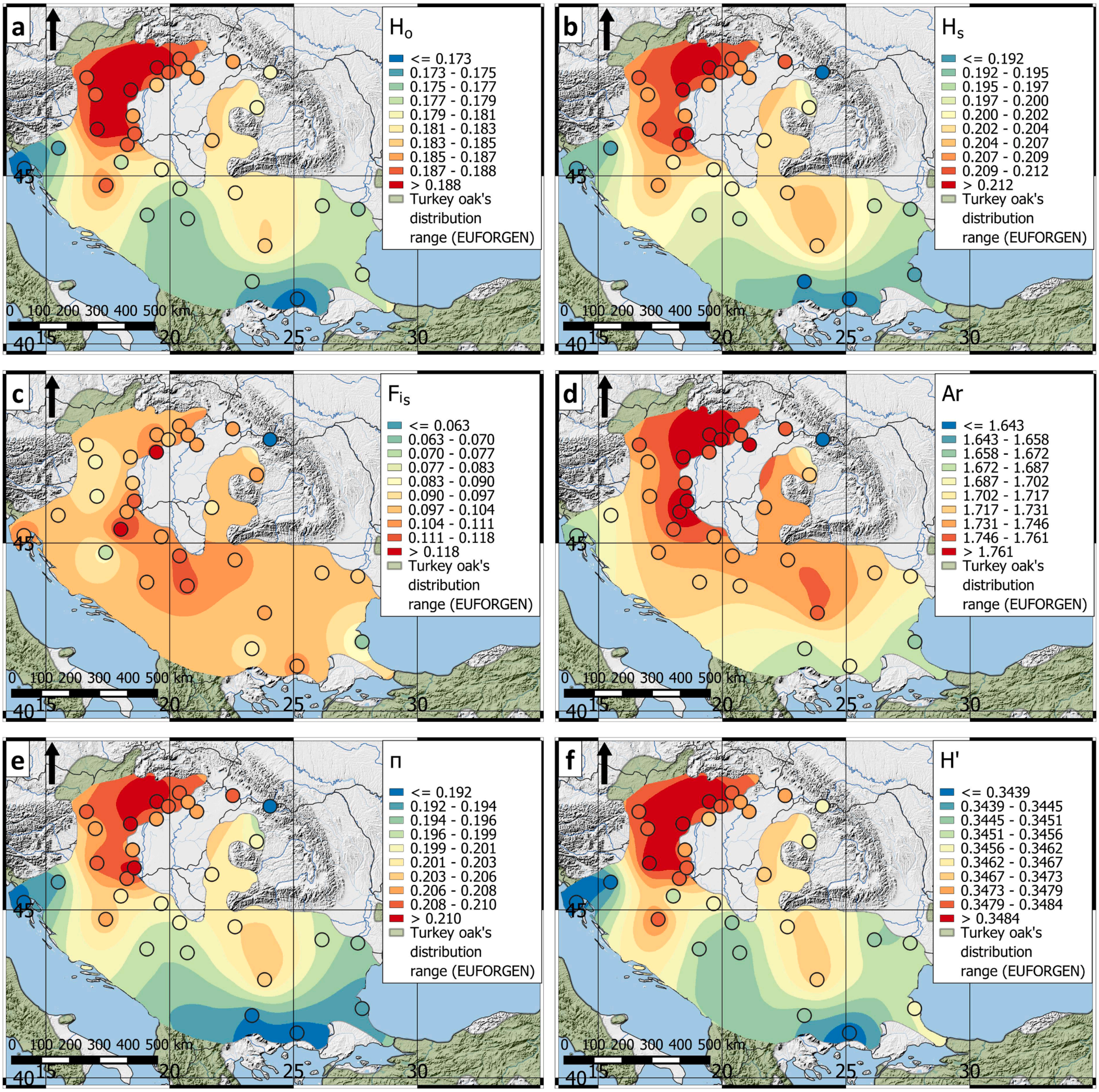

Fig. 3. Patterns of genetic diversity, based on the observed heterozygosity (a), within population gene diversity (b), the inbreeding coefficient (c), allelic richness (d), nucleotide diversity (e), and the Shannon diversity index (f) interpolated across the sampled part of Turkey oak's range. Circles mark the locations of the sampled populations.

level of within-population variance compared to the other populations.

Along the second and third principal axes, RO3 was also separated from the main groups (Fig. 4b). In addition, populations CR2, CR3, and BU1 diverged from their main groups and overlapped with each other. Nevertheless, this overlap was merely a result of the different illustration perspectives; these populations were located at opposite ends of the first principal axis, which accounted for the largest amount of variance.

According to the clear breakpoint in the cross-validation cross-entropy scores of different K values (Figs. 5a), 4 and 5 were selected as the potential numbers of ancestral populations in the TESS3 analysis (with K=5 considered as the optimal K value). Assuming four ancestral populations, the populations CR2, CR3, RO3, RO6, BU1, BU2, BU3, and BUROD were clearly separable from the other sampled stands, constituting three different genetic groups (Fig. 5b). All the other populations had a characteristic composition of different clusters rather than being assigned to a cluster with high probability, indicating their potential admixture. Nevertheless, these characteristic compositions (mainly the ratio of Cluster3 and Cluster4) may have supported the existence of two additional groups: one comprising populations from the Carpathian Basin (the Pannonian group), and the other comprising populations from the central part of the Balkan Peninsula and parts of Romania inside the Carpathian belt (the Central Balkan group).

Introducing five potential ancestral populations made the separation of genetic clusters more pronounced (Fig. 5b). Namely, the larger amount of probability of Cluster5 in the Pannonian group clearly separated these populations from the Central Balkan group (Cluster2). In

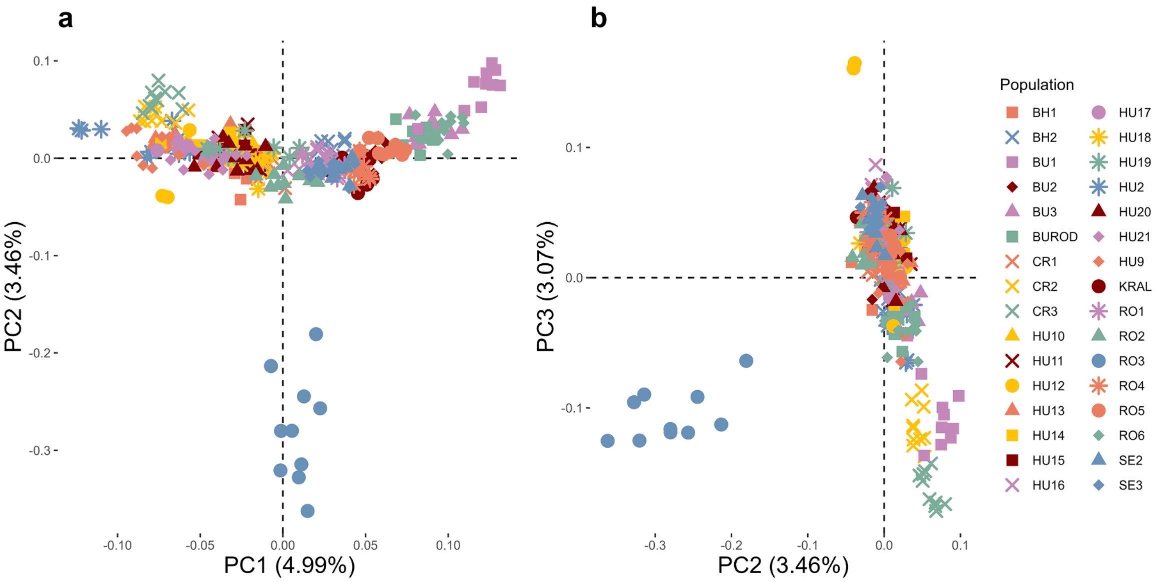

Fig. 4. Results of individual-level principal component analyses in the projection of the first and second (a) and second and third (b) principal axes. Colored markers represent the individuals of different populations. The axis labels indicate the amount of variance accounted for by each principal axis.

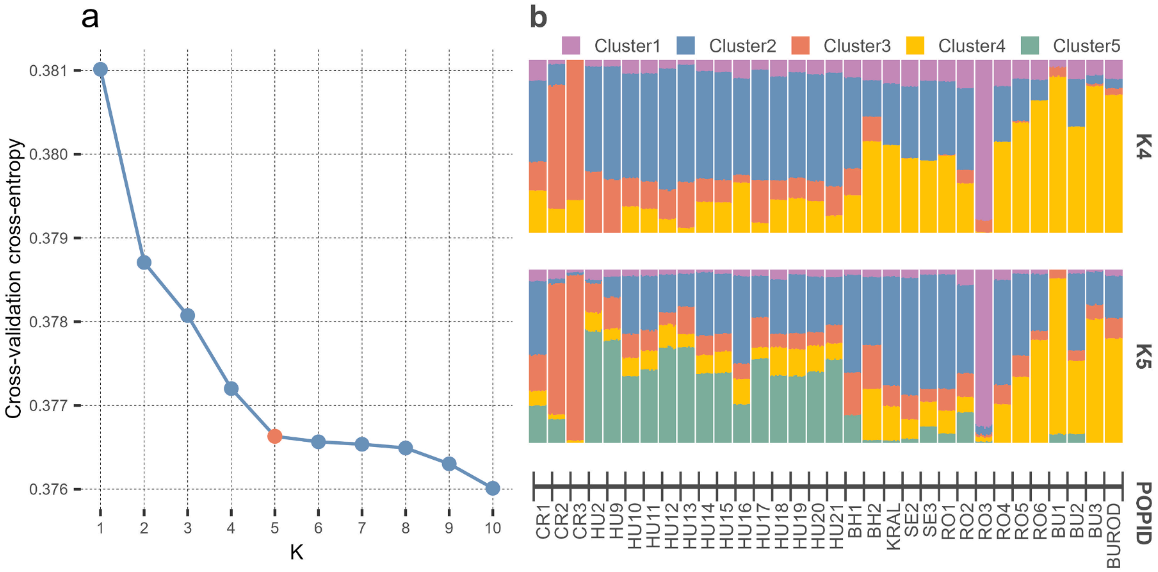

Fig. 5. Selection of the most probable number of ancestral populations (K), based on cross-validation cross-entropy (a) and clustering of sampled individuals assuming four and five ancestral populations using TESS3 (b).

this context, HU16 was an exception, as it had a more similar cluster composition to the Central Balkan group and, in particular, to the RO2 population.

According to the map generated by the kriging of genetic clusters (Fig. 6.), four larger genetic groups covered the sampled part of the distribution range (Cluster2, Cluster3, Cluster4, and Cluster5). In addition, the RO3 population constituted its own group, separating from all the others. From west to east, first, CR2 and CR3 populations represented Cluster3 (Western Balkan group), covering the western corner of the Balkan Peninsula. Inside the Carpathian Basin, two groups, Cluster5 and Cluster2, occupied the western and the eastern part of the region. In addition, these groups constituted an admixture zone in the middle of the Carpathian Basin, clearly indicated by the constitution of corresponding pie charts. Moreover, the admixture of these two groups was also present in the population RO2. Cluster4 comprised the southeasternmost populations sampled and extended to the southeast corner of the Balkan Peninsula. Based on the genetic composition of population BH2, this location was at the meeting point of the Western Balkan, the Central Balkan, and the Eastern Balkan groups, as the approximately even ratio of these three clusters indicated. Similar to the central part of the Carpathian Basin, there was also an admixture zone in the southeast Balkans, where the Central and Southeast Balkan groups came into contact (see genetic composition of RO5, RO6, and BU2).

Nevertheless, the genetic composition of populations represented by pie charts indicated some degree of admixture in almost every part of the sampled regions, excepting only three populations (CR3, RO3, and BU1), where the assignment to a given cluster converged to 100 %.

According to the results of the AMOVA (Table 3), the largest amount of variance was found within samples (86.82 %), while population- and cluster-level variance was much lower, 1.87 % and 1.77 %, respectively. However, despite the lower levels of variance, differentiation was significant at both levels ($p < 0.001$). In addition, between-sample within

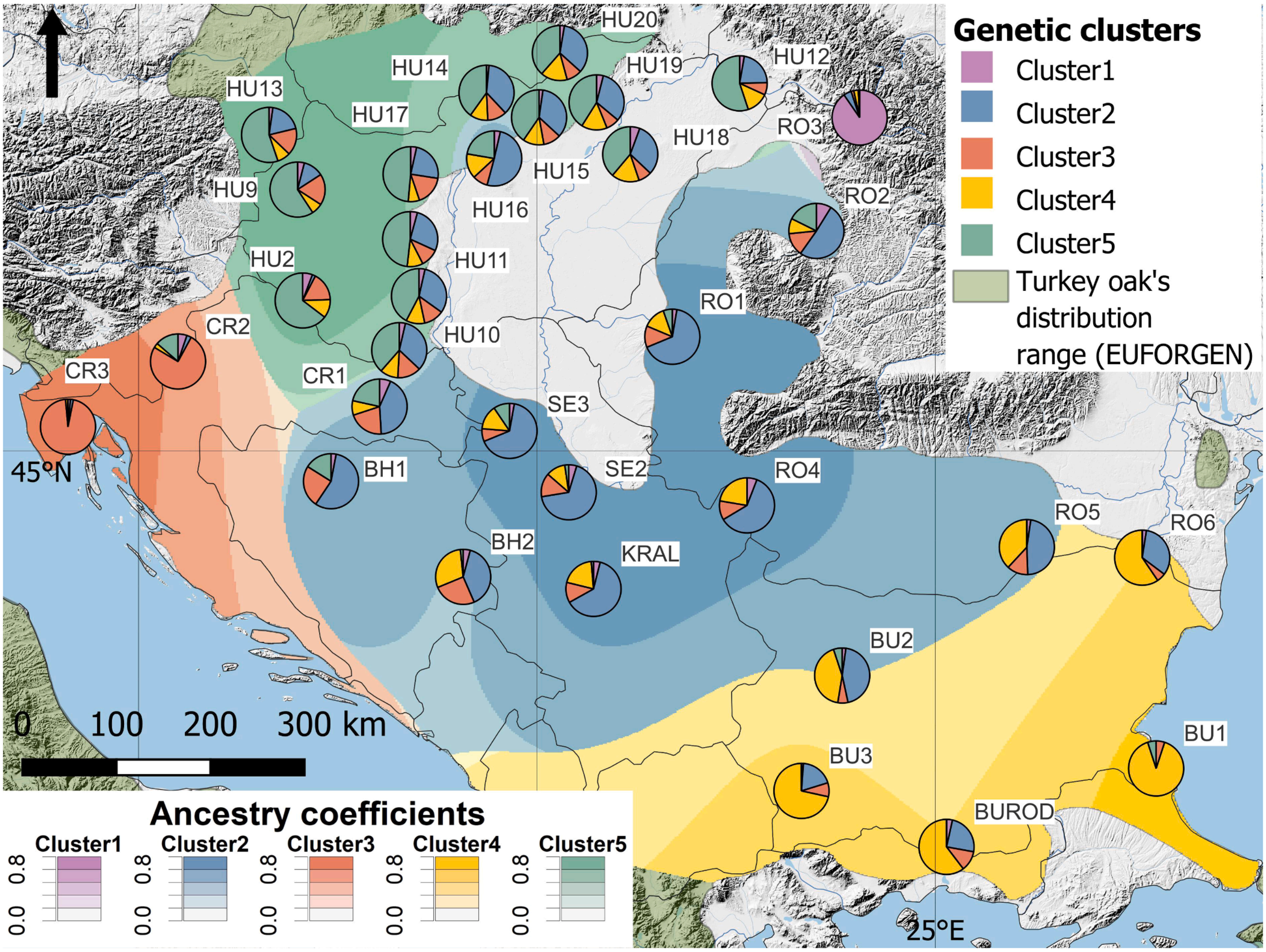

Fig. 6. Ancestry coefficients interpolated across the sampled range of Turkey oak. Individual pie charts represent the ratio of genetic clusters estimated within sampled populations using TESS3.

Table 3
Results of the analysis of molecular variance among genetic clusters and populations (df = degree of freedom, SS – sum of squares, MS – mean squares, % - percentage of variance estimated at different levels).

Source	df	SS	MS	Variance Estimated	%	Phi-Statistics	*p*-Values
Between clusters	4	48378.05	12094.51	64.02	1.77	0.018*	0.001
Between populations within clusters	27	139766.40	5176.53	67.54	1.87	0.019*	0.001
Between samples within population	289	1104306.38	3821.13	344.14	9.54	0.099*	0.001
Within samples	321	1005647.24	3132.86	3132.86	86.82	-	-
Total	641	2298098.07	3585.18	3608.56	100	-	-

*significant

population variance (9.54 %) was also significant. These results may have indicated a modest but complex multi-level population structure.

Cluster level differentiation was further assessed by the pairwise between-cluster F_{st} values (Fig. 7.), where different clusters were clearly separated (all the p values were significant). The maximum value of F_{st} was 0.093 between Cluster1 (population RO3) and Cluster3 (populations CR2 and CR3 from southwest Croatia), while the minimum was 0.008 between Cluster5 (Pannonian group) and Cluster2 (Central Balkan group). Thus, the highest level of differentiation was more than ten times of much as the lowest. The structure of the UPGMA tree supported that Cluster5 and Cluster2 were the closest related. Cluster4 (Eastern Balkan group) was the closest to Cluster2. Cluster3 constituted the outgroup of Cluster2, Cluster4, and Cluster5. In addition, Cluster1 (comprising only RO3) was strongly separated from the other group, constituting the outgroup of all the other clusters.

Pairwise F_{st} values between populations within separate clusters were relatively homogenous and p values were significant for all pairs of populations (Fig. 8.). Inside the two largest groups, Cluster2 and Cluster5, values varied between 0.015 and 0.023. The largest variance among populations was within Cluster4, where the minimum was 0.021 and the maximum was 0.027. Except for the outlier RO3 (the only member of Cluster1), the largest level of differentiation was between the populations of Cluster3 (Western Balkan group) and Cluster4 (Eastern Balkan group), which was in accordance with their geographic distance. The smallest difference was in general among the populations of the two largest groups, the Pannonian (Cluster5) and the Central Balkan (Cluster2) group.

Genetic structuring of populations across a species' range is often

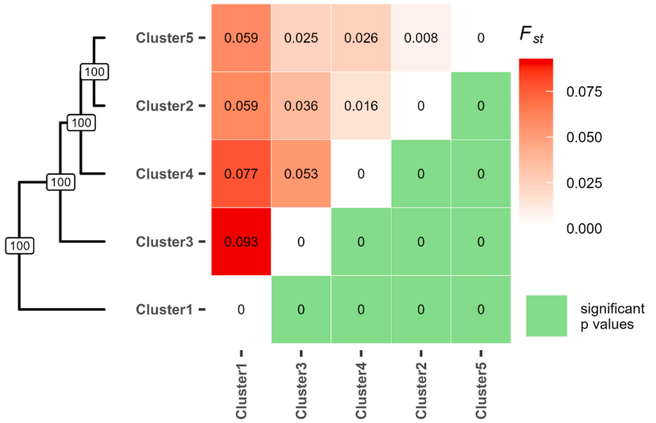

Fig. 7. Heatmap of between cluster pairwise Fst and their corresponding *p* values calculated in Arlequin using 1000 iterations.

associated with adaptive differences among genetic groups, driven by differential selection imposed by varying climatic and site conditions. Consequently, analysis of loci under selection can provide valuable insights into ongoing adaptive processes and help identify the environmental factors that most strongly drive selection.

Using the PCAdapt approach, 14 loci were identified as putatively under selection (Fig. 9a), whereas the F_{st}-based OutFLANK method detected 12 outlier loci (Fig. 9b). Altogether, eight loci were common to both approaches (659161_195, 786271_29, 1124928_81, 1128564_158, 1237384_195, 1799778_309, 2207542_151, 4127820_99), locating on chromosomes 2, 3, 4, 5 and 12 (Table 4).

Based on BlastN and BlastX searches, most matches corresponded to accessions from *Q. suber*, the closest relative of the study species with a well-annotated reference genome (Table 5). Two RAD loci (786271 and 4127820, respectively) were associated with uncharacterized annotations: one matching an uncharacterized protein-coding region and the other an uncharacterized ncRNA. All remaining loci matched protein-coding genes or regions involved in gene expression regulation. Most loci showed high percent identity and low E-values, indicating high similarity between the query sequences and the corresponding database accessions. However, for RAD loci 1124928 and 1237384, low query coverage made these matches uncertain. Only RAD locus 1799778 exhibited low percent identity; for this locus, a significant hit was obtained only by BlastX, while BlastN returned no significant matches.

The LFMM analysis identified two significant genotype–environment associations (Table 6), both involving tempPC2: one with SNP 1124928_81 and the other with SNP 1128564_158. The predictor tempPC2 was primarily driven by the ENVIREM variables Continentality and PETWettestQuarter, as well as the WorldClim variables Bio7 (temperature annual range) and Bio4 (temperature seasonality), together accounting for 45.7 % of the total variance explained by this PC.

4. Discussion

At the species level, genetic diversity, as measured by various indices such as observed heterozygosity, nucleotide diversity, and allelic richness, indicated a relatively high level of diversity in the sampled Turkey oak populations. Although comparisons with other studies were challenging due to differences in sampling regions, genotyping methods, and data processing, Turkey oak populations exhibited slightly lower diversity values than those on sessile oak and pedunculate oak populations sampled in the same regions (Degen et al., 2021; Tóth et al., 2021). In our interpretation, this slight deficit in genetic diversity may have been

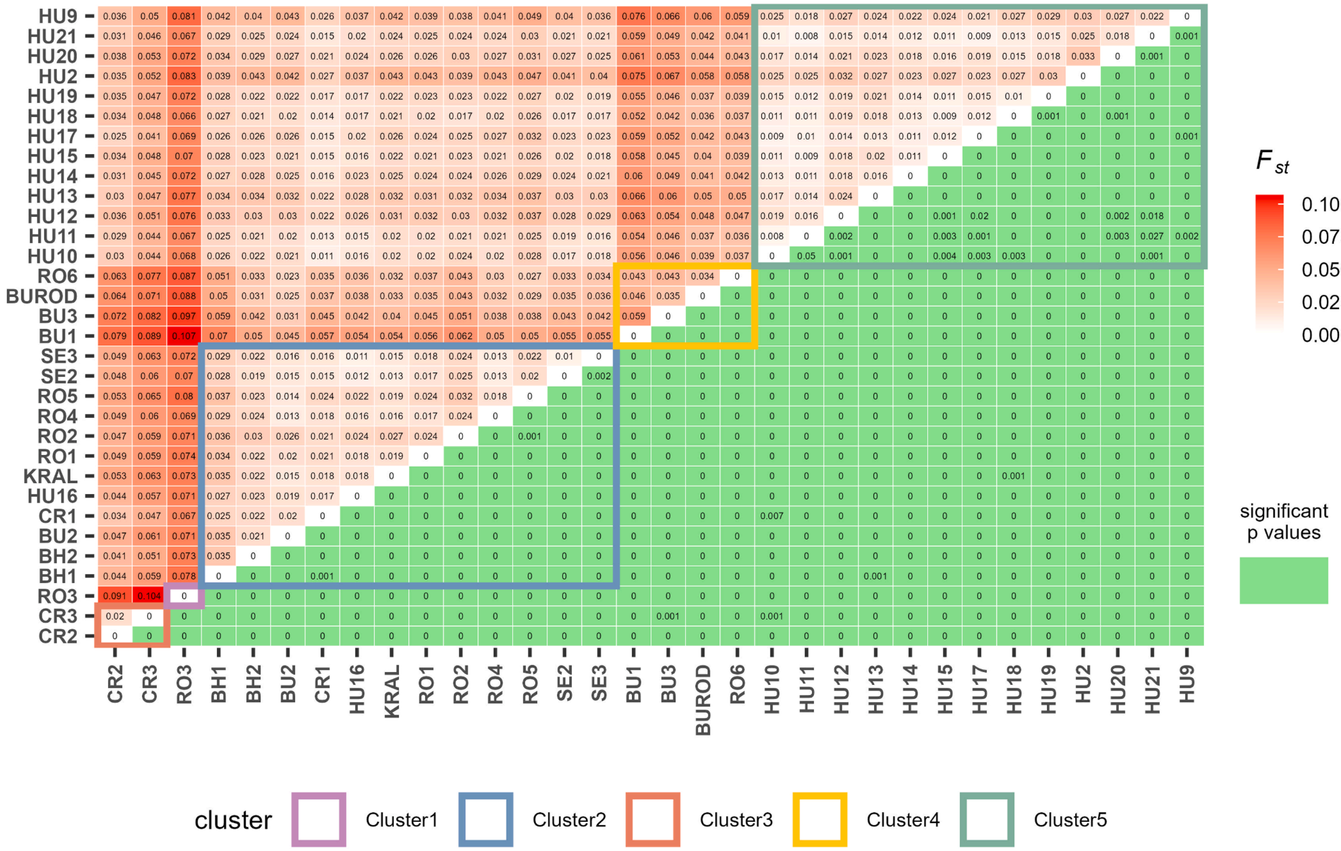

Fig. 8. Heatmap of between-population pairwise Fst and their corresponding *p* values calculated in Arlequin. Colored squares represent populations belonging to genetic clusters defined by Tess3.

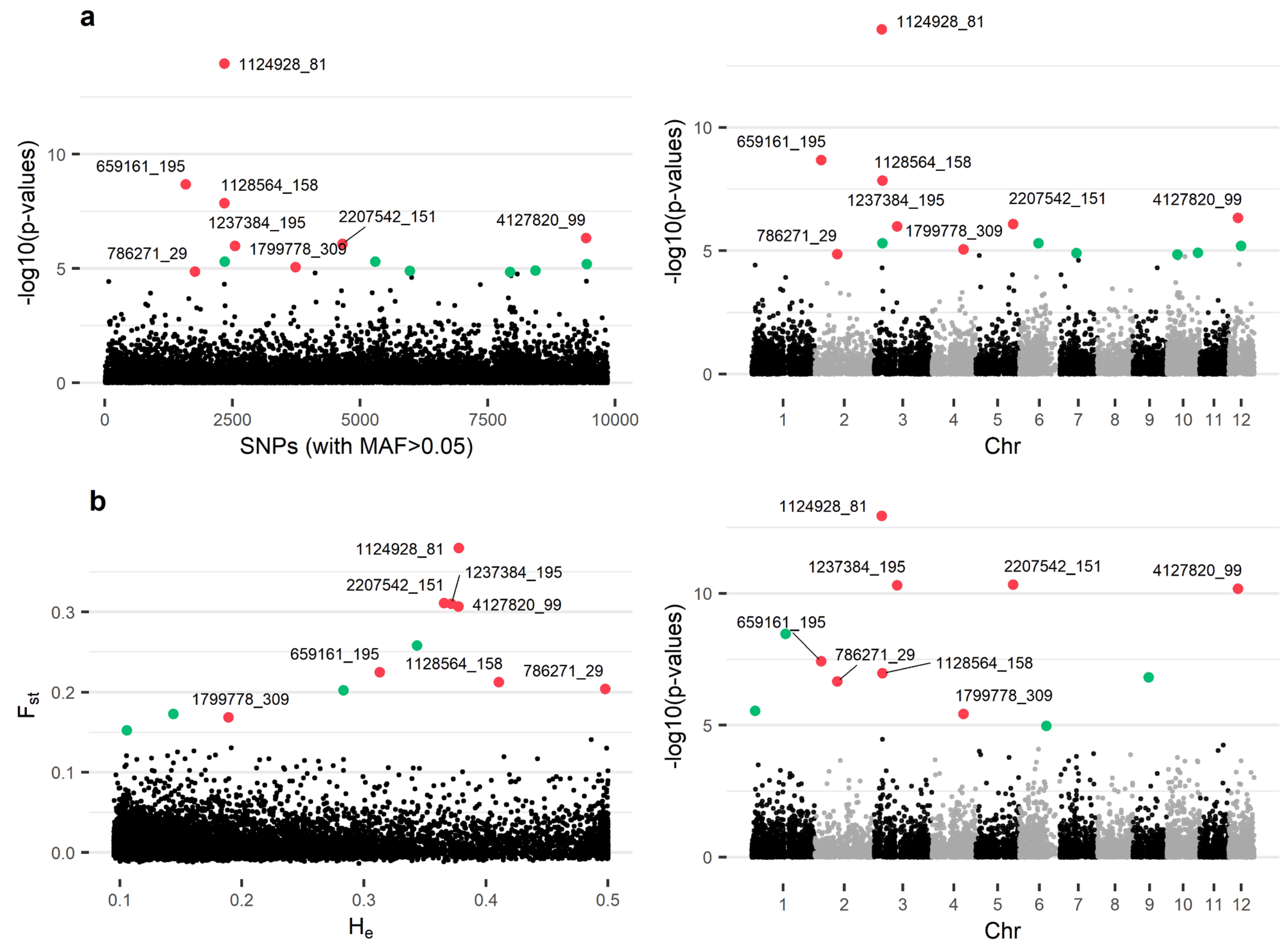

Fig. 9. Results of outlier detection using the PCAdapt (a) and OutFLANK (b) approaches. Commonly detected outliers are labeled and marked in red, while SNP loci marked with green are significant for the specific approaches.

Table 4
Summary of outlier SNP markers commonly detected by the PCAdapt and OutFLANK methods.

SNP	PCAdapt			OutFLANK		
	p-value	*q*-value	-Log10(*p*-value)	*p*-value	*q*-value	-Log10(*p*-value)
659161_195	2.06E-09	1.01E-05	8.69E+ 00	3.75E-08	5.97E-05	7.43E+ 00
786271_29	1.36E-05	9.87E-03	4.86E+ 00	2.16E-07	2.29E-04	6.67E+ 00
1124928_81	1.05E-14	1.03E-10	1.40E+ 01	1.15E-13	1.10E-09	1.29E+ 01
1128564_158	1.39E-08	4.56E-05	7.86E+ 00	1.05E-07	1.44E-04	6.98E+ 00
1237384_195	1.01E-06	1.66E-03	5.99E+ 00	4.91E-11	1.56E-07	1.03E+ 01
1799778_309	8.72E-06	8.56E-03	5.06E+ 00	3.70E-06	3.21E-03	5.43E+ 00
2207542_151	8.16E-07	1.60E-03	6.09E+ 00	4.65E-11	1.56E-07	1.03E+ 01
4127820_99	4.61E-07	1.13E-03	6.34E+ 00	6.72E-11	1.60E-07	1.02E+ 01

at least partly the result of limited gene flow with closely related species. Specifically, Turkey oak is the only representative of section *Cerris* in the sampling regions, and hybridization with co-occurring white oaks (section *Quercus*) is unlikely because of genetic incompatibilities. In contrast, frequent gene flow among members of the white oak section and its significant role in the rapid adaptation of oaks have been documented in several studies (Gerber et al., 2014; Leroy et al., 2017, 2020).

By comparison with the diversity indices reported in our recently published data paper, the values observed here were slightly lower, which was most likely a consequence of differences in the filtering parameters used to prepare the raw dataset (e.g., Hardy-Weinberg equilibrium filtering was not applied in the present study).

Populations of oaks and many other woody taxa have characteristic genetic patterns throughout Europe shaped by the ice ages of the Pleistocene (Magri et al., 2006; Petit et al., 2002). This variability among populations is often manifested in specific chloroplast DNA patterns shared between populations in particular parts of the species' range (Bagnoli et al., 2016; Bordács et al., 2002). The geographic distribution of genetic diversity in European tree populations often constitutes characteristic clines oriented from the southern refugia towards the northwest. Although southern populations, located in the area of former refugia, harbor a large amount of species-level genetic diversity, the level of this diversity can be higher in northern populations, where separate genetic groups are admixed (Petit et al., 2003). This was the

Table 5
BLAST search results for RAD loci of outlier SNPs.

Rad loci	SNP	Chromosome ID	Position	Per. Identity	E-value	Query Cover	Accession	Description
659161	659161_195	OY770007.1	10248478	99.82 %	0.00E+ 00	99 %	XM_065781494.1	PREDICTED: *Quercus suber* G-type lectin S-receptor-like serine/threonine-protein kinase CES101 (LOC112012815), transcript variant X4, mRNA
786271	786271_29	OY770007.1	35321527	88.22 %	0.00E+ 00	79 %	XM_050402844.1	PREDICTED: *Quercus robur* uncharacterized LOC126703767 (LOC126703767), mRNA
1124928	1124928_81	OY770008.1	12040450	98.22 %	3.00E-75	33 %	XM_065764603.1	PREDICTED: *Quercus suber* inactive protein kinase SELMODRAFT_444075 (LOC112039011), transcript variant X2, mRNA
1128564	1128564_158	OY770008.1	12755862	99.73 %	0.00E+ 00	100 %	XM_065761319.1	PREDICTED: *Quercus suber* eukaryotic peptide chain release factor subunit 1–3 (LOC136062361), mRNA
1237384	1237384_195	OY770008.1	35364710	100.00 %	0.00E+ 00	20 %	XM_050430834.1	PREDICTED: *Quercus robur* ABC transporter C family member 13 (LOC126725851), transcript variant X3, mRNA
1799778	1799778_309	OY770009.1	48511475	37.61 %	2.00E-15	91 %	KAK9989376.1	hypothetical protein SO802_029615 [*Lithocarpus litseifolius*]
2207542	2207542_151	OY770010.1	57594196	99.04 %	1.00E-154	61 %	XM_065776610.1	PREDICTED: *Quercus suber* paired amphipathic helix protein Sin3-like 4 (LOC112008577), mRNA
4127820	4127820_99	OY770017.1	14286973	99.58 %	0.00E+ 00	100 %	XR_010626026.1	PREDICTED: Quercus suber uncharacterized LOC136064412 (LOC136064412), ncRNA

Table 6
Results of LFMM analysis on outlier SNP loci (Benjamini-Hochberg–adjusted *p*-values for all predictors).

SNP	tempPC1	tempPC2	tempPC3	precPC1	precPC2	precPC3
659161_195	0.7124	0.5765	0.9353	0.8809	0.7993	0.8167
786271_29	0.9184	0.5765	0.9300	0.8809	0.7993	0.9124
1124928_81	0.7124	0.0160*	0.8564	0.8809	0.7993	0.8050
1128564_158	0.7124	0.0160*	0.9300	0.8809	0.7993	0.8050
1237384_195	0.7124	0.5765	0.2904	0.9326	0.2958	0.8050
1799778_309	0.8704	0.5765	0.9353	0.9196	0.7993	0.8167
2207542_151	0.7124	0.5765	0.2904	0.9326	0.2958	0.8050
4127820_99	0.7124	0.5765	0.2904	0.9326	0.2958	0.8050

* significant (FDR<5 %)

first time that this pattern was detected in the nuclear DNA of Turkey oak populations. As our spatial diversity maps clearly indicated, the level of diversity gradually increased from the southwestern and southeastern populations toward the northwest. The highest levels of diversity was observed in populations of the western part of the Carpathian Basin, while the lowest levels were detected in southeast Bulgaria and southwest Croatia.

This surplus of genetic diversity in northwestern populations could be explained by the population structure detected. Specifically, all sampled populations clustered into five genetic groups, with a large contact zone in the middle of the Carpathian Basin, where the Pannonian and Central Balkan groups admixed. According to this, similar to local white oaks (Bordács et al., 2002; Petit et al., 2003), the Carpathian Basin appears to act as a melting pot of distinct gene pools of Turkey oak originating from separate refugia in the southwestern and southeastern Balkans.

The detected genetic groups correspond closely to those identified in a previous study using chloroplast markers covering the species' entire range (Bagnoli et al., 2016). We observed the same initial east-west differentiation among populations. Additionally, our analysis further subdivided the eastern and western groups into two smaller clusters. According to PCA results, populations of Cluster5 (Pannonian group) were closely related to the members of Cluster3 (populations from southeast Croatia), supporting the southwest Balkan origin of Turkey oak populations in the central and western part of the Carpathian Basin. In contrast, populations on the eastern side of the Carpathian Basin belonged to the Central Balkan group. These findings supported a postglacial colonization of the Carpathian Basin via western and eastern routes originating from western and central/eastern Balkan refugia, respectively.

In addition, there was an important difference between our results based on nuclear markers and the study by Bagnoli et al. (2016), which was based on chloroplast markers. Specifically, we observed a clear admixture zone between the sampled populations of Cluster 5 and Cluster 2, whereas the geographic distribution of chloroplast haplotypes showed no overlap. This suggested that the observed admixture may have primarily been mediated by pollen flow rather than seed dispersal.

In addition to the central part of the Carpathian Basin, another admixture zone occurred between the Central Balkan and the Eastern Balkan groups across northwest Bulgaria and southeastern Romania. Furthermore, population BH2 in the southeast part of Bosnia and Herzegovina exhibited an almost equal mixture of Cluster2, Cluster3, and Cluster4. Apart from three populations (BU1, CR1, and RO3), some degree of admixture was detected in all populations. This pattern suggested that the differentiation among clusters may be relatively recent and/or that ongoing effective gene flow may exist between these groups.

Population HU16 may have represented an illustrative example of the effectiveness of the marker system applied to trace the origin of reproductive material. Although our initial objective was to include only stands of local origin, the genetic structure of this population suggested that it was likely non-autochthonous. Given that the stand was over 120 years old and had probably undergone several cycles of coppice regeneration, determining its exact origin remained challenging. Nevertheless, the proportions of genetic clusters identified through cluster analysis indicated an origin within the Central Balkan group. Notably, its genetic composition was most similar to that of population RO2 in Transylvania, a region historically serving as a major source of oak reproductive material for Hungary over the past centuries.

Another outlier was the population RO3 from multiple points of view. This stand was located in northwest Romania, at the northern limit of the species' range. In this area, there were no extensive stands of Turkey oak; populations were rather sporadic due to the limited number of suitable sites for the species (partly as a consequence of deforestation due to extensive pasturing). This stand was situated on an east-facing slope at approximately 400 m altitude near the eastern chains of the Carpathian Mountains. According to the location and local climatic conditions, this site was probably on the cold edge of the species' niche.

Regarding genetic attributes, this population exhibited the lowest diversity values for almost all indices (population gene diversity, allelic richness, nucleotide diversity). In addition, the lowest but positive inbreeding coefficient indicated a slight excess of heterozygote loci relative to the other populations. Considering these genetic attributes, site conditions, and the sporadic occurrence of the stand, RO3 was probably a founder population, in which genetic diversity may have decreased due to the founder effect (Hampe et al., 2013). Most probably, this founder effect not only reduced the allelic diversity but also changed their frequency and the ratio of homo- and heterozygous loci. As a consequence, this was sufficient for the implemented approaches to separate this population into a distinct cluster (Cluster1) and indicate the largest F_{st} values compared to the other populations.

However, another probable scenario for this phenomenon was that potential sequencing artifacts or sampling effects (because of the small population size) were distorting the results of the genetic diversity indices and population structure. Therefore, to validate the potential founder event a detailed demographic analysis would be important in the future. For this reason, the samples of RO3, together with other outlier samples identified in the population structure analyses, were excluded from the association analyses to prevent potential sequencing artifacts from affecting the results. It was also notable that in the PCA, variance among the individuals of RO3 was much larger than in any of the other populations. While this could have been indicative of genetic drift, sequencing errors cannot be ruled out as a possible explanation.

Although the genetic patterns observed in RO3 may have partly reflected methodological artifacts, ecologically marginal populations at the edge of a species' range are often of particular interest from both evolutionary and conservation perspectives. They may contain unique genetic variants or adaptive potential relevant under future environmental change (Rehm et al., 2015). Therefore, further investigation into the genetic background of RO3 may provide valuable results in the future.

According to F_{st} values, the Pannonian and the Central Balkan groups were most closely related. Most probably, it was because of the extensive gene flow between the two groups, supported by the cluster analysis. However, this contact appears relatively recent, as fossil pollen dating confirms the presence of Turkey oak in the central part of the Carpathian Basin only from approximately 3000–5000 years BP [Neotoma Dataset 4486 (DOI:10.21233/k0tg-pb80), 4487 (DOI: 10.21233/wn8a-n079), 4488 (DOI:10.21233/vr8r-d168) (Nagy-Bodor et al., 1995)]. As another scenario, this contact might have been established multiple times in the past, when populations expanded from the refugia during interglacial times.

Furthermore, within-population differentiation was lowest in the Pannonian and Central Balkan groups, which further supported the recent expansion of these groups. In contrast, populations in the Eastern Balkan group exhibited the highest genetic differentiation. This suggested that the Eastern Balkan refugium was fragmented, with populations surviving glacial phases in multiple smaller refugia, rather than a single, continuous area. Additionally, the geographically structured landscape of the Eastern Balkans may reduce gene flow effectiveness, thereby maintaining the genetic differences accumulated in populations from these smaller refugia.

While the analyses of population structure and genetic differentiation revealed clear spatial patterns among populations, results of outlier detection further suggested that adaptive differentiation was also present. Both PCAdapt and OutFlank proved effective in identifying loci potentially under selection. Altogether, eight SNP loci were consistently detected by both approaches, located on five different chromosomes.

According to BLAST searches, SNP locus 659161_195 was located in a coding region responsible for the production of G-type lectin S-receptor-like serine/threonine-protein kinase, which has been identified as a positive regulator of plant tolerance to salt stress (Sun et al., 2013). Similarly, SNP 1237384_195 was located within the ABC transporter C family member 13 gene, which was previously associated with salt and drought tolerance in pear (Kou et al., 2024). However, this latter annotation is considered unreliable due to the low query coverage. Another SNP detected under putative selection, SNP 2207542_151, was located in a region encoding the paired amphipathic helix protein Sin3-like 4. Homologs of this protein in *Arabidopsis* are involved in chromatin-mediated transcriptional repression, influencing key developmental processes such as seed dormancy and flowering transition.

However, none of these loci were found to be significant in the genotype–environment association analysis. This suggests that, although these loci may have indeed been under selection, the potential drivers of selection were not among the bioclimatic variables included in the analysis. For SNPs 659161_195 and 1237384_195, which are potentially involved in salt stress responses, the inclusion of soil-related variables may help reveal significant associations in future studies.

Only two adjacent loci were found to be significant in the association test. Both markers were significantly associated with the same predictor variable, tempPC2. In this principal component, the most important climate variables were related to temperature fluctuations and extremes. The RAD locus including the SNP locus 1124928_81 was matched with the coding region of the inactive protein kinase gene SELMODRAFT_444075. However, due to low query coverage this match was considered uncertain. SNP locus 1128564_158 was located in a gene encoding the eukaryotic peptide chain release factor subunit 1–3 (eRF1–3). The eRF1–3 is a key factor in translation termination, helping plants adapt to temperature shifts by precisely stopping and restarting protein synthesis to protect cells from heat-induced damage (Smith et al., 2025).

An important conclusion from these analyses was that there was no evidence of significant selection processes linked primarily to precipitation-related predictors. In contrast, in our previous study on sessile oak populations from the same region (in some cases from the exact same locations; Tóth et al., 2023), we found that drought-related factors were the primary drivers of selection. These new results on Turkey oak suggest that these coexisting species may experience different selective pressures even in the same or highly similar environments. Accordingly, assisted migration strategies for these species could benefit from considering these differences in adaptive patterns.

However, additional association tests using different approaches and incorporating new environmental data sources would be important to gain a more detailed and robust understanding of ongoing adaptation in Turkey oak populations.

From a population genetic point of view, these results also allowed us to draw some conclusions for practice. Firstly, our analyses detected the differentiation of populations into distinct genetic groups covering specific parts of the species' range. Consequently, most probably, the traditional transport of oak reproductive material (including also Turkey oak acorns) had already introduced non-autochthonous gene pools into various parts of the study area. For instance, the HU16 population in this study was most likely an example of such a long-distance introduction, as its genetic composition was most similar to a population in Transylvania, which is a traditional source region of oak reproductive materials for Hungary. These non-autochthonous gene pools could differ from the local not just in neutral but also in adaptive traits. Therefore, monitoring the performance of reproductive material from long-distance sources may lead practitioners to valuable conclusions about specific source regions. Particularly, when it is planted along with local reproductive materials, allowing for direct comparisons.

For old, planted stands (like HU16), where the origin is often unknown, next-generation marker technologies may offer opportunities to at least approximate their source regions. If this approximation is possible, these stands could provide invaluable information about long-term adaptability in a given environment, serving as a primitive but accessible alternative to the otherwise lacking provenance trials for this species. Although this would not replace conventional common garden experiments, it could help save time, which is one of the main limitations of such experiments. Therefore, in terms of forest management, monitoring of old, planted stands may, in some cases, be as beneficial as monitoring natural populations.

In the context of genetic diversity, we found characteristic patterns in its geographic distribution. Specifically, diversity increased from the southeast and southwest toward the northwest, with the highest levels observed in populations from the central and western parts of the Carpathian Basin. This region is characterized by the most continental climate within the study area, and many Turkey oak stands here are located at the species' xeric limit. These populations are strongly affected by climate change, mainly through prolonged droughts. In line with this, previous studies have projected a range shift toward higher altitudes (Illés and Móricz, 2022; Móricz et al., 2013). In this context, rich genetic diversity could play a key role in facilitating local adaptation.

Traditionally, oak reproductive material has been transported from the east and southeast toward the northwest within the study region, opposite to the observed diversity gradient. In practical terms, this means that seeds from areas with lower genetic diversity are often introduced into regions where diversity is already higher. However, this does not necessarily indicate a lower adaptive potential. Rare gene variants that confer tolerance to limiting conditions, such as drought, may be unique to – or more frequent in – southeastern populations, where other alleles may have been selected against. This process can result in reduced overall diversity, despite the presence of locally adaptive traits.

Nevertheless, unlike in sessile oak, our genotype-environment association analysis did not detect direct links between selective loci and drought-related climatic variables. In contrast, the significant associations with temperature-related variables suggested that temperature conditions were more likely the primary limiting factors for Turkey oak, rather than limited water availability. Otherwise, this was in line with the well-known thermophilic character of the species.

Additionally, these findings also highlight for practitioners that local stands, such as those in the Carpathian Basin, harbor relatively high levels of genetic diversity. In certain cases, this diversity, if properly managed, may be sufficient to support adaptation without the need to introduce non-autochthonous reproductive material. Management strategies that rely on local genetic resources can enhance adaptive potential, for example, by increasing the efficiency of natural selection. In optimal cases, regeneration from local seed sources can provide tens of thousands of genotypes per hectare, far exceeding the genetic diversity represented by the few thousand saplings typically used in planting. This broader genetic base can increase adaptive capacity. Additionally, using multiple offspring generations may be advantageous, considering fluctuations in mating patterns over time. In some situations, shortening rotation time could also increase the number of generations over time, accelerating natural selection and, in turn, adaptation. In this context, Turkey oak may have great potential due to its relative drought tolerance and frequent masting.

5. Conclusions

In this study, population genetic analyses of Turkey oak revealed characteristic diversity patterns in the Central and Southeast European region. Similar to other oak species native to the study region, a clear diversity cline was identified, showing a northward-increasing diversity gradient.

These results underscore the importance of integrating population genetic investigations into forestry adaptation programs. Notably, the observed diversity gradient runs counter to the planned direction of future reproductive material transfers. Moreover, the higher genetic diversity observed in northwestern populations could provide a strong basis for adaptation in local stands. Consequently, local reproductive material may also be valuable for climate-adaptive reproductive material sourcing in forestry, and it was not necessarily the case that southern populations were the optimal seed sources in all situations.

Analyses of loci under selection and their associations with environmental variables further highlighted the importance of assessing adaptive potential at the species level when planning adaptation programs. Specifically, the genomic loci identified as potentially under selection in Turkey oak differ from those previously reported in sessile oak, sampled from the same or nearby locations. The results suggested that Turkey oak populations in the study region might have been more affected by temperature fluctuations and extremes, unlike co-occurring sessile oak populations, which were previously found to be primarily influenced by water availability.

Based on our findings on genetic diversity and ongoing adaptation challenges, Turkey oak did not show signs of genetic decline in the study region. In fact, the species exhibited the highest population-level diversity in the area with the most extreme continental climate.

Considering that the species is currently expanding its range in this region, is thermophilic, and possesses high genetic diversity, Turkey oak appears to be a particularly valuable species for forestry adaptation in Central Europe.

CRediT authorship contribution statement

Klára Cseke: Writing – review & editing, Supervision, Resources, Methodology. **Zoltán A. Köbölkuti:** Writing – review & editing. **Csilla É . Molnár:** Resources. **Attila Benke:** Writing – review & editing, Supervision, Resources, Project administration. **László Nagy:** Writing – review & editing, Supervision, Resources, Methodology. **Botond B. Lados:** Writing – original draft, Visualization, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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

During the preparation of this work the author(s) used ChatGPT (OpenAI) in order to improve language and readability. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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.

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