Acta fytotechn zootechn, 28, 2025(2): 133–141
http://www.acta.fapz.uniag.sk

Original Paper

Selection Footprints Reflecting Population Stratification of Local Sheep Breeds in the Danube Region

Nina Moravčíková*[1], Karolína Pálešová[1], Adrián Halvoník[1], Monika Chalupková[1], Ivan Pavlík[2], Ján Tomka[2], Luboš Vostrý[3], Hana Vostrá-Vydrová[3], Gábor Mészáros[4], Tijesunimi Ojo[4], Birgit Fuerst-Waltl[4], Johann Sölkner[4], Božidarka Marković[5], Milena Djokić[5], Dušica Radonjic[5], Dragan Stanojević[6], Vladan Bogdanović[6], Radovan Kasarda[1]

[1]*Slovak University of Agriculture in Nitra, Slovakia*
[2]*NAFC – Research Institute for Animal Production Nitra, Lužianky, Slovakia*
[3]*Czech University of Life Sciences Prague, Praha-Suchdol, Czechia*
[4]*Universität für Bodenkultur Wien, Austria*
[5]*University of Montenegro – Biotechnical Faculty, Podgorica, Montenegro*
[6]*University of Belgrade, Faculty of Agriculture, Zemun-Belgrade, Serbia*

Article Details: Received: 2025-06-02 | Accepted: 2025-06-12 | Available online: 2025-06-30

https://doi.org/10.15414/afz.2025.28.02.133-141

This study investigated genetic diversity, population structure, and selection footprints across 16 local sheep breeds from the Danube region using high-density SNP data. The diversity status was derived from the overall heterozygosity and genomic-based inbreeding coefficients (F_{HOM} and F_{IS}). Population stratification was assessed using principal component analysis, phylogenetic networks, and admixture estimation. Selection footprints were identified based on the genome-wide Wright's fixation index (F_{ST}) distribution. Moderate observed and expected heterozygosity levels were found, with the highest values in the Improved Valachian breed ($H_o = 0.44 \pm 0.10$, $H_e = 0.44 \pm 0.08$) and the lowest in the East Friesian ($H_o = 0.37 \pm 0.16$) breed. Inbreeding coefficients aligned with heterozygosity patterns, indicating an increase in inbreeding in geographically or historically separated breeds and reduced inbreeding in recently developed composite breeds, particularly the Improved Valachian and Slovak Dairy sheep. All approaches testing population structure confirmed breed stratification corresponding to geographic and phylogenetic backgrounds, while admixture analysis revealed the highest proportion of genetic admixture in the composite breeds. A genome-wide scan revealed 24 candidate regions under selection pressure across 15 autosomes, encompassing 48 protein-coding genes, including those related to reproduction (*TNP1*, *AMHR2*) and immune response (*SLC11A1*, *IL9*, *JAK3*). Functional enrichment analysis identified overrepresented GO terms related to protein binding, spermatogenesis, hypoxia response, and KEGG pathways such as TGF-beta and VEGF signalling. This study provides insights into breed-specific selection pressures driven by diverse breeding goals and environmental adaptation in sheep breeds in the Danube region. The study also highlights the importance of genomic tools for preserving genetic diversity and supporting sustainable breeding strategies in local populations.

Keywords: selection effect, genetic diversity, high-density SNP data, local breeds

1 Introduction

The domestication of sheep (*Ovis aries*) marks a significant milestone in the history of agriculture, dating back to approximately 11,000 years ago in the Fertile Crescent (Atavliyeva and Tarlykov, 2018). Since then, the species has undergone extensive phenotypic and genetic diversification, driven by both natural and anthropogenic selection (Wang et al., 2019). Among the earliest drivers of anthropogenic selection was the dietary shift associated with transitioning from foraging to farming systems, which introduced novel ecological pressures and management practices (Yurtman et al., 2021; Kaptan et al., 2024). Following domestication, sheep spread into Europe along several major routes, with one of the most important being the migration through the Balkans into the Carpathian Basin. Archaeozoological evidence

---

***Corresponding Author:** Nina Moravčíková, Slovak University of Agriculture in Nitra, Tr. Andreja Hlinku 2, 949 76 Nitra, Slovakia; nina.moravcikova@uniag.sk https://orcid.org/0000-0003-1898-8718

suggests that sheep husbandry was established in the Balkans by the early Neolithic, from where it gradually expanded northwards into the Carpathian region and further into Central Europe. Throughout the Bronze and Iron Ages, and later during the Roman and Medieval periods, livestock movements, trade, and transhumance practices facilitated additional waves of gene flow and breed development (Schmölcke et al., 2018; Bánffy, 2019). In the Danube region, including present-day countries such as Serbia, Montenegro, Slovakia, Austria and Czechia, local breeds evolved under diverse agroecological conditions and cultural influences. These historical processes have contributed to the formation of distinct genetic structures among local sheep populations, reflecting both ancient migration events and more recent selective breeding efforts.

Genomic footprints of these processes include both reduced nucleotide diversity and increased genetic differentiation in specific genomic regions, depending on the nature and strength of selection (Yurchenko et al., 2019; Fonseca et al., 2024). Such patterns are often associated with selective sweeps, where advantageous alleles increase in frequency together with linked loci due to genetic hitchhiking (Barton, 2000; Kim and Stephan, 2003; Stephan, 2019). The nucleotide changes in regions of domestication-related candidate genes suggest that specific traits, such as reproduction, morphology, production performance, physiology, and behaviour, were subjected to strong directional selection during domestication, often manifested by a decrease in genetic variability around the target gene (Çınar et al., 2020; Li et al., 2020; Chen et al., 2021).

Footprints of selection in the genome can be identified using various population genetic tools and statistical methods. One of the most commonly applied approaches is based on determining the fixation index F_{ST}, which measures genetic differentiation between populations. Under neutral expectations, genetic drift and demographic history primarily shape allele frequency differences between populations. However, loci exhibiting unusually high or low F_{ST} values may be significantly affected by divergent selection pressure acting in these regions. In this context, high F_{ST} values usually reflect the effect of local adaptation, while low values suggest negative or balancing selection (Brito et al., 2017). In sheep, F_{ST}-based studies of selection footprints have identified candidate regions associated with important production and reproduction traits, including wool quality, prolificacy, and adaptation to production environments (Guo et al., 2022; Zhang et al., 2023; Yang et al., 2025).

Understanding how selection has shaped genomic variation is particularly relevant for livestock systems across the Danube region, where the maintenance and genetic improvement of locally adapted national sheep breeds remain central to both agricultural sustainability and cultural heritage. Such breeds represent unique genetic resources adapted over centuries to local environmental conditions and traditional management practices. Examples include the Valachian, Tsigai, Sumava, Pivska Pramenka or Zetska Zuja breeds, many of which are listed as national genetic resources playing important roles in marginal and low-input farming systems. Moreover, in several parts of the Danube region, including mountainous and submontane zones, sheep production is tightly linked to pastoral traditions, seasonal transhumance, and multifunctional land use, often prioritising the conservation of original phenotypic traits, such as wool type, horn morphology, and coat colour patterns. These breeds are commonly maintained by smallholders or cooperatives and are frequently integrated into agroecological farming, rural development projects, and agrotourism, supporting both biodiversity conservation and local economies (Oravcová et al., 2018; Mészárosová et al., 2022; Tomka et al., 2022; FAO, 2024). Due to this, the main aim of this study was to quantify genetic connectedness between local sheep breeds in the Danube region and identify selection footprints reflecting their population stratification.

2 Material and Methods

2.1 *Analysed Breeds and Genomic Data*

Genomic data of 739 animals belonging to 16 local sheep breeds originating from Czechia, Montenegro, Slovakia and Serbia were used in this study. Table 1 shows a detailed description of the analysed breeds. Because three different SNP arrays were used for the genotyping of animals, there was a relatively high decrease in the number of available autosomal SNPs with known physical positions after merging datasets. The subsequent quality control of genomic data included filtering of animals and SNPs with call rate higher than 90% and SNPs with minor allele frequency higher than 1% not adhering to Hardy-Weinberg distribution at the level of p <0.0000001. The final database included genotype information of 19,648 SNP markers for 739 animals.

2.2 *Population Stratification Analysis*

The overall average observed (H_o) and expected heterozygosity (H_e), the genomic inbreeding coefficient derived from observed and expected homozygous genotype counts (F_{HOM}) and Wright's inbreeding coefficient (F_{IS}) were calculated using PLINK v1.9 (Chang et al., 2015) to compare the levels of genetic variability among evaluated breeds. The degree of population

Table 1 Summary of the studied populations

Breed	Abbreviation	No. of animals	Country of origin
Improved Valachian sheep	CZIV	39	Czechia
Valachian sheep	CZOV	72	
Sumava sheep	CZS	48	
Bardoka	MEB	23	Montenegro
Pivska Pramenka	MEPP	24	
Sora	MES	28	
Zetska Zuja	MEZZ	29	
Tsigai	RSC	26	Serbia
Vlashko Vitoroga	RSVV	30	
Tsigai	SKC	70	Slovakia
Slovak Dairy sheep	SKD	36	
Improved Valachian	SKIV	70	
Lacaune	SKL	103	
Original Valachian	SKOV	94	
Texel	SKT	5	
East Friesian sheep	SKVF	42	

stratification that expresses the systematic difference in allele frequencies in populations due to different ancestry was quantified by principal component analysis (PCA) using the identity-by-state matrix calculated in PLINK v1.9, discriminant analysis of principal components in the R package adegenet (Jombart, 2008) and genetic admixture analysis using Bayesian approach in admixture (Alexander, 2009). In addition, population structure was tested using NetView (Neuditschko et al., 2012) to construct k-nearest neighbour networks and SplitsTree to generate phylogenetic networks based on Nei's genetic distance matrix (Huson et al., 1998).

2.3 *Testing of Selection Footprints*

Genomic regions under strong selection pressure were identified by determining Wright's F_{ST} index, which is widely used to infer selection footprints based on the assumption that loci under divergent selection exhibit higher differentiation than expected under neutrality. The F_{ST} index was calculated for each SNP marker in the dataset using PLINK v1.9 (Chang et al., 2015). Genomic regions consisting of at least three SNPs exceeding the threshold value (top 1% of extreme F_{ST} values) were considered candidate regions under significant selection pressure, reflecting underlying population stratification potentially driven by local adaptation or artificial selection in each analysed breed.

Protein-coding genes located within these regions were identified using the Ensembl BioMart data mining tool to explore the potential biological significance of the detected selection footprints. The resulting gene list was subsequently subjected to functional enrichment analysis using the Database for Annotation, Visualization, and Integrated Discovery (DAVID) (Sherman et al., 2022), which enabled the identification of significantly enriched Gene Ontology (GO) terms and KEGG pathways ($p < 0.05$), providing insights into the functional categories and biological processes potentially affected by selection.

3 Results and Discussion

3.1 *Degree of Population Stratification*

The highest levels of both observed and expected heterozygosity were found in the Improved Valachian population (H_o = 0.44 ±0.10, H_e = 0.44 ±0.08), while the lowest observed heterozygosity was detected in the East Friesian breed (H_o = 0.37 ±0.16), and the lowest expected heterozygosity in the Texel breed (H_e = 0.31 ±0.18). Although the overall average heterozygosity across populations (H_o = 0.41 ±0.15, H_e = 0.40 ±0.12) indicates a general reduction in heterozygosity, the observed values remain comparable or slightly higher than those reported for other regional or transboundary sheep breeds worldwide (e.g. Davenport et al., 2020; Wanjala et al., 2025). As shown in Figure 1, both the homozygosity-based inbreeding coefficient (F_{HOM}) and the inbreeding coefficient derived from the observed and expected heterozygosity across subpopulations (F_{IS}) revealed, with few exceptions, consistent trends in the overall homozygosity levels across populations. In agreement with the patterns of observed heterozygosity, the highest proportion

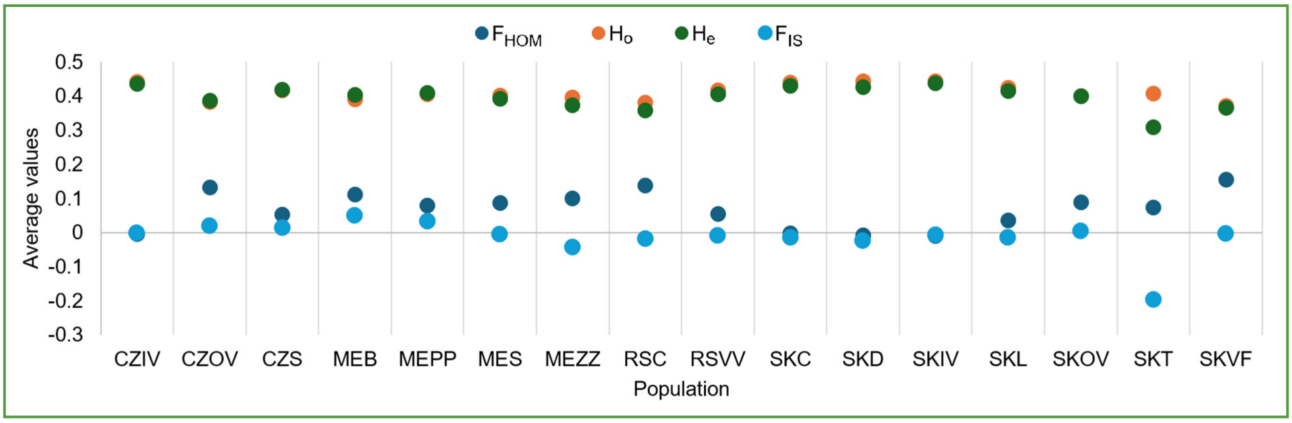

Figure 1 Comparison of average values of genetic diversity indicators across breeds
F_{HOM} – inbreeding coefficient derived from observed and expected homozygous genotype counts, F_{IS} – Wright's inbreeding coefficient, H_o – observed heterozygosity, H_e – expected heterozygosity

of homozygous genotypes was recorded in the East Friesian gene pool (F_{HOM} = 0.16 ±0.06), followed by Tsigai sheep from Serbia (F_{HOM} = 0.14 ±0.04) and Valachian sheep from Czechia (F_{HOM} = 0.13 ±0.08). Conversely, the lowest levels of genomic inbreeding were observed in recently developed breeds, such as the Improved Valachian sheep from Slovakia and Czechia (F_{HOM} = -0.01 ±0.03) and Slovak Dairy sheep (F_{HOM} = -0.003 ±0.02). This result was expected, as these breeds were developed through controlled breeding programs involving crosses of several genetically distinct breeds, which typically leads to increased genetic variability. A comparison of F_{HOM} and F_{IS} values showed generally consistent trends, except for the Texel breed, where opposite patterns were detected (Figure 1). This discrepancy is likely due to the limited sample size available for this population, which may have influenced the accuracy of inbreeding estimates and contributed to bias in *F*-statistics.

The observed variability in heterozygosity and inbreeding levels across the evaluated breeds primarily reflects differences in their breeding histories, management practices, and selection intensity. Similar patterns have been reported in other livestock species, such as local goat breeds maintained in Central and Southeast Europe (Vostrý et al., 2024). Breeds with recent composite origins, such as the Improved Valachian and Slovak Dairy sheep, exhibited higher genetic diversity and lower genomic inbreeding. In contrast, more traditional and geographically separated breeds, such as the Valachian sheep and the Vlashko Vitoroga breed, showed signs of increased homozygosity, likely indicating historical bottlenecks and limited gene flow (Spigler et al., 2017). Moreover, the obtained results underscore the importance of ongoing genomic monitoring to prevent the loss of genetic diversity, particularly in native and locally adapted sheep populations.

Graphical visualisation of the first two principal components (Figure 2A) revealed that individuals were clustered according to their geographical and phylogenetic origins. Breeds with shared ancestry or common founders tended to group more closely together. This pattern was particularly evident in the Improved Valachian populations from Slovakia and Czechia, which formed a tight cluster, indicating minimal genetic differentiation between them. Similarly, the Slovak Dairy sheep clustered near these populations, suggesting shared founder origins or recent gene flow between them. In contrast, the East Friesian and Texel breeds were separated from the other groups, reflecting substantial genetic divergence likely resulting from a distinct breeding history and selection pressures. This clustering pattern was also confirmed by the analysis of the network generated by the NetView approach (Figure 2B) and the phylogenetic tree constructed based on Nei's genetic distance matrix (Figure 2C). Results from both analyses supported the separation of major breed clusters identified by PCA. Geographically more separated breeds with long histories, such as Valachian sheep, Zetska Zuja, Tsigai, Texel or East Friesian, formed distinct branches. In contrast, close relationships between certain breeds, such as the Slovak and Czech Improved Valachian populations, were again evident. The estimated proportion of genetic admixture (Figure 2E) ranged from 3.14% to 11.45%. As expected, the highest admixture levels were detected in the genomes of the Slovak Dairy and Improved Valachian sheep, which both showed multiple ancestral components. This is consistent with their development as composite breeds, originating from breeding programs involving several founder populations to enhance specific production traits and adaptability. Conversely, traditional and regionally conserved breeds such as Šumava, East Friesian, Tsigai, Zetska Zuja or Vlashko Vitoroga displayed more uniform

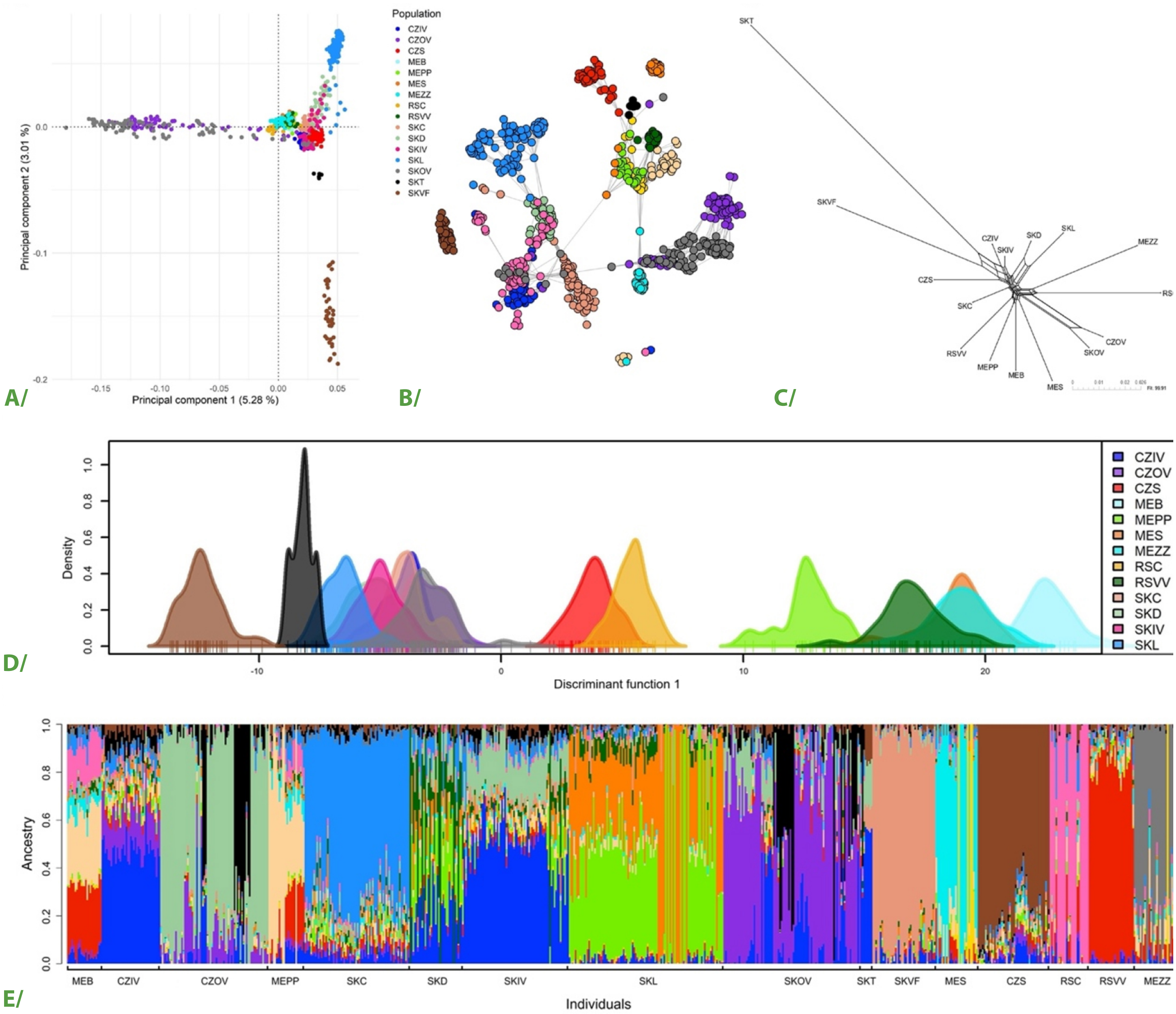

Figure 2 Population stratification based on principal component analysis
A/ – network graph generated using NetView approach; B/ – phylogenetic tree constructed from Nei's genetic distance matrix; C/ – first discriminant function of DAPC analysis; D/ – proportion of genetic admixture among breeds; E/ – CZIV – Improved Valachian sheep, CZOV – Valachian sheep, CZS – Sumava sheep, MEB – Bardoka, MEPP – Pivska Pramenka, MES – Sora, MEZZ – Zetska Zuja, RSC – Tsigai, RSVV – Vlashko Vitoroga, SKC – Tsigai, SKD – Slovak Dairy sheep, SKIV – Improved Valachian, SKL – Lacaune, SKOV – Original Valachian, SKT – Texel, SKVF – East Friesian sheep

ancestry profiles, indicating a stable genetic background shaped primarily by natural and artificial selection, in accordance with specific breeding objectives and environmental conditions.

The genetic structure observed among the analysed sheep breeds is consistent with previous studies on both regional and transboundary livestock populations. Breeds with a history of systematic crossbreeding, such as those recently developed or improved, typically show higher levels of genetic admixture and diversity due to the incorporation of multiple founder populations (Jaafar et al., 2022). In contrast, autochthonous or regionally conserved breeds often form distinct genetic clusters, reflecting their long-term geographic isolation and limited gene flow with other breeds. This was well documented in almost all livestock species, including cattle (Kukučková et al., 2017), sheep (Ramírez-Díaz et al., 2025) and goats (Vostrý et al., 2024).

3.2 Genomic Footprints of Selection Reflected Intensity of Population Stratification

A genome-wide scan of the F_{ST} values revealed 24 candidate genomic regions under strong selection pressure due to divergent breeding objectives and selection strategies applied among the studied breeds. These regions distributed across 15 autosomes were defined based on clusters of at least three SNPs exceeding the threshold defined by the 99th percentile of the obtained F_{ST} values

($F_{ST} \geq 0.12$). The highest proportion of selection footprints was found on autosome 3, whereas the signal showing the highest F_{ST} value was located on autosome 20 (Table 2). Representative results of the genome-wide F_{ST} scan, including the detected selection footprints, are shown in Figure 3.

Annotation of the candidate regions showed 48 protein-coding genes involved in the genetic control of various biological processes. A summary of the genes, including significantly enriched GO terms and KEGG pathways, is shown in Table 2 (GO-enriched genes are highlighted in bold). Notably, several genes were associated with reproductive traits, including *TNP1* (Anjum et al., 2022), which plays a role in spermatids chromatin condensation, and *AMHR2*, a gene associated with gonadal development and sex differentiation (Cutting et al., 2014). Additionally, immune-related genes such as *SLC11A1* (involved in innate immune response and pathogen resistance; Liu et al., 2011), *IL9* (a key driver of immune responses in inflammatory and immune diseases; Neurath and Finotto, 2016), and *JAK3* (part of the JAK-STAT signalling pathway essential for cytokine receptor signalling; Murray, 2007) were identified in regions under selection pressure, suggesting that adaptation to local environments may have been a significant selective force in certain breeds.

To assess the biological importance of detected selection footprints, enrichment analysis of protein-coding genes

Table 2 Summary of detected footprints of selection

Chr	Start (Mbp)	End (Mbp)	Size (Mbp)	Avg. F_{ST}	Protein-coding genes	Significantly enriched GO term/KEGG pathway
1	204.36	204.45	0.09	0.12	***FXR1***	GO:0042803, GO:0007286
2	189.59	189.65	0.06	0.17	–	GO:0007286 GO:0042803, GO:0030041
	217.56	217.98	0.42	0.14	*IGFBP5*, ***TNP1***	
	219.16	219.40	0.24	0.15	***ARPC2,*** *AAMP, PNKD, TMBIM1,* ***CATIP, SLC11A1,*** *CTDSP1*	
3	93.55	93.89	0.33	0.17	*ENSOARG00000026000, ENSOARG00000011524*	GO:0042803, oas04350, oas04060, GO:0001664
	112.16	112.54	0.37	0.13	*OSBPL8, ZDHHC17*	
	132.72	133.02	0.30	0.13	***NPFF, TARBP2,*** *MAP3K12, PCBP2, U6,* ***AMHR2, SP1***	
	159.60	159.88	0.28	0.12	*SLC16A7*	
4	116.45	116.86	0.41	0.12	*INSIG1, CNPY1, RBM33*	
5	4.90	5.15	0.25	0.12	*ARRDC2, KCNN1, CCDC124,* ***SLC5A5,*** *JAK3,* ***INSL3***	GO:0042803, oas04062, GO:0001664 oas04350, oas04060
	44.58	45.05	0.47	0.13	*SLC25A48,* ***IL9,*** *FBXL21P, LECT2,* ***SMAD5,*** *TGFBI, Vault*	
7	44.87	45.18	0.31	0.13	*U6, VPS13C*	
8	40.77	41.17	0.40	0.13	*ENSOARG00000027018*	
10	28.41	28.63	0.23	0.19	*PDS5B*	
	42.66	42.93	0.26	0.14	–	
11	0.01	0.25	0.24	0.13	*ENSOARG00000003921*	
	12.06	12.41	0.35	0.14	*APPBP2, CHCT1, USP32, U6, CA4*	
15	78.45	78.61	0.16	0.13	*ENSOARG00000010872, ENSOARG00000010877, ENSOARG00000012905, ENSOARG00000026848*	
17	59.37	59.47	0.10	0.13	–	
18	44.78	45.07	0.29	0.14	*RALGAPA1, BRMS1L*	
	70.44	70.84	0.40	0.14	–	
19	27.67	28.01	0.34	0.13	*ENSOARG00000024837*	
20	18.79	19.03	0.23	0.19	*ENSOARG00000010358*	
21	3.75	4.26	0.50	0.16	–	

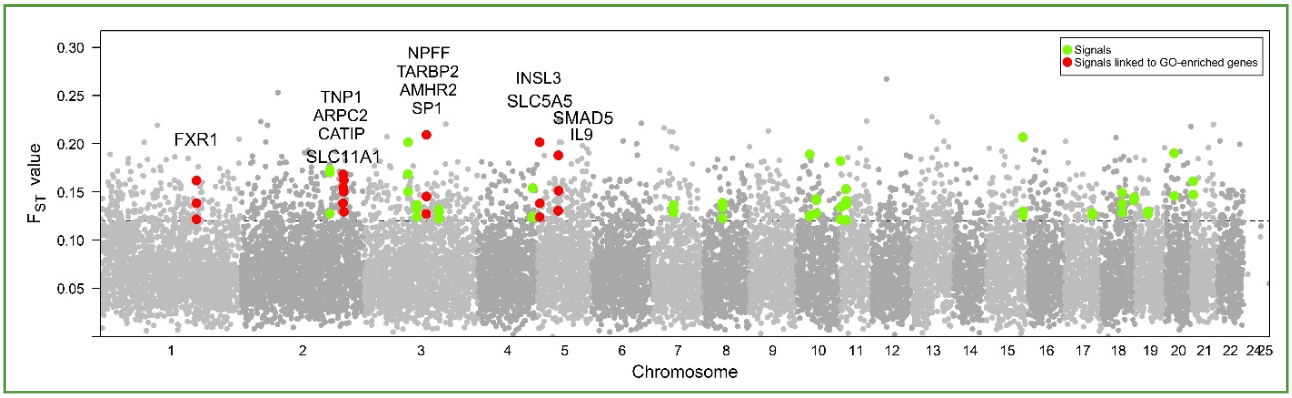

Figure 3 Genome-wide distribution of F_{ST} values and identified selection footprints

within the regions was performed using DAVID. This analysis revealed several significantly overrepresented GO terms and KEGG pathways (*p* <0.05) (Table 2). The most consistently enriched GO term was "protein homodimerization activity" (GO:0042803), which may reflect general cellular functions under selection due to diverse selective pressures. More specific enrichments included "spermatid development" (GO:0007286), indicating that reproductive capability may be a target of artificial selection in commercial and locally adapted breeds, and "G protein-coupled receptor binding" (GO:0001664) responsible for regulating a wide array of physiological processes, including reproduction, development, metabolism, stress responses, and cognition (Kleinau et al., 2024). Some of the genes were significantly involved in two KEGG pathways, TGF-beta signalling pathway (oas04350) and VEGF signalling pathway (oas04370), both of which are associated with growth, development, and tissue remodelling and may reflect historical selection for production traits such as muscle development.

The observed results are consistent with previous studies reporting similar patterns of selection effects in livestock populations. For example, Rodrigues et al. (2025) and Zhang et al. (2021) highlighted the role of immune and reproductive genes in the adaptation of local sheep populations. Moreover, the enrichment of metabolic and signalling pathways parallels results from studies on cattle and goats, where genes involved in energy metabolism, immune function, and environmental stress responses were recurrently under selection (Colombi et al., 2024; Peng et al., 2024).

4 Conclusion

This study highlights substantial variability in genetic diversity and population structure among local sheep breeds in the Danube region. Breeds developed through systematic crossbreeding programs, such as the Improved Valachian and Slovak Dairy sheep, show higher heterozygosity and lower inbreeding, reflecting their broader genetic base. In contrast, traditional breeds with long-term histories exhibit increased homozygosity and distinct genetic clustering, suggesting restricted gene flow and possible historical bottlenecks. Genome-wide scans identified candidate regions under selection associated with reproduction, immune function, and environmental adaptation, shaped by both natural and artificial selection pressures. The results support the view that artificial selection for economically important traits, alongside adaptation to local environments, has significantly influenced the genomic architecture of sheep breeds. The presence of highly differentiated genomic regions containing functionally relevant genes offers a basis for future research focused on key adaptive and production traits. Such insights are essential for developing sustainable breeding strategies that maintain genetic diversity while promoting productivity and resilience under diverse production conditions.

Author Contributions

Conceptualization, R.K., N.M., L.V., J.S., B.F. and G.M.; Methodology, N.M., R.K., G.M. and L.V.; Validation, J.S., L.V., B.F. and G.M.; Formal Analysis, N.M.; Data Curation, N.M., L.V., D.S. and M.D.; Writing – Original Draft Preparation, N.M. and K.P.; Writing – Review & Editing, J.S., A.H., M.CH., I.P., J.T., H.V., G.M., T.O., B.F., B.M., M.D., D.R. and D.S.; Visualization, N.M.; Project Administration, R.K., B.M., L.V., G.M. and D.S.; Funding Acquisition, R.K., B.M., L.V., G.M. and V.B.

Acknowledgements

This research has been supported by the Ministry of Education, Research, Development and Youth of the Slovak Republic (grant no. 1/0316/25), the Slovak Research and Development Agency (grant no. APVV-20-0161 and DS-FR-22-0016), the Ministry of Education, Youth and Sports in the Czech Republic (grant no. 8X23019), the Ministry of Science, Technological Development and Innovation in the Republic of Serbia (grant no. 337-00-140/2023-05/01) and the Ministry of Education, Science and Innovation in Montenegro (grant no. 0604-053/23-1220/2). The support of the MULT 04/2023WTZ project funded by OeAD-GmbH Austria's Agency for Education and Internationalisation and the BMBWF is greatly appreciated. This publication was created thanks to the support of the Research and Innovation operational program for the project: Support of research activities at SPU Nitra in the field of animal production, 313011U414, co-financed from the resources of the European Regional Development Fund.

References

Alexander, D. H., Novembre, J., & Lange K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Res*, 19(9), 1655–1664. https://doi.org/10.1101/gr.094052.109

Anjum, K. H. et al. (2022). Genomic and Computational Analysis of Novel SNPs in *TNP1* Gene Promoter Region of Bos indicus Breeding Bulls. *Genet Res* (Camb), 2022, 9452234. https://doi.org/10.1155/2022/9452234

Atavliyeva, S., & Tarlykov, P. (2018). Genetic history of sheep domestication. *Eurasian Journal of Applied Biotechnology*, 1. https://doi.org/10.11134/btp.1.2018.1

Bánffy, E. (2019). First Farmers of the Carpatian Basin. In Allen, M. J., & Gardiner, J. (Eds.). *The prehistoric society research papers No. 8*. Oxbow Books (pp. 192).

Barton, N. H. (2000). Genetic hitchhiking. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355(1403), 1553–1562. https://doi.org/10.1098/rstb.2000.0716

Brito, L. F. et al. (2017). Genetic diversity and signatures of selection in various goat breeds revealed by genome-wide SNP markers. *BMC Genomics*, 18, 229. https://doi.org/10.1186/s12864-017-3610-0

Chang, C. C. et al. (2015). Second-generation PLINK: rising to the challenge of larger and richer datasets. *Gigascience*, 4, 7. https://doi.org/10.1186/s13742-015-0047-8

Chen, Z. H. et al. (2021). Whole-genome sequence analysis unveils different origins of European and Asiatic mouflon and domestication-related genes in sheep. *Communications Biology*, 4, 1307. https://doi.org/10.1038/s42003-021-02817-4

Çınar, M. U. et al. (2020). Association of TMEM8B and SPAG8 with Mature Weight in Sheep. *Animals*, 10(12), 2391. https://doi.org/10.3390/ani10122391

Colombi, D. et al. (2024). Genomic responses to climatic challenges in beef cattle: A review. *Anim Genet*, 55(6), 854–870. https://doi.org/10.1111/age.13474

Cutting, A. D. et al. (2014). Identification, expression, and regulation of anti-Müllerian hormone type-II receptor in the embryonic chicken gonad. *Biol Reprod*, 90(5), 106. https://doi.org/10.1095/biolreprod.113.116491

Davenport, K. M. et al. (2020). Genetic structure and admixture in sheep from terminal breeds in the United States. *Anim Genet*, 51(2), 284–291. https://doi.org/10.1111/age.12905

FAO. (2024). Genetic diversity of livestock can help feed a hotter, harsher world. FAO. https://www.fao.org/newsroom/detail/Genetic-diversity-of-livestock-can-help-feed-a-hotter-harsher-world/en

Fonseca, P. A. S. et al. (2024). Integration of selective sweeps across the sheep genome: Understanding the relationship between production and adaptation traits. *Genetics Selection Evolution*, 56, 40. https://doi.org/10.1186/s12711-024-00910-w

Guo, Y. et al. (2022). Sequencing reveals population structure and selection signatures for reproductive traits in Yunnan semi-fine wool sheep (*Ovis aries*). *Frontiers in Genetics*, 13, 812753. https://doi.org/10.3389/fgene.2022.812753

Huson, D. H. (1998). SplitsTree: analyzing and visualizing evolutionary data. *Bioinformatics*, 14(1), 68–73. https://doi.org/10.1093/bioinformatics/14.1.68

Jaafar, M. A. et al. (2022). The impact of using different ancestral reference populations in assessing crossbred population admixture and influence on performance. *Front Genet*, 13, 910998. https://doi.org/10.3389/fgene.2022.910998

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24(11), 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Kaptan, D. et al. (2024). The population history of domestic sheep revealed by paleogenomes. *Molecular Biology and Evolution*, 41(10), msae158. https://doi.org/10.1093/molbev/msae158

Kim, Y., & Stephan, W. (2003). Selective sweeps in the presence of interference among partially linked loci. *Genetics*, 164(1), 389–398. https://doi.org/10.1093/genetics/164.1.389

Kleinau, G. et al. (2024). The role of G protein-coupled receptors and their ligands in animal domestication. *Anim Genet*, 55(6), 893–906. https://doi.org/10.1111/age.13476

Kukučková, V. et al. (2017). Genomic characterization of Pinzgau cattle: genetic conservation and breeding perspectives. *Conserv Genet*, 18, 893–910. https://doi.org/10.1007/s10592-017-0935-9

Li, X. et al. (2020). Whole-genome resequencing of wild and domestic sheep identifies genes associated with morphological and agronomic traits. *Nature Communications*, 11(1). https://doi.org/10.1038/s41467-020-16485-1

Liu, Y. et al. (2011). Association Analysis between the Polymorphism of the *SLC11A1* Gene and Immune Response Traits in Pigs. *Asian Journal of Animal and Veterinary Advances*, 6, 580–586. https://doi.org/10.3923/ajava.2011.580.586

Mészárosová, M. et al. (2022). Within- and between-breed selection signatures in the Original and Improved Valachian sheep. *Animals*, 12(11), 1346. https://doi.org/10.3390/ani12111346

Murray, P. J. 2007. The JAK-STAT signaling pathway: input and output integration. *J Immunol*, 178(5), 2623–2629. https://doi.org/10.4049/jimmunol.178.5.2623

Neuditschko, M., Khatkar, M. S., & Raadsma, H. W. (2012). NetView: a high-definition network-visualization approach to detect fine-scale population structures from genome-wide patterns of variation. *PLoS One*, 7(10), e48375. https://doi.org/10.1371/journal.pone.0048375

Neurath, M.F., & Finotto, S. (2016). IL-9 signaling as key driver of chronic inflammation in mucosal immunity. *Cytokine Growth Factor Rev*, 29, 93–99. https://doi.org/10.1016/j.cytogfr.2016.02.002

Oravcová, M., Mačuhová, L., & Tančin, V. (2018). The relationship between somatic cells and milk traits, and their variation in dairy sheep breeds in Slovakia. *Journal of Animal and Feed Sciences*, 27, 97–104. https://doi.org/10.22358/jafs/90015/2018

Peng, W. et al. (2024). Selection signatures and landscape genomics analysis to reveal climate adaptation of goat breeds. *BMC Genomics*, 25(1), 420. https://doi.org/10.1186/s12864-024-10334-x

Ramírez-Díaz, J. et al. (2025). Exploring the complex population structure and admixture of four local Hungarian sheep breeds. *Front Genet*, 16, 1507315. https://doi.org/10.3389/fgene.2025.1507315

Rodrigues, J. L. et al. (2025). Genetic diversity and selection signatures in sheep breeds. *J Appl Genetics*. https://doi.org/10.1007/s13353-025-00941-z

Schmölcke, U., Gross, D., & Nikulina, E. A. (2018). The history of sheep husbandry in Austria from the Neolithic to the Roman Period. *Ann. Naturhist. Mus. Wien, Serie A*, 120, 101–126.

Sherman, B. T. et al. (2022). DAVID: a web server for functional enrichment analysis and functional annotation of gene lists (2021 update). *Nucleic Acids Res*, 50(W1), W216–W221. https://doi.org/10.1093/nar/gkac194

Spigler, R. B., Theodorou, K., & Chang, S. M. (2017). Inbreeding depression and drift load in small populations at demographic disequilibrium. *Evolution*, 71(1), 81–94. https://doi.org/10.1111/evo.13103

Stephan, W. (2019). Selective sweeps. *Genetics*, 211(1), 5–13. https://doi.org/10.1534/genetics.118.301319

Tomka, J., Huba, J., & Pavlík, I. (2022). The state of conservation of animal genetic resources in Slovakia. *Genetic Resources*, 3(6), 49–63. https://doi.org/10.46265/genresj.XRHU9134

Vostry, L. et al. (2024). Genomic analysis of conservation status, population structure, and admixture in local Czech and Slovak dairy goat breeds. *J Dairy Sci,* 107(10), 8205–8222. https://doi.org/10.3168/jds.2023-24607

Wang, W. et al. (2019). Deep genome resequencing reveals artificial and natural selection for visual deterioration, plateau adaptability and high prolificacy in Chinese domestic sheep. *Frontiers in Genetics*, 10, 300. https://doi.org/10.3389/fgene.2019.00300

Wanjala, G. et al. (2025). Genetic diversity and adaptability of native sheep breeds from different climatic zones. *Sci Rep*, 15(1), 14143. https://doi.org/10.1038/s41598-025-97931-2

Yang, C. et al. (2025). Genetic Structure and Selection Signals for Extreme Environment Adaptation in Lop Sheep of Xinjiang. *Biology*, 14(4), 337. https://doi.org/10.3390/biology14040337

Yurchenko, A. A. et al. (2019). High-density genotyping reveals signatures of selection related to acclimation and economically important traits in 15 local sheep breeds from Russia. *BMC Genomics*, 20(S3), 294. https://doi.org/10.1186/s12864-019-5537-0

Yurtman, E. et al. (2021). Archaeogenetic analysis of Neolithic sheep from Anatolia suggests a complex demographic history since domestication. *Communications Biology*, 4, 1279. https://doi.org/10.1038/s42003-021-02794-8

Zhang, W. et al. (2023). Whole-Genome Resequencing Reveals Selection Signal Related to Sheep Wool Fineness. *Animals*, 13(18), 2944. https://doi.org/10.3390/ani13182944

Zhang, Y. et al. (2021). Genome-wide comparative analyses reveal selection signatures underlying adaptation and production in Tibetan and Poll Dorset sheep. *Sci Rep*, 11(1), 2466. https://doi.org/10.1038/s41598-021-81932-y