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Population genetic analysis of *Fagus orientalis* with biogeographical notes

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Keywords: genetic diversity, Holocene, microsatellites, Oligocene, Pleistocene, Pliocene, population structure, prochoresis, recolonization, refugia, speciation.

Summary. The genetic structure of 39 populations of oriental beech (*Fagus orientalis*) from the territory of Crimea, the Caucasus, Asia Minor, and Alborz was studied based on the polymorphism of microsatellite, or single sequence repeats (SSR). Tests for isolation by distance (IBD) conducted in the GenePop program showed a high correlation of genetic differences and the logarithm of the geographic distance in units of geographic coordinates at the level of 0.91. Interpopulation genetic differentiation of *Fagus orientalis* (Fst) ranged from 0.01 to 0.67. The putative relationship of the species populations by the area is presented. A possible prochoresis of the ancestors of *F. orientalis* is reconstructed; probable paths of the formation of the modern area of the species are considered, including the effects of glaciation and volcanism in the Caucasus. Along with refugial populations, examples of Holocene recolonization of the highlands of the Greater Caucasus are given. The observed similarity at the upper boundary of the beech belt in different regions of the Caucasian Isthmus indicates parallelism in the development and establishment of high-mountain populations of the species, or repeated colonizations.

Популяционно-генетический анализ бука восточного (*Fagus orientalis*) с биогеографическими комментариями

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Ключевые слова: видообразование, генетическое разнообразие, голоцен, микросателлиты, олигоцен, плейстоцен, плиоцен, повторная колонизация, прохорез, рефугиумы, структура популяций.

Аннотация. Изучена генетическая структура 39 популяций бука восточного (*Fagus orientalis*) с территории Крыма, Кавказа, Малой Азии и Эльбурса на основе полиморфизма микросателлитных повторов (SSR). Тест на изоляцию дистанций, проведённый в программе GenePop показал высокую корреляцию генетических различий и логарифма географической дистанции в единицах географических координат

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на уровне 0,91. Межпопуляционная генетическая дифференциация *Fagus orientalis* (Fst) составила от 0,01 до 0,67. Рассмотрено предполагаемое родство популяций вида по ареалу. Дана реконструкция возможного прохореза предков *F. orientalis*, рассмотрены вероятные пути становления современного ареала вида, включая воздействия оледенения и вулканизма на Кавказе. Наряду с рефугиумальными популяциями рассмотрены примеры голоценовой реколонизации высокогорья Большого Кавказа. Наблюдаемое сходство на верхней границе букового пояса в различных районах Кавказского перешейка указывает на параллелизм в развитии и становлении высокогорных популяций вида, либо повторные колонизации.

Introduction

The distribution area of *Fagus orientalis* Lipsky (oriental beech) within the former USSR covers the entire Caucasian Isthmus (the Greater and the Lesser Caucasus, the northern edge parts of the Armenian Highlands, isolated in Talysh, Mineralovodsky laccoliths, Stavropol Upland, and mountainous Crimea). In addition to Crimea and the Caucasus, it is found on the Alborz Ridge in northern Iran (Sagheb-Talebi, Schütz, 2002; Bijarpasi et al., 2020; Jahdi et al., 2023), in the north of Asia Minor, in the eastern part of the Balkan Peninsula (in Turkey, Greece, and Bulgaria) (Sokolov et al., 1977; Assyov et al., 2012; Müller et al., 2019), and is indicated for Syria (Menitsky, 2012).

Since the preliminary population genetic analysis of *Fagus orientalis* from Crimea and the Caucasian Isthmus (Aliev et al., 2020), geography of samples has been significantly expanded and covered both foothill and high-mountain populations of the species in all regions of the Russian Caucasus, Crimea, as well as the countries of Transcaucasia, Turkey, and Iran.

The validity of *Fagus orientalis* is debatable. Some foreign authors consider it conspecific with the European *Fagus sylvatica* L. (Denk et al., 2001, 2002, 2005), other authors regard it a subspecies *F. sylvatica* ssp. *orientalis* (Lipsky) Greuter et Burdet (Müller et al., 2019). A. A. Kolakovsky (1982) considered that *F. orientalis* is close to *F. sylvatica* and associates with it by gradual transitional forms – *F. taurica* Popl. (Crimean population) and *F. maesiaca* (Malý) Czeczott (Balkan population). Both species are accepted in domestic literature (Menitsky, 2012; Zernov, 2013; Aliyev et al., 2020) and by some foreign authors (Davis, 1982; Assyov et al., 2012; Bijarpasi et al., 2020; Jahdi et al., 2023; Nasiri et al., 2023).

As previously noted (Aliev et al., 2020), European researchers (Denk et al., 2002) also included materials from Turkey, Georgia, and Northern Iran in their genetic analysis of *F. sylvatica* populations. These authors concluded that the high polymorphism of nuclear rDNA in the ITS sequences of the beeches from western Eurasia, together with the observed clinal variation in morphological characters, suggest the presence of only one species, *Fagus sylvatica*, in Europe and Asia Minor. Previously recognized taxa such as *F. orientalis* and *F. moesiaca* should therefore be considered as synonyms of *F. sylvatica*. Among the Eurasian populations studied by these authors (Denk et al., 2005), the populations from Western Georgia (*F. sylvatica* ssp. *hohenackeriana* sensu Shen p.p.) were the most genetically heterogeneous. All the genetic diversity identified among the European and West Asian populations of the beech was found by them in clones from the Mtirala Mount (Adjara, Georgia) and the village of Tezami (Tbilisi National Park, Georgia) (Denk et al., 2005).

Based on the genetic and morphological analysis of 14 populations of the beech from Greece, Turkey, and Germany (Müller et al., 2019), one population of hybrid origin was identified in northeastern Greece. It was the hybrid between two subspecies co-occurring in southeastern Europe – *Fagus sylvatica* ssp. *sylvatica* L. and *F. sylvatica* ssp. *orientalis* in the known contact zone. The study showed very low genetic differences within the populations of two subspecies: *F. sylvatica* ssp. *sylvatica* (mean G_{ST}: 0.005) and *F. sylvatica* ssp. *orientalis* (mean G_{ST}: 0.008), but significant differences were observed between two subspecies (mean G_{ST}: 0.122).

Iranian scientists (Bijarpasi et al., 2020) compared the genetic structure of Iranian populations of *F. orientalis* with populations of *F. sylvatica* from the hybrid zone in southeastern Europe and with the population of *F. sylvatica* from Central Europe. All populations showed high genetic diversity, similar to other populations of *F. orientalis* and *F. sylvatica* from Europe. Genetic differentiation within the Iranian populations was very low. In contrast, distinct genetic differentiation was found between the Iranian populations and the analyzed European populations (*F. orientalis* and *F. sylvatica*). One EST-SSR was an identifier (G_{ST}: 0.503) between *F. orientalis* and *F. sylvatica* with clear differences in allele frequency between the taxa.

Thus, population genetic studies of *F. orientalis* covered various parts of its wide area, however, throughout the entire distribution area in Crimea, the Caucasus ecoregion, Asia Minor, and Iran, including isolated populations at the boundaries of the species area (Abrau Peninsula, Markotkh Ridge, Stavropol Upland, and recently discovered populations in the extreme south of Armenia in the Shikakhokh Nature Reserve, on the northern slope of the Meghri Ridge (Aliev et al., 2018) and at the mouth of the Samur River (Aliev, 2019, 2021)), genetic studies have never been carried out. In the present work, we attempted to expand on the previously made conclusions (Aliev et al., 2020), as well as significantly complement the reconstruction of possible pathways of prochoresis and the formation of the modern distribution area of *F. orientalis* in the studied regions.

Materials and methods

In 2024, we studied 39 populations of *F. orientalis* (4 of which, located relatively close, were paired into 2 populations) from Crimea, the Caucasus ecoregion, Turkey, and Iran by using molecular genetic methods (Fig. 1, Table 1).

Table 1. Points of sample collection of *Fagus orientalis* for the molecular genetic analysis

Point No.	Point name and location	Number of trees from a point	Altitude above sea level (m)	Coordinates
1	Markoth Ridge, Gelendzhik Resort, Krasnodar Territory, Russia	10	620	39°11'01,00"N, 38°03'18,00"E
3	Alushta Town, Republic of Crimea, Russia	10	250	44°39'19,90"N, 34°22'32,46"E
5	Avadhara Resort, Ritza Relic National Park, Republic of Abkhazia	10	1550–1750	43°30'00,63"N, 40°39'49,17"E
6	Strizhament Mountain, Stavropolye Territory, Russia	10	750	44°49'31,15"N, 41°58'45,33"E
8	Autl Mountain, Sochi National Park, Krasnodar Territory, Russia	10	200–1500	38°27'05,22"N, 48°43'53,71"E
9	Zuhrabkent Village, Suleyman-Stalsky District, Republic of Dagestan, Russia	10	1650–1690	43°56'33,81"N, 39°40'07,91"E
12	Zonkari Mountain, Republic of South Ossetia	10	1270	41°32'37,50"N, 48°08'00,59"E
14	Hyrcanic National Park, Republic of Azerbaijan	10	1750–1800	42°18'42,80"N, 44°11'07,71"E
16	Zubutl Village, Kazbekovsky District, Republic of Dagestan, Russia	10	650	43°00'40,63"N, 46°48'13,28"E
18	Charnali Gorge, Adjara, Republic of Georgia	10	620	41°31'12,22"N, 41°34'27,33"E
21	Goderzky Pass, Adjara, Republic of Georgia	10	1860	41°38'08,60"N, 42°30'07,50"E
26	Kepsha River Gorge, Sochi National Park, Krasnodar Territory, Russia	10	540	43°41'12,21"N, 40°01'14,41"E
31	Khopi Village and Kujba-Yashta Tract, Republic of Abkhazia	5+5	1200–1600	43°16'09,75"N, 40°30'10,04"E
34	Erzy Reserve, Fartanga River, Republic of Ingushetia, Russia	10	960	42°57'34,55"N, 45°05'03,97"E
35	Cubus Mountain, Alania National Park, North Ossetia–Alania, Russia	10	1880	42°53'14,16"N, 43°35'32.20"E
36	Tusheti Pass, vicinity of Omalo Village, Republic of Georgia	10	1450–1870	42°14'58,57"N, 45°29'53,67"E
37	Lagodekhi Reserve, Republic of Georgia	10	850–1880	41°52'27,44"N, 46°18'45,14"E
38	Vendam Village, between Vendam and Sumagalli Villages, Republic of Azerbaijan	10	650–1350	40°54'53,16"N, 48°00'44,74"E
40	Mushak Pass, Tsuntinsky District, Republic of Dagestan, Russia	10	1700–1860	42°02'58,01"N, 46°05'13,32"E

Table 1 (end)

Point No.	Point name and location	Number of trees from a point	Altitude above sea level (m)	Coordinates
41	Tbilisi National Park, Republic of Georgia	10	1300–1350	41°54'58,28"N, 44°54'46,23"E
42	Golubye (Blue) Lakes, Republic of Kabardino-Balkaria, Russia	10	950–1000	43°13'27.56"N, 43°33'5.26"E
46	Khutrak Village, Tsuntinsky District, Republic of Dagestan, Russia	10	1880–2000	42°12'59.06"N, 45°47'12.64"E
47	Kvareli Village, Republic of Georgia	10	795	41°59'17.30"N, 45°50'50.89"E
50	Nokhchi-Keloi Village, Chechen Republic, Russia	10	1170	42°45'11.79"N, 45°54'41.61"E
51	Lower (Nizhniaya) Mara Village, Karachay-Cherkess Republic, Russia	10	1220	43°45'47.83"N, 42° 4'14.07"E
52	Dombay Settlement, Karachay-Cherkess Republic, Russia	10	1360–1620 (1435)	43°20'48.98"N, 41°40'42.95"E
54	Ai-Petri Mountain, Republic of Crimea, Russia	10	1130	44°29'52.70"N, 34° 1'39.55"E
55	Guzeripl Settlement, Republic of Adygea, Russia	10	800–1400 (1200)	44° 1'8.36"N, 40° 3'52.63"E
57	Gebi Village, Republic of Georgia	10	1280	42°43'32.12"N, 43°34'11.90"E
58	Lentekhi Village, Republic of Georgia	10	820	42°47'30.15"N, 42°41'29.41"E
59	Borjomi Town, between Borjomi and Bakuriani Settlement, Republic of Georgia	10	1400–1600 (1500)	41°46'10.36"N, 43°28'36.52"E
60	Shikakhogh Village, Republic of Armenia	10	1350	39° 3'54.20"N, 46°29'12.17"E
61	Dilijan Town, northern slope of Sevansky Ridge, Republic of Armenia	10	1650–1850 (1760)	40°41'7.21"N, 44°50'23.65"E
63	Primorsky Village, Samursky National Park, Republic of Dagestan, Russia	10	0	41°51'6.67"N, 48°33'44.88"E
66	Utrish Reserve, vicinity of Sukko Settlement, from Shikhan and Kaban Mountains, Krasnodar Territory, Russia	5+5	290	44°46'41.57"N, 37°25'5.85"E
68	Sar Kalateh-ye Kharab Shahr Village, East Alborz, Iran	10	965	36°42'25.61"N, 54° 6'0.73"E
70	Vank Village, Karabakh, Republic of Azerbaijan	10	1370	40° 3'51.26"N, 46°31'0.19"E
73	Kodorskoye Gorge, Republic of Abkhasia	10	640	43° 2'6.82"N, 41°17'53.57"E
74	Mahalla Durabey, Turkey	10	1140	39°50'52.35"N, 29°38'23.58"E

From each point, 10 samples were used for the analysis. The minimum distance between samples from one point was 150 m.

DNA was isolated from dry leaves using DiamondDNA Plant kit (LLC "ABT", Russia).

For microsatellite, or single sequence repeats (SSR) analysis, 7 pairs of primers developed earlier for *F. sylvatica* and *F. orientalis* (Pastorelli et al., 2003), yielding stable amplification products, were used. The primer annealing temperature was selected taking into account the reagents we used (Table 2). The amplification was carried out using the ready-made PCR mixture BioMaster HS-Taq PCR ("Biolabmix", Russia) in a volume of 25 μl and with final primer concentration of 400 nM. The amplification was carried out in a CFX96 BioRad thermal cycler (USA) according to the following program: denaturation 95 °C – 60 s, primer annealing – 30 s, elongation 72 °C – 30 s (a total of 33 cycles). Separation of the amplification products was performed by capillary electrophoresis using the QIAxcel Advanced automatic station, Qiagen (Germany) and the QIAxcel DNA High Resolution Kit reagent kit in accordance with the manufacturer's instructions (OL 800 electrophoresis program, sample injection time 10 s). This approach has been successfully used in the analysis of SSR EST-SSR markers of European chestnut (*Castanea sativa* Mil., Fagaceae) (Kara, Orhan, 2023) and microsatellite markers of red oak species (*Quercus*, Fagaceae) (Sullivan et al., 2013).

The obtained matrix of amplified fragment lengths was analyzed using the GENEPOP program version 4.7.5, February 2020 (Raymond, Rousset, 1995; Rousset, 2008).

In the GENEPOP program we obtained a genetic differentiation matrix based on allele frequencies calculated using Markov chains and the "^a" statistic. A population differentiation matrix was also constructed based on the F-statistic (Fst parameter) (Table 2). Fst was estimated using ANOVA (Weir, Cockerham, 1984). The Mantel test for isolation by distance (Mantel, 1967) was also performed in the GENEPOP program.

Principal Component Analysis was conducted using Genetic distance in PHYLIP Version 3.5 program (Fig. 2). The initial SSR polymorphism data were analyzed using Bayesian probabilities in the STRUCTURE 2.3.4 program (Pritchard et al., 2000). Then, a correlation analysis and visualization of the results were performed in the ClustVis program (Metsalu, Vilo, 2015) and a "heat map" was obtained. The heat map shows the inclusion of specific populations in conditional clusters (Fig. 3).

Molecular genetic research was conducted at the Bioengineering Laboratory of the South Siberian Botanical Garden of Altai State University.

Results and Discussion

The results of the genetic analysis indicate general trends in population variability of *Fagus orientalis* in latitudinal and altitudinal directions. The isolation distance test conducted in the GenePop program shows very high correlation between genetic differences and logarithm of geographic distances at the points of geographic coordinates at the level of 0.91, which indicates a geographic principle of microspeciation of *Fagus orientalis*.

In all dendrograms obtained previously (Aliev et al., 2020), the populations from Lagodekhi (Eastern Georgia), Alushta (Crimea, Russian Federation), the Strizhament Mount (Stavropol Upland, Russian Federation), and Avadkhara (Abkhazia) occupied an isolated position, and if they were included in common clusters, they were grouped only among themselves, forming the most ancient branches of evolution.

Table 2. Characteristics of SSR-primers

Point No.	Name of the section	Sequence of forward and reverse primers 5'-3'	Annealing temperature,°C	The observed range of allele sizes (sequence of nucleotides)	Number of alleles, pieces	Fst
1	FS1-15	TCAAACCCAGTAAATTTCTCA GCCTCAATGAACTCAAAAAC	58	84–130	19	0.109
2	FS1-25	GACCCATACCTCTCAGCTTC AGAGATCATTGCAACCAAAC	65	191–216	11	0.194
3	FS1-03	CACAGCTTGACACATTCCAAC TGGTAAAGCACTTTTTCCCACT	58	90–119	12	0.485
4	FS1-11	TGAATTCAATCATTTGACCATTC GGAAGGGTGCTTCAATTTGG	63	110–237	18	0.185
5	FS3-04	AGATGCACCACTTCAAATTC TCTCCTCAGCAACATACCTC	60	102–137	17	0.270
6	FS4-46	GCAGTCCTCCACCATTACTA TACAACAGCAGGCTATCCAT	60	100–139	17	0.458
7	FSM5	ACTGGGACAAAAAAACAAAA GAAGGACCAAGGCACATAAA	60	80–137	20	0.402

Fig. 1. Populations of *Fagus orientalis*, used in molecular genetic analysis (population numbers correspond to Table 1: 1 – Markotkh Ridge, 3 – vicinity of Alushta Town, 5 – resort Avadkhara, 6 – Strizhament Mt., 8 – Autl Mt., 9 – Village Zukhrabkent, 12 – Zonkari Mt., 14 – Hyrcanic National Park, 16 – Zubutl Village, 18 – Charnali Gorge, 21 – Goderzi Pass, 26 – Kepsha Gorge, 31 – Khopi Village, 34 – Erzy Reserve, 35 – Cubus Mt., 36 – Tusheti Village, 37 – Lagodekhi Reserve, 38 – Vendam Village, 40 – Mushak Mt., 41 – Tbilisi National Park, 42 – Golubye (Blue) Lakes, 46 – Khutrak Village, 47 – Kvareli Village, 50 – Nokhchi-Keloi Village, 51 – Lower Mara Village, 52 – Resort Dombay , 54 – Ai-Petri Mt., 55 – Guzeripl Village, 57 – Gebi Village, 58 – Lentekhi Village, 59 – Borjomi Town, 60 – Shikakhogh Reserve, 61 – Dilijan Town, 63 – Primorsky Village, 66 – Utrish Reserve, 68 – Sar Kalateh-ye Kharab Shahr Village (Iran), 70 – Wank Village, 73 – Kodorskoye Gorge, 74 – vicinity of Mahalla Durabey (Turkey).

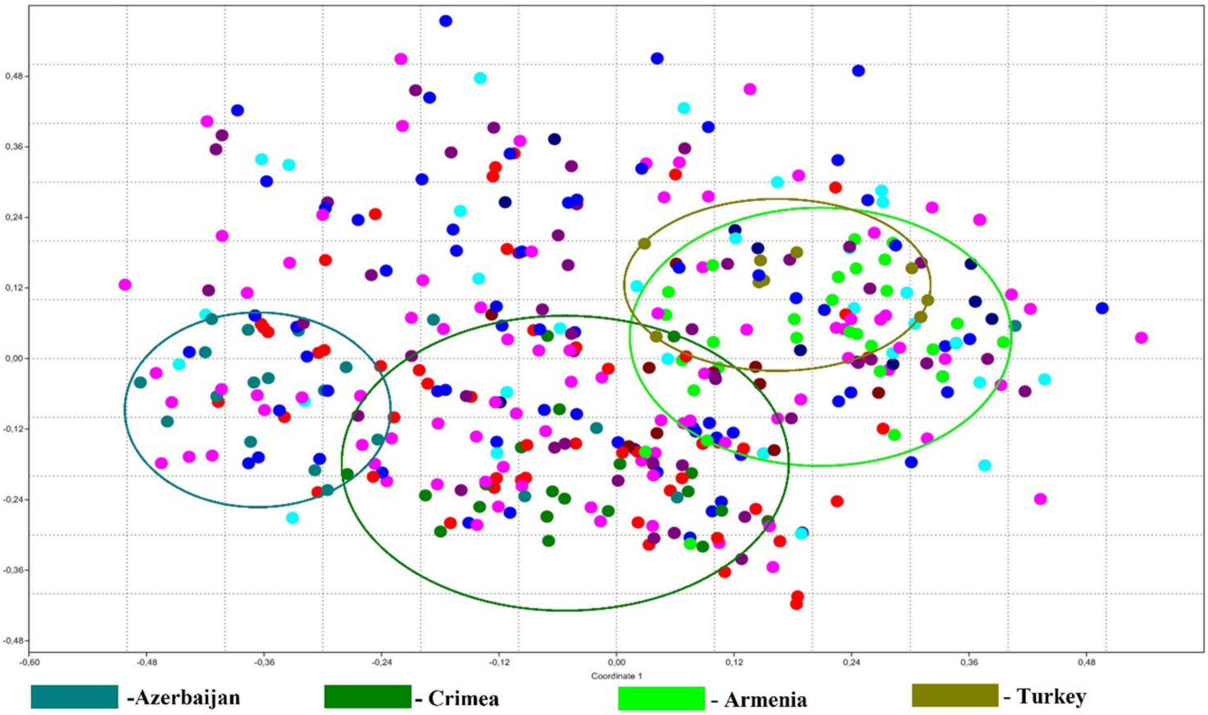

Fig. 2. Principal Component Analysis of the samples of *Fagus orientalis*, based on SSR polymorphism.

It should be emphasized that Lagodekhi is located in the Kakheti refugium of the ancient Colchian biota (Tuniyev, 1990). When analyzed by the UPGMA method, the populations of the *F. orientalis* from Strizhament and the Crimea were significantly far from the North Caucasian populations and the populations of the southern slope of the Greater Caucasus. According to the heat map, the Crimean populations from the vicinity of Alushta and Ai-Petri Mountain are closest to the *F. orientalis* from the Strizhament Mount in the Stavropol Upland and the *F. orientalis* from Avadkhara and Khopi (Abkhazia), which, along with Lagodekhi, suggests a long-term identity of these populations located on the southern slope of the Main Ridge in Abkhazia (Fig. 3).

The population structure was analyzed using the algorithm of Bayes (Bayesian probability method) in the STRUCTURE 2.3.4 program. An admixture model was used for the analysis, as well as correlation models suggesting inheritance of alleles from a common ancestor by gene drift. The analysis was performed in a tenfold repetition for the number of clusters K = 1 to K = 20, with the number of repetitions 10^6 and the value of the 'burn in' parameter 10^6. The optimal number of clusters identified using the STRUCTURE HARVESTER program (Earl, Von Hold, 2012) was 17.

As a result of the Principal Component Analysis based on genetic distances (Fig. 2), clusterization of samples from Azerbaijan, Crimea, Armenia, and Turkey was revealed. Samples from other populations do not form isolated clusters, which indicates a strong variance of genetic SSR characters between populations. This is confirmed by the results of the molecular dispersion analysis (AMOVA). Percentages of molecular variation among the populations were only 14 %, compared to 66 % of molecular variation among individuals.

The STRUCTURE analysis results are visualized as a heat map constructed using unit variation scaling, clustered using maximum distance and Ward linkage. The results of the clustering based on visualization and a heat map constructed using ClustVis are shown in Figure 3, which shows the formation of two large clusters.

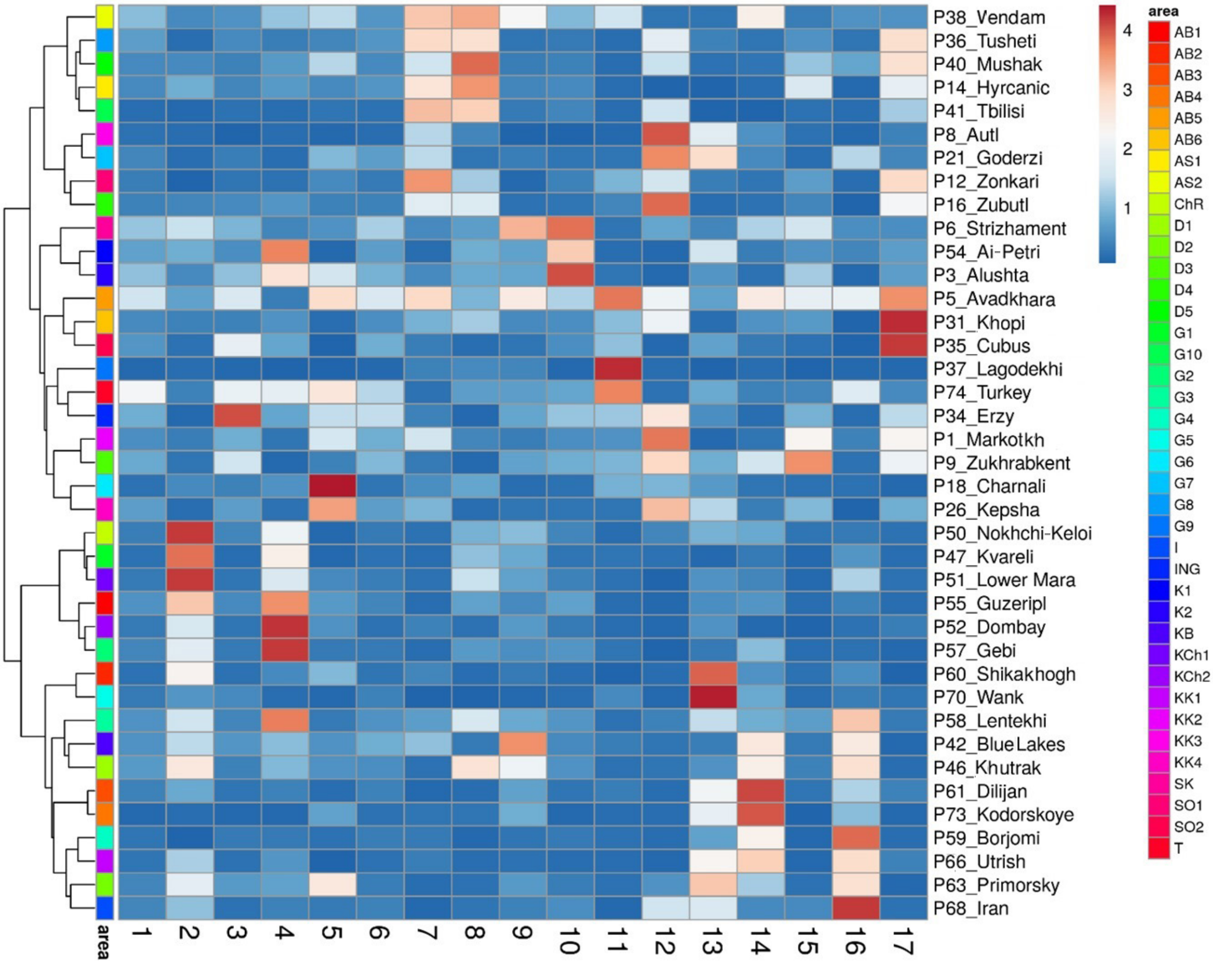

Fig. 3. The results of clustering of *Fagus orientalis* populations, based on SSR polymorphism data.

The first cluster includes two subclusters with the most ancient populations separated from a single area from the mountainous Crimea (surrounding the town of Alushta, Ai-Petri Mountain, Russia) and the Stavropol Upland (Strizhament Mountain, Russia) on the one side, and relict populations in refugia of Colchian mesophilic vegetation (Tuniyev, 1990) on the another side: Colchis in the west (Khopi village, Kujba-Yashta tract, Avadkhara resort, Abkhazia; Charnali gorge, Adjara, Georgia; Kepsha river gorge, Russia), Borjomi in the southwest (Goderzi pass, Adjara, Georgia) and Kakheti (Lagodekhi, Tusheti, Georgia) in the east. The South Ossetian refugium of the Colchian biota is closely related to the Colchian refugium, which occupies an intermediate geographical position between the previously described Borjomi and Kakheti refugia (Tuniyev, 1990) with a population from the vicinity of the village of Zonkari (South Ossetia). The same cluster includes small relict populations from the vicinity of Mahalla Durabey (Turkey), Tbilisi National Park (Georgia), Zukhrabkent village and Zubutl village (Dagestan, Russia), Gyrkan National Park in Talysh and Vendam village on the southern slope of the Eastern Caucasus (Azerbaijan), as well as populations that arose later, during recolonization, and discussed in more detail below.

The time of separation of the mountain forest biota of the Caucasus, Crimea, and the Stavropol Upland is assumed to be the Upper Miocene (Vereshchagin, 1959; Kolakovsky, 1974a, b; Menitsky, 1984). The data on the grouping of the populations in this cluster are consistent with the general picture of the preservation of mesophilic refugia on the southern slope of the Greater Caucasus (Tuniyev, 1990, 1997) and with the data of A. L. Takhtajan (1946) and L. I. Maruashvili (1956) on the possibility of preserving the Colchian refugia in the mid-mountain zone, according to which, during the glacial epochs, the average annual temperature probably decreased by no more than 1.5–2 °C, while precipitation was at least 1500–2000 mm.

In addition to the early separated populations of Crimea and the Stavropol Upland, the first cluster includes samples from relict mesophilic Hyrkan forests in Talysh (Azerbaijan) and samples from the area of former contact of Hyrkan and Colchian flora on the southern slope of the Eastern Caucasus (Lagodekhi, Tusheti – Georgia; Vendam – Azerbaijan). These territories had a common history of formation up to and including the Upper Pliocene. In the Miocene, most Colchian species reached eastern tip of the Greater Caucasus, along its southern slopes, from where they crossed the Karabakh Bridge into the Talysh and came into contact with East Asian species (Tuniyev et al., 2019). N. I. Kuznetsov (1909), I.V. Safarov (1966) and others wrote about the former direct connection of the Colchian-Hyrcanus flora. At present, the floral composition of the Kakheti region of Georgia and Karabakh has many similarities with the forests of Colchis and Talysh (Arushanyan, 1973; Sokolov et al., 1977; Takhtajan, 1978; Gadzhiev et al., 1985). The direct connection of the Talysh with the Lesser Caucasus was disrupted only at the beginning of the Upper Pliocene, due to the formation of the lower Araks trough (Gadzhiev, 1986).

In this work, the involvement of new samples with a wide geography made it possible to identify areas of recent Holocene contact between populations of the northern and southern slopes of the Greater Caucasus. The new data does not refute but significantly expand the previously made conclusions (Aliev et al., 2020): the observed similarity at the upper boundary of the beech belt in various regions of the Caucasian Isthmus indicates parallelism in the development and formation of high-altitude populations of the species. However, we make a significant clarification: the high-altitude populations in Dagestan and North Ossetia–Alania previously had no connection with the foothill populations on the Pastbishchnyj and Lesistyj Ridges in these republics but moved into the highlands of these republics from the southern slope of the Main Ridge, or some of them remained in the mid-mountain belt. This conclusion is supported by the genetic proximity of the populations of the southern slope from Tusheti (Eastern Georgia) and the population from the Mushak Mount (Dagestan) located on the northern slope of the Greater Caucasus. It should be emphasized that the high-altitude populations of *Fagus orientalis* on the northern slope of the Eastern Caucasus are still separated from the foothill belt of beech forests by a belt of semiarid mountain steppes, oreoxerophytes, and places of island pine and birch forest stands.

The settlement of the upper belts of the northern slope of the Caucasus from its southern slope in the Postglacial period is no exception for *Fagus orientalis*. There is more and more documented evidence of this. For example, *Ruscus colchicus* Yeo (Zernov et al., 2020) was recently discovered in the upper forest belt of the Karachay-Cherkess Republic, and typical representatives of the Colchian flora, *Fritillaria ophioglossifolia* Freyn & Sint and *Vaccinium arctostaphylos* L., were found in a high-altitude beech forest in Dagestan (Mushak) (Aliev, 2019, 2021). A number of other species, mainly distributed in central Transcaucasia, also penetrate into the highlands of Dagestan. There are 15 species: *Corydalis angustifolia*, *Paeonia mlokosewitschii*, *Daphne caucasica*, *Erysimum collinus*, *Heracleum wilhelmsii*, etc., whose occurrence in the Bezhta depression is explained by the low passes of the Main Ridge (Murtazaliev, 2023).

For more than three decades, I. I. Tumadzhanov has been studying the florogenesis of beech forests in Dagestan and the entire Caucasus. In his works, he repeatedly criticized the views of N. I. Kuznetsov (1910) in a reasonable manner. Tumadzhanov (1940, 1961, 1971), in particular, noted that the beech forests of the highlands are not fading relics of the tertiary forest flora, as N. I. Kuznetsov imagined, but on the contrary, penetrated and continue to penetrate into Dagestan from Kakheti only in the Postglacial period and displace the dominant pine and birch forests. As arguments, he cited data from spore-pollen analyses and comparative floristics of adjacent areas (Aliev, 2013). Unlike Tumadzhanov, P. L. Lvov (1970a, b) believed that the beech forests of the Bezhta and Shaurinsk depressions lived through the glacial epoch on the spot, and did not enter here from Kakheti in the Postglacial period. In support of his views, Lvov cited data on the geographical distribution and floral composition of isolated sections of beech forests in Dagestan and adjacent areas.

It should be noted that populations from Mushak and Khutrakh in the highland Dagestan, despite their geographical proximity, are located in different clusters on the heat map (Fig. 3), which may indicate their different origins. It is possible that the Khutrakh population has indeed been preserved since the pre-Glacial period, but the Mushak population bears obvious features of a later settlement from the southern slope of Tusheti based on the genetic proximity.

Discussing the highland beech populations, we should focus on volcanism, which, including the last one in the Central Caucasus in the Elbrus, Kazbek, and Kelsky plateau regions about 2000 years ago (Gabrielyan, 1986), had a significant impact on the populations. Probably, the beech populations that persisted or moved in from the southern slope of the Greater Caucasus during the interglacial periods were destroyed by the activity of these volcanoes, and we find modern highland beech forests beyond the influence of paleo-volcanism. This is on the one hand. On the other hand, the beech forests had the opportunity to cross over to the northern slope at the locations of relatively low passes, less than 2500-3000 m a. s. l., which we observe in the area of the Kodorsky (2365 m) and Mushak (2168 m) passes in Dagestan (populations of the Tsuntinsky district). The population of Mount Kubus in North Ossetia–Alania could have arisen due to penetration from the southern slope of the Main Ridge through the Mamison Pass (2911 m). For comparison, the lowest passes between Kabardino-Balkaria and Georgia have heights of 3200–3500 m: Donguz-Orun (3203 m), Becho (3375 m), Twiberi (3607 m), Geziftsik (3452 m) (Shkhagapsoev, 2024); we attribute this fact with the current absence of high-altitude beech forests in Kabardino-Balkaria, Chechnya, and Ingushetia.

The highest passes of the Western Caucasus do not exceed 3000 m – Klukhorsky (2781 m) and Marukhsky (2741 m). All other passes are in the altitude range from 800 m (the bridge between the peaks of Autl – 1880 m and Khuko – 1906 m) to 1800–2200 m (Cherkessky, Aishkha, Pseashkho passes, etc.). They were not an obstacle to the exchange of biota between the two slopes in the past, and in some places they are not that obstacle now. We attribute the similarity between several populations to this fact, taking into account modern horology and the possibility of pollen transfer between neighboring populations. Regardless of the method of analysis, the results indicate a repeated, post-Pleistocene, settlement of the beech into the upper belts of the Western Caucasus.

The second cluster also forms two subclusters (Fig. 3), formed mainly by populations of the eastern part of the Caucasian ecoregion from Dagestan, Azerbaijan, Eastern Georgia and separate populations of the southern slope of the Western Caucasus and the northern slope of the Central–Eastern Caucasus, as discussed below.

The first, smaller subcluster combines the foothill beech populations of the northern slope of the Greater Caucasus and the relict populations of the southern slope in Georgia (Kvareli, Gebi).

The disjunctive populations of the foothill belt of the beech forests of the Eastern–Central Caucasus currently cover the foothills of Dagestan in a semicircle from the village of Zukhrabkent in the south and further extend along the foothill belt of Dagestan, Chechnya, Ingushetia, North Ossetia–Alania to the west of Kabardino-Balkaria. After the Elbrus Gap, the beech belt reappears in the Karachay-Cherkess Republic and then extends continuously along the northern slope of the Western Caucasus. In turn, the foothill beech populations torn apart by multiple eruptions of Elbrus, based on the genetic data of the

Fst1 coefficient, are grouped in the Eastern Caucasus into a common clade – the village of Nokhchi-Keloi (Chechen Republic) – Golubye (Blue) Lakes (Kabardino-Balkaria), and in the Western Caucasus – the village of Nizhnie Mary – the settlement of Dombai (Karachay-Cherkessia) – village Guzeripl (Adygea). According to the Fst1 coefficient, a sample from Kvareli (Eastern Georgia) forms a common cluster with these populations, and according to the heat map, a sample from the Gebi village (Western Georgia) also enters the cluster. The population from Gebi was not affected even by the maximum Würm glaciation, according to Gobejishvili (2004), the Kirtisho valley glacier, 21 km long, stopped above the Gebi village at an altitude of 1300 m. Thus, there is every reason to assume the ancientry of the beech population from the vicinity of the Gebi village.

The second subcluster of the second cluster contains all samples from Armenia, which create a single clade based on genetic distances in the Principal Component Analysis (Fig. 2). This subcluster also includes beech samples from Karabakh (Vank), Kabardino-Balkaria (Blue Lakes), Western Georgia (Lentekhi), Eastern Georgia (Borjomi), Abkhazia (Kodori Gorge), highland Dagestan (Khutrakh), seaside Dagestan at the mouth of the Samur River (Primorsky), the westernmost isolated population from the Navagir Ridge near the Sukko village (Utrish), and eastern Alborz in Iran (near vil. Sar Kalateh-ye Kharab Shahr) (Fig. 3).

Volcanism, which significantly exceeded the volcanic area of the Greater Caucasus, is also important for understanding the current distribution of *Fagus orientalis* in the Lesser Caucasus. The last volcanic eruptions in the Lesser Caucasus and the Armenian Highlands within the former USSR occurred 6-8 thousand years ago. Volcanoes Tondurek and Nemrut on the Van Lake (Turkey) is considered to be active to this day, the last eruptions were recorded in the 15th century (Gabrielyan, 1986). The widest overlap by lavas contributed to the preservation of isolated populations in the upper mountain belt of the northern slopes of the Lesser Caucasus in Northern Armenia (Dilijan) and Karabakh (Azerbaijan).

It was somewhat unexpected that the population from eastern Alborz was in the second cluster, while the population from Talysh combined with samples from the first cluster. At the same time, the populations from marginal areas of Hyrkan flora on the eastern Alborz and its derivatives at the mouth of the Samur River (Primorsky Village, Dagestan, Russia) entered the general clade, indicating genetic similarity greater than with *F. orientalis* from Talysh. Apparently, the existing period of separation of the range of Talysh-Alborz beech populations from the rest of the populations of the Caucasian Isthmus was sufficient to form significant genetic differences. This is confirmed by other authors (Bijarpasi et al., 2020) for Iranian populations from the Alborz which have some differences from European and Turkish populations of *F. orientalis* and are themselves quite polymorphic. It is significant that beeches from Karabakh (Vank, Azerbaijan) and the Priaraxin Lesser Caucasus in Southern Armenia (Shikakhogh) are in a subcluster with marginal populations from Alborz and the mouth of the river Samur. It can be assumed that the time of isolation of these populations from the populations of Talysh and the southern slope of the Eastern Caucasus roughly coincided. Alternatively, distribution route of the beech between the Greater Caucasus and Talysh – Alborz was not the only one but had several possibly parallel branches, both along the mountainous Karabakh Bridge and along the coast of the Caspian Sea. The modern relief of Transcaucasia was formed in the Late Pliocene – Quaternary period. The Caspian Sea during the Akchagyl transgression flooded most of the Kurinsky trough (Museibov, 1986a), creating conditions for the movement of forest vegetation from Alborz along the seashore with numerous river deposits.

The origin of the Talysh-Alborz population cannot be interpreted unambiguously. One of the assumed routes of the beech settlement to the Caucasus is the southern (Aliev et al., 2020). Based on the genetic relationship of populations from Talysh and the southern slope of the Eastern Caucasus, it is likely that *Fagus orientalis* penetrated from Hyrkanic to the Greater Caucasus over the Karabakh Bridge and then in the Pliocene reached Ergeni Ridge in the north. In the eastern part of the Caucasus, along the shores of the Caspian sector of the Pontus, and then the Balakhan basin, there was vegetation described by Baranov (1952) from Ergeni, deciduous but thermophilic, with such species as *Corylus fossilis*, *Alnus incana*, *Quercus* sp., *Castanea* sp., *Parrotia persica*, and representatives of the family Araliaceae. An indicator of a warm climate, as Vereshchagin (1959) rightly wrote, is *Parrotia persica*, currently preserved 10° south in Talysh-Alborz. At the same time, the return route of the beech settlement is more likely. *Fagus orientalis* could have penetrated to the southern coast of the Caspian Sea from the Caucasus via the same Karabakh Bridge. In any case, the noted genetic relationships between the populations of Southern Armenia (Shikakhogh), Karabakh (Vank), the mouth of the Samur River (Primorsky) and eastern

Alborz (near the village of Sar Kalateh-ye Kharab Shahr), on the one hand, and Talysh – the southern slope of the Eastern Caucasus in Azerbaijan (Vendam), on the other, indicate the uniqueness of *Fagus orientalis* and the possible different distribution routes of the species in this part of its area.

The presence in the second cluster of beech samples from the marginal northwestern ridge of the Greater Caucasus – Navagir Ridge on the Abrau Peninsula (Utrish Reserve, Russia) – also requires explanation. Apparently, only in the Pleistocene the species has reached the western limit of its area in the Markotkh Ridge in region of Gelendzhik, since at that time there were a destruction of the Pliocene area into a number of refugia and a downward shift of the high-altitude belts. During this period many high-altitude species descended to the height of 1000–1200 m above sea level, and glacial tongues descended to 450-600 m a. s. l. on the northern slope of the Western Caucasus and to 300–350 m a. s. l. even in the warmest Western Transcaucasia in the valleys of the Inguri and Rioni rivers (Museibov, 1986b; Gobejishvili, 2004). The relics of the Pleistocene period are still observed even at the western tip of the Greater Caucasus, between Anapa and Novorossiysk, surrounded by steppe and sub-Mediterranean flora. The special wind regime of this part of the Black Sea coast leads to the cooling of individual plots not facing the sea, creating conditions comparable to the winter season of the upper belts of the mountains. As a result, such species as *Coeloglossum viride* (L.) C. Hartm., *Gymnadenia conopsea* (L.) R. Br., *Dactylorhyza flavescens* (C. Koch) Holub, *Lilium monadelphum* Bieb., *Viburnum lantana* L., and others can be observed here (Timukhin, Tuniyev, 2018). The westernmost in the Caucasus isolated relict beech forests are currently preserved here.

The obtained result of the genetic evolutionary relationship does not demonstrate a sharp separation of the Markotkh Ridge population from the rest of the populations of the southern slope of the Greater Caucasus, included in the first cluster (Fig. 3). Modern pollen transfer from the continuous beech forests located east of the Markotkh Ridge is also possible. At the same time, the westernmost population from the Navagir Ridge (Utrish), apparently, did not contact secondary with West Caucasian populations. Based on the genetic data of the Fst1 coefficient, the beeches from Utrish form a common clade with the Crimean populations. In this regard, the established links between species of *Quercus* sp. of the Crimea and the Northwest Caucasus should be mentioned (Semerikova et al., 2023). The flora of Crimea is associated with the Anapa-Gelendzhik region by *Juniperus excelsa* M. Bieb., *J. foetidissima* Willd., *Galanthus plicatus* M. Bieb., and many other species. In this regard the Crimean-Novorossiysk biogeographic region stands out.

Despite the secondary contacts of several populations during the interglacial and postglacial periods, or the available pollen transfer with air masses from neighboring diasporas, the most ancient, relict populations of *Fagus orientalis* in the refugial conditions of Adjara, Abkhazia, Kakheti, etc. (Charnali, Kodori Gorge, Lagodekhi) have preserved the maximum similarity in genotypes, which can be considered close to ancestral. Also, these populations continue to differ from all other populations that contacted repeatedly in the past or are in contact over the extended range of the current species' horology. Relict populations from the vicinity of Shikakhogh village (Southern Armenia), Charnali Gorge and Goderzi Pass (Adjara, Georgia), vicinity of village Primorsky at the mouth of the Samur River (southern Dagestan) formed a common clade, based on the genetic data of the Fst1 coefficient. Interestingly, Denk et al. (2005) also indicated the most polymorphic populations of *Fagus orientalis* from Adjara (mt. Mtiral) and near Tbilisi.

Thus, based on the results of the genetic analysis of the populations of *Fagus orientalis* from the Crimean-Caucasian region, Turkey, and Iran, the following view of sequential isolation or the occurrence of secondary contacts between the populations can be assumed: the earliest separation occurred in the populations of the mountainous Crimea, Stavropol Upland and Navagir Ridge. In the conditions of island isolation, they have preserved the unique features of the genotype of the ancestral form. Beeches from Lagodekhi, Gebi, and other refugia of the Colchian flora also seem to be close to their ancestral form.

Based on fossil material on leaves, cupules and nutlets, Denk et al. (2002) stated that in the Oligocene, in the early stage, the spreading of the ancestral form from the northern Pacific to Europe along the northern shores of the Paratethys occurred with a low degree of diversification of characters. In opinion of Menitsky (1984), the main route of settlement of the ancestors of modern deciduous oaks from East Asian countries to the western regions of Eurasia was along the mountain systems of the northern shores of ancient Tethys and the archipelagos of its islands. Kolakovsky (1974a) suggested that the floral exchange between Europe, the Caucasus, and East Asia took place before the Upper Miocene, after the disappearance of the Himalayan sector of the Tethys and its subsequent division into two unrelated basins separated by land that stretched from Afghanistan through central Iran, Asia Minor, the Balkans, and the Alps. The Caucasus from Meotis was a peninsula of the Asia Minor land (Vereshchagin, 1959; Kolakovsky, 1974a), and various ecological conditions have existed in the mountains since the Paleogene, as evidenced by paleobotanical data on the vertical belt of the Tethys subtropical zone (Wolf, 1944; Takhtajan, 1957).

Taking into account the presence of continuous continental communication in the Oligocene not only along the northern shores but also from the south, it is quite logical to assume the existence of two distribution routes of the ancestral beech form, one of which ran along the modern southern shores of the Caspian Sea, Southern Transcaucasia, through Asia Minor to the west, at least to the territory of the modern Balkan Peninsula. This assumption is in good agreement with the paleomaterial: the genus has been known since the Cretaceous, and in the former USSR since the Paleogene, and in the Caucasus it is very often found in a fossil state (Kolakovsky, 1982). In Colchis from the Sarmatian to the Cimmerian, *Fagus attenuata* prevailed, and *F. orientalis* Lipsky ssp. *fossilis* appeared from the Pontus, which, according to Kolakovsky (1982), is very common in Upper Tertiary and Quaternary flora.

The southern mountainous land, extending from Afghanistan through Central Iran, Asia Minor, the Balkans and up to the Alps, is considered to be the established fact of the continuous existence of a mountainous belt of arid climate since the Cretaceous period, with corresponding subtropical hemixerophilic phyto-landscapes (Krishtofovich, 1954; Kolakovsky, 1974a, b) where it could carry mesophilic biotopes in higher belts.

In the Miocene, the processes of “borealization” took over almost the entire Caucasus. Thus, from the Middle Sarmatian in some localities in Eastern Georgia, up to 70 % of trees already belong to deciduous species (Palibin, 1935). Comparing this flora with the Upper Miocene flora of Asia Minor, Grossheim (1936) concluded that they show great proximity and are characterized by the same mixture of boreal and subtropical elements.

In the Pliocene, *Fagus orientalis* occupied all mesophilic areas of the Caucasian Isthmus. The beginning of the primary disjunction of the *F. orientalis* range should be considered the Middle-Upper Pliocene, when the ridges of the Greater and Lesser Caucasus underwent significant glaciation (Gvozdetsky, 1963; Markov et al., 1965) and the Lesser Caucasus was separated from the Talysh-Alborz by the Araks trough.

The Pleistocene history of the Caucasus is, first of all, the glacial impact in the axial part of the Greater Caucasus and in the highest areas of the Lesser Caucasus and the Armenian Highlands. It was associated with glacial and pluvial periods of pulsation of the basins of the Black and especially the Caspian Seas, as well as the indirect impact of the European glacier. During this period, mountain heights increased in the Greater Caucasus by 1000 m and in the Lesser Caucasus and the Armenian Highlands by 500–700 m (Museibov, 1986a).

As we told before, Pleistocene volcanism played a significant role in the Central Caucasus and the Armenian Highlands (Timukhin, Tuniyev, 2018). Isolated in the highlands in some populations, the former continuous beech forests fell out as a result of the glaciation of the Greater and Lesser Caucasus, and the remaining populations were destroyed due to the powerful eruption of the volcanoes of Elbrus, Kazbek and the largest volcanoes of the Kelsky plateau (Didi-Nepiskalo, Patara-Nepiskalo, Keli, East Khorisar, and South Narvankhokh) in the Greater Caucasus and practically throughout the Lesser Caucasus and the Armenian Highland from Javakheti (Georgia) to Karabakh (Azerbaijan).

The beech populations from the refugial conditions of the southwestern Transcaucasia (Charnali River Gorge), limestone northwestern Colchis (Kodori Gorge), and some other populations have the peculiarity and clearly relict features in the genotype. However, the multiple shifts of the forest belt in the Pleistocene contributed to the mixing of the gene pool of the midland-highland and relict foothill populations, and therefore, apparently, we do not see such a clear picture of isolation as with the populations of the Crimea and the Stavropol Upland.

Both nuclear and chloroplast markers show that most *Fagus sylvatica* populations in Central, Eastern, and Northern Europe have a very homogeneous genetic structure, whereas populations in Western and Southern Europe have a rather heterogeneous genetic structure with a number of isolated populations in the Iberian, Apennine, and Balkan peninsulas and southern France (Margi et al., 2006). Paleobotanical findings indicate the preservation of at least several *F. sylvatica* populations in the Pleistocene refugia of Europe during the last Ice Age and possible ways of recolonization in the Postglacial period. Moreover, the latest paleobotanical data allowed us to revise the previously formed opinion about refugia in Europe, the picture was much more complicated. According to Margi et al. (2006), the entire modern *F. sylvatica* range in Central and Northern Europe was formed from Western European refugia in southern France, the eastern Alps-Slovenia-Istria, and possibly southern Moravia and southern Bohemia. Whereas the populations that survived in the last glacial in the Mediterranean region did not penetrate into Central Europe.

This new vision sheds light on the genetic divergence during the recolonization of the European range by the *F. sylvatica* and indicates the independence of refugia in southern France and Slovenia, rather than their marginal position as the southern populations, since their geographical and genetic distance from the populations of Spain and the Balkans is observed. As an example, the population from the Balkans did not colonize the Carpathians, and *F. sylvatica* from the center of the Apennine Peninsula penetrated northern Italy only in the second half of the Holocene (Margi et al., 2006). Most European Ice Age refugia were preserved in mountainous regions with a shady and humid regime. Thus, the current genetic diversity of *F. sylvatica* populations in Europe is explained not by a single glacial episode but by multiple interglacial and glacial cycles during at least the Middle Pleistocene.

Similarly with Europe, local features and the presence of unique alleles are observed in *Fagus orientalis* in all regions of the Caucasian Isthmus, due to the well-known microclimatic and microhabitat conditions. Such conditions, so characteristic of the Caucasus mountains, contribute to the accumulation of original features in individual localities. Interestingly, *F. sylvatica* in Europe, despite the noted phenotypic differences due to the characteristics of biotopes, has little genetic diversity (Wortemann et al., 2011). High genetic diversity, similar to other populations of *F. orientalis* from Balkan-Asia Minor-Caucasus range and *F. sylvatica* from Europe is indicated for the Alborz population of *F. orientalis* (Bijarpasi et al., 2020).

The observed similarity at the upper boundary of the beech belt in various regions of the Caucasian Isthmus may be a reflection of parallelism in the development and formation of high-altitude populations of *F. orientalis*, as in the case of populations with approximately equal hypsometric characteristics of biotopes from Goderzky Pass, Mount Autl and Zukhrabkent village, or the late Holocene “detaching” of populations on the northern slope during the ascent of all belts upward from the southern slopes in the Holocene and their separation by the mountain meadow belt in modern conditions, as in the case of populations from Mount Mushak and Tusheti, Kubus Mountains and the southern slope of the Western Caucasus.

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REFERENCES / ЛИТЕРАТУРА

Aliev Kh. U. 2013. *Sravnitelnaya kharakteristika bukovykh lesov Dagestana* [*Comparative characteristics of beech forests of Dagestan*]. Dissertation ... Candidate of Biological Sciences: 03.02.08, 03.02.01. Makhachkala. 197 pp. [In Russian] (***Алиев Х. У.*** Сравнительная характеристика буковых лесов Дагестана. Дисс. ... канд. биол. наук: 03.02.08, 03.02.01. Махачкала, 2013. 197 с.).

Aliev Kh. U. 2019. New species of vascular plants for the flora of Dagestan. *Bot. Zhurn.* 104(10): 135–138. [In Russian] (***Алиев Х. У.*** Новые виды сосудистых растений для флоры Дагестана // Бот. журн., 2019. Т. 104, № 10. С. 135–138). https://doi.org/10.1134/S0006813619100028

Aliev Kh. U. 2021. The importance of beech forests in the preservation of valuable species of the flora of Dagestan. In: VIII All-Russian Conference with International Participation “Mountain ecosystems and their components”, dedicated to the Year of Science and Technology in the Russian Federation. *BIO Web Conf.* 35: 00003. https://doi.org/10.1051/bioconf/20213500003

Aliev Kh. U., Koltunova A. M., Kutsev M. G., Tuniev B. S. 2020. Population genetic analysis of *Fagus orientalis* Lipsky from the territory of the Crimea and the Caucasus. *Turczaninowia* 23, 4: 17–31. [In Russian] (***Алиев Х. У., Колтунова А. М., Куцев М. Г., Туниев Б. С.*** Популяционно-генетический анализ бука восточного (*Fagus orientalis* Lipsky) с территории Крыма и Кавказа // Turczaninowia, 2020. Т. 23, № 4. С. 17–31). https://doi.org/10.14258/turczaninowia.23.4.3

Aliev Kh. U., Tuniev B. S., Aghasyan A. L. 2018. Geobotanical characteristics and structure of the relict beech forest in the Shikakhokhsky Nature Reserve (Southern Armenia). *Takhtajania* 4: 31–36. [In Russian] (***Алиев Х. У., Туниев Б. С., Агасян А. Л.*** Геоботаническая характеристика и структура реликтового букняка в Шикахохском заповеднике (Южная Армения) // Takhtajania, 2018. Вып. 4. С. 31–36).

Arushanyan R. I. *1973*. Relics of Nagorno-Karabakh and their new locations. *Bot. Zhurn. 58(5)*: *700–706*. [In Russian] (***Арушанян Р. И.*** Реликты Нагорного Карабаха и новые местонахождения их // Бот. журн., 1973. Т. 58, № 5. С. 700–706).

Assyov B., Petrova A., Dimitrov D., Vassilev R. 2012. *Conspectus of the Bulgarian vascular flora*. Sofia. 489 pp.

Baranov V. I. 1952. *O chyem govoryat peschaniki Kamyshina i peski Ergeney* [*What talking about the sandstones of Kamyshin and sands of Ergeney*]. Stalingrad: Regional Book Publ. 48 pp. [In Russian] (***Баранов В. И.*** О чём говорят песчаники Камышина и пески Ергеней. Сталинград: Обл. книгоизд-во, 1952. 48 с.).

Bijarpasi M. M., Müller M., Gailing O. 2020. Genetic diversity and structure of Oriental and European beech populations from Iran and Europe. *Silvae Genetica* 69: 55–62.

Davis P. H. 1982. *Fagus orientalis* L. In: P. H. Davis *Flora of Turkey*. Vol. 7. Edinburgh: University Press. Pp. 657–658.

Denk Th., Frotzier N., Davitashvili N. 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). *Biol. J. Linn. Soc.* 72: 287–332. https://doi.org/10.1006/bijl.2000.0502

Denk Th., Grimm G., Hemleben V. 2005. Patterns of molecular and morphological differentiation in *Fagus* (Fagaceae): phylogenetic implications. *Am. J. Bot.* 92(6):1006–1016.

Denk Th., Grimm G., Stögerer K. K., Langer M., Hemleben V. 2002. The evolutionary history of *Fagus* in western Eurasia: Evidence from genes, morphology and the fossil record. *Plant Syst. Evol.* 232: 213–236.

Earl D. A., von Holdt B. M. 2012. Structure harvester: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conserv. Genet. Res.* 4: 359–361. https://doi.org/10.1007/s12686-011-9548-7

Gabrielyan G. K. 1986. Volcanism and seismic phenomena. In: *Fizicheskaya geografiya Zakavkazya* [*Physical Geography of Transcaucasia*]. Yerevan: Yerevan University Press. Pp. 36–41. [In Russian] (***Габриелян Г. К.*** Вулканизм и сейсмические явления // Физическая география Закавказья. Ереван: изд-во Ереванского ун-та, 1986. С. 36–41).

Gadzhiev F. A. 1986. Elburz region. Hyrcanian province. In: *Fizicheskaya geografiya Zakavkazya* [*Physical Geography of Transcaucasia*]. Yerevan: Yerevan University Press. Pp. 295–297. [In Russian] (***Гаджиев Ф. А.*** Эльбурская область. Гирканская провинция // Физическая география Закавказья. Ереван: изд-во Ереванского ун-та, 1986. С. 295–297).

Gadzhiev V. D., Alekperov A. M., Efendiev M. R., Mustafaeva R. K. 1985. *Zakatalskyy zapovednik* [*Zakataly Reserve*]. Moscow: Agropromizdat. 184 pp. [In Russian] (***Гаджиев В. Д., Алекперов А. М., Эфендиев М. Р., Мустафаева Р. К.*** Закатальский заповедник. М.: Агропромиздат, 1985. 184 с.).

Gobejishvili R. 2004. Late Pleistocene (Würmian) glaciation of the Caucasus. In: *Quaternary Glaciations – Extent and Chronology*. Amsterdam: Elsevier. Pp. 129–134.

Grossheim A. A. 1936. Analysis of the flora of the Caucasus. *Tr. botan. instituta Azerb. fil. AN SSSR* [*Proceedings of Botanical Institute of Azerbaijan branch of the USSR Academy of Sciences*] 1: 1–257. [In Russian] (***Гроссгейм А. А.*** Анализ флоры Кавказа // Тр. ботан. ин-та Азерб. фил. АН СССР, 1936. № 1. С. 1–257).

Gvozdecky N. A. 1963. *Kavkaz. Ocherki prirody* [*Caucasus. Nature essay Kavkaz*]. Moscow: Geografgiz. 264 pp. [In Russian] (***Гвоздецкий Н. А.*** Кавказ. Очерк природы. М.: Географгиз, 1963. 264 с.).

Jahdi R., Nejad A. S., Behjou F. K. 2023. Assessing the state of forest health in Oriental beech (*Fagus orientalis* L.) dominated forests in Iran. *Annals of Silvicultural Research* 48(2): 60–72.

Kara D., Orhan E. 2023. Tolerance evaluation and genetic relationship analysis among some economically important chestnut cultivars in Türkiye using drought-associated SSR and EST-SSR markers. *Sci. Rep.* 13: 20950. https://doi.org/10.1038/s41598-023- 47951-7

Kolakovsky A. A. 1974a. Some data on the paleogeography of the Caucasus in connection with the formation of its flora. *Trudy Sukhumsk. Bot. Sada* [*Proceedings of the Sukhumi Botanical Garden*] 20: 115–131. [In Russian] (***Колаковский А. А.*** Некоторые данные по палеогеографии Кавказа в связи с формированием его флоры // Труды Сухумского бот. сада, 1974. Вып. 20. С. 115–131).

Kolakovsky A. A. 1974b. Vertical zonation of forest vegetation of Colchis in the Tertiary period. *Trudy Tbilisskogo instituta lesa* [*Proceedings of the Tbilisi Forest Institute*] 21: 98–115. [In Russian] (***Колаковский А. А.*** Вертикальная поясность лесной растительности Колхиды в третичное время // Труды Тбилис. ин-та леса, 1974. Т. 21. С. 98–115).

Kolakovsky A. A. 1982. *Fagus orientalis* Lipsky. In: A. A. Kolakovsky. *Flora Abkhazii* [*Flora of Abkhazia (in 4 volumes)*]. Vol. 2. Pp. 202–204. [In Russian] (***Колаковский А. А.*** *Fagus orientalis* Lipsky. // А. А. Колаковский Флора Абхазии (в 4-х т.). Т. 2. Тбилиси: Мецниереба, 1982. С. 202–204).

Krishtofovich A. N. 1954. The origin of xerophytic plant formations in the light of paleobotany. In: *Pustyni SSSR i ich osvoyeniye* [*Deserts of the USSR and their development*]. Vol. 2. Moscow; Leningrad: Publ. of Academy of Sciences of

USSR. Pp. 583–596. [In Russian] (***Криштофович А. Н.*** Происхождение ксерофитных растительных формаций в свете палеоботаники // Пустыни СССР и их освоение. Т. 2. М.; Л.: Изд-во АН СССР, 1954. С. 583–596).

Kuznetsov N. I. 1909. Principles of division of the Caucasus into botanical and geographical provinces. *Zapiski Imperatorskoy Akademii nauk po fiziko-matematicheskomu otdeleniyu* [*Notes of the Imperial Academy of Sciences on the Physics and Mathematics Department*]. Vol. 24, No. 1. St. Petersburg: Typografiya *Imperatorskoy Akademii nauk*. 174 pp. [In Russian] (***Кузнецов Н. И.*** Принципы деления Кавказа на ботанико-географические провинции (Доложено в заседании Физико-Математического Отделения 23 января 1908 г.) // Записки Императорской Академии наук по физико-математическому отделению. Т. 24, № 1. СПб.: Тип. Имп. Акад. наук, 1909. 174 с.).

Kuznetsov N. I. 1910. *Nagornyy Dagestan i znacheniye ego v istorii razvitiya flory Kavkaza: Dolozheno v soyedinyennom zasedanii Otdeleniya geografii, matematiki i geografii fizicheskoy I.R.G.O. 26 oktyabrya 1910 g.”* [*Mountainous Dagestan and its importance in the history of the development of the flora of the Caucasus. Reported at the joint meeting of the Department of Geography Mathematics and Physical Geography of the Imperial Russian Geographical Society on October 26, 1910*]. St. Petersburg: Typografiya M. M. Stasyulevicha. 48 pp. [In Russian] (***Кузнецов Н. И.*** Нагорный Дагестан и значение его в истории развития флоры Кавказа: Доложено в соедин. заседании Отд. географии, мат. и географии физической И.Р.Г.О. 26 окт. 1910 г. СПб.: тип-я М. М. Стасюлевича, 1910. 48 с.).

Lvov P. L. 1970a. Regional features of beech forests of Dagestan. *Sbornik nauchnykh soobshcheniy Dagestanskogo otdeleniya VBO* [*Collection of scientific reports of the Dagestan branch of the All-Russian Botanical Society*] 2: 3–12. [In Russian] (***Львов П. Л.*** Региональные особенности буковых лесов Дагестана // Сборник научных сообщений Дагестанского отделения ВБО, 1970. Вып. 2. С. 3–12).

Lvov P. L. 1970b. Towards the spread of beech forests in Dagestan. *Bot. Zhurn.* 55(9): 1243–1246. [In Russian] (***Львов П. Л.*** К распространению буковых лесов в Дагестане // Бот. журн., 1970. Т. 55, № 9. С. 1243–1246).

Mantel N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27: 209–220.

Margi D., Vendramin G. G., Comps B., Dupanloup I., Geburek Th., Gömöry D., Latalowa M., Litt Th., Paule L., Roure J. M., Tantau I., Knaap W. O., Petit R. J., Beaulieu J.-L. 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist,* 171(1): 199-221. https://doi.org/10.1111/J.1469-8137.2006.01740.X

Markov K. K., Lazukov G. I., Nikolaev V. A. 1965. *Chetvertichnyy period (lednikovyy period – antropogenovyy period)* [*Quaternary period (Ice Age – Anthropogenic period)*]. Vol. 1. Moscow: Publ. MGU. 371 pp. [In Russian] (***Марков К. К., Лазуков Г. И., Николаев В. А.*** Четвертичный период (ледниковый период – антропогеновый период). Т. 1. М.: Изд-во Моск. ун-та. 1965. 371 с.).

Maruashvili L. I. 1956. *Tselesoobraznost peresmotra sushchestvuyushchikh predstavlenyy o paleogeograficheskikh usloviyakh lednikovogo vremeni na Kavkaze* [*The advisability of revising existing ideas about the paleogeographic conditions of the Ice Age in the Caucasus*]. Tbilisi: Mezniyereba. 126 pp. [In Russian] (***Маруашвили Л. И.*** Целесообразность пересмотра существующих представлений о палеогеографических условиях ледникового времени на Кавказе. Тбилиси: Мецниереба, 1956. 126 с.).

Menitsky Yu. L. 1984. *Duby Azii* [*Oaks of Asia*]. Leningrad: Nauka. 284 pp. [In Russian] (***Меницкий Ю. Л.*** Дубы Азии. Л.: Наука, 1984. 284 с.).

Menitsky Yu. L. 2012. *Fagus* L. In: *Conspectus Florae Caucasi.* Vol. 3, part 2. St. Petersburg; Moscow: KMK Scientific Press Ltd. P. 286. [In Russian] (***Меницкий Ю. Л.*** *Fagus* L. // Конспект флоры Кавказа: в 3-х томах. Т. 3, ч. 2. СПб.–М.: Тов-во науч. изд. КМК, 2012. С. 286).

Metsalu T., Vilo J. 2015. ClustVis: A web tool for visualizing clustering of multivariate data using Principal Component Analysis and heatmap. *Nucleic Acids Res.* 43: 566–570. https://doi.org/10.1093/nar/gkv468

Müller M., Lopez P. A., Papageorgiou A. C., Tsiripidis I., Gailing O. 2019. Indications of Genetic Admixture in the Transition Zone between *Fagus sylvatica* L. and *Fagus sylvatica* ssp. *orientalis* Greut. & Burd. *Diversity* 11(90): 1–11. https://doi.org/10.3390/d110600090

Murtazaliev R. A. 2023. Analysis of the flora of Dagestan. *Botanicheskiy vestnik Severnogo Kavkaza* [*Botanical Bulletin of the North Caucasus*] 1: 38–64. [In Russian] (***Муртазалиев Р. А.*** Анализ флоры Дагестана // Ботанический вестник Северного Кавказа, 2023. № 1. С. 38–64).

Museibov M. A. 1986a. History of relief development. In: *Fizicheskaya geografiya Zakavkazya* [*Physical Geography of Transcaucasia*]. Yerevan: Yerevan University Press. Pp. 50–54. [In Russian] (***Мусеибов М. А.*** История развития рельефа // Физическая география Закавказья. Ереван: изд-во Ереванского ун-та, 1986. С. 50–54).

Museibov M. A. 1986b. Ancient and modern glaciation. In: *Fizicheskaya geografiya Zakavkazya* [*Physical Geography of Transcaucasia*]. Yerevan: Yerevan University Press. Pp. 101–104. [In Russian] (***Мусеибов М. А.*** Древнее и современное оледенение // Физическая география Закавказья. Ереван: изд-во Ереванского ун-та, 1986. С. 101–104).

Nasiri M., Yousefzadeh H., Shirvany A., Etemad V., Espahbodi K., Amirchakhmaghi N., Rajora O. P. 2023. Effects of fifty years of shelterwood harvesting on genetic diversity and population structure of Oriental beech (*Fagus orientalis* L.) in the relict Hyrcanian forest. *For. Ecol. Manag.* 529: 120623. https://doi.org/10.1016/j.foreco.2022.120623

Palibin I. V. 1935. Stages of development of the flora of the Caspian countries since the Cretaceous period. *Sovetsk. Bot.* 3: 10–50. [In Russian] (***Палибин И. В.*** Этапы развития флоры Прикаспийских стран со времени мелового периода // Сов. ботаника, 1935. № 3. С. 10–50).

Pastorelli R., Smulders M. J. M., Van't Westende W. P. C., Vorman B., Giannini R., Vettori C., Vendramin G. G. 2003. Characterization of microsatellite markers in *Fagus sylvatica* L. and *Fagus orientalis* Lipsky. *Mol. Ecol. Notes.* 3: 76–78.

Raymond M., Rousset F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J. Heredity* 86: 248–249.

Rousset F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Mol. Ecol. Resour.* 8: 103–106.

Pritchard J. K., Stephens M., Donnelly P. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155(2): 945–959.

Sagheb-Talebi Kh., Schütz J.-Ph. 2002. The structure of natural oriental beech (*Fagus orientalis*) forests in the Caspian region of Iran and potential for the application of the group selection system Forestry. *An International Journal of Forest Research* 75(4): 465–472.

Safarov I. V. 1966. Zelkova, its biological and ecological characteristics and economic importance. *Izv. Akad. nauk Azerbajdzansk. S.S.R., Ser. Biol. Med. nauk* [*News of the Academy of Sciences of the Azerbaijan SSR. Biological Sciences Series*] 1: 18–24. [In Russian] (***Сафаров И. В.*** Дзельква, её биолого-экологические особенности и хозяйственное значение // Известия АН Азербайджанской ССР. Серия биол. и мед. наук, 1966. Вып. 1. С. 18-24).

Semerikova S. A., Aliev Kh. U., Semerikov N. V., Semerikov V. L. 2023. Phylogeography of Oak Species in the Caucasus Based on Results of Chloroplast DNA Analysis. *Russ. J. Genet.* 59(7): 669–684.

Shkhagapsoev S. Kh. 2024. *Petrophilic floral complex of Kabardino-Balkaria: composition, structure, ecology*]. Nalchik: Publ. House of M. and V. Kotlyarovs 254 pp. [In Russian] (***Шхагапсоев С. Х.*** Петрофильный флористический комплекс Кабардино-Балкарии: состав, структура, экология. Нальчик: изд-во М. и В. Котляровых, 2024. 254 с.).

Sokolov S. Ya., Svyazeva O. A., Kubli V. A. 1977. Сем. Facaceae Dum. In: *Arealy derevyev i kustarnikov SSSR* [*Tree and shrub habitats of the USSR*]. Vol. 1. Leningrad: Nauka. Pp. 112–125. [In Russian] (***Соколов С. Я., Связева О. А., Кубли В. А.*** Сем. Facaceae Dum. - Буковые // Ареалы деревьев и кустарников СССР. Т. 1. Л.: Наука, 1977. С. 112–125).

Sullivan A. R., Lind J. F., McCleary T. S., Romero-Severson J., Gailing O. 2013. Development and characterization of genomic and gene-based microsatellite markers in North American red oak species. *Plant Molecular Biology Reporter* 31: 231–239.

Takhtajan A. L. 1946. On the history of the development of vegetation of Armenia. *Acta Instituti Botanici Academiae Scientarium SSR Armeniae* 4: 51–107. [In Russian] (***Тахтаджян А. Л.*** К истории развития растительности Армении // Труды Ботанического института АН Арм. ССР, 1946. Т .4. С. 51–107).

Takhtajan A. L. 1957. On the origin of the temperate flora of Eurasia. *Bot. Zhurn.* 42(11): 1635–1653. [In Russian] (***Тахтаджян А. Л.*** К вопросу о происхождении умеренной флоры Евразии // Бот. журн., 1957. Т. 42, № 11. С. 1635–1653).

Takhtajan A. L. 1978. *Floristicheskiye oblasti Zemli* [*Floristic regions of the Earth*]. Leningrad: Nauka. 219 pp. [In Russian] (***Тахтаджян А. Л.*** 1978. Флористические области Земли. Л.: Наука. 219 с.).

Timukhin I. N., Tuniyev B. S. 2018. Pleistocene refugia of high-mountain flora at foothills of Northern Colchis (Krasnodar Territory, Sochi). In: *Botanika v sovremennom mire. Trudy XIV Syezda Russkogo botanicheskogo obshchestva i konferentsii "Botanika v sovremennom mire"* [*Botany in the modern world. Proceedings of the XIV Congress of the Russian Botanical Society and the conference "Botany in the modern world"*]. Vol. 1. Makhachkala: ALEF. Pp. 201–203. [In Russian] (***Тимухин И. Н., Туниев Б. С.*** Плейстоценовые рефугиумы высокогорной флоры в предгорьях Северной Колхиды (Краснодарский край, Сочи) // Ботаника в современном мире. Труды XIV Съезда Русского ботанического общества и конференции «Ботаника в современном мире» (г. Махачкала, 18-23 июня 2018 г.). Т. 1: Систематика высших растений. Флористика и география растений. Охрана растительного мира. Палеоботаника. Ботаническое образование. Махачкала: АЛЕФ, 2018. С. 201-203).

Tumadzhanov I. I. 1940. Beech and beech forests in Nagorno-Dagestan. *Trudy Tbilissk. Bot. Inst.* [*Proceedings of the Tbilisi Botanical Institute*] 7: 57–83. [In Russian] (***Туманжанов И. И.*** Бук и буковые леса в Нагорном Дагестане // Труды Тбилисского ботанического института, 1940. Т. 7. С. 57–83).

Tumadzhanov I. I. 1961. History of the forests of the North Caucasus. In: M. I. Neyshtadt, V. K. Gudelis (eds.). *Voprosy golotsena: Sbornik statey k VI Mezhdunarodnomu kongressu INKVA v Varshave* [*Questions of the Holocene: Collection of articles for the VI International The INQUA Congress in Warsaw*]. Vilnius. Pp. 249–266. [In Russian] (***Туманжанов И. И.*** История лесов Северного Кавказа // Вопросы голоцена: Сборник статей к VI Междунар. конгрессу ИНКВА в Варшаве. Ред. М. И. Нейштадт, В. К. Гуделис. Вильнюс, 1961. С. 249–266).

Tumadzhanov I. I. 1971. Botanical and geographical features of Highland Dagestan in relation to the paleogeography of the Pleistocene and Holocene. *Bot. Zhurn.* 56(9): 1239–1251. [In Russian] (***Тумаджанов И. И.*** Ботанико-географические особенности Высокогорного Дагестана в связи с палеогеографией плейстоцена и голоцена // Бот. журн., 1971. Т. 56, № 9. С. 1239–1251).

Tuniyev B. S. 1990. On the Independence of the Colchis Center of Amphibian and Reptile Speciation. *Asiatic Herpetological Research* 3: 67–84.

Tuniyev B. S. 1997. About exact borders of the Colchis biogeographical province. *Russian Journal of Herpetology* 4(2): 182–185.

Tuniyev B. S., Orlov N. L., Ananjeva N. B., Agasyan A. L. 2019. *Snakes of the Caucasus: taxonomic diversity, distribution, conservation*. St. Petersburg; Moscow: KMK Scientific Press. 276 pp.

Vereschagin N. K. 1959. *Mlekopitayuchchiye Kavkaza* [*Mammals of the Caucasus*]. Moscow; Leningrad: Publ. of Academy of Sciences of USSR. 703 pp. [In Russian] (***Верещагин Н. К.*** Млекопитающие Кавказа. М.–Л.: изд-во АН СССР, 1959. 703 с.).

Vulf E. V. 1944. *Istoricheskaya geografiya rastenyy. Istoriya flor zemnogo shara* [*Historical geography of plants. History of floras of the globe*]. Moscow; Leningrad: Publ. of Academy of Sciences of USSR. 545 pp. [In Russian] (***Вульф Е. В.*** Историческая география растений. История флор земного шара. М.–Л.: изд-во АН СССР, 1944. 545 с.).

Weir B. S., Cockerham C. C. 1984. Estimating F-Statistics for the Analysis of Population-Structure. *Evolution* 38: 1358–1370.

Wortemann R., Herbette S. T. S., Fumanal B., Alia R., Ducousso A., Gomory D., Roeckel-Drevet P., Cochard H. 2011. Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiology* 31: 1175–1182. https://doi.org/10.1093/treephys/tpr101

Zernov A. S. 2013. *Illyustrirovannaya flora yuga Rossiyskogo Prichernomorya* [*Illustrated flora of the south of the Russian Black Sea region*]. Moscow: KMK Scientific Press Ltd. 588 pp. [In Russian] (***Зернов А. С.*** Иллюстрированная флора юга Российского Причерноморья. М.: Тов-во науч. изд. КМК, 2013. 588 с.).

Zernov A. S., Adzhiev R. K., Filin A. N. 2020. Additions to the flora of the Karachay-Cherkess Republic. Message 5. *Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol.* 125, 6: 48–50. [In Russian] (***Зернов А. С., Аджиев Р. К., Филин А. Н.***, Дополнения к флоре Карачаево-Черкесской республики. Сообщение 5 // Бюл. МОИП. Отд. биол., 2020 Т. 125, вып. 6. С. 48–50).