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Insights into the genetic diversity and population structure of domestic geese in Russia: an exploratory study of native breeds using microsatellite markers

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Introduction: Presently, domestic geese remain genetically less studied farm animals. Goose breeding is a traditional branch of animal husbandry in Russia. Currently, the Russian goose gene pool includes 21 breeds of domestic and foreign origin; however, many populations have experienced a substantial decline and some are approaching extinction. Therefore, studies of genetic diversity and population structure are essential for developing effective conservation and breeding strategies aimed at preserving biodiversity.

Methods: Using 17 microsatellite (STR) markers, we investigated the genetic diversity and population structure of six Russian goose populations maintained exclusively in a conservation flock: Tula Fighting (TULA), Kholmogory White (KHLM_W), Kholmogory Gray (KHLM_G), Large Gray (LRGR), Vladimir Clay (VLDM), and Chinese Gray (CHGR). Genetic relationships among populations were analyzed to reconstruct genetic differentiation patterns and provide insights into their evolutionary history and conservation management.

Results: Genetic diversity indices varied considerably among populations. KHLM_W and KHLM_G exhibited the highest allelic richness ($A_R \geq 3.534 \pm 0.260$), whereas lower values were observed in the remaining populations (1.970 ± 0.213 in VLDM to 3.170 ± 0.193 in TULA). Expected heterozygosity (uH_E) ranged between 0.191 ± 0.050 in VLDM and 0.599 ± 0.036 in KHLM_G. Among all populations, KHLM_G showed the highest polymorphism levels across diversity indicators (A_R = 4.118 ± 0.196, H_O = 0.457 ± 0.054, uH_E = 0.599 ± 0.036). The inbreeding coefficient (uF_{IS}) indicated a generally low extinction risk across populations, although VLDM demonstrated a potentially vulnerable status (0.258). PCA, Neighbor-Joining, Neighbor-Net, and STRUCTURE analyses consistently identified two major genetic clusters, with TULA or LRGR occupying an intermediate position depending on the analytical approach.

Discussion: Genetic relationships inferred from microsatellite data were consistent with previous phenetic analyses and historical evidence regarding breed origins. Evolutionarily, CHGR and KHLM populations were associated with the Chinese lineage derived from the swan goose (*Anser cygnoides*), whereas LRGR represented the European lineage originating from the graylag goose (*A. anser*). Composite TULA and VLDM formed a European subgroup, while

TULA also exhibited features of an intermediate lineage. These initial findings demonstrate that Russian goose populations represent unique genetic reservoirs containing valuable adaptive diversity and emphasize their importance for conservation and future breeding programs.

KEYWORDS

A. cygnoides, *Anser anser*, gene pool, genetic diversity, microsatellite (STR) markers, population and evolutionary genetics, Russian goose breeds

1 Introduction

The genetic resources of farm animals, including poultry, constitute important components of global biodiversity and play an indispensable role in maintaining ecological balance and supporting human wellbeing (Moiseyeva, 1996; Qi et al., 2025). Livestock production in general, and poultry farming in particular, has substantial socioeconomic importance worldwide (Tereshchenko, 2008). Among poultry sectors, goose breeding occupies a distinct position due to its long historical tradition and economic significance. Currently, goose production continues to expand under different organizational systems, including industrial enterprises, commercial farms, and household production systems (Royter and Solovyov, 2021). The importance of goose production is associated with several valuable biological and economic characteristics. Goose meat is considered a high-quality product because of its complete protein content, abundance of B-group vitamins, favorable fatty acid composition, and relatively low cholesterol level compared with meat from other poultry species. In addition, geese provide valuable products such as liver, fat, down, and feathers, thereby increasing their economic importance (Tereshchenko et al., 2008). Geese also possess several production advantages, including large body size, high adaptability to intensive farming systems, and relatively strong resistance to diseases (Xu et al., 2004). Furthermore, indigenous waterfowl genetic resources, as carriers of unique and valuable genotypes, represent important subjects for evolutionary studies and biodiversity conservation programs (Romanov et al., 1995; 1999). These resources contribute significantly to ecosystem maintenance and provide a foundation for the sustainable development of waterfowl production systems (Li et al., 2012; Lai et al., 2018; Warzecha et al., 2019; Zinovieva et al., 2025; Qi et al., 2025).

An important component of preserving local animal genetic resources is their continuous monitoring of genetic diversity and population structure, along with investigation of genetic relationships and breed origins (Bondarenko and Kutnyuk, 1995; Bondarenko and Podstreshny, 1996; Moiseyeva et al., 2009; Dementieva et al., 2022). Such information provides an essential basis for developing evidence-based conservation strategies aimed at preventing the erosion of unique genetic resources and maintaining breed resilience under increasing anthropogenic and environmental pressures (Moiseyeva et al., 2003; Tagirov et al., 2010).

The Russian Federation possesses a unique gene pool of indigenous goose breeds that originated under diverse environmental and climatic conditions through long-term traditional breeding practices (IRPS, 1905; Martsev and Grishina, 2016). Currently, 28 goose breeds, including both native and imported populations, are officially recognized and approved for breeding in Russia (MARF, 2025; Zinovieva et al., 2025). These include several indigenous breeds (Table 1), such as Kholmogory (KHLM), Tula Fighting (TULA), Vladimir Clay (VLDM), and Large Gray (LRGR), as well as the Chinese Gray (CHGR) breed, which was introduced into Russia in the 18th century and subsequently adapted successfully to local conditions (Grishina, 2015). Among these populations, KHLM geese represent one of the oldest indigenous breeds and are characterized by large body size, hardiness, and high reproductive performance. TULA geese have historically been valued for their fighting abilities and distinctive conformation traits. The VLDM breed is characterized by favorable meat production traits, high egg productivity, and disease resistance. LRGR geese, developed from European (Toulouse) and local (Romny) breeds, exhibit rapid growth and excellent fattening ability. CHGR geese, characterized by high egg production and favorable incubation traits, contributed substantially to the development of several native composite goose breeds (see other breed-specific information provided in Appendix).

Despite its economic viability and potential, commercial goose farming in Russia lags behind global standards. One of the industry's key challenges is the threat of losing the unique germplasm flocks created at the All-Russian Poultry Research and Technological Institute (Sergiev Posad, Moscow Oblast, Russia) in the 1970s and 1980s (Bondarenko et al., 1986). Presently, the Upper Volga Federal Agricultural Research Center (UVFARC) is home to Russia's only gene pool collection for 21 goose breeds (Martsev and Grishina, 2016; Grishina and Zharkova, 2020; Martsev, 2020; UVFARC, 2026). Of particular value are the reserve breeds (TULA, VLDM, KHLM, Arzamas, Adler, and Pskov Bald) that are preserved exclusively in collection flocks and are at risk of extinction. While inferior to commercial crossbreds in overall productivity, these breeds possess unique economically important traits, i.e., strong bones, high-quality eggs, disease resistance, and increased eggshell strength (Grishina, 2011).

Furthermore, local goose populations face additional threats associated with global environmental changes. Climate change, biological invasions, habitat degradation caused by anthropogenic activities, environmental pollution, and land-use transformation increasingly expose indigenous goose populations to unprecedented challenges (Watermeyer et al., 2021). Similar trends involving the erosion of genetic diversity under the combined influence of global and local factors have been reported in many countries (Romanov et al., 2009). For example, in China, the introduction of modern European goose breeds characterized by rapid growth rates and high feed efficiency has resulted in their predominance within the commercial goose industry and has consequently contributed to a substantial decline in the population size of rare indigenous goose breeds (Qi et al., 2025). In Poland, fourteen goose breeds/populations have been incorporated into the national program for the

conservation of animal genetic resources (Warzecha et al., 2019), including the Zatorska population developed through crossing four varieties originating from either graylag (*Anser anser*) or swan goose (*A. cygnoides*) lineages (Jaszczak et al., 1996; Zawadzka et al., 1997).

Therefore, current strategies for preserving the genetic diversity of indigenous genetic resources increasingly require a shift from traditional phenotypic characterization toward molecular genetic approaches (Romanov and Weigend, 1999; 2001; Dementieva et al., 2021; Dotsev et al., 2025). Advances in high-throughput technologies and modern biotechnological tools have created new opportunities for monitoring genetic diversity and population structure in unique poultry populations, thereby facilitating the conservation and sustainable utilization of their valuable genetic characteristics (Zakharov-Gesekhus et al., 2007).

Molecular genetics provides robust and reliable instruments for investigating the genetic structure and diversity of animal populations (Katerinich et al., 2014; Francis, 2017). Early applications of DNA markers in domestic and wild geese involved analyses of restriction fragment length polymorphisms (Quinn and White, 1987; Quinn et al., 1987), mitochondrial DNA (Shields and Wilson, 1987; Van Wagner and Baker, 1990; Quinn et al., 1991; Avise et al., 1992; Quinn and Wilson, 1993; Nelson et al., 1996; Zink, 1996; Worthy et al., 1997), minisatellite DNA fingerprints (Hillel et al., 1989; Choudhury et al., 1993; Grunder et al., 1994; Millar et al., 1994; Rave et al., 1994; Rave, 1995; Larsson et al., 1995; Tegelstrom and Sjoberg, 1995; Tegelstrom and von Essen, 1996; Zawadzka et al., 1997), interspersed repetitive DNA families (Zhu et al., 1990; 1991), endogenous avian viral genes (Grunder et al., 1993), and random amplified polymorphic DNA (Horn et al., 1996; Shiau et al., 1996; Siwek et al., 2000; Bednarczyk et al., 2002). More recently, monitoring genetic diversity in animal populations has increasingly relied on advanced molecular approaches, among which microsatellite analysis remains one of the most informative and widely used techniques. Microsatellites, are also referred to as simple sequence repeats (SSRs) and short tandem repeats (STRs; Edwards et al., 1991), are tandemly repeated DNA sequences consisting of motifs typically ranging between one and ten nucleotides in length (Tautz, 1989). Microsatellite markers have been successfully applied for evaluating genetic diversity, investigating genetic relationships, breed/population identification, and monitoring inbreeding in both domestic and wild goose populations (Cathey et al., 1998; Fields and Scribner, 1997; Maak et al., 2003; Huang et al., 2005; Cao et al., 2014).

The utility of microsatellite markers for assessing the genetic status of rare and valuable domestic goose genetic resources has been demonstrated in many studies in China and Taiwan (Tu et al., 2006; Liu et al., 2006; Li et al., 2007; Lai et al., 2018), Poland (Warzecha et al., 2019), Slovakia (Mindek et al., 2014; 2018), and several other countries (Baublys et al., 2006; Juodka et al., 2012; Shnaf and Anwar, 2018; Abdel Moniem et al., 2019; 2021). For example, Qing-Ping et al. (2009), using 26 microsatellite loci to analyze the genetic diversity and population structure of local geese from the Taihu region of China, reported substantial genetic variation, alongside relatively low levels of inbreeding, despite reductions in breeding ranges. Lai et al. (2018), using 14 microsatellite markers from the genome of White Roman geese, demonstrated differences between private and breeding-station populations of Chinese geese, revealing heterogeneous population structure and emphasizing the need for optimized breeding strategies. The usefulness of microsatellite analysis for endangered local breeds was also demonstrated by Mindek et al. (2018), who performed a preliminary assessment of genetic diversity in Slovak-origin goose populations. These authors showed that low genetic diversity, genetic uniqueness, and small effective population size reflected the critical status of these populations, which preserve the genetic legacy of now-extinct indigenous geese. Likewise, an investigation of Polish goose breeds based on 15 microsatellite markers revealed high intrabreed variability in the White Kołuda breed, indicating substantial breeding potential (Warzecha et al., 2019). Collectively, these findings demonstrate the high informativeness of microsatellite markers for evaluating genetic diversity, detecting inbreeding risks, and designing conservation and breeding strategies for both endangered and commercially important goose populations (Liu et al., 2006).

Furthermore, contemporary goose research increasingly incorporates more advanced molecular genetic approaches, including whole-genome analyses, genomic evaluation of breeding value, and identification of genes associated with economically important traits, which are becoming standard tools in modern breeding and genetic studies (Qi et al., 2026; Zhou et al., 2026; Zhu et al., 2026; Chen et al., 2026). Nevertheless, goose populations maintained in the Russian Federation remain relatively understudied. Available studies have primarily focused on individual productive and biological characteristics (Galina et al., 2018; Ivanov et al., 2021; Grishina, 2023), whereas their genetic diversity and uniqueness based on genetic marker variation remain insufficiently characterized. Consequently, breeding programs continue to rely largely on traditional approaches. Preliminary studies of several Russian goose breeds using a limited number of microsatellite loci and relatively small sample sizes have been conducted to evaluate biodiversity and identify candidates for semen cryopreservation programs (Kharzinova et al., 2025; Zinovieva et al., 2025). However, further investigation of genetic diversity in Russian goose populations using contemporary molecular approaches remains essential for the development of effective breeding strategies and for the conservation and maintenance of indigenous genetic resources.

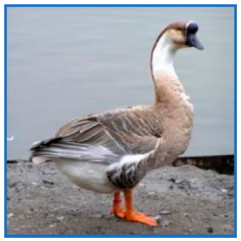
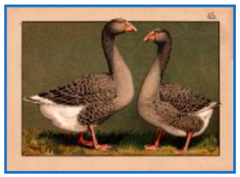
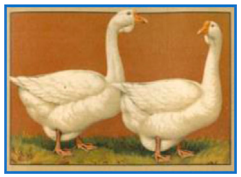
In this exploratory study undertaken as a substantial extension of our preliminary work (Kharzinova et al., 2025; Zinovieva et al., 2025), we investigated the genetic diversity of six populations representing five goose breeds from the UVFARC gene pool using microsatellite-based analysis. In addition, we examined genetic relationships among the studied populations to assess their current population structure and gene flow patterns. The results obtained provide a basis for improving the management of goose genetic resources and for optimizing future breeding and conservation programs.

2 Materials and methods

2.1 Ethics statement

The current study did not involve any endangered or protected animals. All procedures were performed according to the ethical guidelines of the L. K. Ernst Federal Research Center for Animal

TABLE 1 Goose breeds/varieties from the Russian gene pool collection examined using 17 microsatellite markers in this study.

Breed (code)	Origin and description	References
Chinese Gray (CHGR) 	Originated in Manchuria and subsequently spread throughout China before being introduced into Europe and Russia during the 18th century. Characterized by a prominent frontal knob at the base of the bill (gene *Kb*) . The plumage is gray-brown with a dark stripe extending along the neck and back (gene *Ns*) . CHGR geese were crossed with native Russian populations and contributed to the development of the Kuban, Pereyaslav, Kholmogory (KHLM), and Linda breeds. Included in the State Register of Breeding Achievements (SRBA; Rosinformagrotech, 2022) in 1993. Differs from the standard (white) Chinese goose mainly in plumage coloration, likely associated with variation in the candidate gene *KIT*	Fisinin and Zlochevskaya (1989); Pigarev (1989a); Martsev (2020); Zinovieva et al. (2025)
Tula Fighting (TULA) 	One of the oldest indigenous goose breeds in Russia, developed through traditional selection beginning in the 17th–18th centuries specifically for goose fighting, a historically popular activity in Russia, particularly in the Tula Governorate. Since the 19th century, the breed has also gained economic importance. Plumage occurs in white, gray (genes *C* and *G*) , and gray-piebald variants. The breed is characterized by aggressive behavior, a strong constitution, and exceptional endurance. Included in the SRBA (Rosinformagrotech, 2022) in 1993	Martsev (2020); Pigarev (1989c); Zinovieva et al. (2025)
Large Gray (LRGR) 	Developed in the mid-20th century. Breeding work began in Ukraine in the 1930s through crossing Romny and Toulouse geese followed by selective breeding. In 1941, development continued in Tambov Oblast using the same parental breeds. Plumage is predominantly gray (genes *C* and *G*) with white ventral regions. The breed is classified as dual-purpose (meat–fat type). Included in the SRBA (Rosinformagrotech, 2022) in 1993	Fisinin and Zlochevskaya (1989); Pigarev (1989b); Martsev (2020); Zinovieva et al. (2025)
Vladimir Clay (VLDM) 	Developed at the Pioneer Breeding Plant in Vladimir Oblast between the 1960s and 1980s. Created from Toulouse geese (for meat traits and body conformation) and KHLM geese (for reproductive performance, body size, and hardiness). Characterized by a distinctive clay-colored plumage pattern (genes C , *G* , *Sp* , *sd* (*TYRP1* or *MLANA*) and *Vc*). Included in the SRBA (Rosinformagrotech, 2022) since 1993.	Fisinin and Zlochevskaya (1989); Martsev (2020); Zinovieva et al. (2025)
Kholmogory White (KHLM_W) 	One of the best-known traditional Russian goose breeds. It is presumed to have originated in the Central Black Earth Belt region of Russia during the first half of the 19th century through crossing local geese with Chinese geese to improve reproductive performance. Characteristic features include a frontal knob at the base of the bill (gene *Kb*) , a dewlap under the bill (gene *Dl*) , and a ventral skin fold ("purse"). Plumage is predominantly white, although gray (genes *C* and *G*) and piebald variants also occur. The breed is valued for high meat productivity and cold tolerance and is widely distributed across several Russian regions, including Belgorod, Bryansk, Voronezh, Kursk, and Oryol Oblasts. Included in the SRBA (without color specification) in 1993 (Rosinformagrotech, 2022).	Fisinin and Zlochevskaya (1989); Pigarev (1989d); Martsev (2020); Zinovieva et al. (2025)

(*Continued*)

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TABLE 1 Continued

Breed (code)		Origin and description	References
Kholmogory Gray (KHLM_G)		A plumage variant of the KHLM breed distinguished primarily by its characteristic wild-type coloration, with gray-brown feathers on the back and wings and lighter ventral regions (genes C^+ and G^+). Other phenotypic and productive characteristics are similar to those of the standard KHLM breed	Fisinin and Zlochevskaya (1989); Pigarev (1989d); Martsev (2020); Zinovieva et al. (2025)

Genes:
[a]Autosomal dominant gene (ADG) for the frontal knob at the base of the bill (*Kb*).
[b]ADG, for the dark neck stripe (*Ns*).
[c]KIT, proto-oncogene, receptor tyrosine kinase (*KIT*; Wen et al., 2021).
[d]ADG, for plumage color (C^+; major color factor) and sex-linked (Z chromosome) dominant gene (SLZDG) for gray plumage coloration and absence of buff dilution (G^+).
[e]tyrosinase-related protein 1 (*TYRP1*; Xu et al., 2022; Wen et al., 2023a).
[f]melan-A (*MLANA*; Yang et al., 2022; Olli et al., 2026). Image credits: CHGR (Wikimedia Foundation, 2006; CC BY-SA, 3.0); TULA (IRPS, 1905; PD-old-70); LRGR (Wikimedia Foundation, 2005; CC BY-SA, 3.0); KHLM_W (IRPS, 1905; Wikimedia Foundation, 2007; PD-old-70); VLDM, and KHLM_G, authors' photographs.
[g]ADG, for absence of spotting (Sp^+), sex-linked (Z chromosome) recessive gene for absence of blue dilution (sd^+), and SLZDG, for brown dilution (Ve).
[h]Autosomal dominant gene for the neck skin fold (dewlap; *Dl*) (Bondarenko et al., 1986).

Husbandry (LKEFRCAH). Protocol No. 3 of 2 June 2025 was approved by the LKEFRCAH Commission on the Ethics of Animal Experiments for conducting work on the goose flocks at UVFARC. Tissue samples from all geese were collected in 2025 by trained personnel under strict veterinary precautions. These procedures were carried out in accordance with the Rules for Organizing Laboratory Research (Testing) in the Implementation of Veterinary Control (Supervision) approved by the Council of the Eurasian Economic Commission, Decision No. 80 of 10 November 2017 (EEC, 2026).

2.2 Animals and sample collection

In this study, a total of 127 geese from the main flock maintained in the UVFARC bioresource collection (Novy, Suzdal District, Vladimir Oblast, Russia) were analyzed. The sampling included six populations representing four breeds and two KHLM varieties: LRGR (n = 14), VLDM (n = 18), TULA (n = 20), Kholmogory Gray (KHLM_G; n = 21), and Kholmogory White (KHLM_W; n = 22) of Russian origin, and CHGR (n = 32) of foreign origin (Table 1). The housing, management, and feeding of the birds were carried out in accordance with established standards and procedures described elsewhere (Tereshchenko et al., 2008). Tissue samples (blood and feather pulp) were collected as biological material and used as a source of genomic DNA. All biological material was subsequently deposited in the Genetic Material Bank of Domestic and Wild Animal and Poultry Species, part of the Network Bioresource Collection of Farm Animals (Agreement with the Russian Ministry of Science and Higher Education No. 075-15-2021-1037 dated 28 September 2021), established and maintained at the LKEFRCAH. The study was conducted in 2025–2026 using equipment from the LKEFRCAH Shared-Use Center for Bioresources and Bioengineering of Farm Animals.

2.3 DNA extraction and microsatellite genotyping

Genomic DNA was extracted using two commercial kits depending on tissue type. The DNA-Extran-1 kit was used for blood samples, whereas the DNA-Extran-2 kit (Sintol Scientific and Production Company, Moscow, Russia) was applied for feather pulp, following the manufacturer's instructions. DNA quality and quantity were assessed using fluorometry (Qubit 4.0, Invitrogen/Life Technologies, USA) and spectrophotometry (NanoDrop™ 8000, Thermo Fisher Scientific, Inc., USA) instruments. Only samples with a DNA concentration of 15 ng/μL or higher and an absorbance ratio A260/A280 of 1.8 or above were retained for further analysis.

Genotyping was performed based on polymorphism analysis at 17 STR loci: *Aalu1b*, *Afa35*, *Ans02*, *Ans25*, *Afa30*, *Afa19*, *Afa13*, *Afa19b*, *Bcau1*, *Ans13*, *Afa02*, *Ans07*, *Ans21*, *Afa17*, *Afa18*, *Ans18*, and *CKW18* (Volkova et al., 2026; Table 2). These markers were originally developed from microsatellite sequences of *A. anser*, *A. cygnoides* and other anseriform species and were validated for cross-species amplification in previous studies (Weiß et al., 2008; Andres and Kapkowska, 2011; Kleven et al., 2015).

A detailed description of the PCR test system, including reagent kits and reaction conditions, is provided elsewhere (Volkova et al.,

TABLE 2 Characterization of 17 microsatellite loci used for short tandem repeat (STR) genotyping in this study.

Multi-plex primer panel	Locus (GenBank accession No., source species)	Forward (F) and reverse (R) primer (5′→3′)	STR motif	Allele size range (bp)	Annealing tempera-ture (°C)	References
1	*Aal μ1* (U63689, *Anser albifrons*)	F: CATGCGTGTTTAAGGGGTAT R: TAAGACTTGCGTGAGGAATAG	$(GT)_{15}$	78–88	60	Weiß et al. (2008)
	Afa35 (KT698203, *A. fabalis*)	F: ACCCTGCCAGATCTCTTGTC R: GCCCATTTTTCTAAAGAAGATGCC	$(AGAC)_{10}(AGAA)_{7}$	125–193	60	Kleven et al. (2015)
	Ans02 (EU833383, *A. anser*)	F: TTCTGTGCAGGGGCGAGTT R: AGGGAACCGATCACGACATG	$(AG)_{17}$	207–221	60	Weiß et al. (2008)
	Ans25 (EU833378, *A. anser*)	F: CACTTATTAATGGCACTTGAAA R: GTTCTCTTGTCACAACTGGA	$(GT)_{18}$	262–272	60	Weiß et al. (2008)
	Afa30 (KT698198, *A. fabalis*)	F: GTCTTGCACCACTTCACCAG R: GAGACTGGCACCCAGAAAAAG	$(AGAT)_{10}$	132–144	60	Kleven et al. (2015)
	Afa19 (KT698187, *A. fabalis*)	F: AGAAACCCAAATTTTTATGTTGTTGTC R: GCTACTGCCCATTTCCACAG	$(TTTG)_{7}$	177–189	60	Kleven et al. (2015)
	Afa13 (KT698181, *A. fabalis*)	F: TCTTATCTCCAAACAAGCTGGG R: GGTAGGAGGTGCTATAGGCG	$(TATC)_{11}$	210–226	60	Kleven et al. (2015)
	Aph19 (AJ515894, *Anas platyrhynchos*)	F: ATGGAGCAAGCAATCGTCTG R: AGCGTGAGGGTCTGCAGA	$(CA)_{8}$	234–238	60	Weiß et al. (2008)
	Bca μ1 (AF025889, *Branta canadensis*)	F: TGCTTTTTACCCCCAGTGTTCT R: AGAATCTGCTATATTATTTCCAGCTC	$(TA)_{15}CA$	115–125	60	Andres and Kapkowska (2011)
	Ans13 (KT276345, *A. anser*)	F: GCTAAGGTTGTTGCATTGATC R: TAGAGGCACAGACAAAGCAGA	$(CA)_{9}$	131–138	60	Weiß et al. (2008)
	Afa02 (KT698170, *A. fabalis*)	F: CGAATCACGAGGCACAAGAG R: TCCATTTGTAGGTGAGAAAATATGC	$(TATC)_{11}$	186–218	60	Kleven et al. (2015)
	Ans07 (EU833363, *A. anser*)	F: GACTGAGGAACTACAATTGACT R: ACAAAGACTACTACTGCCAAG	$(CA)_{11}$	233–246	60	Weiß et al. (2008)
2	*Ans21* (EU833375, *A. anser*)	F: TTCAGCATAAGTTCAGGCATG R: TATGGGTTAGTGTTCTTCTCA	$(AT)_{2}(GT)_{5}AT$	174–190	60	Weiß et al. (2008)
	Afa17 (KT698185, *A. fabalis*)	F: CAAATCAGGCCCACACTGAC R: TGCCCTCTTCATCCTTAGCG	$(ATAG)_{12}$	222–250	60	Kleven et al. (2015)
	Afa18 (KT698186, *A. fabalis*)	F: ACCCTCTATACCCTCTGGGC R: TCCTCAGTCATTTCTTTAACACAC	$(TCTA)_{8}$	194–210	60	Kleven et al. (2015)
	Afa25 (KT698193, *A. fabalis*)	F: TGCATCAGTGTACCATTTGAG R: ATGCTGAGGCAACTCTACCC	$(ATGT)_{11}$	236–240	60	Kleven et al. (2015)
	Ans18 (EU833373, *A. anser*)	F: GTGTTCTCTGTTTATGATATTAC R: AACAGAATTTGCTTGAAACTGC	$(AC)_{12}AT(AC)_{6}$	231–237	60	Weiß et al. (2008)
	CKW18 (AY720929, *A. cygnoides*)	F: AATGTGCTGTGTCACATTCTCC R: CATCATCCAACGATTCAGACAT	$(CAAAA)_{7}$	244–248	60	Andres and Kapkowska (2011)

2026). In brief, PCR was carried out in a 9 μL reaction volume containing 1× PCR buffer, 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.1 μM of each primer, and 1 U of Taq DNA polymerase. The thermal cycling protocol consisted of initial denaturation at 95 °C for 10 min, followed by 30 cycles of 95 °C for 30 s, annealing at 60 °C for 35 s, and extension at 72 °C for 60 s, with a final extension at 72 °C for 15 min. Amplification was performed using a MiniAmp thermal cycler (Applied Biosystems, Waltham, MA, USA).

TABLE 3 Parameters[a] of genetic diversity of gene pool breeds of geese based on the polymorphism analysis of 17 microsatellite loci.

Population[b]	n	A_R (M ± SE)	P_r All (n)	HO (M ± SE)	uH_E (M ± SE)	uFI_S [CI 95%]	PIC
LRGR	14	2.588 ± 0.173	2	0.361 ± 0.051	0.412 ± 0.051	0.062 [−0.094, 0.218]^{ns}	0.595 ± 0.026
VLDM	18	1.970 ± 0.213	0	0.150 ± 0.052	0.191 ± 0.050	0.258 [−0.008, 0.524]^{ns}	0.493 ± 0.020
TULA	20	3.170 ± 0.193	4	0.341 ± 0.055	0.423 ± 0.049	0.186 [0.039, 0.333]*	0.632 ± 0.021
KHLM_W	22	3.534 ± 0.260	2	0.422 ± 0.058	0.528 ± 0.050	0.180 [0.007, 0.352]*	0.676 ± 0.029
KHLM_G	21	4.118 ± 0.196	2	0.457 ± 0.054	0.599 ± 0.036	0.223 [0.057, 0.389]*	0.727 ± 0.022
CHGR	32	3.045 ± 0.275	2	0.366 ± 0.050	0.435 ± 0.053	0.137 [0.015, 0.259]*	0.635 ± 0.027

[a]Parameters: *n*, number of animals; M, mean value; SE, standard error; A_R, rarefied allelic richness; P_r *All* (*n*), number of private alleles found exclusively in a single population; H_O, observed heterozygosity; uH_E, unbiased expected heterozygosity; uF_{IS}, unbiased inbreeding coefficient; CI, 95%, variations in the uF_{IS}, coefficient at a confidence interval of 95%; *PIC*, polymorphism information content; ns, not significant ($p > 0.05$); *$p < 0.05$.

[b]Populations: LRGR, large gray; VLDM, vladimir clay; TULA, tula fighting; KHLM_W, kholmogory white; KHLM_G, kholmogory gray; CHGR, chinese gray.

Fragment analysis was conducted using capillary electrophoresis and a LOCUS Seqtor 1616 genetic analyzer (Helikon Company LLC, Moscow, Russia). Allele sizes were determined using the internal size standard SD-450 (Synthol, Moscow, Russia). Raw data were scored using GeneMarker® software (v. 3.0.1, SoftGenetics LLC, State College, PA, USA; Hulce et al., 2011). The resultant genotype matrix was compiled in Microsoft Excel and subsequently exported for downstream analyses in GenAlEx (v. 6.5; Peakall and Smouse, 2006; 2012) and R statistical environment (v. 3.5.0; R Core Team, 2012). Polymorphic information content (PIC) was estimated using CERVUS (v. 3; Kalinowski et al., 2007).

Linkage disequilibrium (LD) was not explicitly tested in this study. The selected markers originate from different genomic regions. Given the limited sample sizes available for the rare breeds analyzed here, which would render LD tests statistically underpowered, we assumed independence among loci for downstream analyses. Our primary focus here was, subsequently, population genetic characterization rather than marker panel validation.

Marker informativeness based on PIC values was estimated using CERVUS. Deviations from Hardy–Weinberg equilibrium (HWE) were assessed for each locus within each population using the χ^2 test implemented in GenAlEx.

2.4 Estimation of intrapopulation genetic diversity indices and multilocus heterozygosity

Data processing and diversity analyses were performed in the R environment (v. 3.5.0), whereas data visualization was conducted in R (v. 4.0) using the ggplot2 package (v. 4.0.0; Wickham, 2009). Intrapopulation genetic diversity parameters were estimated, including rarefied allelic richness (A_R), i.e., allelic diversity standardized using a rarefaction approach (Kalinowski, 2004); observed heterozygosity (H_O); unbiased expected heterozygosity (uH_E; Nei, 1978); and the inbreeding coefficient (uF_{IS}) with 95% confidence intervals (CI) based on uH_E. These parameters were calculated using the R environment component diveRsity (v. 1.9.89; Keenan et al., 2013). Private allele frequencies in each population were calculated in GenAlEx. In addition, multilocus heterozygosity (MLH) was calculated for each individual based on the proportion of heterozygous loci across the 17 microsatellite markers. MLH estimates were obtained using a custom script.

2.5 Assessment of population genetic structure

Population genetic structure was assessed using two complementary analytical approaches. First, principal component analysis (PCA) was used to visualize genetic relationships among individuals and populations in a reduced multivariate space (Mishra et al., 2017) while retaining the major components of genetic variation (Elhaik, 2022). PCA was performed in the R package *adegenet* (Jombart, 2008; Jombart and Ahmed, 2011), and results were visualized using ggplot2 (GitHub, 2022). Second, Bayesian clustering analysis was conducted using the STRUCTURE software (v. 2.3.4; Pritchard et al., 2000; Pritchard Lab, 2016), based on multilocus genotypes.

The admixture model with correlated allele frequencies was applied. The number of assumed genetic clusters (*K*) was set from 1 to 10. For each *K* value, 10 independent runs were performed with a burn-in period of 100,000 iterations followed by 500,000 Markov chain Monte Carlo iterations. The most likely number of genetic clusters (*K*) in the dataset was inferred using the Δ*K* method of Evanno et al. (2005).

2.6 Analysis of genetic differentiation

Pairwise genetic differentiation matrices were calculated using Wright's fixation index (F_{ST}; Weir and Cockerham, 1984) and Jost's genetic differentiation index (*D*; Jost, 2008). Both measures were computed using the R package diveRsity (Keenan et al., 2013). To visualize genetic relationships among populations, Neighbor-Joining (NJ; Saitou and Nei, 1987) and Neighbor-Net (NN; Huson and Bryant, 2006) approaches were employed based on pairwise F_{ST} and Jost's *D* distance matrices. NJ dendrograms were constructed using the T-REX web server (Boc et al., 2012), while NN networks were generated using the SplitsTree software (v. 6.4.17; Huson and Bryant, 2006; 2024). Both approaches were used as complementary tools for visualizing patterns of genetic differentiation rather than phylogenetic reconstructions.

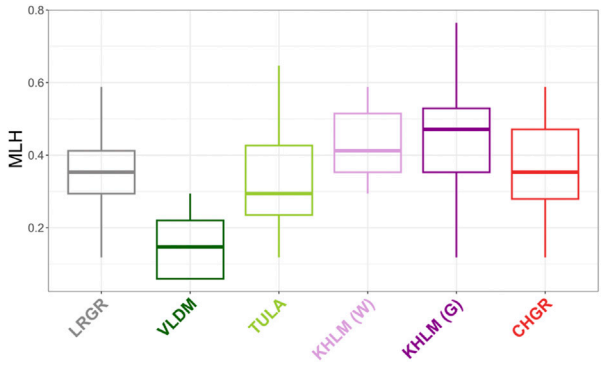


FIGURE 1
Boxplot analysis of multilocus heterozygosity (MLH) in the studied goose populations based on the analysis of polymorphism of 17 microsatellites. Populations: LRGR, Large Gray; VLDM, Vladimir Clay; TULA, Tula Fighting; KHLM_W, Kholmogory White; KHLM_G, Kholmogory Gray; CHGR, Chinese Gray. Boxplots show interquartile range (Q1–Q3), with a horizontal line inside conforming to the median, and whiskers to minimum-to-maximum value range.

3 Results

3.1 Marker informativeness and HWE

The PIC values for the 17 microsatellite loci varied from 0.544 (*Bcau1*) to 0.869 (*Aalu1b*), with a mean of 0.755 ± 0.073 (Supplementary Table 1), proving their informativeness and suitability in the current population genetic analyses in geese. Remarkably, 15 of the 17 loci exhibited PIC values above 0.650, indicating that the selected microsatellite panel was highly informative.

The results of χ^2 tests for HWE at each locus (Supplementary Table 2) demonstrated that the number of loci with significant deviations ($p < 0.05$) ranged between 2 in LRGR and 7 in KHLM_G. The greatest number of deviations (7 loci) in KHLM_G involved highly significant departures at *Ans13, Ans07*, and *Ans21* ($p < 0.001$). CHGR showed deviations at five loci, while KHLM_W exhibited deviations at six loci. TULA and VLDM displayed deviations at five loci each. LRGR showed the fewest deviations, with only *Ans13* ($p < 0.001$) and *Ans07* ($p < 0.01$) departing from HWE. VLDM also had the highest number of monomorphic loci (6), suggesting its reduced allelic diversity.

3.2 Intrapopulation genetic diversity

Based on multilocus SSR genotypes at 17 microsatellite loci, intrapopulation genetic diversity parameters were estimated for the studied goose populations (Table 3). Detailed information on private allele frequencies presented in Supplementary Table 3.

The A_R values varied from 1.970 (VLDM) to 4.118 (KHLM_G), with KHLM_W exhibiting the second highest value (A_R = 3.534). TULA and CHGR showed intermediate values (A_R = 3.170 and A_R = 3.045, respectively), whereas LRGR displayed the lowest diversity among the remaining populations (A_R = 2.588). Analysis of private alleles revealed 12 unique alleles distributed across five populations. TULA harbored their highest number (n = 4), including the allele *Ans18-231* at a notably high frequency of 0.750. LRGR, KHLM_W, KHLM_G and CHGR each possessed two private alleles, whereas VLDM had none. The presence of private alleles was observed at particularly high frequencies in TULA (*Ans18-231*, 0.750) and LRGR (*Ans13-134*, 0.536).

Population-specific PIC values per population (Table 3) varied from 0.493 ± 0.020 in VLDM to 0.727 ± 0.022 in KHLM_G. KHLM_W exhibited the second highest mean PIC (0.676 ± 0.029), followed by TULA (0.632 ± 0.021), CHGR (0.635 ± 0.027), and LRGR (0.595 ± 0.026).

Values of H_O and uH_E followed a similar pattern. The lowest values were detected in VLDM (H_O = 0.150; uH_E = 0.191), whereas the highest were observed in KHLM_G (H_O = 0.457; uH_E = 0.599). Both KHLM populations exhibited comparable heterozygosity levels (H_O = 0.422–0.457; uH_E = 0.528–0.599), despite differences in A_R. In the remaining populations, intermediate heterozygosity values were observed (H_O = 0.341–0.366; uH_E = 0.412–0.435). Across all populations, uH_E values commonly exceeded H_O, indicating a general deficit of heterozygotes. The uF_{IS} coefficient ranged between 0.062 in LRGR and 0.258 in VLDM. Herewith, statistically significant heterozygote deficiency ($p < 0.05$, Table 3) was detected in TULA, CHGR, and both KHLM populations, based on uF_{IS}-specific 95% CI not overlapping zero. In contrast, the uF_{IS} CI for LRGR and VLDM overlapped zero (Table 3) and independent exact tests confirmed that these populations did not show significant deviations from HWE.

3.3 MLH analysis

Based on individual genotype proportions of polymorphic alleles across 17 microsatellite loci, MLH was calculated for all studied goose populations (Figure 1; Supplementary Table 4). The lowest MLH values were observed in VLDM (mean = 0.150 ± 0.020; median = 0.147), indicating reduced individual genetic variability in this population. In contrast, the highest MLH values were detected in KHLM_G (mean = 0.457 ± 0.033; median = 0.471), followed closely by KHLM_W (mean = 0.422 ± 0.021; median = 0.412). Intermediate MLH levels were recorded in CHGR (mean = 0.366 ± 0.020), LRGR (0.361 ± 0.030), and TULA (0.341 ± 0.031).

Analysis of the distribution of individual MLH values revealed population-specific differences in variability. The widest range was observed in KHLM_G (0.118–0.765), accordant with its high mean MLH and overall genetic variability. KHLM_W exhibited a narrower distribution (0.294–0.588), with the highest minimum MLH value among all populations, indicating relatively uniform individual heterozygosity. Comparable MLH ranges were detected in LRGR and CHGR (0.118–0.588), whereas TULA showed a slightly broader range (0.118–0.647), reflecting moderate within-population variability.

3.4 Population structure and genetic differentiation

3.4.1 PCA clustering patterns

To characterize relationships among individuals assess patterns of genetic similarity and infer population structure, PCA was

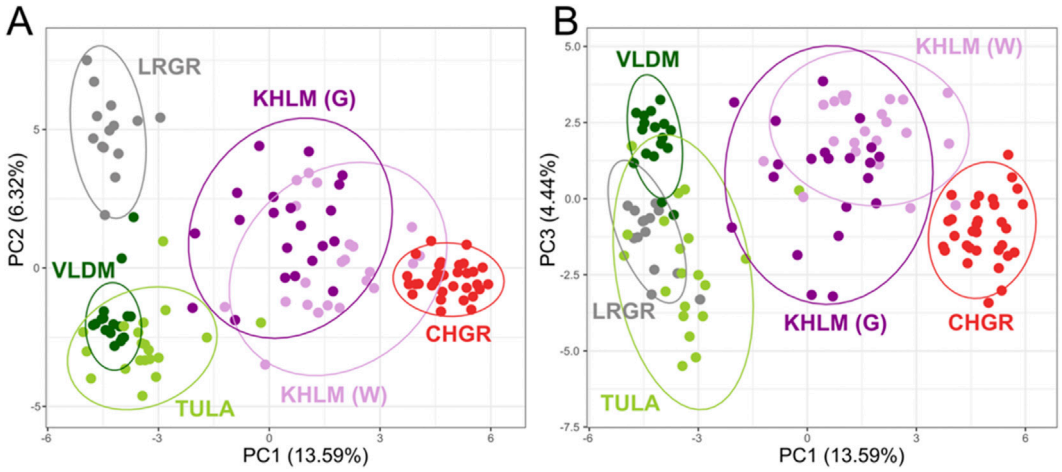


FIGURE 2
Principal component analysis (PCA) of the germplasm goose breeds/populations based on polymorphism analysis of 17 microsatellites. PCA clustering patterns are shown **(A)** for the first (PC1) and second (PC2) principal components and **(B)** for the first and third (PC3) principal components. Populations: LRGR, Large Gray; VLDM, Vladimir Clay; TULA, Tula Fighting; KHLM_W, Kholmogory White; KHLM_G, Kholmogory Gray; CHGR, Chinese Gray.

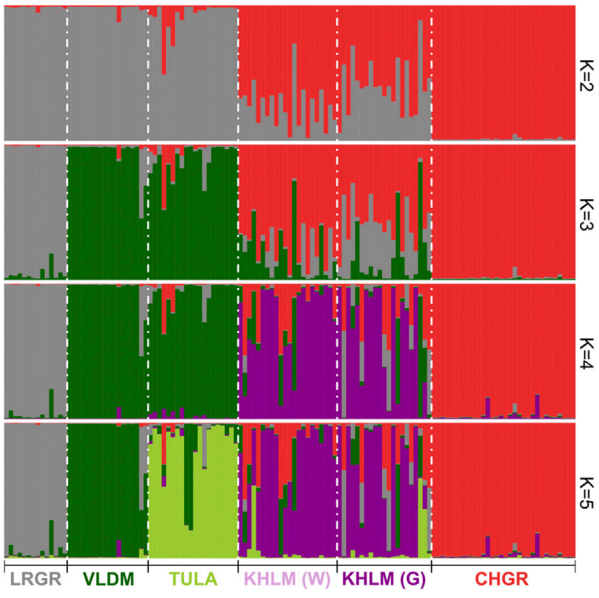


FIGURE 3
Cluster analysis results for the goose gene pool breeds/populations based on 17 polymorphic microsatellites and using the STRUCTURE program for the number of clusters from K = 2 to 5. Populations: LRGR, Large Gray; VLDM, Vladimir Clay; TULA, Tula Fighting; KHLM(W), Kholmogory White; KHLM(G), Kholmogory Gray; CHGR, Chinese Gray.

performed (Figure 2). The first principal component (PC1), accounting for 13.59% of the total microsatellite variation, separated KHLM and CHGR from the remaining populations, although partial overlap was observed (Figure 2A). Furthermore, the KHLM_G and KHLM_W populations showed substantial overlap, forming a common cluster with considerable within-group variability. PC2 (6.32% the total variation) further differentiated the populations, resulting in the formation of a distinct LRGR cluster. In contrast, TULA and VLDM individuals occupied a common region in the lower-left quadrant of the PC1–PC2 plane, with VLDM forming a relatively consolidated subcluster within the broader TULA distribution. The TULA population exhibited greater dispersion of individuals, indicating lower within-population genetic homogeneity. In turn, the combined KHLM cluster was positioned near the PC2 axis.

PC3 (4.44% the total variation) primarily reflected genetic variation at the individual level. Examination of individual distribution in the PC1–PC3 projection revealed a somewhat different clustering pattern (Figure 2B). In comparison with the PC1–PC2 projection, overlap between CHGR and KHLM individuals decreased, indicating greater separation of these populations along PC3. Although the KHLM populations continued to overlap substantially, KHLM_W individuals were primarily concentrated in the upper-right quadrant of the PC1–PC3 plane, whereas KHLM_G individuals showed broader dispersion along the PC3 axis. The remaining populations formed a relatively compact elongated cluster occupying the lower and central regions of the PC1–PC3 plane, while VLDM maintained comparatively high within-group variability.

3.4.2 Bayesian clustering analysis using STRUCTURE

To investigate population genetic structure in greater detail and assess patterns of genetic assignment and admixture among individuals, Bayesian clustering analysis was performed using STRUCTURE software (Pritchard et al., 2000; Figure 3).

Analysis of the complete dataset without prior population information identified K = 2 as the most likely number of clusters according to the Evanno ΔK method (ΔK = 5460.4). To provide a more detailed representation of population structure, clustering patterns for K values varying from three to five were

TABLE 4 Matrix of pairwise values of the F_{ST} fixation index and pairwise genetic distances according to the Jost's *D* index in the studied goose breeds based on 17 polymorphic microsatellites.

Population	LRGR	VLDM	TULA	KHLM_W	KHLM_G	CHGR
LRGR		0.343	0.248	0.302	0.184	0.469
VLDM	0.106		0.219	0.356	0.295	0.545
TULA	0.126	0.035		0.244	0.170	0.409
KHLM_W	0.290	0.190	0.198		0.029	0.155
KHLM_G	0.137	0.152	0.113	0.029		0.174
CHGR	0.488	0.368	0.322	0.085	0.132	

F_{ST}, values are shown above the diagonal, and *D* values below the diagonal for paired comparisons. Populations: LRGR, large gray; VLDM, vladimir clay; TULA, tula fighting; KHLM_W, kholmogory white; KHLM_G, kholmogory gray; CHGR, chinese gray.

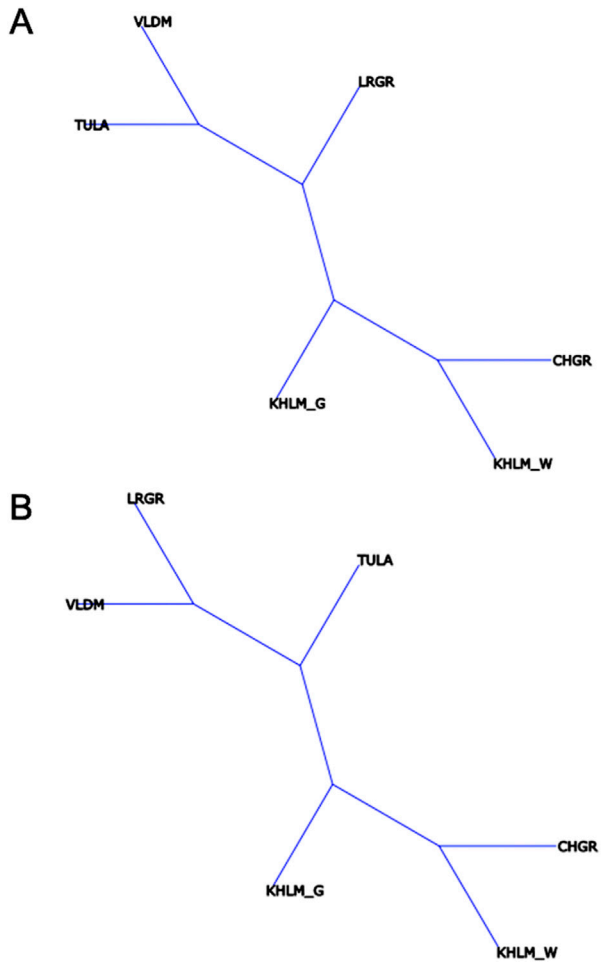


FIGURE 4
Neighbor-Joining (NJ) dendrograms of genetic relationships among the studied goose populations constructed from matrices of pairwise genetic distances based on F_{ST} **(A)** and Jost's *D* **(B)** Populations: LRGR, Large Gray; VLDM, Vladimir Clay; TULA, Tula Fighting; KHLM_W, Kholmogory White; KHLM_G, Kholmogory Gray; CHGR, Chinese Gray.

also examined. At $K = 2$, two major genetic clusters were identified. One cluster was predominantly represented by CHGR individuals, whereas the second included individuals from LRGR, VLDM, and TULA populations. Both KHLM populations exhibited pronounced admixture patterns, containing genetic components from both clusters, although the CHGR-associated component predominated. At $K = 3$, the overall pattern observed for KHLM populations remained largely unchanged. However, TULA and VLDM formed a distinct common cluster, whereas LRGR showed increased genetic separation from the remaining populations. At $K = 4$, a specific genetic component characteristic of both KHLM populations became evident, while residual admixture with other populations remained detectable. Further subdivision was observed at $K = 5$, where TULA and VLDM exhibited additional differentiation with the emergence of population-specific genetic components. Nevertheless, several TULA individuals retained mixed ancestry patterns shared with other populations. In contrast, the genetic structure of KHLM_W and KHLM_G remained largely stable relative to $K = 4$, characterized by a predominant common genetic component and persistent low-level admixture. LRGR and CHGR coherently displayed high genetic homogeneity across all clustering levels.

3.4.3 Genetic differentiation

To quantify the degree of genetic divergence among the studied goose populations, pairwise matrices of the fixation index (F_{ST}) and Jost's *D* values were calculated (Table 4). According to the F_{ST} estimates, the greatest genetic differentiation was observed between CHGR and VLDM (0.545), followed by CHGR and LRGR (0.469). The lowest F_{ST} value was detected between the two KHLM populations (0.029), indicating a high degree of genetic similarity. Among pairwise comparisons involving different breeds, the lowest F_{ST} values were found for KHLM_W–CHGR (0.155), KHLM_G–CHGR (0.174), and KHLM_G–TULA (0.170). The Jost's *D* estimates ranged between 0.029 and 0.488 and generally revealed patterns similar to those obtained with F_{ST}. As with the fixation index, the lowest differentiation was observed between KHLM_W

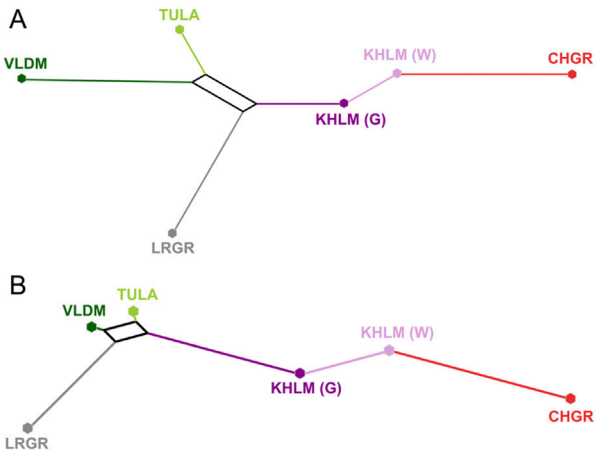


FIGURE 5
Neighbor-Net-based dendrograms of genetic relationships among the studied goose breeds as constructed on the basis of the matrices of pairwise genetic distances F_{ST} **(A)** and Jost's D **(B)** A box-like mesh on the dendrograms reflects possible genetic networks. Populations: LRGR, Large Gray; VLDM, Vladimir Clay; TULA, Tula Fighting; KHLM(W), Kholmogory White; KHLM(G), Kholmogory Gray; CHGR, Chinese Gray.

and KHLM_G (D = 0.029). However, unlike the F_{ST} results, the lowest interbreed divergence was detected between VLDM and TULA (D = 0.035), whereas the highest value was recorded for CHGR–LRGR (D = 0.488).

The matrices of pairwise F_{ST} and Jost's D values were subsequently visualized using NJ and NN dendrograms (Figures 4, 5). Both dendrogram pairs revealed similar topologies, forming two major clusters and providing complementary insights into the genetic structure and divergence of the populations. The first cluster comprised CHGR along with the KHLM populations, including a close association between CHGR and KHLM_W. The second cluster included LRGR, VLDM, and TULA. Differences between the two dendrograms were primarily associated with the internal arrangement of populations within the second cluster. In the topology constructed from F_{ST} values (Figures 4A, 5A), TULA and VLDM formed a closer subcluster, whereas LRGR occupied a distinct branch. In contrast, the dendrogram based on Jost's D values (Figures 4B, 5B) placed LRGR and VLDM as a paired branch, while TULA diverged independently from the central trifurcation node.

4 Discussion

4.1 Usefulness of microsatellite markers for studying goose populations and breeds

The present study focused on six populations representing five goose breeds maintained in a germplasm collection. These populations were selected for their status as locally adapted breeds with no prior microsatellite-based characterization and represent rare genetic resources that reflect the diversity of Russian goose breeds. Several of these populations currently contain fewer than 100 individuals, highlighting their potential genetic vulnerability (Zharkova, 2020).

Previous studies (e.g., Liu et al., 2006; Mindek et al., 2018) have demonstrated the utility of microsatellite markers for assessing the genetic status of rare and valuable goose genetic resources, although the number of loci employed has varied from 14 (Lai et al., 2018) and 15 (Warzecha et al., 2019) to 26 (Qing-Ping et al., 2009). In the current exploratory study, the application of a panel of 17 microsatellite loci previously developed by our research group made it possible to perform the first preliminary assessment of allele frequency patterns and population genetic relationships among Russian goose gene pool populations. The marker panel proved informative for primary population genetic characterization in geese. The majority of loci showed PIC values exceeding the threshold of 0.5 (Supplementary Table 1), which, according to the criteria of Botstein et al. (1980), classified them as highly informative markers. Such levels of polymorphism indicated the suitability of the selected loci for assessing genetic diversity and resolving population structure, comparable to or exceeding the informativeness of panels used in previous studies on other goose breeds. However, as discussed below (Section 4.5), several methodological constraints should be considered when interpreting these results, reinforcing the preliminary nature of this exploratory study.

4.2 Genetic diversity and MLH comparisons across the studied populations

Among the studied populations, VLDM displayed a particularly distinctive pattern of genetic diversity. As noted by Ibeagha-Awemu and Erhardt (2005), temporal changes in allele frequencies underlie the estimation of major population genetic parameters, including heterozygosity, inbreeding coefficients, and genetic distances. In the present study, allele frequency analysis revealed that VLDM was characterized by the lowest level of genetic diversity among all populations examined (Table 3). The MLH analysis (Supplementary Table 4) further supported the distinct genetic profile of VLDM. This population exhibited the lowest multilocus heterozygosity values among all groups analyzed. The median MLH value was 0.147, indicating that half of the individuals possessed heterozygous genotypes at fewer than 14.7% of loci. Moreover, the low mean MLH value, along with the relatively narrow range of individual values (0.059–0.294), suggests a high degree of genetic homogeneity and a predominance of homozygous genotypes within the population. Such patterns are frequently observed in populations that have undergone prolonged reductions in effective population size and subsequent erosion of genetic diversity (Bosse and van Loon, 2022).

Interestingly, although VLDM showed the highest uF_{IS} value (Table 3), this excess of homozygotes did not reach statistical significance. This may be due to the limited sample size (n = 18) and reduced statistical power, or it may indicate that the pronounced homozygosity is relatively uniform across individuals rather than arising from cryptic substructure. Given the small population size of VLDM, a lack of statistical power appears not to diminish the biological relevance of the observed homozygosity pattern.

The reduced genetic variation observed in VLDM may be explained by several historical and demographic factors. This breed was developed as a composite population derived from KHLM_W and Toulouse Gray geese (Fisinin and Zlochevskaya, 1989; Martsev, 2020). During breed formation, only individuals exhibiting the desired clay plumage color alongside favorable productive and reproductive traits were selected for further propagation (Fisinin and Zlochevskaya, 1989; Frolova et al., 2013). Such intensive directional selection during the establishment phase may have reduced the effective number of founder individuals and limited the diversity of alleles retained within the emerging population. Subsequently, this breed experienced a marked reduction in population size, reaching critically low numbers in recent decades (Fisinin and Zlochevskaya, 1994; Zharkova, 2020). Such reductions in effective population size are often accompanied by bottleneck events, genetic drift and the progressive loss of allelic variation (García-Castro and Márquez, 2024).

While the possible role of long-term selection in shaping the current genetic composition of VLDM cannot be excluded (Zhang et al., 2026), the microsatellite markers used in the present study do not allow direct identification of selection signatures. More sophisticated genomic approaches would be valuable for investigating potential selective sweeps and for further elucidating the mechanisms underlying the reduced diversity observed in this breed.

In contrast to VLDM, the remaining populations retained substantially higher levels of genetic diversity, with the two KHLM populations being the most variable (Table 3; Supplementary Table 4). These findings conform to our earlier phenetic studies, which also identified the greatest degree of diversity in this breed (Romanov, 1994). At the same time, both KHLM populations showed statistically significant heterozygote deficiency. Positive uF_{IS} values combined with relatively high allelic diversity may indicate the existence of a hidden population substructure within the sampled birds. Such a pattern may be in agreement with the Wahlund effect (Wahlund, 1928; Garnier-Géré and Chikhi, 2013), when pooling individuals originating from genetically differentiated subgroups results in lower H_O estimates compared to expected values.

LRGR showed the second lowest diversity among the populations (Table 3), with the uF_{IS} value not significantly different from zero, indicating HWE. This relative genetic homogeneity may be consistent with its more recent origin as a composite breed derived from Romny and Toulouse geese (Domenik, 2016; Smorchkova, 2023). TULA and CHGR displayed intermediate diversity levels. Both populations showed significant heterozygote deficiency, indicating deviations from HWE. The observed intermediate diversity in CHGR might be in line with its Chinese origin and the preservation of breed-specific genetic components despite its widespread historical use in developing other breeds.

The distribution of private alleles (Table 3) further highlighted population-specific differentiation and agreed with the findings of Abdel Moniem et al. (2020). These authors emphasized the importance of private alleles for breed specification and demonstrated that they provide evidence of genetic separation, with a high number of breed-specific alleles reflecting the genetic uniqueness of each goose breed. TULA harbored the highest number of private alleles (n = 4), including the allele *Ans18-231* at a notably high frequency of 0.750, underscoring its uniqueness and conservation value. LRGR, KHLM_W, KHLM_G, and CHGR each possessed two private alleles (Supplementary Table 3). Conversely, the complete absence of private alleles in VLDM reinforces its genetically depleted status and emphasizes the urgent need for conservation measures to preserve its remaining genetic variation.

The levels of genetic diversity observed in our study were broadly conforming to those reported in other microsatellite-based studies of domestic goose breeds. Abdel Moniem et al. (2020) reported H_O values varying from 0.37 (Wanxi) to 0.62 (Emden) and expected heterozygosity (H_E) from 0.43 to 0.70 across nine goose populations. These ranges are concordant with the values found in our study. Parada et al. (2012) reported H_O varying from 0.45 to 0.55 and H_E from 0.38 to 0.51 in eight Polish conservative goose flocks; these values aligned with our intermediately varied populations (TULA and CHGR). In comparison, studies on Chinese indigenous grey geese reported mean heterozygosity ranging between 0.49 and 0.69 (Tu et al., 2006), which encompasses the higher diversity observed in our KHLM populations. In contrast, VLDM displayed substantially lower diversity, comparable to the most genetically depleted populations reported in the literature, such as the Egyptian goose populations studied by Abdel-Kafy et al. (2021), which showed low diversity indices (H_O = 0.277; H_E = 0.352) and a high inbreeding coefficient (F_{IS} = 0.203).

The mean PIC values varied considerably among the studied populations (Table 3). The elevated PIC values in the KHLM populations were compatible with their higher allelic richness, whereas the reduced PIC in VLDM reflected its diminished genetic variability. These estimates were generally comparable to, and in several cases higher than, those reported by Abdel Moniem et al. (2020) for 14 goose breeds (0.449–0.730). In particular, the PIC values for KHLM_G, KHLM_W and TULA exceeded the majority of the values observed in that study, while the lowest PIC recorded in VLDM fell within the lower range of their dataset.

4.3 Population structure and genetic differentiation

The PCA (Figure 2) and STRUCTURE (Figure 3) analyses further highlighted the distinctive genetic organization of the studied goose populations. In particular, both approaches consequentially demonstrated a high degree of genetic homogeneity and consolidation within the VLDM population, suggesting preservation of a relatively stable breed-specific genetic component in consistency with patterns of population consolidation and genetic drift. A close association between VLDM and TULA was also observed across several analytical approaches, including PCA clustering, Bayesian inference, and analyses of genetic relationships (Figures 2–4). This pattern may indicate the presence of shared ancestral genetic backgrounds and/or partially overlapping historical sources used during breed formation. TULA geese are considered among the oldest Russian breeds and were historically selected primarily for goose fighting. Although available historical records do not provide evidence for intentional crossbreeding

between TULA and VLDM, their genetic affinity detected in the present study (Figure 4; Table 4) suggests that both populations may have inherited genetic material from partially related ancestral populations.

Furthermore, the PCA results showed the relatively low cumulative proportion of variance explained by the first three principal components (Figure 2). This pattern is commonly observed when genetic divergence among populations is moderate, a substantial part of the total variation is distributed within populations, and/or population structure is complex and multi-dimensional rather than dominated by a few major axes (Patterson et al., 2006). In the theoretical framework for PCA of genetic data, Patterson et al. (2006) found that, when the number of markers is sufficiently large, there will be $K-1$ significant eigenvalues and corresponding eigenvectors that capture population structure. Hereby, the remaining components primarily reflect within-population variance and sampling noise. Consequently, with a more limited marker set, the signal of population structure may be less concentrated in the leading principal components. In the present study, the use of 17 microsatellite loci may, therefore, have contributed to the modest proportion of variance captured by the first three axes.

The STRUCTURE analysis provides additional insights into possible ancestry patterns within the studied populations. At $K = 2$, two major genetic components were identified. One component predominated in CHGR and, to a considerable extent, in both KHLM populations, whereas the other was dominant in LRGR, VLDM, and most TULA individuals. Considering the known evolutionary history of domestic geese and the dual origin of domestic forms, which involves two distinct ancestral lineages, i.e., the graylag goose and swan goose (Scherf, 1995), it is tempting to interpret these broad ancestry patterns as reflecting contributions from the two major ancestral domestication lineages. Similar evidence for ancestral contributions has previously been reported in cytogenetic investigations (Silversides et al., 1988; Jaszczak et al., 1996; Zawadzka et al., 1997). However, because no wild reference populations were included in the present study, such interpretation should be considered hypothetical. Future whole-genome studies of the Russian goose breeds analyzed here would be crucial for phylogenetic analyses to test this hypothesis further, as recently demonstrated for Chinese and European goose breeds (Wen et al., 2023b).

Increasing the number of assumed ancestral populations revealed progressively finer population subdivision patterns. At $K = 3$, an additional component emerged and was represented to varying degrees across multiple populations, particularly in TULA and VLDM. Rather than representing a discrete ancestral lineage, this component may reflect historical admixture processes and shared ancestry among populations derived from different genetic backgrounds. At $K = 4$, the overall clustering pattern remained largely stable, although an additional component became evident in the KHLM populations, suggesting further internal population structuring and potentially reflecting their complex breeding history. At $K = 5$, an additional component appeared predominantly within TULA individuals, indicating a higher degree of within-population heterogeneity compared with the other breeds examined.

Analyzing pairwise genetic differentiation matrices (F_{ST} and Jost's D) calculated to quantify the degree of genetic divergence among populations (Table 4), we came to the conclusion about a wide spectrum of genetic differentiation. The highest differentiation was observed between CHGR and VLDM, and the lowest between the two KHLM subpopulations. The F_{ST} and Jost's D estimates obtained were broadly accordant with those reported in other microsatellite-based studies of domestic geese. For example, Li et al. (2012) reported pairwise F_{ST} values varying from 0.04 between Panshi Grey goose and Yongkang Grey goose to 0.47 between Panshi Grey goose and Landes goose among six Chinese goose breeds. The highest F_{ST} value observed in our study (for the CHGR–VLDM pair, 0.545) slightly exceeded that maximum, suggesting particularly pronounced genetic divergence between these two populations.

The differences detected between the F_{ST} and Jost's D estimates in our study can be explained by the specific properties of these statistical approaches. Several authors (Gerlach et al., 2010; Meirmans et al., 2011; Hopper et al., 2018; Kharzinova and Zinovieva, 2020), following the work of Jost (2008), demonstrated that the F_{ST} fixation index does not always adequately reflect the degree of genetic differentiation when highly polymorphic markers, such as microsatellites, are used. Even when populations share no alleles, F_{ST} values may remain comparatively low because the index is constrained by high levels of within-population diversity. Consequently, F_{ST} may underestimate actual differentiation. By contrast, Jost's D is less sensitive to intrapopulation diversity and more directly quantifies differences in allele composition among populations. In the present study, comparison of both metrics provided complementary information on genetic relationships among the surveyed goose populations. Relative to F_{ST}, Jost's D revealed a clearer genetic affinity between VLDM and TULA and generally emphasized stronger differentiation among the studied breeds. Thus, simultaneous use of both approaches allowed a more detailed characterization of population relationships than either metric alone.

The complex ancestry of KHLM populations was further supported by the concordance of outcomes from the PCA (Figure 2), STRUCTURE (Figure 3), and genetic differentiation analyses (Table 4). Although KHLM_W and KHLM_G exhibited minimal genetic distances and strong overlap in multivariate analyses, both populations also demonstrated substantial admixture with other breeds. Across all clustering levels, the KHLM populations maintained a common predominant genetic component while simultaneously retaining genetic contributions associated with other populations. Across all clustering levels, the KHLM populations maintained a common predominant genetic component while simultaneously retaining genetic contributions associated with other populations. Historical evidence suggests that KHLM geese originated through hybridization between local Russian geese and Chinese geese. The present molecular findings are remarkably consonant with that historical hypothesis. The shared ancestry inferred from STRUCTURE patterns and the comparatively low genetic distances between KHLM and CHGR may reflect retention of genomic components originating from Chinese goose ancestry. Long-term selection, recurrent intercrossing, and subsequent breed consolidation (Adminka,

2026; Own Farming, 2025b) likely contributed to the preservation of both substantial genetic diversity and signatures of historical admixture in present-day KHLM populations.

In contrast to KHLM, which demonstrated pronounced admixture and a complex internal structure, CHGR displayed the opposite pattern. CHGR geese formed a genetically distinct and relatively homogeneous group according to PCA and STRUCTURE analyses (Figures 2, 3). Furthermore, this population exhibited the greatest degree of genetic divergence relative to the remaining breeds and occupied an isolated position within the networks of genetic relationships (Figure 5). These observations agreed with the origin of Chinese geese from the domesticated swan goose lineage (*A. cygnoides*) and indicate the preservation of breed-specific genetic components despite their widespread historical use in developing numerous other goose breeds.

LRGR also exhibited relative genetic isolation, forming a separate cluster in the PCA space and occupying an isolated position in the genetic relationship analyses (Figures 2, 4A, 5). However, its divergence from the remaining populations was less pronounced than that observed for CHGR. This intermediate position may reflect the comparatively recent origin of LRGR through interbreeding of older Romny and Toulouse geese (Domenik, 2016; Smorchkova, 2023) and its stronger historical links with other domestic European goose populations.

Comparison of NJ and NN approaches further emphasized complementary aspects of population relationships. NJ trees (Figures 4A,B) represent a simplified model of genetic relationships based on assumed divergence patterns. Such trees assume predominantly bifurcating relationships and may force populations into separate branches even when historical gene flow exists. In contrast, NN is designed to accommodate reticulate genetic relationships and therefore can reveal signals of admixture, migration, and introgression. The network structures obtained in Figure 5 included box-like connections among populations, indicating potential reticulate relationships and gene exchange. Although NJ and NN produced generally similar two-cluster topologies in the present study, the NJ approach emphasized divergence patterns, whereas NN additionally captured signals of subsequent genetic exchange among populations.

Taken together, these results suggest that LRGR, VLDM, and CHGR exhibit comparatively consolidated genetic structures, whereas TULA appears genetically more heterogeneous and may preserve signals of more complex historical ancestry. The KHLM populations occupy a distinctive intermediate position and demonstrate evidence of mixed ancestry patterns congruous with their proposed historical origin involving local and Chinese-derived goose populations. This inference is concordant not only with the STRUCTURE and PCA results but also with the other genetic structure statistics, which show that CHGR and KHLM populations exhibit the lowest genetic divergence in terms of shared allele frequencies (Jombart, 2008). This further supports the retention of ancestral genomic components originating from Chinese goose lineages. Nonetheless, all such interpretations should be considered preliminarily and with caution because they may also be influenced by historical gene flow resulting from intentional or accidental interbreed crossings, as well as by the relatively limited sample sizes, number of microsatellite markers used in the present study and their inherent constraints. Overall, the combined use of alternative genetic differentiation metrics and tree/network approaches provided a more balanced assessment of genetic relationships among the surveyed goose populations and allowed a clearer characterization of their genetic structure within the limitations of the present exploratory study.

4.4 General insights: diversity and conservation implications

The analysis of microsatellite polymorphism demonstrated that the surveyed goose populations differed substantially both in their levels of genetic diversity and in the structure of their genomes. VLDM was characterized by high genetic homogeneity and low intrabreed diversity, emphasizing the need for priority conservation measures. In contrast, KHLM exhibited comparatively high levels of genetic variability and a more complex population structure.

Genetic isolation was observed in LRGR and CHGR, with CHGR exhibiting the highest degree of isolation and LRGR showing a moderate but distinct genetic separation from the remaining populations. TULA occupied an intermediate position and displayed considerable intrabreed heterogeneity. Most of these findings are in line with the historical development of the studied breeds and may reflect the effect of long-term breed-forming processes driven by selection, hybridization, and demographic factors. On the other hand, because the demographic history was not directly investigated in the present study, such interpretations should be considered hypothetical until further validated in future research.

An important aspect in studies of poultry diversity concerns the classification of breeds according to their origin and evolutionary relationships. During the Soviet period, domestic and imported goose breeds were traditionally classified according to both their ancestry and economically important characteristics into three principal groups (Saleev and Ionova, 1982):

a. Chinese-origin geese, including Chinese, Kuban, Pereyaslav, and Gorky breeds, characterized by relatively high egg production but comparatively low body weight.
b. Western European geese, including Toulouse, LRGR, Vishtines, Emden, Rhenish, and Italian breeds, typically characterized by a looser body constitution and relatively high productivity.
c. Eastern European geese, including Romny, Arzamas, and Shadrinsk (Ural) breeds, generally characterized by high viability but lower productivity.

Within this framework, CHGR represents a typical member of the Chinese-origin group, whereas LRGR belongs to the Western European lineage. TULA, KHLM_W, KHLM_G, and VLDM can generally be assigned to the Eastern European group. The present molecular findings broadly support this historical classification, while also providing important refinements regarding genetic relationships among breeds.

The present molecular findings are generally in keeping with our earlier phenetic analyses (Romanov, 1994) and with historical records describing breed origins. Two principal ancestral lineages appear to have shaped the genomes of the investigated populations: the Chinese lineage derived from the swan goose and the European

lineage originating from the graylag goose, with the latter domesticated approximately 7,000–7,500 years ago (Scherf, 1995; Wen et al., 2023b).

In accordance with this lineage framework, LRGR (as well as the Shadrinsk breed employed in the preliminary investigation by Kharzinova et al., 2025) appears more closely associated with the European lineage represented by *A. anser*-derived domestic geese. This observation agrees with the documented contribution of European breeds, including Romny and Toulouse geese, to the formation of LRGR. The relatively isolated yet less divergent genetic position of LRGR may therefore reflect its more recent composite origin within the European domestic goose background.

Interestingly, VLDM and TULA occupied an intermediate position between the major ancestral patterns. Our molecular analyses suggest that TULA possesses a relatively heterogeneous and potentially synthetic genomic structure that may reflect ancient hybridization events followed by prolonged traditional breeding practices. VLDM, despite its similarly intermediate clustering position, differs markedly in exhibiting high genetic consolidation and reduced diversity, possibly due to historical founder effects and recent demographic constraints (Grishina, 2015). Taken together, these findings suggest that the historical development of Russian goose breeds cannot be fully explained by simple linear descent models. Rather, their present genomic architecture likely reflects complex interactions among ancestral lineages, repeated hybridization events, local selection practices, and subsequent breed consolidation processes.

4.5 Methodological considerations, exploratory nature of the study and future prospects

The current study represents an exploratory investigation of genetic diversity and population structure in native Russian goose breeds using microsatellite markers. As the first comprehensive molecular screening of these specific populations, it provides vital baseline insights required to guide future large-scale genomic mapping and conservation efforts.

Several limitations, however, should be taken into account when interpreting these results. First, sample sizes per population were relatively small, ranging from 14 to 32 individuals, which may reduce the precision of diversity estimates and the statistical power of certain analyses. Specifically, these limited cohorts precluded formal testing for LD, as such tests would lack sufficient statistical power. Furthermore, deviations from HWE were observed in several populations. Notably, these deviations were population-specific rather than systematic across all breeds. If these deviations had been caused by technical artifacts, such as null alleles or locus monomorphism, they would likely appear uniformly across the entire dataset. Instead, their population-specific nature strongly suggests that they reflect genuine biological processes operating within these isolated, closed conservation flocks, including non-random mating, genetic drift, inbreeding, or the Wahlund effect. Nevertheless, the exact magnitude of these parameters should be interpreted with caution, and larger cohorts will be required in future studies to fully validate these localized evolutionary trends.

Second, the panel of 17 microsatellite markers, although comparable in size to those employed in similar livestock studies, offers limited genomic coverage and may not fully capture the complex genetic architecture of the examined breeds. This constraint was further compounded by locus monomorphism in certain populations, most notably in VLDM, where six loci were monomorphic, thereby reducing the effective number of informative markers (Supplementary Table 2). Finally, the diversity estimates and admixture patterns presented here reflect a static snapshot of the genetic composition of these populations at the time of sampling. These patterns might also be influenced by the potential limitations of the STRUCTURE software in recovering exact population frameworks under uneven sampling conditions (Puechmaille, 2016). Given these factors, continuous genetic monitoring is essential to track potential losses of diversity or sudden shifts in population structure.

Importantly, the individuals analyzed here represent the entire gene pool of these breeds currently accessible and maintained within the conservation flock. Despite extensive efforts to locate purebred representatives across Russia, no additional unrelated individuals are presently available. Excluding breeds with limited sample sizes from the analysis would create permanent gaps in the understanding of their genetic architecture, potentially increasing the risk of genetic resource loss and hindering the development of effective conservation strategies. Despite these constraints, the results provide a useful first approximation of the genetic status of these rare populations and have already been shared with the gene pool enterprise responsible for their maintenance.

Such critically low population sizes underscore the urgency of integrating molecular genetic data into routine breeding management. Historically, managed populations of this size face an extreme risk of irreversible genetic erosion without coordinated institutional oversight. As successfully demonstrated in both domestic and wild avian populations experiencing severe demographic bottlenecks (e.g., Ryder et al., 2016; Robledo-Ruiz et al., 2023; Ali, 2024), these baseline genetic profiles are therefore vital for designing science-based, targeted mating strategies to minimize inbreeding and secure state-level conservation support for preserving Russia's avian genetic heritage.

Future investigations should transition to genome-wide approaches, including whole-genome sequencing (WGS; Ren et al., 2025) and high-density single-nucleotide polymorphism (SNP) analyses (Wang et al., 2024), which will allow for formal LD testing and a more robust assessment of HWE dynamics. Currently, genomic resources for poultry are rapidly expanding, with multiple high-quality genome assemblies available for *Anser* species, including *A. anser* and *A. cygnoides* (Li et al., 2020; Zhao et al., 2024; Jiang et al., 2026; NCBI, 2026). Implementing advanced genomic technologies, such as genotyping-by-sequencing (Grzegorczyk et al., 2021; Yang et al., 2026), restriction site-associated DNA sequencing (Yu et al., 2015), reduced-representation sequencing (Wright et al., 2019), and differential gene expression analyses (Ran et al., 2021), will substantially improve our understanding of genome architecture and economically important traits in this relatively understudied poultry species (Chen et al., 2023; Gao et al., 2023; Wen et al., 2023b; Wang et al., 2024; Sun et al., 2024; Huang et al., 2025; Ren et al., 2025).

To our knowledge, this study represents the first attempt to characterize the genetic diversity of Russian goose germplasm using a targeted STR panel. Based on the identified microsatellite genotypes, selected individuals have already been designated for artificial insemination, germplasm cryobanking (Martsev and Grishina, 2016), and future WGS projects (Kharzinova et al., 2025; Zinovieva et al., 2025). Securing the genetic potential of native breeds while simultaneously improving their productivity remains a pivotal challenge in animal husbandry (Gadyuchko et al., 2003; Moiseyeva et al., 2006; Baydevlyatova et al., 2009; Bondarenko and Khvostik, 2020a). Ultimately, the development, conservation, and sustainable use of Russian poultry genetic resources—which hold a unique place within Eurasian poultry biodiversity (Semyenova et al., 2002; Romanov et al., 2009; Dementieva et al., 2020)—will depend on the continuity of such molecular-guided initiatives.

Based on our findings, we recommend the following strategic actions:

a. Immediate conservation intervention by implementing urgent rescue measures for the VLDM breed due to its critically low genetic diversity and high number of monomorphic loci.
b. Systematic genetic monitoring to establish routine, long-term genetic screening for all populations maintained in the conservation flock, with a particular focus on the vulnerable VLDM and LRGR breeds.
c. Marker-assisted breeding by incorporating private allele data and individual multilocus genotypes into routine breeding programs to maximize overall genetic variance.
d. Advanced genomic mapping by initiating high-density SNP and WGS studies to investigate fine-scale ancestry patterns, runs of homozygosity (Dementieva et al., 2020), and signatures of selection associated with adaptive and production traits.

5 Conclusion

This study represents the first stage of molecular genetic research on native (LRGR, VLDM, TULA, and KHLM) and foreign-origin (CHGR) goose breeds maintained in the Russian germplasm collection. The inclusion of two KHLM populations differing in plumage color (KHLM_W and KHLM_G) additionally enabled assessment of intrabreed genetic structure. The results demonstrated that all studied goose populations possess distinctive characteristics with respect to their genetic diversity and population structure. The lowest level of genetic diversity was observed in VLDM, whereas the highest values of rarefied allelic richness and heterozygosity were found in both KHLM populations. Despite differences in allelic richness and patterns of intrapopulation variability, KHLM_W and KHLM_G exhibited high genetic similarity, retaining a common predominant genetic component and showing minimal genetic divergence. Analyses of population structure and genetic relationships further confirmed the complex history of KHLM formation and revealed the relative genetic affinity between VLDM and TULA. More broadly, the observed separation into two major genetic groups—a European cluster (LRGR–TULA–VLDM) and a Chinese-associated cluster (CHGR–KHLM_W–KHLM_G)—is generally in agreement with earlier phenetics-based classifications of goose breeds from the former USSR (Romanov, 1994) and with current concepts regarding the origin and microphylogeny of domestic geese from the two ancestral wild species, graylag goose and swan goose (Liu et al., 2006; Abdel Moniem et al., 2019; 2021; Grzegorczyk et al., 2021; Chen et al., 2023). The identified breed-specific genetic components emphasize the importance of conserving the germplasm of these populations as valuable genetic resources for future breeding and biodiversity preservation (Khvostik and Bondarenko, 2021). These exploratory results also indicate the necessity of gradually integrating traditional conservation practices with modern molecular approaches, including routine genetic monitoring, diversity management, cryobanking, and genomic characterization.

The present findings substantially expand current knowledge regarding the genetic diversity and population structure of Russian goose breeds. Nevertheless, the study should be regarded as preliminary because the analyzed populations originated from a single germplasm collection and may not fully represent the present-day diversity of these breeds across their breeding ranges. Future work should therefore include larger sample sizes from additional breeding and conservation farms and apply high-resolution genomic approaches, including whole-genome analyses, to validate and refine the observed patterns. Even at this stage, however, the obtained results provide an important scientific and practical foundation for developing effective strategies aimed at preserving the unique genetic resources of Russian goose breeds.

Data availability statement

The microsatellite genotype data generated and analyzed during the current study is publicly available in Figshare at https://doi.org/10.6084/m9.figshare.32685129.

Ethics statement

The animal study was approved by the LKEFRCAH Commission on the Ethics of Animal Experiments. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

VK: Formal Analysis, Writing – original draft, Project administration, Data curation, Investigation, Supervision, Conceptualization, Writing – review and editing. AD: Conceptualization, Validation, Visualization, Methodology, Writing – review and editing, Software, Investigation, Data curation, Formal Analysis. VV: Investigation, Validation, Writing – review and editing, Formal Analysis, Software, Data curation. NC: Writing – review and editing, Methodology. VB:

Funding acquisition, Writing – original draft. DG: Resources, Writing – original draft. IS: Writing – original draft, Resources. AM: Writing – review and editing, Methodology, Validation. AR: Resources, Writing – original draft. VN: Writing – original draft, Resources. MR: Formal Analysis, Visualization, Data curation, Software, Writing – review and editing, Conceptualization, Validation, Writing – original draft. NZ: Project administration, Conceptualization, Investigation, Funding acquisition, Supervision, Writing – review and editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was used in the creation of this manuscript. We used large language models for editorial assistance limited to formatting references, translating the original Russian manuscript and historical Latin and Russian sources into English, reviewing, consistency checks, and language polishing. Specifically, ChatGPT-5.5 (ChatGPT; OpenAI) and Google AI Mode (October 2026; Google LLC) were used. The authors verified the factual accuracy of all AI-assisted text, checked for plagiarism, and accept full responsibility for the manuscript. No generative AI system is listed as an author and none performed original data analysis or drew scientific conclusions.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fgene.2026.1926455/full#supplementary-material

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Appendix: Historical account of goose breeds in Russia: The Magic Swan Geese

Before analyzing the genetic diversity and population structure of Russian geese, it is important to briefly consider their historical origin and breeding development. Geese occupied a prominent place in Russian folklore and rural culture (Shein, 1900; Afanasev, 1975; Pokrovsky, 1994), frequently appearing in fairy tales and other traditional genres under the names *Magic Swan Geese* or simply *Swan Geese* (not to be confused with the biological species name swan goose *A. cygnoides*).

The formation of domestic goose breeds in Russia resulted from centuries of breeding, introduction of foreign populations, and interbreeding (Silaeva, 2004a; 2004b). Early naturalists, including Pallas (1811) and Baldamus (1877), suggested that Russian domestic geese originated through crosses between local *A. anser*-derived geese and Chinese geese descended from *A. cygnoides* (Knipovich and Sobichevsky, 1893). Although these hypotheses predated modern genetics, they represent the earliest concepts of Russian goose origins. Pallas (1811) also described unusually large Russian geese from the Arzamas region and noted their use in traditional goose fighting.

According to Abozin (1895), 1900, (1908), three ancient Russian fighting breeds—TULA, Arzamas, and KHLM—formed the historical core of Russian goose breeding. He considered TULA the oldest breed and proposed that Arzamas and KHLM originated from it. Goose fighting represented a unique feature of Russian poultry culture, and both TULA and Chinese geese were actively exhibited at major poultry exhibitions during the late 19th and early twentieth centuries (Somova, 1886; RPS, 1887; IRPS, 1899; RSAPF, 1907). After World War II, restoration programs included TULA, KHLM, and Chinese geese (Zelenskaja, 1942; Sapovalov, 1945). The present study investigates three historical breeds (TULA, KHLM, and Chinese) together with two more recently developed breeds (LRGR and VLDM).

TULA, traditionally divided into straight-, convex-, and concave-billed types (Abozin, 1895), is one of the oldest Russian goose breeds and was selected primarily for goose fighting (Saleev and Ionova, 1982). The breed was widely distributed across central Russia, particularly in the Tula Governorate, and historical authors considered it morphologically closest to *A. anser* (Abozin, 1895; Own Farming, 2025a). Today, it is regarded as endangered (Martsev and Grishina, 2016).

KHLM is another oldest Russian breeds. Most authors suggested that it originated during the 19th century from crosses between local white geese and Chinese geese, possibly involving TULA (Saleev and Ionova, 1982; Fisinin and Zlochevskaya, 1989; 1994; Pigarev, 1989d; VNIIplem, 1996; Martsev, 2020). Alternative historical accounts proposed crosses of Chinese and Arzamas geese or directly between TULA and Chinese geese (Abozin, 1895; 1896; 1908; 1913; Own Farming, 2025b; GeoMedia, 2026; Veterinary Encyclopedia, 2026). By 1980, approximately 18,500 KHLM geese remained in the USSR, after which numbers declined because of replacement by more productive breeds (Fisinin and Zlochevskaya, 1989).

LRGR, developed during the 1930s–1940s by reproductive crossing of Romny and Toulouse geese, historically included the Borki and Tambov Steppe varieties (Saleev and Ionova, 1982; Fisinin and Zlochevskaya, 1989; 1994; Pigarev, 1989b; VNIIplem, 1996; Martsev, 2020). It became one of the most widespread indigenous goose breeds in the USSR before declining following the introduction of imported commercial breeds and the post-Soviet collapse of goose production (Fisinin and Zlochevskaya, 1989). Earlier genetic studies relied mainly on biochemical markers, i.e., ovoprotein polymorphisms (Podstreshny et al., 2001; Khvostyk and Bondarenko, 2008; Bondarenko and Khvostik, 2020b).

VLDM originated from reproductive crossing between KHLM_W and Toulouse geese, followed by selection for clay-colored plumage (Saleev and Ionova, 1982; Fisinin and Zlochevskaya, 1989; 1994; Martsev, 2020). Once common in Vladimir Oblast, its population declined from about 230 birds in 1980 to only 40 in 1990 and 91 adults by 2020, making it critically endangered (Fisinin and Zlochevskaya, 1989; 1994; Zharkova, 2020).

Chinese geese, represented by white and gray varieties, descend from *A. cygnoides* domesticated in East Asia approximately 3,000–5,000 years ago (Scott, 1957; Saleev and Ionova, 1982; Scherf, 1995; Silaeva, 2004a; Romanov, 1994; Wen et al., 2023b). Known to earlier European travelers (Yule, 1913; Yule and Cordier, 1903; Polo, 1958; Haw, 2006), they have played a major role in the development of numerous Russian breeds (Saleev and Ionova, 1982; Fisinin and Zlochevskaya, 1994; VNIIplem, 1996). Historical descriptions (see also Supplementary Figure 1) by Pallas (1811), Albin (1734), Frisch (1763) and Teplov (1774) document their long-standing presence in Russia and Europe. Pallas (1811) and Darwin (1859) also noted their ability to produce fertile hybrids with domestic graylag-derived geese, an observation that anticipated modern concepts of goose domestication. Chinese geese were once widespread in Russia but declined sharply after the 1980s owing to replacement by more productive commercial breeds (Fisinin and Zlochevskaya, 1989).