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Genetic diversity and relationships of *Vitis vinifera* L. in the south caucasus

Franco Röckel^{1*} , Kristine Margaryan^{2,3} , Vugar Salimov⁴ , David Maghradze^{5,6} , Gabriella De Lorenzis⁷ , Osvaldo Failla⁷ , Valérie Laucou⁸ , Thierry Lacombe⁸ , Rauf Asadullayev⁴ , Movlud Huseynov⁹ , Afet Huseynova⁴ , Reinhard Töpfer¹ , Oliver Trapp¹ and Erika Maul¹

Abstract

The South Caucasus is recognized as one of the primary centres of grapevine domestication and harbours an extraordinary wealth of wild and cultivated grapevine diversity. Understanding the genetic structure and relationships of this germplasm is essential both for conservation and for the valorisation of local varieties in viticulture, wine making and breeding. The objectives of the present study consisted of the exploration of grape genetic diversity and the investigation of genetic relationships existing in Armenia, Azerbaijan and Georgia. Germplasm studied included 425 non-redundant accessions, genotyped using 24 nSSR-markers, from these three countries and from Western to Eastern Europe. The total sample set included 366 *Vitis vinifera* subsp. *sativa* varieties, 50 *Vitis vinifera* subsp. *sylvestris* individuals and 9 interspecific crosses. A Bayesian clustering analysis and diversity parameters revealed that Armenia and Azerbaijan share a common gene pool, whereas the Georgian gene pool is mainly independent, with few intermixes. First-order parentage analysis identified 208 first-degree relationships with 196 grape varieties (46%) being involved, while 231 genotypes (54%), respectively 180 (42%) *sativa* and 51 (12%) *sylvestris* did not show any genetic relatedness. Two reconstructed genetic profiles are proposed, suggesting that these are likely key ancestors within the Georgian gene pool. This treasure of genetic diversity from one of the cradles of wine culture holds immense potential for research and breeding with an unique cultural-historical background. Therefore, further surveys and research are essential for the conservation, sustainable management, and utilization of the grapevine genetic biodiversity of the South Caucasus.

Keywords Grapevine, Genetic resources, nSSR markers, Armenia, Azerbaijan, Georgia

*Correspondence:

Franco Röckel
franco.roeckel@julius-kuehn.de

¹Julius Kühn Institute (JKI), Institute for Grapevine Breeding Geilweilerhof, Siebeldingen, Germany

²Laboratory of Plant Genomics, Institute of Molecular Biology, National Academy of Sciences of Armenia, Yerevan, Armenia

³Research Institute of Biology, Yerevan State University, Yerevan, Armenia

⁴The Azerbaijani Scientific Research Institute of Viticulture and Wine making, Baku, Azerbaijan

⁵Faculty of Viticulture-Winemaking, Caucasus International University, Tbilisi, Georgia

⁶National Wine Agency of Georgia, Tbilisi, Georgia

⁷Department of Agricultural and Environmental Sciences, University of Milan, Milan, Italy

⁸UMR AGAP Institut, Univ Montpellier, CIRAD, INRAE, Institut Agro, UMT Génovigne, équipe « Diversité, Adaptation et Amélioration de la Vigne », Montpellier, France

⁹UNEC- Azerbaijan State University of Economics, Baku, Azerbaijan



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Introduction

Grapevine (*Vitis vinifera* L.) was one of the first domesticated fruit trees in southwest Asia and the Mediterranean basin, besides olive, fig, date palm, pomegranate and sycamore fig. These fruit trees were predestined for early cultivation due to the easy maintenance of the genotype via simple vegetative propagation by cuttings layering [88]. In 2024, grapes covered an area of 7,09 million ha. Nearly half of the production was allotted to table grapes (49,2%), followed by wine grapes (43,2%) and raisins (7,6%) (<https://www.oiv.int>).

Since the 19th century, the South Caucasus has been considered the centre of grape diversity, where, the cultivated grapevine *Vitis vinifera* L. subsp. *vinifera* (synonym subsp. *sativa*) evolved via domestication from its wild progenitor *Vitis vinifera* subsp. *sylvestris* (Gmelin) Hegi [47]. This opinion was shared by Nikolai Ivanovich Vavilov, who developed the idea of seven centres of origin of cultivated plants in the world [85]. He wrote: “Transcaucasia is the principal centre whence the forms of the wild and of the cultivated grapes have originated. The great number of various indigenous grape varieties in Georgia, Armenia and Azerbaijan, showing the whole scale of diversity of colour, size of fruit and seeds, suggests that the process of form origination is centred in Transcaucasia. [...] Wild grapes, sometimes referred to as *Vitis sylvestris* Gmel., are undoubtedly to be found in abundance in the forests. [...] In autumn, when the fruit is ripening, a traveller passing through the forests of Transcaucasia might think himself in the Garden of Paradise.”

Nowadays, grape domestication for wine production is meant to have occurred in Vavilov’s Triangle, the region lying between the southern slopes of the Caucasus mountain range, east of the Taurus mountains in south-eastern Anatolia and north of the Zagros mountains [47]. Archaeological excavations [4, 7, 20, 31, 59, 60] corroborate these findings as well as multidisciplinary studies regarding morphological, oenological and resistance-related genetic traits of the wild and cultivated Caucasian grapevine, proving the diversity of that outstanding genepool [6, 48, 68, 73, 74, 83]. Recent scientific focus on the grapevine genetic resources of the Caucasus started in 2003 in the framework of the first international regional project titled “Conservation and sustainable use of grapevine genetic resources in the Caucasus and Northern Black Sea Region” [44]. It was coordinated by IPGRI with the main goal of strengthening the national capacity in the countries of the region to ensure the long-term maintenance of *Vitis* genetic resources, including both the traditional varieties and the wild resources.

Molecular analysis of a wide geographical spectrum of non-redundant *sativa* genotypes, including 2096 cultivars preserved in the INRAE Vassal grape repository,

revealed structuring of cultivated varieties according to use, geographic origins and human selection [3]. The results supported the theory of domestication in Vavilov’s Triangle and expansion via northern and southern routes from East to West, and a third towards Asia. Relatedness among 583 *Vitis sativa* varieties and 59 *Vitis sylvestris* samples, preserved in the USDA grape germplasm collection, points in the same direction, suggesting primary domestication in the Near East and secondary events via introgression from local *Vitis sylvestris* as the grapes migrated westwards [63]. Same conclusions have been reached when 783 cultivated varieties were analysed together with a pool of 384 Italian genotypes and others from the Balkans and Eastern Mediterranean and Caucasus [61]. The most extensive study to date by Dong et al., [21] analysed 2448 non-redundant *V. vinifera* (1604 cultivated and 844 wild genotypes) and proposed two independent domestication events, separated for wine and table grapes. Based on their estimation, domestication happened around 11.000 years ago in the South Caucasus for a first pool of wine grapes and in the Near East at the same time, but followed by different events of wild introgression until 7.000 years ago for table grapes and a second, bigger pool of wine grapes. Furthermore, diversity analysis indicated the differentiation of wild and cultivated accessions by ten distinct genetic ancestries (i.e. four wild and six cultivated) reflecting geographical origin and use.

Many grape cultivars have been described in the South Caucasus region, demonstrating the richness of the local germplasm [38, 45, 54, 66]. Numerous investigations on genetic grape diversity focused on this germplasm [14, 51, 76, 77]. Analysis of 159 wild and cultivated *V. vinifera* accessions of Georgian, Azerbaijani and European origin based on nine nSSR (nuclear Simple Sequence Repeats) loci, clearly separated Georgian and Azerbaijani genotypes and determined a closer genetic relationship between the Georgian and European genepool [16]. This finding was confirmed in two similar studies [17, 78]. Genetic investigation of 1378 wild and cultivated individuals of South Caucasus (Armenia, Azerbaijan and Georgia), the Caspian Sea region (Turkmenistan and Pakistan) and Europe (Croatia, France, Italy and Spain) using 20 nSSR markers, inferred three genetically distinct groups: (1) Western European *Vitis sylvestris*, (2) Eastern European *Vitis sylvestris* and (3) *sativa* varieties with a few *Vitis sylvestris* intermixed [72]. Another study by Marrano et al., [55] of genetic relationships concerned 13 wild and 66 cultivated samples from Central Asia and 40 Georgian varieties, analysed with 22 nSSRs. The cultivated compartment of Georgia and Central Asia was clearly distinguished. Genetic analysis of 42 Georgian varieties and 26 wild individuals using 15.317 SNPs differentiated two groups according to their geographic

origin in the Georgian territory (Eastern and Western parts of the country) and a third group including wild grapes [15]. No first-degree relationships were detected.

In recent years, the most representative and comprehensive analysis of Armenian grapevine germplasm has been initiated through close collaboration between the Institute of Molecular Biology, NAS RA, and the Julius Kühn Institute, Institute for Grapevine Breeding Geilweilerhof (JKI-ZR). The efforts aim at the preservation, promotion, and prominence of native grapevine germplasm, with a particular focus on recovering the untapped biodiversity and breeding potential of *Vitis vinifera* L. in Armenia [50, 51]. More than 700 genotypes were collected from old vineyards, home gardens, and private collections across the country. To ensure accurate cultivar identification, a symbiotic approach combining both genotypic and phenotypic characterization was applied to each accession. One of these studies provided a comprehensive characterization of 221 unique varieties, including mutants, neglected or minor autochthonous cultivars, as well as new bred cultivars created within national breeding programs, mainly during the Soviet era. For 67 genotypes, no references or corresponding genetic profiles were available. 125 “unknown” genotypes have been precisely characterized. Among them, 50 varieties were officially named by Armenian governmental bodies (National Academy of Sciences of Armenia, Ministry of Economy of Armenia) and registered in the *Vitis* International Variety Catalogue (VIVC, www.vivc.de) in 2025. A genetic survey of 221 Armenian cultivated genotypes with 24 nSSRs revealed 62 full parentages with 53 out of them having not been previously reported and 185 half-kinships [50]. However, kinships of Azerbaijani and Georgian varieties were not deeply investigated yet and ancestry research including grape varieties of all three Caucasian countries at once was not done on a larger scale until now.

Pedigrees of a small number of South Caucasian ancient varieties and several modern crosses were determined in the scope of a large-scale kinship study using 20 nSSRs [41] and 6,770 SNPs [13], respectively. Examination of identity revealed that a vast proportion of the Caucasian germplasm is not duplicated in Western European collections [57] and that trueness to type of accessions in South Caucasian grapevine collections needs to be further investigated [29, 50, 57, 64]. To overcome that issue in Armenia, determination of identity was performed for all genotypes conserved in the Armenian National Grapevine Collection.

Despite the numerous studies on grapevine diversity in the South Caucasus, gaps still remain in the comprehensive understanding of the relationships and structure among germplasm from Armenia, Azerbaijan and Georgia when analysed together on a larger scale. In

particular, Azerbaijani and Georgian varieties have not yet been investigated in depth with respect to kinship, and no integrative study has merged datasets from the three countries to assess genetic structure and parentage analysis simultaneously, so far. This present investigation aims to fill this gap by combining and analysing genetic profiles from different projects, thereby providing the first large-scale evaluation of genetic diversity, structure, and kinship relationships across the entire South Caucasian germplasm. The focus is at (1) inspecting genetic diversity and structure of the South Caucasian gene pool itself and (2) deciphering relationships between individual grapevine varieties including country and region-specific connections. For that purpose, genetic profiles of three studies were merged, explicitly from the cooperation between the Julius Kühn Institute, Institute for Grapevine Breeding Geilweilerhof (JKI-ZR) in Germany and the Research Institute for Viticulture and Winemaking in Baku / Azerbaijan (AZE007), COST Action FA1003 [25] and a survey of grape germplasm still existing in Armenia [50].

The consolidation of these complementary datasets provided the most extensive representation of South Caucasian grapevine diversity analysed to date. This comprehensive framework enabled robust comparative analyses, revealing both shared and distinct genetic patterns across Armenia, Azerbaijan, and Georgia, while also uncovering novel relationships among cultivated and wild accessions.

Materials and methods

Origin of the plant material

The genetic profiles of 425 non-redundant accessions from three projects were selected: (1) 79 accessions from the cooperation between the Julius Kühn Institute, Institute for Grapevine Breeding Geilweilerhof (JKI-ZR) in Germany and the Research Institute for Viticulture and Winemaking in Baku / Azerbaijan (AZE007), (2) 206 accessions from COST Action FA1003 (East-West Collaboration for Grapevine Diversity Exploration and Mobilization of Adaptive Traits for Breeding) [57] and (3) 140 accessions from a study of Armenian genetic diversity (genetic profiles already published), 16GE-042 project, HESC RA/BMBF [50]. The detailed number of accessions per project and the number of *V. vinifera* subsp. *sativa* varieties, *V. vinifera* subsp. *sylvestris* and interspecific crosses (I.C.) are reported in Supplemental Table S1. The detailed number of accessions per country is shown in Table 1, including the two genetic profiles inferred via Colony (see parentage analysis). For all analysed samples, the origin of the data, the supposed geographic origin according to bibliographical citations given in the *Vitis* International Variety Catalogue (VIVC) (www.vivc.de, 5 July 2025) and passport data extracted

Table 1 Number and type of analysed accessions by country/region

Country of origin	No. of vitis sativa and I.C. varieties	No. of vitis sylvestris accessions	Total no. of non-redundant accessions
Armenia	110		110
Azerbaijan	73	50	123
Armenia/Azerbaijan	5		5
Armenia/Georgia	2		2
Georgia	117		117
Western-Eastern Europe, Asia	59		59
Interspecific crosses (I.C.)	9		9
Inferred Georgian genotypes	2		2
Total	377	50	427

from VIVC (colour of berry skin, utilisation, flower sex, chlorotype, *Vitis* species, breeder and pedigree given by breeder, pedigree by molecular markers) are shown in Supplemental Table S1. In addition, 59 varieties from Western to Eastern Europe and Asia were included to the sample-set to increase the discovery of putative genetic relationships. For example, ‘Luglienga Bianca’, ‘Madeleine Angevine’, ‘Muscat of Alexandria’, ‘Pinot Noir’, two I.C., ‘Villard Blanc’ and ‘Dattier de Saint-Vallier’ were added for validation of breeder’s records.

Genotyping of the accessions from Azerbaijan

Although modern SNP markers offer higher genomic resolution, nSSR markers were chosen for this study due to their high multi-allelic diversity and the associated cost-effectiveness even with a smaller number of loci, as well as their direct comparability with existing data from previous projects. Seventy-nine accessions from the German-Azerbaijani cooperation were genotyped. DNA was extracted from fresh or dried young leaves or from woody cuttings with the DNeasy 96 plant mini kit (QIAGEN, Düsseldorf, Germany) following to the manufacturer’s instructions. The following 24 nuclear microsatellite loci, which exhibited a high degree of heterozygosity, polymorphism, and reproducibility in previous studies [11, 23, 41, 57, 72, 81], were analysed in multiplex PCRs: VVS2, VVMD5, VVMD7, VVMD21, VVMD24, VVMD25, VVMD27, VVMD28, VVMD32, VrZAG62, VrZAG67, VrZAG79, VrZAG83, VMC4f3.1, VMC1b11, VVIb01, VVIh54, VVIN16, VVIN73, VVIp31, VVIp60, VVIq52, VVIv37, VVIv67 [10, 42, 62, 80, 82] and the flower sex marker ATP3 [75]. ATP3 differentiates female and male versus hermaphrodite plants [28]. All forward primers were 5’-labelled with a fluorescent dye (FAM, HEX, TAMRA or ROX) and markers with different labels and non-overlapping fragment lengths were grouped in seven multiplex pools, comprising two to five

Table 2 Geographic origin of the samples used to calculate genetic diversity parameters and genetic structure

Country/region of origin	No. of vitis sativa varieties	No. of vitis sylvestris accessions	Total no. of accessions
Armenia	104		104
Azerbaijan	66	50	116
Georgia	104		104
Eurasia	15		15
Total	287	50	339

nSSR markers. PCR was conducted with the 2x KAPA2G Fast PCR Kit (Düren, Germany). Therefore, 1 ng of DNA was deployed to prepare 5 µL reaction mixtures containing the master mix and 100 pmol each of the two primers. The final reaction was carried out in a GeneAmp PCR system 9700 thermal cycler (Applied Biosystems, Schwerte, Germany) with an initial denaturation of 3 min at 95 °C, followed by 30 cycles of denaturation at 95 °C (15 s), annealing at 60 °C (30 s), and extension at 72 °C (30 s). A final extension was performed at 72 °C for 5 min. For the subsequent fragment length determination by capillary electrophoresis on an ABI 3130xl Genetic Analyzer (Applied Biosystems, Life Technologies, Waltham, MA, USA), 1 µL of the PCR product was applied and the results were evaluated with GeneMapper 4.0 software (Applied Biosystems, Life Technologies, Waltham, MA, USA). Allele sizes in base pairs were determined by comparing the fragment peaks with the internal size standard. To harmonize amplification shifts among different multiplexes, the results of single peaks were corrected according to the standard cultivars ‘Cabernet franc’ and ‘Muscat à petits grains blancs’. Final genetic profiles (in base pairs) of the analysed accessions are provided in Supplemental Table S2.

Genetic diversity parameters and genetic structure

For the calculation of genetic diversity parameters and genetic structure, modern crosses (mainly from the 20th century) of the South Caucasus were not included due to contributing alleles of foreign varieties not native to the South Caucasus, like ‘Muscat of Alexandria’ and ‘Muscat of Hamburg’. Likewise, the I.C. ‘Villard Blanc’ and ‘Dattier de Saint-Vallier’ offspring contributing alleles originating from North American species were excluded from analysis. From the original dataset, in total 339 genotypes were retained, consisting of 287 traditional Caucasian and Eastern European grapevine varieties and 50 wild *Vitis sylvestris* accessions from Azerbaijan. The geographic origin of the samples is shown in Table 2. The predefined groups based on the geographical origin used for Structure analysis are indicated in Supplemental Table S1.

GenAlEx (version 6.5) was used to determine the number of different alleles (Na), the number of effective alleles

(Ne), number of private alleles (No. Private Alleles), number of locally common alleles found in 50% or fewer populations (No. LComm Alleles ($\leq 50\%$), Shannon's Information Index (I), observed heterozygosity (Ho), expected heterozygosity (He) and the fixation index / inbreeding coefficient (F) [67].

Bayesian clustering was performed with Structure (version 2.3.4) to infer the number of genetic populations (K) and to assign genotypes to populations based on genetic ancestry values independent of their geographic origin [26, 27, 32, 69]. Configuration was set as follows: admixture model, correlated allele frequencies, putative populations (K) tested from 1 to 8 with a burning time and replication number of 50,000, respectively and 10 independent iterations for each run. The stability and convergence of MCMC chains (Markov chain Monte Carlo) was ensured by visual inspection of the α and F_{ST} data plots in Structure for each run and the comparison of the $LnP(D)$ (estimated log-likelihood of the data) for each iteration within each K. In addition, it was verified that there was no label switching (multimodality of ancestry values) for any genotype within the 10 iterations for each K. The most likely number of clusters (best K) was assessed using the ad hoc delta K statistic (ΔK) as described by Evanno et al., [24] using Structure Harvester [22]. The respective Structure bar plot was created via Clumpak [40]. Additionally, the R software environment (<https://www.r-project.org/>) was used to further explore the data. The pairwise fixation index F_{ST} was calculated (implemented in R/hierfstat) to quantify the genetic differentiation between populations and statistical significance assessed using 1,000 bootstrap replicates to determine the 95% confidence intervals [30]. Population structure with a discriminant analysis of principal components (DAPC; implemented in R/adegenet) was applied [34]. Groups were defined a priori based on the origin of the samples. The optimal number

of principal components was determined via cross-validation (xvalDapc) with 30 replicates, and all discriminant functions (n.da) retained as recommended for a small number of populations.

Parentage analysis

Cervus software (version 3.0.7) was applied using the 24 nSSRs to infer parents-progeny Trios and first-degree relationships [36]. We only accepted perfect matches (no mismatch at any locus) with a confidence level of 95% and an assumed error rate of 0.02. Colony software (version 2.0.6.6), a likelihood-based method for pedigree reconstruction, was used to determine prominent missing progenitors, e.g. parents completing full-sibs and revealing further parent-offspring relationships, as well as to infer their allelic profiles [35]. Only reconstructed allelic profiles showing a 100% match at the first and second estimated allele on all 24 nSSR markers and where no further alleles were proposed, have been retained.

Results

Grapevine genetic diversity and genetic structure in the South Caucasus

Genetic data from 24 nSSRs of 339 retained genotypes with an autochthonous genetic background were divided into four genetic groups/populations based on their geographic origin and compared with the *Vitis sylvestris* outgroup (Table 2). With the allelic profiles, statistical indices were calculated and diversity within and among the groups was determined (Table 3). The number of different alleles (Na) and the number of effective alleles (Ne) do not differ significantly among the different groups, ranging from 9.71 to 11.63 and 4.55 to 5.25, respectively. Nevertheless, the number of private alleles was 0.42 for Azerbaijan and 0.46 for Georgia, as well as 1.21 for *Vitis sylvestris* and 1.29 for Armenia indicating a moderate, but higher level of genetic variability in these last two groups. I value was slightly higher in Armenia (1.84), compared to the other groups (~1.7), while No. LComm values were similar across groups, with Georgia (1.58) and Armenia (1.5) slightly higher. For nSSR markers efficiency, the observed and the expected heterozygosity (Ho, He) are considered to evaluate the genetic variability among the tested samples, with lower values of Ho in conjunction with the results of the fixation index / inbreeding coefficient indicating the existence of inbreeding. Based on our results for the cultivated varieties, the differences between Ho and He were not significant and the inbreeding coefficient is zero or slightly negative, specifying random mating, whereas the fixation index of 0.1 for the *Vitis sylvestris* population indicates a minor degree of inbreeding.

To identify the genetic structure among the three geographical groups in relation to the wild grape *Vitis*

Table 3 Allelic patterns of the 339 selected genotypes at 24 nSSR loci based on their origin

Parameter	Armenia	Azerbaijan	Georgia	<i>Vitis sylvestris</i>
Na	11.63	10.25	9.96	9.71
Ne	5.25	4.80	4.69	4.55
No. Private Alleles	1.29	0.42	0.46	1.21
I	1.84	1.74	1.70	1.70
No. LComm Alleles ($\leq 50\%$)	1.50	1.38	1.58	1.38
Ho	0.78	0.79	0.76	0.67
He	0.78	0.76	0.75	0.75
F	0.00	-0.03	-0.02	0.10

Na=number of different alleles, Ne=number of effective alleles, I=Shannon's Information Index, No. LComm Alleles ($\leq 50\%$) = number of locally common alleles found in 50% or fewer populations, Ho=observed heterozygosity, He=expected heterozygosity, F=fixation index / inbreeding coefficient

sylvestris from the territory of Azerbaijan, a Bayesian clustering analysis implemented in the program Structure was conducted (Fig. 1A). A clear subdivision on the population level could be detected. Based on the method of Evanno et al., [24], $K = 3$ captures the uppermost level of genetic structure, indicating three different clusters (Supplemental Fig. 1). Most individuals showed a major membership proportion of ≥ 0.70 to one of the three proposed groups based on the averaged ancestry values for $K = 3$ (Supplemental Table S3), with only 13% of individuals being admixed and Georgia showing the highest number of admixed samples (around 30%). Pop1, accounting for 182 genotypes, grouped mainly Armenian (92) and Azerbaijani (59) individuals and a few Georgian (10) samples, Pop2 grouped mainly Azerbaijani (49 out of 64) individuals, *Vitis sylvestris* and some Georgian samples (14 out of 64), while Pop3 grouped mainly Georgian samples (42 out of 49). The results indicate a significant overlap between the Armenian and Azerbaijani gene pools, whereas the Georgian varieties were mainly independent, with a significantly higher degree of intermixing, especially with the wild grape *Vitis sylvestris*. This could only

be observed at a low rate for Armenian or Azerbaijani varieties, although the *Vitis sylvestris* samples originated from Azerbaijan.

To further validate the found results, a discriminant analysis of principal components (DAPC) (Fig. 1B) and the pairwise fixation index F_{ST} (Supplemental Fig. 2) were utilised. Both additional analyses confirmed the Structure analysis, suggesting three genetic groups. The samples from Armenia and Azerbaijan cannot be distinguished, displaying one genetic group. From the Armenian and Azerbaijani samples, wild grapes are clearly separated and distinctive along discriminant function 2 (Df2), which accounts for 6.09% of the variance, whereas the Georgian samples are differentiated along Df1, explaining 6.42% of the variance. The Georgian samples are much closer to the Armenian and Azerbaijani cultivated grapes. Based on the obtained results, genetic differentiation within the South Caucasus grape gene pool is very low, indicating a high level of interconnection, with Georgia exhibiting the closest continuity between wild and cultivated forms.

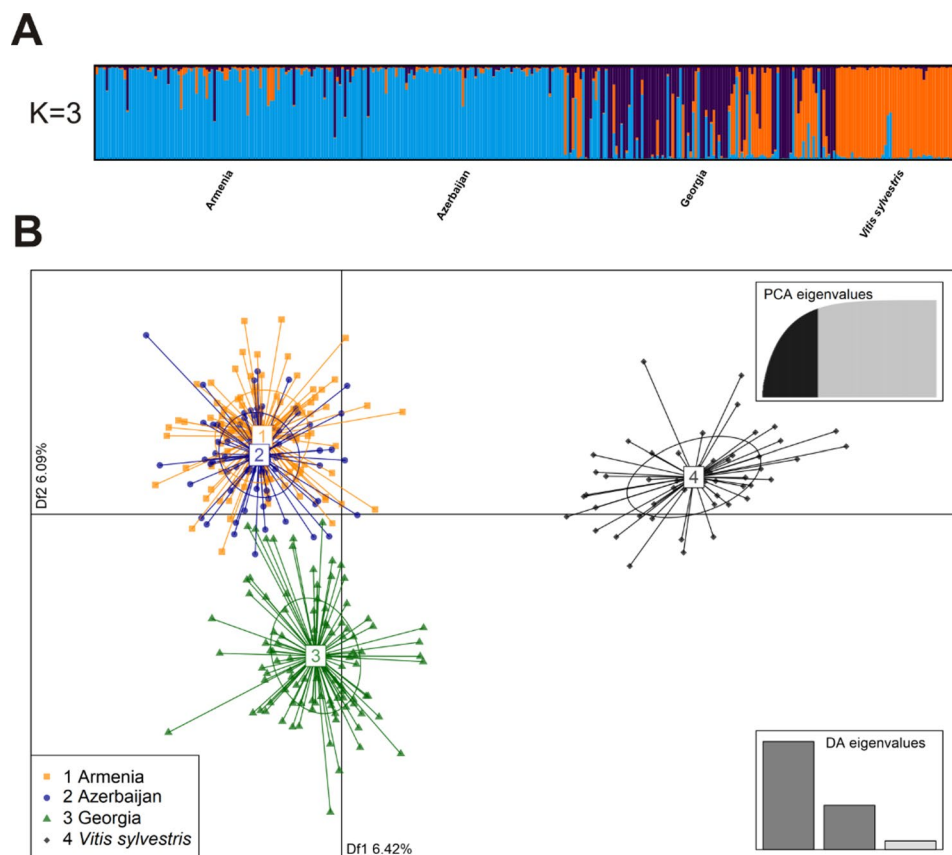


Fig. 1 Bayesian clustering (A) and discriminant analysis of principal components (DAPC) (B) results of the 339 selected accessions based on their origin. (A) Barplot (Q-matrix) displaying the admixture proportions as estimated by Structure for $K = 3$. Each accession is represented by a single vertical bar divided into three colour segments representing its genetic proportions in each cluster. (B) Df = discriminant function, PCA = principal component analysis, DA = discriminant analysis

Kinship analysis

The initial data set for kinship analysis comprising 24 nuclear microsatellite markers included 425 non-redundant genotypes.

Colony, a likelihood-based method for pedigree reconstruction was performed based on the 425 unique accessions, aiming at the identification of missing ancestors in the data set. From the proposed reconstructed genetic profiles only two genetic profiles resulted, which theoretically came into consideration as putative parents, keeping in mind that several distinct genotypes very closely related (full-sibs or half-sibs) could have been genitors as well. The two genetic profiles were retained as possible ancestors, because for each locus exactly two alleles were proposed and compared to the about 8,000 unique genetic fingerprints of the JKI-ZR-SSR marker database (over 6,600 genetic profiles assignable to specific varieties are available at <https://www.vivc.de/> perfect match corresponded to the Georgian table grape variety ‘Mskhviltsvala Tetri’, genotyped at 6 loci in the scope of the GrapeGen06 project [56] and available via private access in the European *Vitis* Database (www.eu-vitis.de). Interestingly, this variety was also found as a single old vine in 2022 in the Tavush region of Armenia, neighbouring the Georgian border [53]. The second inferred genotype (designation in VIVC: Reconstructed Genotype 51 (GEORGIA), VIVC variety number: 42428) was not present in the four nSSR marker databases of JKI-ZR, INRAE Vassal grape repository, CREA Conegliano (Manna Crespan, personal communication) and University of Trento (Stella Grando, personal communication) and its derived role should therefore be interpreted with caution.

First order parentage analysis (the putative parent and the progeny shared at least one allele on all analysed loci) using Cervus software identified 208 first-degree relationships with 196 grape varieties (46%) being involved, while 231 genotypes (54%), representing 180 (42%) *sativa*, did not show any genetic relatedness. For all putative parentages, no mismatch was accepted at the analysed nSSR loci. LOD scores of the 208 first-degree relationships, prime names and VIVC-variety numbers are listed in Supplemental Table S4. In addition, chlorotype (maternally inherited) [2] and flower sex are provided, useful for the determination of cross direction. Respective information was taken from the VIVC. The category of the variety (traditional or modern cross), parent offspring combination (Trio: full parentage verified; Duo: verification of parent-offspring relationship), relationship between the cultivars (parent-offspring (PO), offspring (Off), parent 1 (P1) and parent 2 (P2) and comments, mainly referring to previously detected parentages are shown in Supplemental Table S4.

Full parent-offspring and parent-offspring combinations

Forty-eight Trios were detected. Two of them, ‘Csaba Gyoengye’ and ‘Muscat of Hamburg’, being of Western European origin, were not considered hereinafter. They served as references for LOD scores. Thus, from the 46 remained Trios, 22 were traditional varieties and 24 represented modern crosses. List of Trios is reported in Supplemental Table S5. Most of the 22 traditional varieties originated in Georgia (16), four were from Azerbaijan and two from Armenia. Georgian offspring had Georgian ancestors only, whereas for Armenian and Azerbaijani offspring, parents were from the two countries, sometimes mixed or all two from the opposite country. From the 24 modern crosses, 20 belonged to *sativa* and four were IC. Twelve of them were bred in Georgia, nine in Azerbaijan and one in Armenia, Moldova and Uzbekistan, respectively. From the 46 full parentages, 45 Trios were detected in this study for the first time.

From the 427-genotype panel, 104 Duos (i.e. sharing of one or more alleles at each nSSR locus) were inferred, from which 73 were traditional varieties and 31 represented modern crosses. Duos are reported in Supplemental Table S4. Territorial links of cultivars are displayed in Supplemental Table S6. Most Duos of traditional varieties sharing the same country of origin, turned out to be from Georgia (35), followed by Azerbaijan (11). Armenia contributed 5 and Uzbekistan 1 PO-combination. In six cases, Armenian and Azerbaijani varieties were related. The remaining 16 PO-combinations represent intertwining relationships between Caucasian and Eurasian varieties or were of unknown origin. From Georgia, 11 modern crosses were in the data set, 8 from Azerbaijan and 6 from Armenia. Twenty-nine Duos of 25 traditional varieties and 4 modern crosses, were already found in prior studies (Supplemental Table S4). Hence, 75 Duos are reported here for the first time.

Role of the two genitors inferred via colony

‘Mskhviltsvala Tetri’ and ‘Reconstructed Genotype 51 (GEORGIA)’ appeared to have been progenitors of six putative full parentages (Fig. 2). In addition, seven full-sibs of ‘Reconstructed Genotype 51 (GEORGIA)’ and ‘Gabasha’ were identified and an offspring of ‘Reconstructed Genotype 51 (GEORGIA)’ and ‘Grdzelmtevana Institutis’. ‘Mskhviltsvala Tetri’ and ‘Reconstructed Genotype 51 (GEORGIA)’ were also due to most likely 4 and 9 half kinships, respectively.

Main contributors to kinships

The frequency of contributors to kinships is reported in Supplemental Table S7. The most prominent variety identified in this dataset was ‘Reconstructed Genotype 51 (GEORGIA)’ with 23 parent-offspring (PO) relationships,

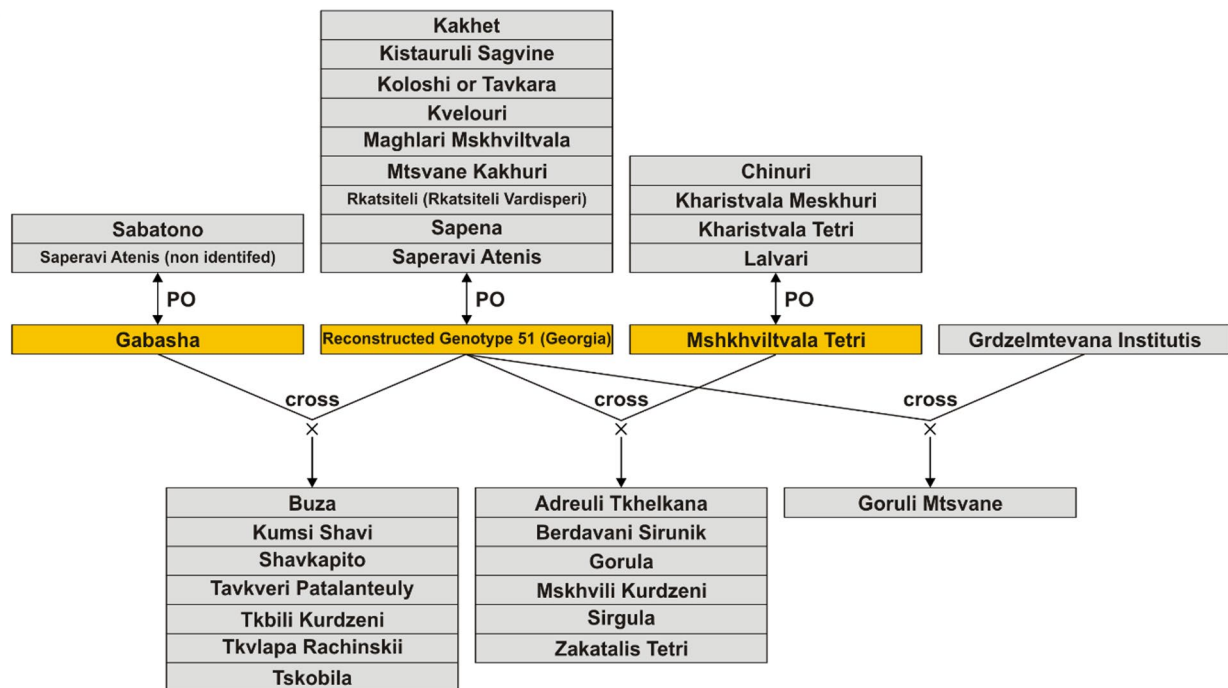
A**B**

Fig. 2 Pedigree tree for the most prolific grapevine varieties of Georgia (A) and Azerbaijan (B). PO = parent-offspring relationship

followed by ‘Muscat of Alexandria’ used in breeding programs, ‘Mskhviltvala Tetri’, ‘Shaani belyi’ and ‘Gabasha’ with 13, 10, 9 and 9 POs, respectively (Fig. 2). The high number of ‘Tebrizi’, ‘Sultanina’ and ‘Rkatsiteli’ relationships with 9, 8 and 8 POs, respectively, reflect breeder’s activities. The formerly non-identified ‘Genotype 77’ from Tavush region [50], named ‘Berdavani Sirunik’, displayed 6 POs.

Discussion

Genetic diversity and genetic structure

The historical origins and development of grapevine genetic resources in the South Caucasus can be considered largely analogous, owing to the shared geographical region. According to Dong et al., [21], the wet climate of the Early Holocene facilitated the expansion of suitable habitats for *Vitis sylvestris* populations (Syl-E) across a wide area, including the South Caucasus. This period marks a likely starting point for grapevine cultivation in this region. However, the evolution and selection of

cultivated grapevines in the South Caucasus have been shaped by various historical, ecological, and cultural factors. Key contributors to this process include the macro- and microclimate, such as the humid conditions of Western Georgia versus the more arid climates of Eastern Georgia, Armenia, and Azerbaijan. The geographical diversity, from the Greater Caucasus Mountain range to the lowlands of Colchis and the Kura-Arax, also played a significant role with soil variations driven by climatic and geological factors [86]. The region’s position at the cross-roads of Asia and Europe, intersected by key trade routes (including branches of the Silk Road), significantly facilitated the introduction and exchange of grapevine varieties. Furthermore, during the 10th century AD, when Azerbaijan began to adopt Islam, the population preferably selected table grapes, unlike Georgia and Armenia, where the adoption of Christianity in the 4th century AD led to the continued development of grapevine varieties suited for winemaking. Other factors, such as human migration, the transfer of grapevine varieties between

regions or the long-standing dominance of large unified states further contributed to the complex viticultural history.

Negrul et al., [65] classified the diverse gene pool of Eurasian grapevine varieties into three *proleses* based on morphological traits: *orientalis*, *pontica* and *occidentalis* (Negr.), which was later validated through molecular markers (e.g., Bacilieri et al., [3]. Despite the relatively small geographic area of the South Caucasus, grapevine varieties from this region are primarily classified into two broad groups, *pr. pontica* and *orientalis* (Negr.). The Western Georgian varieties are typically classified within the *pontica* (Negr.) group (*subpr. Georgica* (Negr.)), while a small number of varieties from Eastern Georgia, Armenia, and Azerbaijan fall within the *orientalis* (Negr.) group, particularly in the *Caspica* (Negr.) subgroup. This classification may help explain the closer genetic relationship between Armenian and Azerbaijani grapevine varieties, in contrast to the distinction of Georgian varieties (see Fig. 1B). The cultivated grapevine gene pools of Armenia, Azerbaijan, and Georgia exhibit comparable levels of genetic diversity and population structure, suggesting that viticulture in the South Caucasus has followed parallel evolutionary and cultural paths. Allelic richness and effective allele numbers are similar across the three countries, and the narrow differences between observed and expected heterozygosity, along with low fixation indices, imply that these groups largely retained the signatures of random mating. A significant distinction lies in the frequency of private alleles, with Armenian cultivars harbouring nearly three times as many unique alleles as those from Azerbaijan or Georgia. This discrepancy is not solely due to sampling strategies but reflects recent extensive surveys in Armenia, which revealed both historically documented landraces and previously unknown grapevine lineages [50]. The observed genetic relatedness between the Armenian and Azerbaijani grapevine gene pools is most likely the result of a combination of biological and socio-political factors. At the biological level, both regions appear to have drawn upon overlapping populations of *Vitis sylvestris* native to the South Caucasus, which would have provided a shared ancestral genetic foundation. This overlap was most likely further reinforced over the centuries through trade, migration, and agricultural exchange, which facilitated the movement of grapevine material across political territories. The Russian Empire, which dominated the South Caucasus from the early 19th century, and the subsequent Soviet era during the 20th century, further intensified these interactions through the centralization of viticulture. During this period, Armenia was designated as a centre for brandy production, Georgia for wine production, and Azerbaijan for both table grape and wine production [45]. Large-scale breeding programs

were implemented, and the exchange of plant material between research institutions in the three republics was routine.

In conclusion, the data indicate that Armenian and Azerbaijani cultivars share a closely related genetic background, while Georgian varieties appear more genetically connected to wild grapes. To fully unravel these relationships, further comprehensive studies across research fields will be crucial to clarify the true structure of the South Caucasus grapevine gene pool, with important implications for viticulture, conservation and breeding.

Kinship analysis

In the past, huge efforts were made to elucidate the complex genetic relationships within the cultivated compartment of grapes using nSSR- and/or SNP-markers as reflected in more than 100 respective articles recorded in the VIVC. Multiple reasons are driving these efforts. Here are some examples:

- unravelling the ancestors of famous varieties like ‘Merlot’ [9], ‘Tempranillo’ [33] and ‘Barbera’ [70]. Numerous ancestors of these renowned grapes are minor or rediscovered varieties like ‘Blaue Zimmettraube’, which represented the missing link for the full parentage of ‘Blauer Portugieser’ (‘Blaue Zimmettraube’ x ‘Silvaner’) [58].
- detection of founder and migrating varieties like ‘Heunisch Weiss’ [8] and ‘Heben’ [87].
- validation of breeders’ records to have certainty on trait transfer to the offspring [5, 19, 41].
- examination of varieties relationships and understanding of genetic admixture in a geographically smaller [12, 49, 89] and broader context [13, 18, 41].

All the above quoted criteria apply to genetic relationships found in the South Caucasian genepool. However, the direction of crosses could not be determined, as chloroplast markers were not included in this study.

In previous studies, Colony software successfully reconstructed genetic profiles, completing complex pedigree networks and proving the existence of a once distinct cultivar landscape and presumable loss [12, 50, 70]. That was the case in this research as well. Colony software inferred two clear-cut genetic profiles, where for each of the 24 nSSRs only two alleles were proposed. One of them corresponded to the white table grape variety ‘Mskhivtvala Tetri’ from Kartli province, Georgia, whereas ‘Reconstructed Genotype 51 (GEORGIA)’ was not present in any of the four consulted nSSR-databases. There are several scenarios possible: (1) ‘Reconstructed Genotype 51 (GEORGIA)’ was replaced by

better performing progenies, (2) became rare and (3) got lost or (4) it is still present in old vineyards (5) and/or maintained in one of the Georgian grape vine collections. Sargolzaei et al., [79] enumerated about 525 varieties existing in Georgia. From that number only 119 were involved in this study and approximately another 100 genotypes were checked in consulted nSSR-data bases. Thus, there is a strong possibility that the missing 'Reconstructed Genotype 51 (GEORGIA)' may still be identified through further investigation of additional germplasm collections, particularly from Eastern Europe and Central Asia.

'Mskhviltvala Tetri' and 'Reconstructed Genotype 51 (GEORGIA)' uncovered a high number of genetic relationships between Georgian varieties. The two varieties created six full-sibs 'Adreuli Tkhelkana', 'Gorula', 'Mskhvili Kurdzeni', 'Sirgula', 'Zakatalis Tetri' and 'Berdavani Sirunik' (= Genotype 77 in Margaryan et al., [50]. 'Berdavani Sirunik' was found in Tavush region, village Berdavan close to the Georgian border. Another seven full-sibs are offspring of 'Reconstructed Genotype 51 (GEORGIA)' and 'Gabasha', namely 'Buza', 'Kumsi Shavi', 'Shavkapito', 'Tavkveri Patalanteuly', 'Tkbili Kurdzeni', 'Tkvlapa Rachinskii' (synonym 'Tkvlapha Rachuli') and 'Tskobila'. 'Goruli Mtsvane' is an offspring of 'Reconstructed Genotype 51 (GEORGIA)' and 'Grdzelmtevana Institutis'. 'Goruli Mtsvane' is a renowned wine grape in Kartli province (a map of Georgia with its provinces is given in Supplemental Fig. 3), also spread in Kakheti and Imereti regions in a small amount [38, 71], as well as its half-sib 'Mtsvane Kakhuri', grown in Kakheti province. 'Reconstructed Genotype 51 (GEORGIA)' is inferred as a likely progenitor of 'Rkatsiteli', the most prominent to cite and the most emblematic Georgian white grape variety, mainly spread in Kakheti province and also in the neighbouring Kartli province, covering the 3rd position of the World vineyard area for 1990 [1]. This finding is in contrast to a previous study [3], where, owing to a small number of Georgian genotypes, Caucasian germplasm showed a low frequency of family-related individuals. This had led to the assumption of a slower breeding activity in that region. Very likely, 'Mskhviltvala Tetri' and 'Reconstructed Genotype 51 (GEORGIA)' that appear to have been the main Georgian genitors might have produced further offspring, which were not included in the data set shaping the country's variety diversity. A similar situation was observed, for example, in the Italian variety landscape [13].

With 16 Trios and 35 Duos of traditional and 12 Trios and 11 Duos of modern varieties, far more relationships were detected among Georgian cultivars. One reason might be that Georgia contributed the highest number of genotypes to the panel. Azerbaijan accounted for four Trios and 11 Duos of traditional and nine Trios and eight

Duos of modern varieties. From the Armenian genepool where 62 Trios and 185 half-kinships were found in a previous study [50], only relationships of those varieties from the AZE007 and COST Action FA1003 samples were considered. Thus, only two Trios and five Duos of traditional Armenian varieties and one Trio and six Duos of modern crosses were detected. However, examination of the varieties used, taken from VIVC (Supplemental Table S1), provided an interesting issue: 34% of the 65 Azerbaijani traditional varieties revealed mono use as table grapes, 11% of 102 Armenian and 3% of 97 Georgian traditional varieties, respectively. Could a simple explanation for the low number of genetic relationships in the Azerbaijani genepool mean that table grapes were less in the focus of strict selection than wine grapes? Could this explain why the table grapes group from Eastern Europe was shown to be by far the most diverse [3]? Another idea to take into account is that, since Antiquity and the Middle Ages, wine grapes used to be preferably propagated vegetatively, whereas table grapes were more often propagated by seeds [41]. Hence, the number of sexual crosses (and improvement) is much more important for table grapes.

Detected Trios of traditional varieties are suggesting national/regional restricted spontaneous hybridization, at least with respect to Georgia. From today's point of view and according to the bibliography, 'Reconstructed Genotype 51 (GEORGIA)' seem to have been present in Racha-Lechkhumi, Kartli and Kakheti provinces, where most of its offspring are still grown (a map of Georgia with its provinces is given in Supplemental Fig. 3). Genetic relatedness of half sibs 'Goruli Mtsvane', 'Sapena' and 'Rkatsiteli', neighbouring each other in a single cluster, was indicated in the study of De Lorenzis et al., [15] using an 18 K SNP-Chip. In fact, the first main cluster of the cited study, composed of 17 varieties, includes twelve offspring of the three main progenitors analysed in this study, corroborating the findings of the present work. Genetic relatedness of the remaining five varieties with one of the three founder grapes is in all probability. Interestingly, Georgian ampelographers described morphological similarity of half sibs 'Kumsi Shavi', 'Kvelouri' and 'Buza' and the similarity of 'Mskhviltvala tetri' and 'Gorula', which are not easy to distinguish from each other [39], confirming the outcome of the present study. In addition, according to phenotypical observations, 'Mskhviltvala tetri' progenitor of full sibs 'Gorula' (Kartli) and 'Sirgula' (Kakheti) was said to belong to the same group of varieties [84]. Detailed comments regarding the varieties involved in Trios and a map of Georgia with its provinces is given in Supplemental Table S8. Differentiation of Armenian and Azerbaijani contributors of Trios revealed weaker, indicating a common genepool. For example, the non-identified genotype 'AZE007 N° 104'

turned out to be the presumed progeny of the renowned 'Areni Sev' and ancient 'Hatisi' from the Armenian gene-pool. The two Azerbaijani varieties 'Azerbaijani Novrast' and 'Gyalshan' most likely are a cross of 'Shafei/Ambari' from Armenia/Azerbaijan and 'Shaani Belyi' from Azerbaijan and a cross of 'Shrkhan' from Armenia and 'Ala Shaani' from Azerbaijan, respectively.

Twenty-two Duos of traditional varieties showed geographically mixed ancestry that is to say with different countries of origin. For example, the Duo 'Sultanina' and 'Naose' questioned the country of origin of the two varieties given in VIVC, Turkey and Afghanistan, respectively. In addition, several spontaneous offspring of 'Sultanina' were deduced [13, 41, 43], pointing to its more South Caucasian or even Central Asian origin and consequently establishing the link to 'Naose' from Afghanistan. However, due to the very early diffusion of Sultanina, it is difficult to know its place of birth. Accordingly, because the country of origin of 'Sultanina' is undeterminable, Central Asia was entered as the region of origin in VIVC. Likewise, 'Dana Burnu' very probably originated in Azerbaijan and not in Turkey, due to its presence under various names in Azerbaijani grape collections and owing to the two inferred PO-relationships with 'Ala Shaani' and 'Shaani belyi'. This observation was corroborated by Structure-analysis in the present study. Because grapes are not bound to countries, further geographical origins were specified. For example, 'Dzrali' and 'Lalvari' are considered to have originated on Armenian or Georgian territory. Thus ARM/GEO was determined as country of origin. They were found in Tavush region of Armenia, however their ancestry and synonyms 'Shaba' for 'Dzrali' and 'Buera' and 'Zerdagi' for 'Lalvari' indicate also Georgian origin. These synonyms do not appear in ancient literature. However, identity was stated during COST Action FA1003 via comparison of genetic profiles and ampelographic features description [37, 45, 46].

In the three South Caucasian countries, grape breeders were highly active in creating new wine and table grapes during the 20th century. From Armenian, Georgian and Azerbaijani breeders 178, 79 and 20 modern crosses are registered in the VIVC, respectively. In the present study, some varieties, for which no breeders' data were available, were identified as modern crosses according to their parents (Supplemental Tables S4 and S5). For instance, Georgian grape breeders often used 'Muscat of Alexandria', 'Rkatsiteli', 'Tavkveri' and 'Tebrizi'. 'Angur Kalan', 'Chaouch Rozovyi' and 'Shaani belyi' were often employed by Azerbaijani breeders. With regard to that knowledge, we supposed that 'Ag Beilagani', 'Nagshabi' and 'Sultany Kishmishy' are most likely modern Azerbaijani varieties. 'Meskhuri Shavi' from Meskheta region in Georgia, proved to be a progeny of the female 'Tavkveri' and 'Pinot'. 'Elmin', 'Khart Khart (non-identified)' and

'Nr. 17' turned out to be half-sibs with the French fungal resistant cultivar 'Dattier de Saint-Vallier' as progenitor. Most likely 'Dattier de Saint-Vallier', created in France around the 1930's or 1940's, existed in Azerbaijani grape collections under a different name, because nothing is known about this variety in that country. On the other hand, parentage given by breeders for 'Elmin' was 'Tebrizi' x "Mixture of pollen of fungal resistant varieties", corroborating this finding. However, instead of 'Tebrizi', 'Chaouch Rozovyi' is proposed as the female parent. Hence, the present study also allowed validating and adapting breeders' records. Some cross combinations were only half confirmed, e.g. for 'Aguna'. Instead of 'Muscat of Hamburg' and 'Tebrizi' the cross parents were 'Muscat of Alexandria' and 'Tebrizi'. 'Nakhulbakhevi' and 'Saamo' were supposed to be offspring of 'Muscat of Alexandria' and 'Tebrizi', and 'Muscat of Alexandria' and 'Angur Kalan', respectively. 'Muscat of Alexandria' was confirmed, whereas 'Tebrizi' and 'Angur Kalan' were rejected. In these two cases, the second parent was not present in the data set. Respective information for all crosses is shown in Supplemental Tables S4 and S5.

45 out of 46 Trios were detected for the first time. The progenitors of 'Kishmish Kishrau' were previously reported [41, 50, 64]. The pedigree of 'Tchragi Spitak', for which the parents 'Tchragi Erkser' and 'Genotype 60' were proposed by Margaryan et al., [50], was modified. In the present study 'Tchragi Erkser' was confirmed and the Armenian/Azerbaijani variety 'Shafei/Ambari' was identified as the second parent (Supplemental Table 5). 29 Duos of 25 traditional varieties and 4 modern crosses were already found in prior studies (Supplemental Table S4). Hence, 75 Duos are reported for the first time, shedding light on the relatedness of South Caucasian germplasm and contributing new relationships for the VIVC.

The South Caucasian sample-set, comprising Armenian, Azerbaijani and Georgian accessions, consisted of 193 traditional varieties (excluding modern crosses). From this sample set, 63 (33%) varieties showed genetic relationships, whereas 130 (67%) were unrelated. Missing relatives might have disappeared, unfortunately and thus will never be recovered. However, they could still be present in the countries germplasm repositories or may still exist in old vineyards. Further efforts intending recovery of South Caucasus grape germplasm is needed to find missing ancestors before stating the presence of genetic erosion.

In conclusion, our results demonstrate that the South Caucasus represents a reservoir of unique grapevine genetic resources, with Armenia showing the highest allelic richness, Azerbaijan a distinctive proportion of table grapes, and Georgia a strong interconnection of local varieties shaped by a few key ancestors. Grapevine cultivation represents a strategically important

agricultural sector in these countries whose relevance extends beyond economic value. The contribution shapes rural livelihoods, landscape stability, and diversified agricultural economies, which are key components of regional food security frameworks. The genetic diversity within grapevine populations plays thereby a fundamental role in addressing the mentioned and future challenges. A broad genetic base enhances the capacity of viticultural systems to adapt to environmental stressors, including drought, heat, and emerging pathogens. In particular, the preservation and utilization of local and indigenous grapevine varieties are crucial, as these genotypes often possess unique adaptive traits shaped by long-term evolution under specific environmental conditions, like the recent discovery of the resistance locus *Ren1* in Armenian wild grapes [52]. These findings therefore lay a long-awaited foundation and underscore the need for the integrated use of this genetic diversity to promote breeding, sustainable viticulture and preserve the cultural heritage of one of the cradles of grapevine breeding.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40066-026-00645-5>.

Supplementary Material 1: Figure 1. Delta K plot.

Supplementary Material 2: Figure 2. Pairwise fixation index *F_{st}*.

Supplementary Material 3: Figure 3. Map of Georgia and its provinces.

Supplementary Material 4. Tables S1 to S8.

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Author contributions

FR: methodology, visualization, writing original draft, review and editing KM: formal analysis of Armenian grapevine germplasm, review and editing VS: formal analysis of Azerbaijani grapevine germplasm, review and editing DM: formal analyses of Georgian grapevine Germplasm, review and editing GDL: formal analysis, review and editing OF: formal analysis, review and editing VL: SSR data and database comparison, review and editing TL: formal analysis, review and editing RA: formal analysis of Azerbaijani grapevine germplasm MH: formal analysis of Azerbaijani grapevine germplasm AH: formal analysis of Azerbaijani grapevine germplasm RT: formal analysis, supervision OT: formal analysis, supervision EM: conceptualization, project administration, writing original draft, review and editing.

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Data availability

The authors confirm that all data generated or analysed during this study are included in this published article.

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Competing interests

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