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11TH HARDWOOD CONFERENCE PROCEEDINGS

Róbert Németh, Christian Hansmann, Holger Militz, Miklós Bak, Mátyás Báder

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Editors: Róbert Németh, Christian Hansmann, Holger Militz, Miklós Bak, Mátyás Báder

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Uncovering genetic structures of natural Turkey oak populations to help develop effective climate change strategies for forestry

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Keywords: *Quercus cerris* L., ddRAD-seq, SNP, Balkan Peninsula, population genetics, reference mapping, cork oak

ABSTRACT
Turkey oak (*Quercus cerris* L.) is a widespread species of the genus *Quercus* section *Cerris*, distributed from central and southeast Europe to Asia Minor. The species has long been known for its enormous phenotypic-genotypic variability and extreme adaptability. Throughout its vast distribution range, Turkey oak occupies countless ecological niches with very different site conditions. According to the last projections, climate change is putting high pressure on the natural forest tree populations to adapt to the rapidly changing conditions. Due to their high variability and adaptability, oaks have great potential in forestry climate adaptation efforts. This is particularly true for the Turkey oak. According to recent results of climate-based modelling of species' future distribution, Turkey oak could be a winner of climate change in Central Europe, significantly increasing its distribution and abundance. As a result, its importance in forestry and the wood industry could significantly increase in the future. However, for effective adaptation strategies, it is necessary to collect detailed information on the ecological characteristics of the species, drought adaptation strategies, genic diversity and genetic structure of wild populations throughout its range. Furthermore, as this species has previously played only a marginal role in the wood industry, its growing importance would require more detailed information on its wood properties and alternative uses for its wood. In this study, we used our recently published reference-mapped genome-wide SNP dataset to investigate the genetic diversity and population structure of eight natural Turkey oak populations from Hungary and the Balkan Peninsula. Based on the diversity indices, we found that the studied population carried a relatively high amount of genetic diversity. According to various clustering approaches (fastStructure, PCA and DAPC), the studied populations were divided into four genetically distinct groups, corresponding to two Balkan, one Hungarian and one ambiguous group. The genetic isolation of these groups was found to be statistically significant and further validated by Barrier analysis, which revealed significant gene flow barriers between clusters. According to our results, Balkan populations appear to be genetically more diverse and structured, and therefore, wild populations of this biogeographical region are promising for further studies of the species' adaptation to climate change. In addition, the genetic consistency of the Hungarian populations may indicate common refugial origin. On the other hand, the outlier ambiguous group formed by one Hungarian population is probably a legacy of a historical long-distance human-assisted movement of reproductive material. In conclusion for practice, may be an important question for future studies whether strong genetic structuring of Turkey oak populations is also manifested at the phenotypic level, for instance in different stem quality and/or wood properties of genetic groups.

INTRODUCTION

Changing environmental conditions is both challenging for the forestry and wood industry sectors. For forestry, more extreme site conditions, new pests and diseases are increasing the risk of mortality in forest stands. As part of the natural adaptation of forest tree species and active forestry adaptation efforts, the composition of species in natural and planted stands could change in the future (Bolte et al. 2009). Based on climate projections for the central European region, especially for the Carpathian basin, dramatic changes are expected in site conditions and as a consequence in the species composition of natural forest stands (Buras and Menzel 2019). Thus not only the wood quality is expected to decrease, but the species of primary input material for the wood industry could also change. Accordingly, forests' economic returns may decrease both for forestry and the wood industry (Hanewinkel et al. 2013).

According to the results of climate projections, whereas some tree species are expected to decrease its distribution and abundance, a few species are expected winners of climate change in the Central European region, such as Turkey oak (*Quercus cerris* L.), pubescent oak (*Quercus pubescens* Willd.). or silver linden (*Tilia tomentosa* Moench) (Thurm et al. 2018). However, these are mainly species which had formerly only a secondary role in the wood industry or were not processed at all. Currently, it is an urgent question both in forestry and wood industry how these species are inserted into the applied technologies.

As a member of high-potential alternative forest tree species, Turkey oak may significantly increase its role in forestry in the future. Due to its relatively high drought tolerance and masting not as hectic as white oaks, Turkey oak may be a promising alternative option for forestry. Throughout its vast distribution range, from the Italian and Balkan peninsulas to Asia Minor, the species occurs in a wide variety of habitats, demonstrating its strong ecological plasticity. According to the most recent results of population genetic studies, Turkey oak carries a relatively high genetic variability and has a strong genetic structure through the distribution range (Özer 2014; Bagnoli et al. 2016). On the one hand, this high genetic diversity could be the basis of efficient adaptation but also meant that distinct populations throughout the range could have differing phenotypic behaviour as well (eg. growth, drought tolerance or wood properties).

Although it was previously processed almost exclusively for firewood, it is already the most widespread oak species in Hungary (occupying more than 200 000 ha) and may increase its area in the coming decades (Illés and Móricz 2022). Thus its wood may be available in higher and higher quantity in the future.

In our current study, we examined the genetic diversity and genetic structures in eight natural Turkey oak populations from the Balkans and the Carpathian basin. For population genetic analyses we used our recently published dataset, which is the first high-resolution genomic dataset available for this species generated by double digest restriction site-associated DNA sequencing (ddRAD-seq).

Based on the thousands of genome-wide single nucleotide polymorphisms (SNP) we found strong genetic structures among Hungarian and Balkan populations. Among Hungarian populations (except one outlier stand) we did not find any genetic structuring which may refer to their common refugial origin. Amongst the Balkan stands we found a significant genetic barrier which divides the stands into two genetic groups, which refers to different refugial origins of stands. According to our findings, the strong genetic structures and relatively high genetic diversity of this species are promising for further studies to examine the genetic background of drought adaptation and wood properties.

MATERIALS AND METHODS

For our population genetic analyses, we used our recently published dataset (Lados et al. 2024), which comprises the genomic SNP data of 88 Turkey oak individuals from eight Hungarian and Balkan populations (five from Hungary, two from Bulgaria and one from Kosovo). The dataset was generated by a reduced representation method ddRAD-seq, which allows for an effective sampling of the whole nuclear genome, obtaining thousands of genome-wide single nucleotide polymorphisms (SNP). Our published dataset consists of both *de novo* and reference-mapped SNPs. Reference mapping was carried out by using the cork oak (*Quercus suber* L.) genome (Ramos et al. 2018), as this species is the closest relative of Turkey oak which has a reference genome available. In the course of our current study we used the reference mapped SNP data (containing 26 059 genome-wide SNPs) for population genetic computations.

For basic population genetic analysis, we used the "adegenet" (Jombart and Ahmed 2011), "pegas" (Paradis 2010), "hierfstat" (Goudet and Jombart 2022) and "poppr" (Kamvar et al. 2014) packages in the statistical software R (R Core Team 2022). First, because only preliminary filtering was carried out on the raw dataset, to obtain reliable population genetic inference, we applied careful filtering by using the "missingno" function of the "poppr" package, removing any loci with missing data more than 5% and then genotypes with more than 5%. After that, we also filtered out those loci that are significantly out of Hardy-Weinberg equilibrium (HWE; $p<0.05$) using the "hw.test" function with 1000 bootstrap resampling in the package "pegas" to estimate HWE for every locus. Finally, 18 584 loci were discarded as contained missing values greater than 5%, three genotypes had more than 5% missingness (QCER-HU2-9, QCER-KO1-10, QCER-KO1-2) and 1110 loci were significantly out of HWE. After filtering, 6359 loci were kept for further analysis.

To compute basic population genetic indices we used the "basic.stat" and "allelic.richness" functions in the package hierfstat and "private_alleles" functions in "poppr". The per loci values were averaged or summed (for private alleles) over populations.

During the investigation of population structure, we applied different statistical approaches. The Bayesian clustering program fastStructure was implemented with 100 cross-validation. In addition, we also used principal component analysis (PCA) implemented in "ade4", the discriminant analysis of principal components (DAPC) implemented in "adegenet", and the analyses of molecular variance (AMOVA) also implemented in "adegenet" to further validate the results of fastStructure. Significance testing in AMOVA was carried out by using "randtest" function in "ade4" with 999 repetitions.

Finally, we also examined the existing geneflow barriers among populations under study, using Barrier v2.2 program (Taberlet et al. 1998). To obtain bootstrap values for the barriers, we implemented a custom R code to generate 1000 bootstrap F_{st} matrices. Each matrix was generated by using the "dist.genepop" function in "adegenet" to compute pairwise F_{st} between populations.

RESULTS AND DISCUSSION

Results

Based on the population genetic indices computed, the eight populations under study show relatively small differences in diversity, excluding the HU1 population (Table 1). Although the number of sampled individuals changes over populations which not favour comparisons, heterozygosity values show an interval from 0.222 to 0.250 across populations, with a gentle excess of homozygotes suggested by the positive values of the inbreeding coefficient (except BU1 and HU1 populations with negative values). In addition, the slightly higher values of the allelic richness suggest a higher number of alleles per locus in Hungarian populations than in Balkan ones.

As for the exceptions, in the case of the number of private alleles, there is an outlier among the studied populations, the HU1. Only this Hungarian population from Zselickisfalud carries private alleles, 18 in number. Another exception is that the HU1 and BU1 populations have an excess of heterozygosity based on the negative values of the inbreeding coefficient.

Table 1: Population genetic indices of the examined populations (where Pop=populations ID, n=number of sampled individuals, H_o=observed heterozygosity, H_s=gene diversity, N_p=number of private alleles, A_r=allelic richness, F_{is}=inbreeding coefficient, CI=95% confidence interval for mean F_{is})

Pop	*n*	H_o	H_s	N_p	A_r	F_{is}	CI	
BU1	10	0.229	0.225	0	1.676	-0.012	-0.025	-0.005
BU2	10	0.228	0.235	0	1.730	0.023	0.023	0.043
KO1	8	0.224	0.230	0	1.712	0.019	0.018	0.039
HU1	12	0.250	0.238	18	1.718	-0.034	-0.062	-0.044
HU2	12	0.230	0.238	0	1.735	0.021	0.024	0.042
HU3	8	0.235	0.239	0	1.739	0.006	0.007	0.027
HU4	12	0.236	0.240	0	1.745	0.012	0.010	0.028
HU5	13	0.236	0.241	0	1.745	0.019	0.015	0.030

The result of the analyses of principal components shows significant structuring of populations (Figure 1). The first principal component accounts for 3.87%, the second for 2.85% of the total variance, dividing the eight studied populations into four genetic clusters. As for the four clusters, five individuals of BU1 built their own group separating from the two other Balkan populations. BU2 and KO1 build a second Balkan group, and HU2, HU3, HU4, and HU5 build a consistent Hungarian group together with three individuals of HU1. Finally, nine individuals of the HU1 population build a fourth strongly differentiating group. As the separation of BU1 from the other Balkan populations is mainly along the second principal component but HU1 separating from the Hungarian populations mainly along the first principal component, it seems the differentiation of HU1 is more pronounced than BU1.

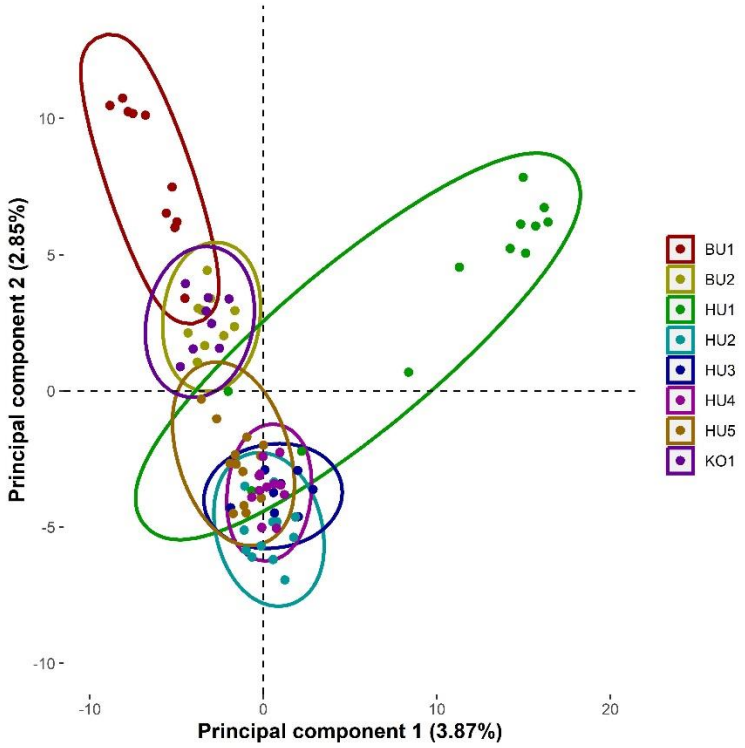

Figure 1: Principal component analyses for the 85 individuals of the eight populations

In another approach, the Bayesian clustering program fastStructure suggests only three genetic clusters (Figure 2a). However, based on the admixture pattern that appears in the BU2 and KO1 populations, these are considerable as a slightly separating group from BU1. With this consideration, similar to the results of the principal component analyses, we identified four genetically consistent groups. The first group is composed of the individuals of BU1, the second comprises BU2 and KO1, the third is all the Hungarian ones except HU1 and the fourth is a strongly separating group composed of HU1 alone.
To support the results of the latter analyses, we also carried out the discriminant analyses of the principal components (DAPC). As Figure 2b shows, it suggests a similar population structure to the latter analyses with a more pronounced separation of BU1 from the group of BU2 and KO1 populations.
The results of AMOVA (Table 2) confirm significant population and cluster level differentiation, both the clusters built by fastStructure and DAPC. Cluster level variation accounts for 2.97% of the total variance for fastStructure and 3.60% for DAPC.

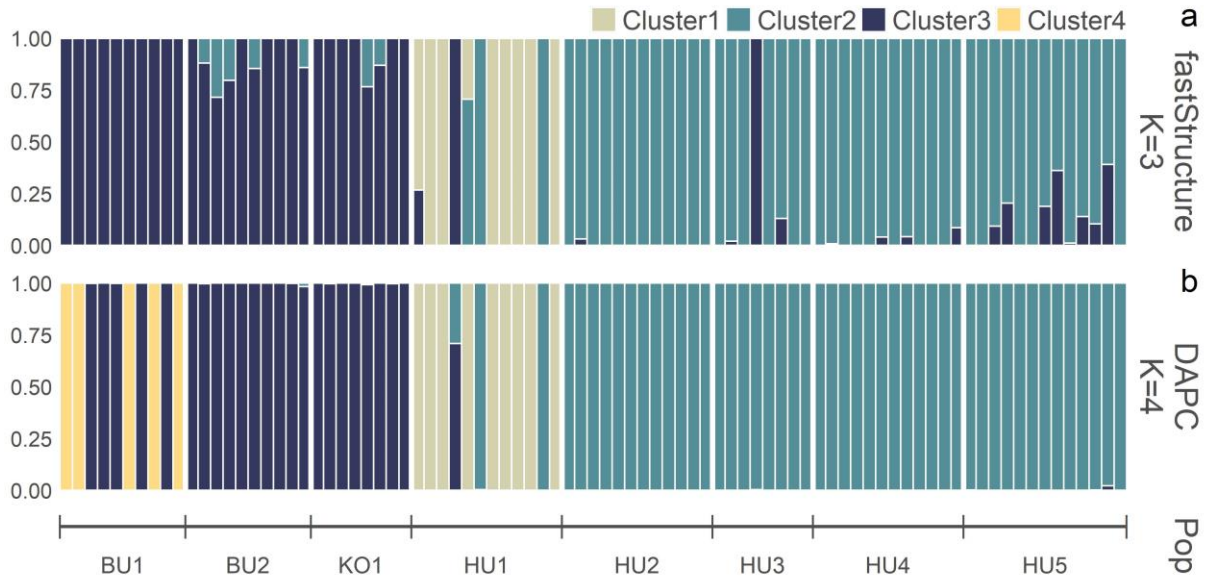

Figure 2: Results of clustering by fastStructure (a) and DAPC (b) (each bar on the plots corresponds to the probability of ancestry of a given individual)

In the final analyses, we examined the existing gene flow barriers among populations with the program Barrier. As a result, we found three significant barriers. Going from east to west, the first barrier divides Balkan populations into two groups separating BU1 from the others. The second barrier is between the Hungarian and Balkan populations, and the third separates HU1 from all the other populations.

Table 2: Analyses of molecular variance (where df=degree of freedom, SS=sum of squares, MS=mean squares, Sigma= variance, %=percentage of the total variance, Φ =phi statistics, *=significant p value on 0.05 significance level)

Source of variation	*df*	*SS*	*MS*	*Sigma*	*%*	*Φ*	*p*
Clustering with fastStructure							
Between clusters	2	8335.11	4167.55	46.41	2.97	0.0297	0.001*
Between populations within clusters	8	14908.88	1863.61	25.45	1.63	0.0168	0.001*
Between samples within population	74	110988.00	1499.84	7.37	0.47	0.0049	0.399
Total	169	260465.00	1541.21	1564.33	100.00		
Clustering with DAPC							
Between clusters	3	11392.84	3797.62	56.41	3.60	0.0360	0.001*
Between populations within clusters	7	13020.82	1860.12	25.36	1.62	0.0168	0.001*
Between samples within population	74	109818.30	1484.03	-0.53	-0.03	-0.0004	0.527
Total	169	260465.00	1541.21	1566.33	100.00		

Discussion

The genetic system of Turkey oak is characterized by a long lifespan, wind pollination, large, mainly gravity-distributed acorns and mass occurrence throughout its vast range. Accordingly, population genetic statistics suggest a relatively high-level extent of diversity (see observed heterozygosity), low level of inbreeding, and large effective population size (eg. clustering methods were unable to separate Hungarian populations, these considerable as a single population). However, for two populations, the number of private alleles and the excess of heterozygotes may suggest pronounced differentiation from the others. Although the number of private alleles detectable strongly depends on the filtering parameters applied to a given dataset, in our study we found such alleles only in the HU1 population from Zselickisfalud, Hungary. The appearance of private alleles only in this population may be a sign that the HU1 population is separating from the other stands. As for BU1, we did not detect any private alleles

(with the filtering parameters applied), however, the excess of heterozygosity may refer to individuals of at least two different genetic groups occur in this stand (as the results of PCA and DAPC show).
Based on the results of multiple clustering approaches the eight populations under study could be separated most likely into four genetic groups. These groups are an admixed southeast Balkan group composed of BU1 (according to PCA and DAPC), a central Balkan group composed of BU2 and KO1, a consistent Hungarian group comprising the individuals of HU2, HU3, HU4 and HU5, and finally a strongly differentiating admixed group composed of HU1. Considering the biogeographic history of the species, the detected population structures may refer to the population genetic effect of the last glacial period, as our results are consistent with the recent findings on the species' plastid diversity (Bagnoli et al. 2016). According to this, genetic groups may represent descendant populations of different glacial refugia. Thus in the case of the studied Balkan populations, our results refer to at least two separate refugia for this region. However, the populations of the Hungarian group may originate from a common refugium as we observed only a low level of differentiation between them. As for the outlier HU1 population, based on the mentioned biogeographic findings, the strong differentiation of this stand does not seem logical. The thing that each clustering approach supported admixture in this population with the members of the other Hungarian stands may refer that this population has no local origin, and this stand may be a result of a historical long-distance reproductive material movement. The reproductive materials of the individuals causing admixture may have come from the neighbouring stands in a natural way or from the original stand that inhabited that area previously.
The Barrier analyses of the gene flow between populations revealed three genetic barriers supported with high bootstrap values. Going from east to west, the first barrier divides Balkan populations into two groups, the second barrier divides Hungarian and Balkan populations, and the third barrier separates HU1 from all the other stands. Considering the locations of the statistically significant barriers, these are consistent with the results of cluster analyses.

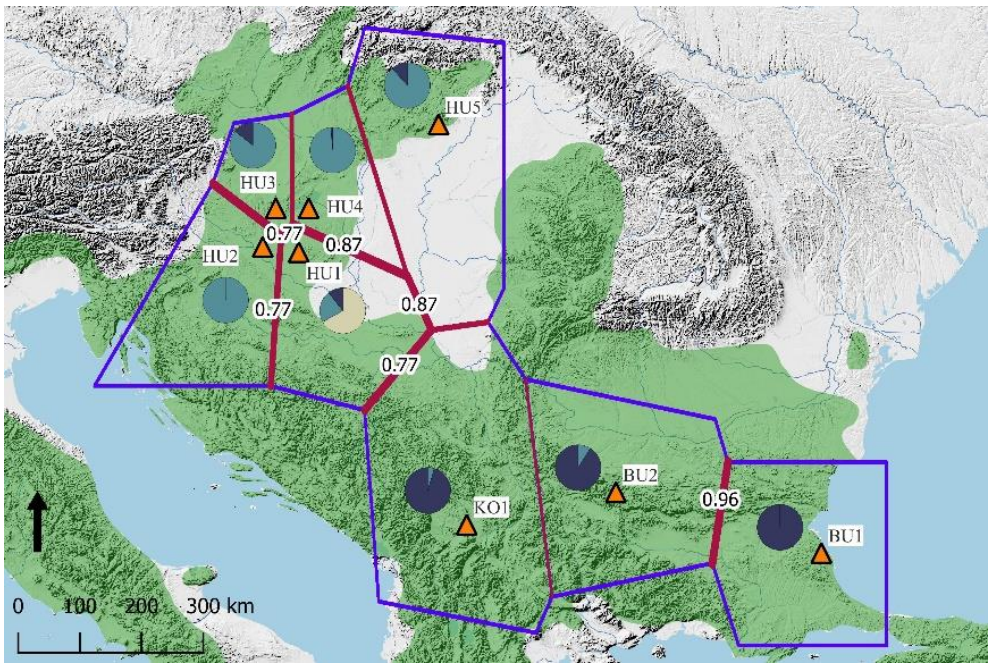

Figure 3: Results of Barrier analyses (red lines are the genetic barriers, bootstrap values on the lines show the support of the given barrier, and piecharts show the genetic structure of populations based on fastStructure clustering approach)

Our AMOVA results support statistically significant cluster and population level differentiation both for the clusters of fastStructure and DAPC. According to the higher percentage of variance on the cluster level, and the composition of Figure 2 (b), in this case, the DAPC approach was more efficient in detecting population structure. The otherwise relatively low percentage of variance on cluster and population levels seems consistent with the species' genetic system.

CONCLUSIONS

In our study, we investigated the population genetic aspects of eight central and southeast European Turkey oak populations. By using our recently published high-resolution genomic SNP dataset generated by ddRAD-seq, we provided deep insight into the species' population structure first time. Population genetic indices computed based on genome-wide data support a relatively high level of diversity of the studied populations corresponding to the species' genetic system. In addition, the occurrence of private alleles and deviation in heterozygosity may be a sign of differentiation and admixture in HU1 and BU1 populations.

According to all clustering approaches implemented, we found strong genetic structures among populations. Four genetically distinct groups were identified, strongly separating Hungarian populations from the Balkan ones. In addition, PCA and DAPC were able to separate the BU1 population from the two other Balkan populations. Interestingly the HU1 population strongly separated from the otherwise consistent Hungarian group. In our interpretation, it may be a legacy of a historical long-distance reproductive material movement. If this is the case, it would be useful to further investigate this stand as this can provide valuable information as a "historical provenance test".

In conclusion for the practice, strong genetic structuring of this species throughout its native range may be manifested not only in neutral traits but also in adaptive ones. Accordingly, in the case of Turkey oak, the geographic origin of reproductive materials may have different effects on several traits influencing the climate adaptation potential, growth traits and wood properties. As Turkey oak could be an alternative for forestry in climate adaptation, it would be important in the future to investigate the genetic background of its adaptation to harsh conditions and the options for the improvement of its wood quality. As we found relatively high genetic diversity coupled with genetic structuring, Balkan populations are promising for further studies on the genetic background of adaptation to changing environmental conditions and genetic traits influencing wood quality. However, as our current dataset has obvious limitations because of the low sample size and the few sampled populations relative to the vast distribution range, in the first step, it would be important to extend this dataset to obtain reliable data for more individuals evenly covering the distribution range.

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