

Theses of Doctoral (Ph.D.) Dissertation

**POPULATION STRUCTURE AND GENETIC CHARACTERIZATION OF
INDIGENOUS GOAT BREEDS FROM DIFFERENT CLIMATIC ZONES AS A
CLIMATE CHANGE AND ADAPTATION MECHANISM**

NELLY KICHAMU
Ph.D. candidate

Supervisor:
Prof. Dr. Szilvia Kusza, D.Sc.



**UNIVERSITY OF DEBRECEN
Doctoral School of Animal Science**

Debrecen, 2026

1. INTRODUCTION

Climate change has created significant challenges for agricultural productivity, food security, and ecosystem stability, with developing countries being particularly affected. In these contexts, livestock species that can thrive under harsh environmental conditions are increasingly important for sustainable food systems and rural livelihoods. Among these, the domestic goat (*Capra hircus*) holds considerable significance. Goats were among the first animals to be domesticated, with evidence tracing their origins to the Zagros Mountains of the Fertile Crescent in Southwest Asia approximately 10,000 years ago. Today, goats play an essential role in the livelihoods of smallholder farming communities worldwide, owing to their remarkable ability to adapt to a wide range of challenging environments, including arid, semi-arid, desert, and mountainous regions. Their small body size, high reproduction rate, and resilience to harsh conditions make goats a vital resource for smallholder farmers, particularly women, in resource-constraint settings. Breeding indigenous goats that are adapted to local climates and resistant to diseases is therefore considered essential for maintaining a stable and sustainable food supply.

However, the genetic diversity of indigenous goat populations is increasingly threatened by crossbreeding with exotic breeds, limited conservation efforts, traditional management practices, and insufficient attention from breeding programs. This genetic erosion undermines their adaptive capacity to withstand the pressures of climate change. It is therefore crucial to understand the genetic diversity and population structure of these indigenous populations in order to inform effective conservation and management strategies. This doctoral research thus focused on assessing the population structure and genetic diversity of indigenous goat populations across different regions, with particular emphasis on their climate adaptation mechanisms, guided by the following objectives:

1. To perform genetic characterization of Kenyan indigenous goat breeds using pedigree information.
2. To evaluate the genomic characteristics of African, Asian, and European native goat breeds.
3. To determine the genomic relationships among native goats from Africa, Asia, and Europe.
4. To identify signatures of selection that underlie the adaptation of these goat populations.

2. MATERIALS AND METHODS

2.1. Ethics statement

This doctoral research was approved by the Scientific and Ethics Committee of the Center for Agricultural Genomics and Biotechnology of the University of Debrecen.

2.2 Genetic characterization of Kenyan native goat breeds using pedigree

2.2.1 Animal species and data for pedigree analysis

Pedigree data for Galla and SEA were obtained from the national studbook maintained by the Kenya Stud Book (KSB), including records from two state sheep and goat breeding farms and four private farms across Kenya. A total of 7,324 animals were analyzed ($n = 5,224$ Galla, comprising 3,460 females and 1,762 males; $n = 2,162$ SEA, comprising 1,220 females and 942 males), born between 1983 and 2022, were used in this study.

2.3 Genetic characterization of European, Asia, and African goats using molecular data

2.3.1 Animal species, sample collection regions, and genotyping

Blood samples of 372 goats from Africa, Asia, and Europe (Table 1) were collected from the jugular vein by an experienced veterinary officer, following all the standard protocol and requirements. The samples were then stored in the laboratory freezer at temperatures below -20°C , awaiting processing to Whatman FTA cards. The whole process from DNA isolation to variant calling and genotyping using the CaprineSNP70K Bead Chip array (Illumina, USA) was done by NEOGEN Company, Scotland.

Table 1. Breed name, continent, country, and number of animals sampled

Country	Continent	Breed name	Breed code	Numbers
Ethiopia	Africa	Keffa	KEF	30
		Woyto-Guji	WG	25
Kenya		Galla	GAL	25
		Small East African	SEA	25
Tanzania		Pare White	PWT	25
		Maasai East African	MEA	25
Hungary	Europe	Hungarian Native	HUN	40
Romania		Banat White	BWT	12
Bosnia-Herzegovina		Domaća Balkanska Šarena Koza	DBSK	20

Country	Continent	Breed name	Breed code	Numbers
Philippines	Asia	Philippine Native Antipas Cotabato group	PHIN	25
Kazakh		Local goat population from Darbazo	DAB	20
		Local goat population from Kenes	KENS	20
		Local goat population from Kosseit	KOSS	20
		Local goat population from Shokpar	SHOK	20
		Local goat population from Ushterek	USH	20
		Local goat population from Kundyzdy	KUN	20
Total				372

2.3.2 Quality control

Quality control (QC) for genotyped data was done using the PLINK version 1.9 (PURCELL et al., 2007). Before QC, the study had a total of 372 goat samples, each with 64,264 autosomes after removing the sex chromosomes. First, the raw genotyped were converted to the binary PLINK format (.bed, .bim, and .fam). After this, the following threshold was applied: individuals with more than 10% missing genotypes, and SNPs with a call rate of below 95%, SNPs with minor allele frequency (MAF) < 0.01 were excluded.

Hardy–Weinberg equilibrium (HWE) test was performed on control samples to detect potential genotyping errors. All variants with significant deviations ($p < 1 \times 10^{-6}$) from HWE, animals with first-line relations (parent-offspring and sibling-sibling), and SNPs at linkage disequilibrium were excluded. During the quality control process, the following exclusions were made: 2,000 variants with missing genotype, 1 sample with missing genotype data, and 3,575 variants not meeting the minor allele threshold were removed. Besides, 2,086 variants were removed due to the HWE test, 5,484 variants were linkage disequilibrium (LD) pruned and excluded by --indep-pairwise 50 5 0.2 command. The remaining SNPs for analysis of genetic diversity and population structure were 371 samples and 51,119 SNPs, with an average call rate of 0.97.

2.4 Statistical analysis

2.4.1 Genetic characterization of Kenyan native goat breeds using pedigree

ENDOG software version 4.8 (GUTIERREZ & GOYACHE, 2005) was used to assess the pedigree completeness (PC), generation interval (GI), inbreeding coefficient (F), average relatedness (AR), effective population size (Ne), and effective number (fe) of founders and ancestors (fa) in the study goats.

2.4.2 Estimating pedigree completeness (PC)

The following parameters were used to measure pedigree completeness: (a) Number of maximum traced generations (MG), (b) Number of complete generations (CG), using the formula proposed by GINJA et al. (2017).

$$CG = \left(\frac{1}{2}\right)n$$

Where n is the number of generations separating the individual from each known ancestor.

2.4.3 Estimation of generation interval (GI)

GI is defined as the average age of parents at the birth of their offspring (CASTRO-VÁSQUEZ et al., 2023; HONG et al., 2024) and was assessed using four different pathways, including: Buck-son (Lss), Buck-daughter (Lsd), Doe-son (Lds), and Doe-daughter (Ldd). To get the average GI of all four pathways, the following formula was applied:

$$GI = \frac{Lss + Lsd + Ldd + Lds}{4}$$

2.4.4 Inbreeding coefficient (F) and average relatedness coefficient (AR)

F was defined as the level of relationship between two individuals who share common ancestors. F was calculated using the formula proposed by BIJMA & WOOLLIAMS (2000), while the change in inbreeding rates per year ($\Delta F/y$) and per generation ($\Delta F/g$) were derived by regressing F values against year of birth. The average relatedness coefficient (AR) is defined as the probability that any offspring randomly chosen originates from a specific animal in the pedigree data (RASHIDI et al., 2015; GUTIÉRREZ & GOYACHE, 2005). AR was also computed using the method described by BERNARDES et al. (2016).

2.4.5 Estimation of effective population size (Ne)

Ne is the number of individuals in an ideal population that would result in the same rate of inbreeding as observed in the actual population (MANUNZA et al., 2025) and was

calculated by regressing individual inbreeding on the mean MG, mean CG (BARROS et al., 2011). Besides, the Individual change in inbreeding ΔFi was calculated using the formula defined by GOYACHE et al. (2003). The realized Ne was then calculated by averaging the individual increase in inbreeding.

2.4.6 Assessment of effective number of founders (f_e) and ancestors (f_a)

These parameters are used to characterize the genetic variability of a given population, based on the gene origin for animals with complete parental information. The f_e , which is the number of animals producing the same level of genetic diversity if randomly mated. The f_e was evaluated using the formula by BERNARDES et al. (2016). The genetic contribution of ancestors (f) was assessed by applying the formula proposed by BOICHARD et al. (1997). While the f_a was computed based on the marginal contribution, following the method by BOICHARD et al. (1997).

2.5. Statistical analysis using molecular data (70K goats beadchip)

2.5.1 Analysis of within-population genetic diversity

Observed heterozygosity (H_o) for each population was calculated to understand their level of genetic diversity. Three genomic inbreeding coefficients (F_{hat1} , F_{hat2} , and F_{hat3}) were computed in PLINK, following the framework established in the GCTA software (YANG et al., 2011). Runs of Homozygosity (ROH) were identified using the consecutive runs method implemented in detectRUNS without linkage disequilibrium pruning (BISCARINI et al., 2019) in R (R CORE TEAM, 2016). The analysis required a minimum of 15 SNPs per run, with a maximum gap of one million base pairs between adjacent SNPs and a minimum run length of 250 kilobases. Each ROH was allowed one heterozygous and one missing genotype per segment. Detected ROH were categorized into five length classes (0–6, 6–12, 12–24, 24–48, and >48 Mb), and their frequency was calculated for each population. The genomic inbreeding coefficient based on ROH (F_{ROH}) was then summarized both per length category and for each population overall. The overall mean values were computed by averaging across all populations included in the dataset. Historical Ne of each population was estimated using the LD-based method in the SNeP software version 1.11 (BARBATO et al., 2020). To compare the current and historic Ne , the GONe software (COOMBS et al., 2012) was used while setting default parameters. Results from SNeP and GONe were then visualized in R ggplot2 (WICKHAM, 2016).

2.5.2 Population structure and relationship between and among the studied goat populations

Genomic relatedness among the goat populations was evaluated using a Neighbor-Net network based on Reynolds' pairwise genetic distances (F_{ST}) and visualized in SplitsTree v4 (HUSON & BRYANT, 2006). To quantify genetic differentiation between populations, the F_{ST} matrix was computed using the StAMPP package (PEMBLETON et al., 2013). Further, principal component analysis (PCA) was used to assess the population structure and done using PLINK v2.0 and visualized in R with Tidyverse (CHANG et al., 2015; WICKHAM, 2016; R CORE TEAM, 2016). Proportion of individual ancestry were estimated with ADMIXTURE v1.3 (ALEXANDER et al., 2015) on the LD-pruned dataset, while testing K values from 1 to 20 and selecting the optimal K based on the lowest cross-validation error; the resulting bar plots were visualized in the BITE v2 package in R (MILANESI et al., 2017; R CORE TEAM, 2016). Gene flow among populations was inferred using the maximum-likelihood framework in TreeMix v1.13 (PICKRELL & PRITCHARD, 2012), starting with five migration edges and increasing m stepwise until the model explained about 99.8% of the variance.

2.5.3 Identification of signatures of positive selection for adaptation within the populations

Two methods were used to assess the signatures of selection within the studied goat populations, including Extreme Runs of Homozygosity islands (eROHi) and the Integrated Haplotype Score (iHS). The eROHi was assessed using the output files generated from ROH above. The iHS method was evaluated using the Rehh package (GAUTIER & VITALIS, 2012) implemented in R software. The candidate regions were then identified and calculated using a sliding window method, applying thresholds to those used in the identification of ROH islands. Those genes within 250 kilobases upstream and downstream of this region were annotated using BioMart (DURINCK et al., 2005) based on the *Capra hircus* reference genome (ARS1) from the Ensemble database (HUBBARD et al., 2002). Reviews from multiple published scientific literature were also useful in determining the functions of identified genes.

threatened with extinction (FAO, 1998). The increase may arise from the breeding program that encouraged mating between related individuals in the population.

N_e was consistently low in both breeds, indicating a small number of individuals contributed genetically to the population. In Galla goats, N_e ranged from 2.5 to 4.4 for MG, with a single outlier value (48.6), which may be likely due to errors in pedigree recordings. In SEA goats, N_e values remained low between 2 and 6 generations, which are consistently below the FAO minimum threshold of 50 required to maintain long-term genetic diversity (FAO, 1998). These low N_e values indicate the presence of a strong genetic drift and a small number of founders in both breeds, with SEA goats demonstrating even lower N_e in many generations. Higher values of 52.65 were reported by MANDAL et al. (2021) in Indian Jamunapari goats and 69 in Markhoz goats (RASHIDI et al., 2015). However, missing pedigree information can lead to an overestimation of N_e . In general, these results indicate the narrow genetic base in this breed due to increased F , AR , with alarming small N_e , suggesting that these populations had few ancestors, which makes them more susceptible to further loss in genetic diversity.

Table 2. Population parameters for maximum and complete generations for Galla goats

Maximum generation (MG)							Complete generation (CG)					
G	No	F%	% Inbred	F for inbred	AR	N_e	No	F%	% Inbred	F for inbred	AR	N_e
0	77	0			0.01		122	0			0.04	
1	336	0			0.05		1,072	0.17	64.83	0.267	0.1	2.8
2	427	0.19	21.56	0.22	0.07	2.5	1,377	0.41	100	0.41	0.2	1.7
3	398	0.23	23.62	0.24	0.1	14.5	1,309	0.56	100	0.56	0.24	1.9
4	230	0.35	34.97	0.35	0.12	3.1	806	0.65	100	0.65	0.26	2.4
5	411	0.34	34.01	0.34	0.12		416	0.71	100	0.71	0.35	2.8
6	411	0.42	42.61	0.43	0.12	4.4	120	0.68	100	0.68	0.25	
7	493	0.49	50.33	0.5	0.18	3.8						
8	462	0.59	59.2	0.59	0.22	2.6						
9	437	0.59	60.87	0.61	0.27	48.6						
10	474	0.65	100	0.65	0.27	3.5						
11	287	0.69	100	0.69	0.27	3.9						
12	270	0.69	98.52	0.69	0.34							
13	199	0.75	100	0.75	0.33	2.8						
14	81	0.79	100	0.79	0.35	3						

Table 3. Population parameters for maximum and complete generations for SEA goats

Maximum generation (MG)							Complete generation(CG)					
G	No	F%	% Inbred	F for inbred	AR	Ne	No	F%	% Inbred	F for inbred	AR	Ne
0	64	0	0	0.01	0		66	0			0.02	
1	184	0	0	0.09	0	2.3	340	0.14	46.18	0.31	0.26	3.3
2	115	0.2	100	0.28	0.2		428	0.22	69.86	0.32	0.39	5.5
3	321	0.16	66.67	0.26	0.25	2.4	460	0.42	100	0.42	0.45	1.9
4	199	0.37	100	0.41	0.37		619	0.58	100	0.58	0.77	1.7
5	182	0.34	87.91	0.45	0.39	2.3	249	0.7	100	0.7	0.82	1.8
6	56	0.5	100	0.67	0.5	3.9						
7	115	0.56	100	0.76	0.56							
8	126	0.42	100	0.68	0.42	4.3						
9	174	0.61	99.43	0.78	0.61							
10	162	0.59	100	0.78	0.59	4.8						
11	214	0.65	100	0.8	0.65	4.6						
12	173	0.69	100	0.82	0.99	5.8						
13	75	0.71	100	0.81	0.71	1.2						
14	2	0.8	100	0.85	0.83							

G, number of generations; *No*, number of animals; *F*%, inbreeding coefficient expressed as a percentage; % inbred, proportion of inbred animals; *F* for inbred, inbreeding coefficient for inbred animals; *AR*, average relatedness of each animal.

3.1.3 Generation intervals (GI)

GI estimates showed clear differences between the two breeds across the four pathways (Table 4). From the results, Galla goats recorded a shorter generation interval (3.94 years) than SEA goats (4.56 years), suggesting faster generational turnover, probably due to earlier reproductive maturity, although farmer management decisions also influence these intervals. Similar values were reported by JOEZY-SHEKALGORABI et al. (2016) and GINJA et al. (2017) in South Khorasan Cashmere and Creole Goats in America. The relatively long generation interval observed may be attributed to traditional management practices, whereby farmers retain does and selected bucks in the herd for several years rather than replacing them frequently, resulting in a slower turnover of breeding animals across generations.

Galla breed had the longest GI in the buck–son pathway (6.44 years), followed by daughter (3.94 years), doe–son (3.95 years), and doe–daughter (3.69 years). The SEA goats reported longer GI in all the pathways with buck–son (4.95 years), buck–daughter (4.55 years), doe–son (4.75 years), and doe–daughter (4.39 years). The differences in these pathways indicate that male parents contribute to genetic diversity of the population at a later

age as compared to female parents, especially in Galla breeds where the buck–son contribution was very long.

Table 4. Generation interval and average age of parent at birth of offspring in four different pathways for Galla and SEA

Generation interval in year					Average age of the parent at the birth of offspring (year)			
Pathway	Galla goat		SEA		Galla goat		SEA	
	No.	Interval	No.	Interval	No.	Mean age $\pm$ SD	No.	Mean age $\pm$ SD
Buck-Son	18	6.44 $\pm$ 0.36	11	4.95 $\pm$ 0.74	1,814	4.22 $\pm$ 0.05	837	4.82 $\pm$ 0.07
Buck-daughter	1,342	3.94 $\pm$ 0.05	503	4.55 $\pm$ 0.09	3,313	4.19 $\pm$ 0.03	1,255	4.64 $\pm$ 0.06
Doe-Son	19	3.95 $\pm$ 0.47	11	4.75 $\pm$ 0.97	1,808	3.68 $\pm$ 0.05	836	4.55 $\pm$ 0.10
Doe-Daughter	1,312	3.69 $\pm$ 0.06	502	4.39 $\pm$ 0.12	3,276	3.66 $\pm$ 0.04	1,254	4.26 $\pm$ 0.07
Total	2,691	3.83 $\pm$ 0.04	1,027	4.39 $\pm$.12	10,211	3.94 $\pm$ 0.02	4,182	4.56 $\pm$ 0.04

3.1.4. Effective number of founders (*fe*) and ancestors (*fa*)

Pedigree recording was adequate in both breeds, however, only a few ancestors contributed substantially to the current genetic diversity in these populations (Table 5). The Galla breed recorded more individuals and founders (5,222 and 99, respectively) than the SEA breed (2,162 and 61, respectively). Despite this, both breeds showed a very low *fa* (*fa* = 7 in Galla and *fa* = 2 in SEA), resulting in an identical ratio of (*fa/fe* = 1) in both populations. A similar (*fa/fe*) ratio was reported by OLIVEIRA et al. (2016) in Spanish Murciano-Granadina goats. In contrast, RASHIDI et al. (2015) reported a much higher ratio of 7.10 in the Iranian Markhoz breed, indicating a substantial genetic bottleneck caused by lack of transfer of founder alleles to subsequent generations and, consequently, a risk to the preservation of original genetic diversity.

Furthermore, only 3 ancestors accounted for 50% of the genetic variability in Galla, while 1 ancestor explained the same proportion in SEA, highlighting severe founder bottlenecks in both breeds. The founder contribution ratios (*fe/f*) were 0.07 for Galla and 0.03 for SEA, confirming that only a small proportion of founders shaped the present gene pool. Such reliance on a few numbers of breeding animals increase the risk of further loss of genetic diversity in these breeds.

Table 5. Gene origin for Galla and SEA breeds

Parameters	Galla	SEA
Total number of animals	5,222	2,162
Animals with both parents known	5,100	2,096
Animals with one unknown parent	99.5	65
Animals with unknown parents	122	66
Number of founders (<i>f</i>)	99	61
The effective number of founders (<i>fe</i>)	7	2
The effective number of ancestors (<i>fa</i>)	7	2
The number of ancestors explains 50% of the genetic variability	3	1
Ratio <i>fe/f</i>	0.07	0.03
Ratio <i>fa/fe</i>	1	1

3.2 Analysis of within-population genetic diversity

A moderate genetic diversity was observed across all populations (Table 6), with a mean H_O of between 0.34 ± 0.03 (PHIN) and 0.441 ± 0.01 (SHOK) and most populations recording between 0.36 ± 0.03 and 0.44 ± 0.01 . These moderate diversity values are likely maintained by ongoing gene flow resulting from the intermixing of animals across herds and regions through grazing, breed exchange, and seasonal migration in search of water and pasture (KICHAMU et al., 2024a). Such gene flow prevents excessive genetic drift and helps sustain heterozygosity within populations (BENSOUF et al., 2025). Similar levels of moderate genetic diversity have been reported in other indigenous goat breeds (GEBRESELEASH et al., 2024; NANTONGO et al., 2024; MUKHINA et al., 2022; ONZIMA et al., 2018).

The F_{hom} values varied across the populations, with PHIN (0.317 ± 0.07) and the KOSS (0.183 ± 0.10) having the highest values. Some African populations, MEA (-0.01 ± 0.03) and WG (0.000 ± 0.02), recorded minimal or negative F_{hom} values, indicating low inbreeding or possible outbreeding. In contrast, PHIN recorded the highest inbreeding values across all estimates ($F_{hat1} = 0.232$, $F_{hat2} = 0.274$, $F_{hat3} = 0.274$), likely attributable to geographic isolation or N_e similar to those reported by LEON-APODACA et al. (2024), LI et al. (2022), and PEGOLO et al. (2025). F_{ROH} values (Figure 2A) further confirmed this pattern, with KOSS (0.094), SEA (0.070), and PHIN (0.062) recording the highest values, while SHOK (0.008) and WG (0.007) showed the lowest, reflecting relatively higher genetic diversity. Populations such as PHIN and KOSS should therefore be prioritized in conservation and breeding programs to preserve their genetic potential and long-term viability. Shorter ROH

length (0–12 Mb) dominated across all the populations (Figure 2B), suggesting past bottlenecks associated with domestication or breed formation (HUANG et al., 2024; PEGOLO et al., 2025).

Table 6. Summary statistics of observed heterozygosity, inbreeding coefficients

FID	H_o	F_{hom}	F_{hat1}	F_{hat2}	F_{hat3}
BAW	0.43 ± 0.02	0.035 ± 0.04	0.136 ± 0.04	0.018 ± 0.04	0.077 ± 0.04
DBSK	0.425 ± 0.02	0.047 ± 0.04	0.173 ± 0.03	0.028 ± 0.04	0.1 ± 0.04
GAL	0.393 ± 0.02	0.119 ± 0.05	0.012 ± 0.05	0.129 ± 0.05	0.071 ± 0.05
HUN	0.427 ± 0.01	0.043 ± 0.03	0.139 ± 0.03	0.029 ± 0.03	0.084 ± 0.03
KEF	0.386 ± 0.02	0.134 ± 0.04	0.004 ± 0.04	0.149 ± 0.04	0.077 ± 0.04
KENS	0.433 ± 0.01	0.029 ± 0.03	0.108 ± 0.03	0.025 ± 0.03	0.066 ± 0.03
KOSS	0.391 ± 0.05	0.122 ± 0.11	0.183 ± 0.1	0.119 ± 0.11	0.151 ± 0.11
KUN	0.427 ± 0.02	0.043 ± 0.05	0.097 ± 0.05	0.04 ± 0.05	0.069 ± 0.05
MEA	0.394 ± 0.02	0.116 ± 0.04	-0.01 ± 0.03	0.127 ± 0.05	0.059 ± 0.04
PWT	0.396 ± 0.03	0.113 ± 0.07	0.017 ± 0.06	0.12 ± 0.08	0.069 ± 0.07
PHIN	0.34 ± 0.03	0.237 ± 0.07	0.317 ± 0.07	0.232 ± 0.07	0.274 ± 0.07
SEA	0.385 ± 0.04	0.137 ± 0.08	0.017 ± 0.07	0.149 ± 0.08	0.083 ± 0.07
SHOK	0.441 ± 0.01	0.011 ± 0.02	0.08 ± 0.02	0.008 ± 0.02	0.044 ± 0.02
USH	0.434 ± 0.04	0.027 ± 0.08	0.151 ± 0.09	0.011 ± 0.08	0.081 ± 0.08
WG	0.39 ± 0.01	0.127 ± 0.02	0 ± 0.02	0.142 ± 0.02	0.071 ± 0.02
DAB	0.413 ± 0.04	0.073 ± 0.08	0.14 ± 0.07	0.068 ± 0.09	0.104 ± 0.08

Mean ($\pm$ standard deviation) of observed heterozygosity (H_o) and inbreeding coefficients (F_{hom} , F_{hat1} , F_{hat2} , F_{hat3}) for each population. Values represent the average genetic diversity and inbreeding levels, with standard deviations reflecting variability among individuals within each group. F_{ROH} representing genomic-based inbreeding

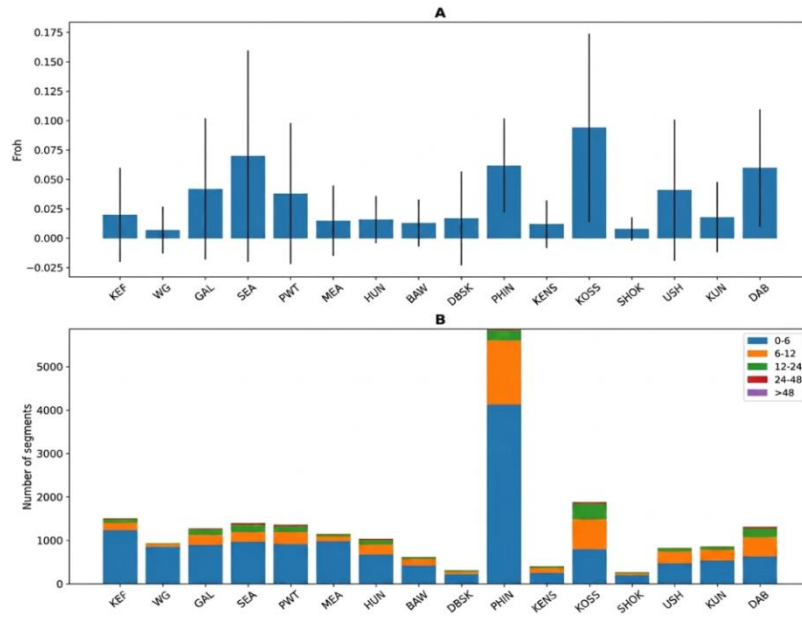


Figure 2. ROH Analysis results; (A) Inbreeding coefficients based on runs of homozygosity (F_{ROH}) and (B) The ROH class by length

3.3 Intra and interpopulation relationships and population structure

Relationships within and between populations were evaluated in two ways: the divergence time analysis with SplitsTree software and the neighbor-joining tree. The Neighbor-joining tree based on F_{ST} values (Figure 3), revealed four population clusters based on geographic regions and migration histories. The Philippines population positioned itself far from the others, indicating greater differentiation. This distinct position may result from the country's geographic isolation and historical bottlenecks, given its archipelagic nature and lack of association with other Asian countries (LARENA et al., 2021).

The Ushterek population from Kazakhstan (Central Asia) clustered closely with European breeds, implying historical admixture or shared ancestry. This clustering may be due to the sharing of some demographic events, like trade and migration between these continents. This finding is consistent with Kazakhstan's role as a primary dispersal route for goats through the Eurasian Steppe to Europe and Central Asia, facilitating genetic admixture and shared ancestry (TABATA et al., 2019). TreeMix analysis was used to investigate population relationships and potential gene flow among goat populations. The model fit improved with additional migration edges, stabilizing after five edges (Figure 4A and B), indicating that the migration events stabilized at $m = 5$. The resulting SplitTree (Figure 4C) illustrated five historically significant gene flow events, which are shown by colored arrows representing migration intensity ($m = 5$).

The TreeMix results aligned with the neighbor-joining tree, with populations clustering according to geographic location and breed history. The first migration edge from GAL to PWT, MEA, SEA, WG, and KEF indicating significant gene flow among African populations, with GAL serving as a genetic link across the region. This pattern reflects shared boundaries, trans boundary livestock migrations, and the extensive spread of GAL across East Africa, consistent with previously reported weak population structure and admixture among African indigenous goats (BENJELLOUN et al., 2015; ONZIMA et al., 2018; MDLADLA et al., 2018).

DAB and KUN formed a tight genetic cluster, reflecting their close geographic proximity and shared traditional pastoralism system in Kazakhstan, where communal grazing and periodic livestock movements facilitate free interbreeding between neighboring flocks (KICHAMU et al., 2024b). BAW, USH, DBSK, and HUN clustered together, likely reflecting shared ancestry through historical gene flow among adjacent countries. PHIN diverged early from other clusters, indicating a distinct genetic makeup, while SHOK, KENS, and KOSS showed short migration edges, highlighting ongoing genetic admixture within these populations.

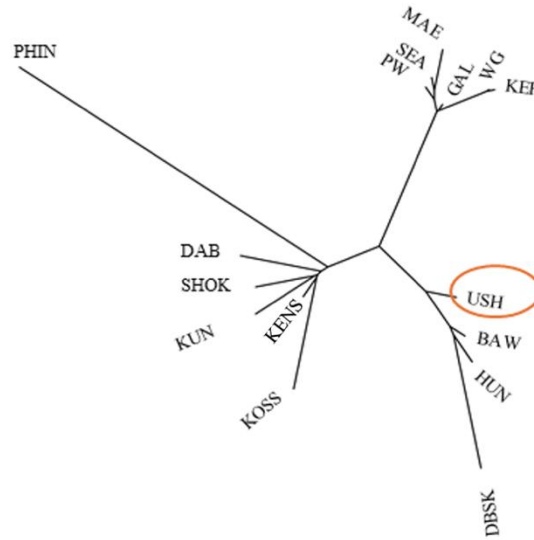


Figure 3. Neighbor network based on distance matrix from pairwise F_{ST} values

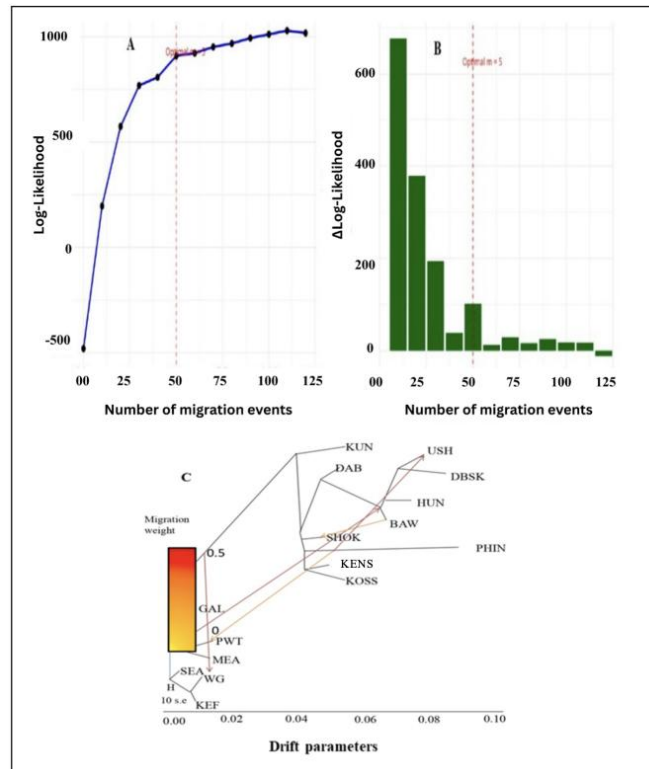


Figure 4. Population structure for studied goats; (A) Change in log likelihood and number of migration events, (B) inferred maximum likelihood population graph, and (C) TreeMix showing the migration edges of study goats

Further, PCA was used to assess the interpopulation relationships (Figure 5). The PCA results were similar to those of neighbor-joining trees. PC1 accounted for 25.66% of the total variation, while PC2 explained 16.64%. The most significant principal component, PC1, separated the African population from the Central Asian (Kazakhstan) and Southeast Asian (Philippines) populations. In contrast, PC2 differentiated the European population from the Southeast and some Central Asian populations.

Figure 6A presents the population structure at the optimal K value, and Figure 6B shows the optimal K with the lowest cross-validation error at K = 10. Results clustered the population into four groups along the continental lines. GAL, MEA, PWT, and SEA populations are highly admixed. The level of admixtures in this population suggests some gene flow amongst them, which may have arisen from the type of production systems employed in those, especially smallholding and pastoralists system that lacks structured breeding programs and encourages communal grazing systems (KICHAMU et al., 2024a).

A similar pattern but less admixture was observed in European populations (HUN, DBSK, BAW), suggesting higher genetic homogeneity. Likely due to the closed production

system and selective breeding for desirable traits, as well as the imposition of strict breed standards, this may have limited the level of gene flow into the population. In contrast, a distinct and mixed co-ancestry pattern was observed in the Kazakh population groups (KENS, KOSS, KUN, SHOK, USH, DAB), while a single co-ancestry was seen in the PHIN population results that are consistent with PCA and indicate a genetically distinct lineage.

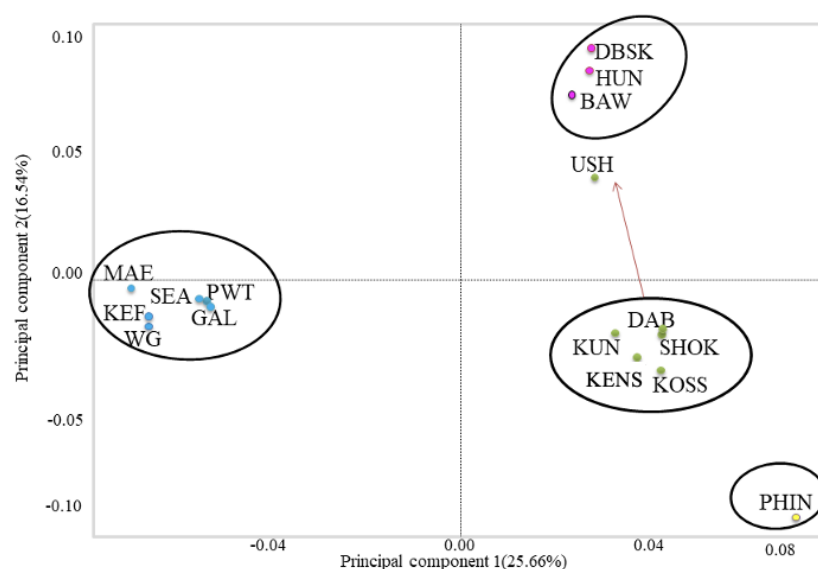


Figure 5. Population structure for the studied goat populations by principal component analysis (PCA)

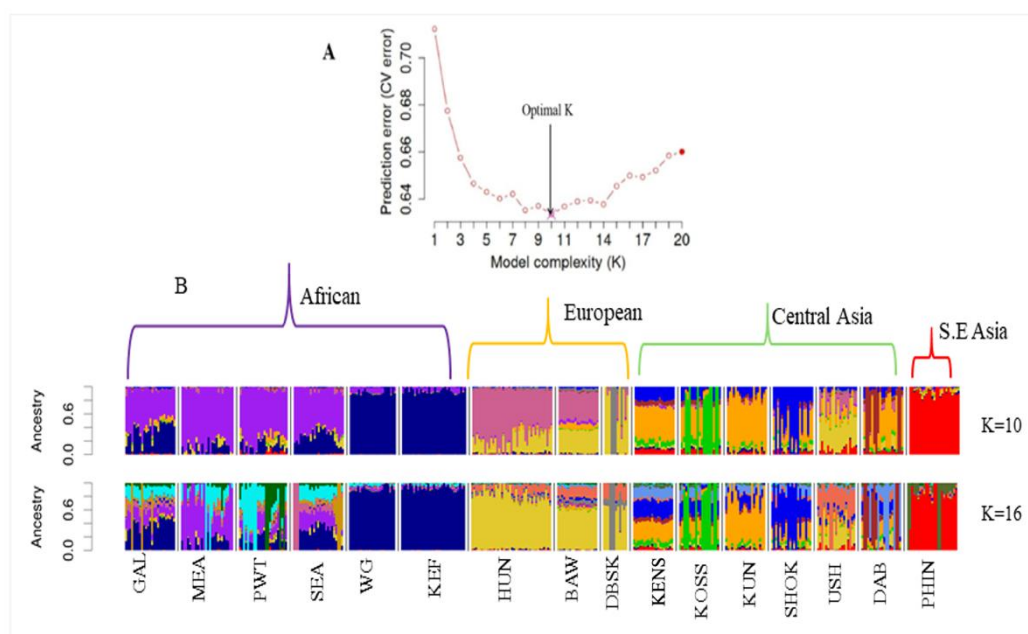


Figure 6. Population structure for the studied goat populations; (A) Cross-validation error plot and (B) Admixture analysis plot

3.3.1 Effective population size (N_e)

The SNeP results showed a declining trend in N_e across all populations (Figure 7A). The BAW and HUN of Europe, GAL, MEA, PWT, SEA from East Africa, and KENS from Kazakhstan maintained relatively higher N_e values at the initial generation (generation 98) but later underwent a steady decrease toward the present generation (generation 13). In contrast, the DBSK population from Europe, KOSS, and DAB from Kazakhstan recorded consistently lower N_e values (<400) throughout the generations.

This trend may reflect recent demographic changes, possibly driven by environmental pressures, reduced genetic diversity, or human-mediated activities, including selective breeding for traits of economic importance, thus leading to the population bottleneck effect. Besides, to understand the ancient N_e and how these population size has changed over generations including (declines, expansions and recoveries), the GONe software was used (Figure 7B) which revealed larger population sizes, with the SEA (1,600,000), GAL (160,000), and PHIN (120,000) populations recording the highest values, suggesting that this breeds had a historically wider genetic pool. Besides, the medium values were observed in WG (80,000), DAB (40,000), KEF (20,000), and DBSK (16,000), while PWT (10,000), MEA (8,000), and KOSS (6,000) have smaller historical population sizes. Interestingly, the entire population showed a sharp decline in the current generation. Similar demographic reductions have been reported in most small ruminants across the globe, a case driven by climatic stresses, bottlenecks and human selection (KLIMENKO et al., 2025; COLLI et al., 2018).

Despite having a significant historical N_e in some populations, all the populations experienced reductions in recent generations. This reduction was expected, given the current increase in animal-based protein due to a growing population, which has led to the selection of vital traits to help meet the demand, including selective breeding for high-yielding, good feed conversion, and fast-growing individuals. A practice that encourages the use of a few breeding animals for a prolonged period. Thus, affecting the N_e over time.

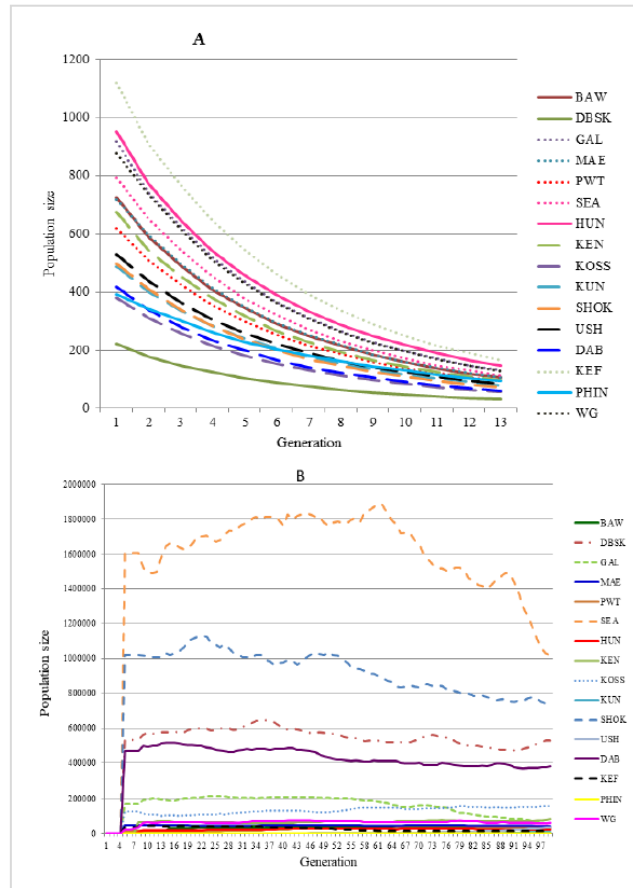


Figure 7. Effective population sizes (N_e) of studied goats. (A) Recent N_e estimated with SNeP and (B) Historical and detailed N_e using GONE software

3.4. Identification of signatures of selection for resistance and adaptation

The eROHi method identified a total of 34 candidate genes under selection, including 11 in Africa, 11 in Europe, 1 in Kazakhstan, and 11 in the Philippines populations; most of them were found localized in chromosome 13. In comparison, the iHS method detected 39 genes in chromosomes 3, 5, 7, 8, 12, 18, 21, 23, and 27, including Europe (19), Kazakhstan (8), Africa (6), and the Philippines (6) (Figure 7 and 8). Notably, there was no overlap in candidate genes observed in the two methods. Among these genes 14 of them were identified as important gene (Figure 9) that plays crucial role in this goat population including immunity (*PRPF6*, *DIP2C*, *CD58*), adaptation (*DIP2C*, *ATP1A1*, *SOX18*), reproduction or fertility (*OPRL1*, *DIP2C*, *ATP12A*, *NPBWR2*), milk fat content (*NFX1*) and growth development (*NTRK3*, *ADAMTSL3*, *SOX18*, *ZNF512B*, *DNAJC5*). Genes such as *DIP2C*, *SOX18*, and *ATP1A1* are linked to heat tolerance, ion transport, vascular regulation, and cellular homeostasis, suggesting adaptation to hot and arid environments (ELAYADETH-MEETHAL et al., 2021) Meanwhile, *PRPF6*, *CD58*, and members of the *S100* gene family are involved in

immune regulation, inflammation, and pathogen defense, indicating selection for disease resistance in challenging environments (CROSBY et al., 2004; SINGH et al., 2022). Overall, these results suggest that indigenous goats have undergone selection for both environmental resilience and enhanced immune competence across diverse ecological regions.

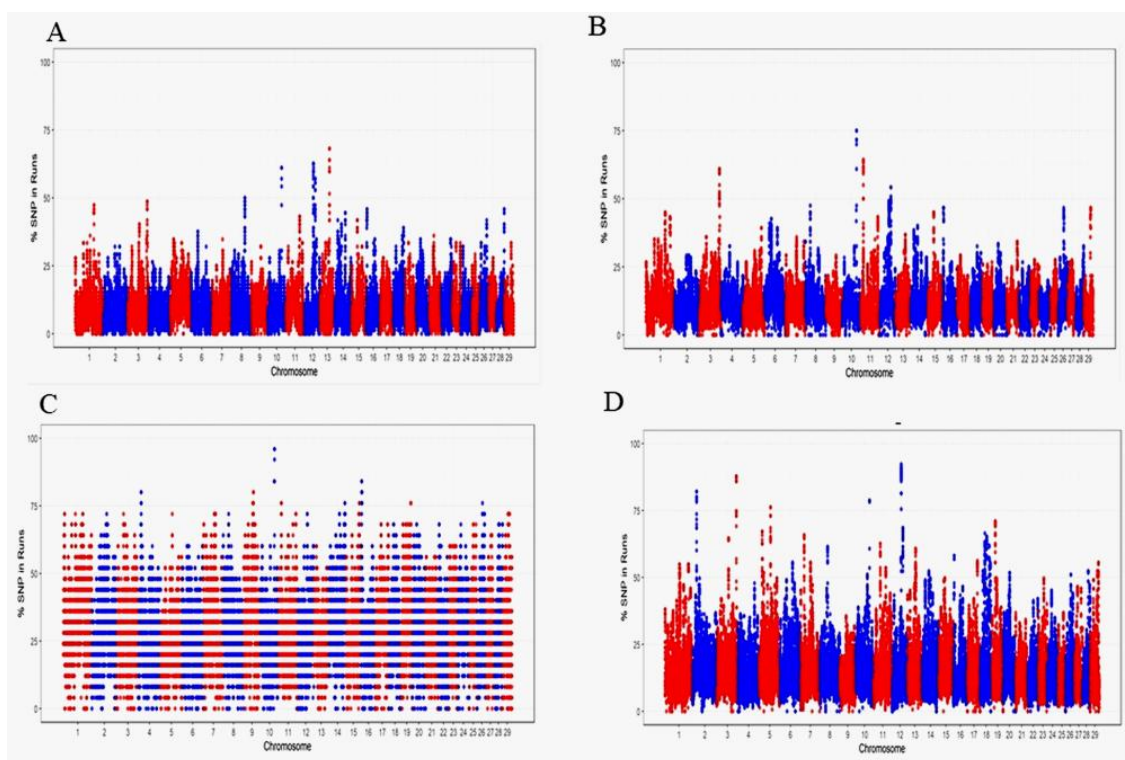


Figure 7. Manhattan plots based on eROHi showing the percentage of SNPs in runs per chromosome for (A) European goats, (B) Kazakhstan goats, (C) Philippine goats, and (D) African goats

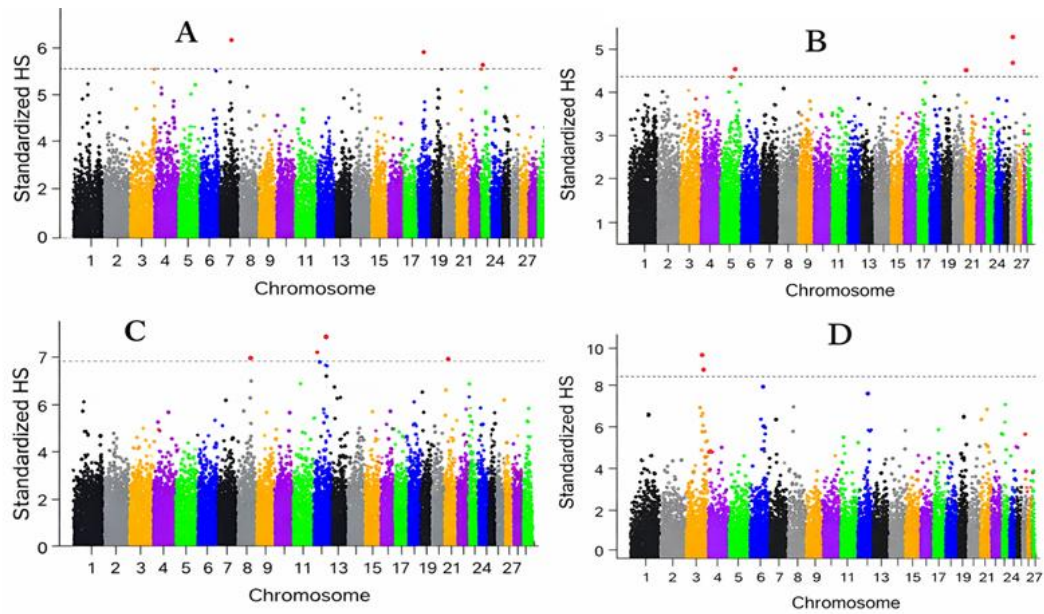


Figure 8. Manhattan plot based on standardized iHS per clustered population. A) African population, B) Philippine population, C) European population, and D) Kazakhstan population

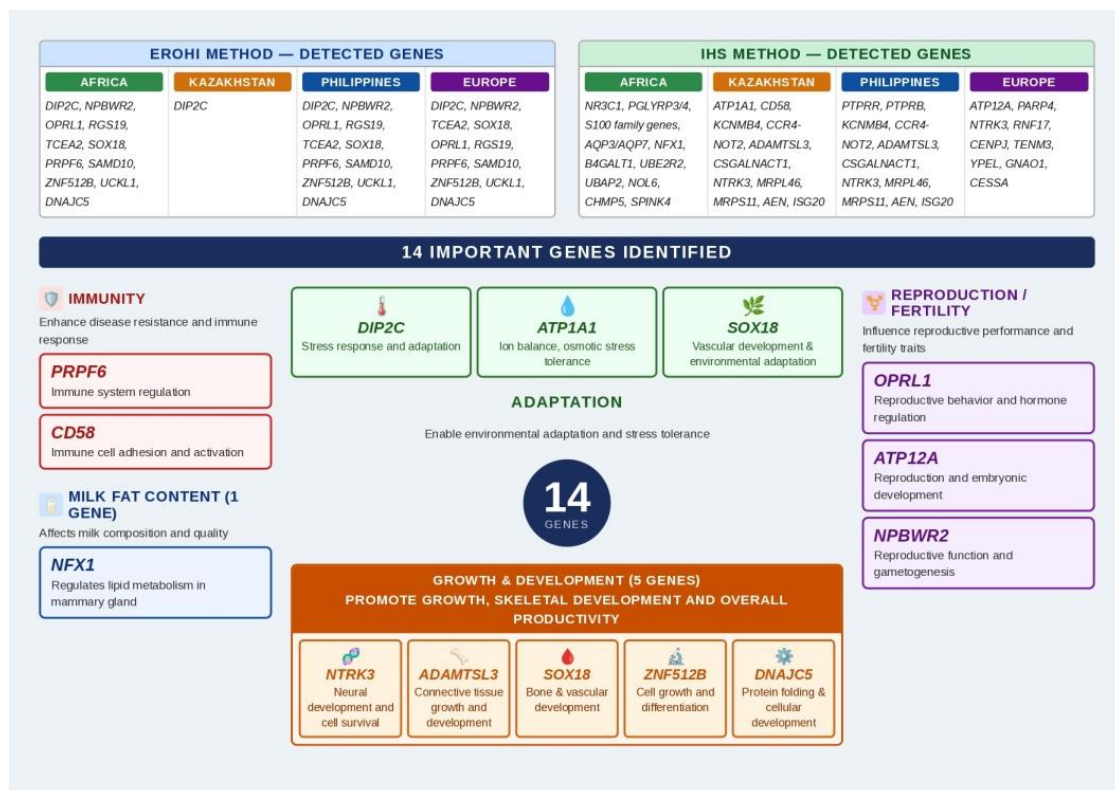


Figure 9. Signatures of positive selection mapped by the eROHi and iHS methods for all the goat populations

3.5 Comparison between pedigree-based and genomic estimates of genetic diversity in Galla and SEA goats

Both pedigree and genomic analyses show that Galla and SEA goats have low genetic diversity and increasing inbreeding. Pedigree data found rising inbreeding across generations, very small effective population sizes, and few effective founders, while genomic data confirmed low heterozygosity, positive inbreeding coefficients, and mostly short ROH segments, indicating that much of the inbreeding is ancient rather than recent.

4. CONCLUSIONS

This doctoral study provides a detailed assessment of indigenous goat populations in selected countries of Europe, Africa, and Asia, which reveals valuable insights into their genetic diversity, population structure, and evolutionary changes. Pedigree analysis of Kenyan indigenous GAL and SEA populations revealed low effective population size, increasing inbreeding levels, and high genetic relatedness. These may be underestimated due to the incompleteness of pedigree data and the extensive production system employed in the region. Besides, only a few animals contributed to 50.00% of the genetic diversity within the breeds, thereby increasing vulnerability to inbreeding depression and potential extinction risk.

For genomic analysis, the moderate observed heterozygosity values across these populations indicate a fair level of genetic health. However, some populations, like the PHIN, recorded a higher inbreeding coefficients and lower heterozygosity, which suggest reduced genetic diversity and some potential inbreeding depression. In contrast, SHOK, KENS, and WG recorded a high genetic diversity and low inbreeding levels, which underscore their importance as reservoirs of genetic diversity.

The Runs of Homozygosity results revealed the dominance of short homozygous segments across the studied goat populations, demonstrating the presence of historical inbreeding events. Furthermore, the decline in effective population size was observed across all breeds, reflecting an ongoing genetic drift and limited gene flow within the populations. These factors may speed up the erosion of genetic diversity if not well monitored and managed. The population structure analysis showed the clustering of populations according to their geographical origin, which confirms how location and regional breeding history can influence the genetic differentiation of a given breed population. However, the USH population from Kazakhstan showed a genetic shift towards the European clusters, suggesting possible historical admixture or shared ancestry with European breeds.

Additionally, the detection of various selection signatures that are linked to important traits across the genome for these goat populations, namely immune response (*PRPF6*, *DIP2C*, *CD58*), adaptation (*DIP2C*, *ATP1A1*), reproduction and fertility (*OPRL1*, *DIP2C*, *ATP12A*), milk butter fat content (*NFX1*), and growth and development (*NTRK2*, *ADAMTSL3*, *SOX18*), underscores the presence of adaptive mechanism brought about by the environmental pressures, husbandry practices, and human induced selection. These mechanisms highlight the genetic basis of economically and biologically important characteristics while emphasizing the vital role of selection in shaping the genomic architecture of these indigenous goats.

These results, therefore, necessitate the development of sustainable and conservation breeding programs that are aimed at managing the genetic diversity, addressing the decline in population size, and preserving the available adaptive traits contained in these indigenous goats. Strengthening the level of monitoring and evaluation of this genetic diversity, adoption of a controlled breeding system, and conservation of locally adapted breeds will be essential for ensuring the long-term resilience of these goat populations, especially in the current face of climate change and increasing demand for animal protein.

5. NEW SCIENTIFIC RESULTS

1. Despite limitations in pedigree completeness, pedigree analyses of GAL and SEA goats revealed pronounced genetic erosion, reflected by very low founder and ancestor representation ($f_e = f_a = 7$ and 2, respectively), with only 3 and 1 ancestors accounting for 50% of total genetic diversity. Inbreeding increased in both populations (GAL: $F = 0.04\%$; SEA: $F = 0.05\%$) per generation, accumulating to average inbreeding of 0.46 and 0.44, respectively, while N_e was critically low (5.19 and 4.77, respectively) indicating severe founder bottlenecks, strong genetic drift, and increased risk of extinction.
2. The study identified the Philippine Native Antipas Cotabato group as having high inbreeding coefficients and low heterozygosity ($F_{ROH} = 0.062$, $F_{hom} = 0.237$, $H_O = 0.34$), while several African populations, including Galla, Maasai East Africa, Pare White, and Small East Africa, showed high levels of admixture, indicating vulnerability in genetic diversity. Complementing this, N_e declined across all studied populations, from 1,160 at generation 1 to < 400 at generation 13, with Bosnian Domaća Balkanska Šarena Koza (DBSK) and Kazakh Kosseit (KOSS) starting with < 400 in generation 1 to < 60 in the current generation. These populations are therefore at risk of losing their adaptive potential and require immediate conservation and genetic management interventions to prevent extinction.
3. Most of the studied goat populations recorded shorter ROH length (0-24 Mb), indicating the presence of ancient inbreeding. These trends provide an insight into historical dynamics within indigenous goat populations.
4. The studied goat populations were clustered into four groups (European, African, Philippine, and Kazakhstan) based on their geographical region or location, confirming the influence of geographical isolation and local adaptation in shaping the genetic structure of goat populations due to varied environmental conditions and specific regional breeding strategies used. Except for the Ushterek population from Kazakhstan, which grouped closer to European goats, indicating the existence of shared ancestry or historical admixture from previous events, such as the interregional trade between various Eurasian regions.
5. The study identified potential selection signatures in genes, including *ATP1A1*, *PRPF6*, *DIP2C*, *SOX18*, and *CD58*, that were linked to heat tolerance, adaptation across varied environmental conditions, and immune response. A finding that reveals the genetic basis of resilience in indigenous goats, hence suggesting their potential adaptation to challenging environmental conditions.

6. PRACTICAL RESULTS

1. The low effective population size, accumulation of inbreeding, and low founder representation in Kenyan Galla and SEA, can be controlled by developing structured sire rotation programs where breeding bucks can be systematically rotated across flocks and sub-populations on a defined schedule to reduce the probability of repeated related mating and limit the rate of inbreeding accumulation within local herds.
2. The identified significant genes associated with immunity and adaptation, including *ATP1A1*, *PRPF6*, *DIP2C*, and *CD58*, can be incorporated into marker-assisted selection breeding programs to improve these crucial traits in indigenous goat populations while preserving genetic diversity.
3. The consistently low effective population size ($N_e < 400$) observed in Domaća Balkanska Šarena Koza, Kosseit, and Darbaza populations' warrants their classification as at-risk breeds. Targeted conservation breeding programs should therefore be established for these populations to prevent further genetic loss and ensure their long-term sustainability.
4. Populations with high genetic diversity should be prioritized as parent stock and maintained as genetic reservoirs for future breeding programs, given their lower relatedness and reduced inbreeding risk. Conversely, populations with high inbreeding levels should be managed through the introduction of external flocks of the same breed to control inbreeding, improve productivity, and enhance overall resilience.
5. The declining effective population size observed across all populations, particularly in recent generations, poses a significant risk of genetic erosion. To address this, conservation measures such as establishing gene banks and promoting community-based breeding and management programs should be implemented to ensure the long-term survival and sustainable utilization of these indigenous goat genetic resources.
6. The admixture levels identified in some populations can inform breeding and conservation strategies aimed at restoring breed to its original genotype. This can be achieved by selecting individuals with the highest genetic purity or phenotypic characteristics closest to the original breed, thereby ensuring that future generations maintain the desired breed traits and standards.

7. BIBLIOGRAPHY

1. ALEXANDER, D. H. – SHRINGARPURE, S. S. – NOVEMBRE, J. – LANGE, K. (2015): Admixture 1.3 software manual. Los Angeles: UCLA Human Genetics Software Distribution.
2. BARBATO, M. – OROZCO-TERWENGEL, P. – TAPIO, M. – BRUFORD, M. W. (2020): SNeP: A tool to estimate trends in recent effective population size trajectories using genome-wide SNP data. *Frontiers in Genetics*, 11, 550. <https://doi.org/10.3389/fgene.2020.00550>
3. BARROS, E. A. – RIBEIRO, M. N. – ALMEIDA, M. J. O. – ARAÚJO, A. M. (2011): Population structure and genetic variability of the Marota goat breed. <http://www.uco.es/organiza/servicios/publica/az/php/az.php>
4. BENJELLOUN, B. – ALBERTO, F. J. – STREETER, I. – BOYER, F. – COISSAC, E. – STUCKI, S. – BENBATI, M. – IBNELBACHYR, M. – CHENTOUF, M. – BECHCHARI, A. – LEMPOEL, K. – et al. (2015): Characterizing neutral genomic diversity and selection signatures in indigenous populations of Moroccan goats (*Capra hircus*) using WGS data. *Frontiers in Genetics*, 6, 107. <https://doi.org/10.3389/fgene.2015.00107>
5. BENSOUF, I. – DHI, B. I. – BEJAOU, S. – OULED AHMED, H. – KHEMIRI, H. – M'HAMDI, N. (2025): Genetic diversity and population structure of the indigenous goat population in Tunisia's northwest. *Archives Animal Breeding*, 68(2), 409–423. <https://doi.org/10.5194/aab-68-409-2025>
6. BERNARDES, P. A. – GROSSI, D. A. – SAVEGNAGO, R. P. – BUZANSKAS, M. E. – RAMOS, S. B. – ROMANZINI, E. P. – GUIDOLIN, D. G. F. – BEZERRA, L. A. F. – LÔBO, R. B. – MUNARI, D. P. (2016): Population structure of Tabapuã beef cattle using pedigree analysis. *Livestock Science*, 187, 96–101. <https://doi.org/10.1016/j.livsci.2016.03.002>
7. BIJMA, P. – WOOLLIAMS, J. A. (2000): Prediction of rates of inbreeding in populations selected on best linear unbiased prediction of breeding value. *Genetics*, 156(1), 361–373. <https://doi.org/10.1093/genetics/156.1.361>
8. BISCARINI, F. – COZZI, P. – GASPA, G. – MARRAS, G. (2019): Detect runs of homozygosity and runs of heterozygosity in diploid genomes. <https://hdl.handle.net/2318/1792948>

9. BOICHARD, D. – MAIGNEL, L. – VERRIER, E. (1997): The value of using probabilities of gene origin to measure genetic variability in a population. *Genetics Selection Evolution*, 29(1), 5–23.
10. CASTRO-VÁSQUEZ, R. – VÁSQUEZ-LOAIZA, M. – CRUZ-MÉNDEZ, A. – DOMÍNGUEZ-VIVEROS, J. – CAMACHO-SANDOVAL, J. – SABORÍO-MONTERO, A. (2023): Genealogical information analysis of Gyr and Nelore cattle from Costa Rica. *Ciência Rural*, 53(10), e20220236. <https://doi.org/10.1590/0103-8478cr20220236>
11. CHANG, C. C. – CHOW, C. C. – TELLIER, L. C. – VATTIKUTI, S. – PURCELL, S. M. – LEE, J. J. (2015): Second-generation PLINK: Rising to the challenge of larger and richer datasets. *Gigascience*, 4(1), s13742-13015-10047-13748. <https://doi.org/10.1186/s13742-015-0047-8>
12. COLLI, L. – MILANESI, M. – TALENTI, A. – BERTOLINI, F. – CHEN – CRISÀ, A. – DALY, K. G. – DEL CORVO, M. – GULDBRANDTSEN, B. – LENSTRA, J. A. – ROSEN, B. D. (2018): Genome-wide SNP profiling of worldwide goat populations reveals strong partitioning of diversity and highlights post-domestication migration routes. *Genetics Selection Evolution*, 50(1), 58. <https://doi.org/10.1186/s12711-018-0422-x>
13. COOMBS, J. – LETCHER, B. – NISLOW, K. (2012): GONe: Software for estimating effective population size in species with generational overlap. *Molecular Ecology Resources*, 12(1), 160–163. <https://doi.org/10.1111/j.1755-0998.2011.03057.x>
14. CROSBY, K. – YATKO, C. – DERSIMONIAN, H. – PAN, L. – EDGE, A. S. (2004): A novel monoclonal antibody inhibits the immune response of human cells against porcine cells: identification of a porcine antigen homologous to CD58. *Transplantation*, 77(8), 1288–1294. <https://doi.org/10.1097/01.TP.0000120377.57543.D8>
15. DURINCK, S. – MOREAU, Y. – KASPRZYK, A. – DAVIS, S. – DE MOOR, B. – BRAZMA, A. – HUBER, W. (2005): BioMart and Bioconductor: a powerful link between biological databases and microarray data analysis. *Bioinformatics*, 21 (16), 3439–3440
16. ELAYADETH-MEETHAL, M. – THAZHATHU VEETIL, A. – ASAF, M. – PRAMOD, S. – MALONEY, S. K. – MARTIN, G. B. – RIVERO, M.J. – SEJIAN, V. – NASEEF, P. P. – KURUNIYAN, M. S. – LEE, M. R. (2021): Comparative expression profiling and sequence characterization of ATP1A1 gene associated with heat tolerance in tropically adapted cattle. *Animals*, 11(8), 2368. <https://doi.org/10.3390/ani11082368>

17. FAO. (1998): Secondary guidelines for development of national farm animal genetic resources management plans: Management of small populations at risk. 59–83. FAO, Rome, Italy. <https://www.fao.org/documents/card>
18. GAUTIER, M. – VITALIS, R. (2012): rehh: An R package to detect footprints of selection in genome-wide SNP data from haplotype structure. *Bioinformatics*, 28(8), 1176–1177. <https://doi.org/10.1093/bioinformatics/bts115>
19. GEBRESELEASH, H. B. – NIGUSSIE, H. – WANG, C. – LUO, C. (2024): Genetic diversity, population structure and selection signature in Begait goats revealed by whole-genome sequencing. *Animals*, 14(2), 307. <https://doi.org/10.3390/ani14020307>
20. GINJA, C. – GAMA, L. T. – MARTÍNEZ, A. – et al. (2017): Genetic diversity and patterns of population structure in Creole goats from the Americas. *Animal Genetics*, 48(3), 315–329. <https://doi.org/10.1111/age.12529>
21. GOYACHE, F. – GUTIERREZ, J. P. – FERNANDEZ, I. – GOMEZ, E. – ALVAREZ, I. – DIEZ, J. – ROYO, L. J. (2003): Using pedigree information to monitor genetic variability of endangered populations: The Xalda sheep breed of Asturias as an example. *Journal of Animal Breeding and Genetics*, 120(2), 95–105. <https://doi.org/10.1046/j.1439-0388.2003.00378.x>
22. GUTIÉRREZ, J. P. – GOYACHE, F. (2005): A note on ENDOG: A computer program for analysing pedigree information. *Journal of Animal Breeding and Genetics*, 122(3), 172–176. <https://doi.org/10.1111/j.1439-0388.2005.00512.x>
23. HONG, J. – KIM, Y. – CHO, E. – LEE, J. – KIM, Y. – PARK, H. (2024): Application of deep learning with bivariate models for genomic prediction of sow lifetime productivity-related traits. *Animal Bioscience*, 37(4), 622–630. <https://doi.org/10.5713/ab.23.0264>
24. HUANG, C. – ZHAO, Q. – CHEN, Q. – SU, Y. – MA, Y. – YE, S. – ZHAO, Q. (2024): Runs of homozygosity detection and selection signature analysis for local goat breeds in Yunnan, China. *Genes*, 15(3), 313. <https://doi.org/10.3390/genes15030313>
25. HUBBARD, T.– BARKER, D.– BIRNEY, E.– CAMERON, G.– CHEN, Y.– CLARK, L.– COX, T.– CUFF, J.– CURWEN, V.– DOWN, T.– DURBIN, R.– EYRAS, E.– GILBERT, J.– HAMMOND, M.– HUMINIECKI, L.– KASPRZYK, A.– LEHVASLAIHO, H.– LIJNZAAD, P.– MELSOPP, C.– ... CLAMP, M. (2002): The Ensemble genome database project. *Nucleic Acids Research*, 30 (1), 38–41. <https://doi.org/10.1093/nar/30.1.38>

26. HUSON, D. H. – BRYANT, D. (2006): Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution*, 23(2), 254–267. <https://doi.org/10.1093/molbev/msj030>
27. JOEZY SHEKALGORABI, S. – MAGHSOUDI, A. – TAHERI YEGANEH, A. – RAJABI MARAND, B. (2017): Genetic variability of Iranian Adani goat breed using pedigree analysis. *Journal of Animal and Plant Science*, 27(3), 677–680. <https://doi.org/10.1080/1828051X.2017.1321129>
28. JOEZY SHEKALGORABI, S. – MAGHSOUDI, A. – TAHERI YEGANEH, A. – RAJABI MARAND, B. (2016): Pedigree analysis of Cashmere goat breed of South Khorasan. *Italian Journal of Animal Science*, 15(4), 590–594. <https://doi.org/10.5367/0000000006778536800>
29. KICHAMU, N. – ASTUTI, P. K. – WANJALA, G. – STRAUSZ, P. – BAGI, Z. – KUSZA, S. (2024a): A review on Indigenous goats of East Africa: A case for conservation and management. *Biology*, 13(6), 419. <https://doi.org/10.3390/biology13060419>
30. KICHAMU, N. – WANJALA, G. – CZISZTER, L. T. – STRAUSZ, P. – ASTUTI, P. K. – BAGI, Z. – KUSZA, S. (2024b): Assessing the population structure and genetic variability of Kenyan native goats under extensive production system. *Scientific Reports*, 14(1), 16342. <https://doi.org/10.1038/s41598-024-67374-2>
31. KLIMENKO, V. V. – TERESHIN, A. G. – MIKUSHINA, O. V. – POPOVA, N. V. (2025): Global scenarios and forecasting. *Global Scenarios and Forecasting*, 16(1), 3–24. <https://doi.org/10.30884/jogs/2025.01.01>
32. LARENA, M. – SANCHEZ-QUINTO, F. – SJÖDIN, P. – et al. (2021): Multiple migrations to the Philippines during the last 50,000 years. *Proceedings of the National Academy of Sciences*, 118(13), e2026132118. <https://doi.org/10.1073/pnas.2026132118>
33. LEON-APODACA, A. V. – KUMAR, M. – DEL CASTILLO, A. – CONROY, G. C. – LAMONT, R. W. – OGBOURNE, S. – CAIRNS, K. M. – BORBURGH, L. – BEHRENDORFF, L. – SUBRAMANIAN, S. – SZPIECH, Z. A. (2024): Genomic consequences of isolation and inbreeding in an island dingo population. *Genome Biology and Evolution*, 16(7), evae130. <https://doi.org/10.1093/gbe/evae130>
34. LI, G. – TANG, J. – HUANG, J. – JIANG, Y. – FAN, Y. – WANG, X. – REN, J. (2022): Genome-wide estimates of runs of homozygosity, heterozygosity, and genetic load in two Chinese indigenous goat breeds. *Frontiers in Genetics*, 13, 774196. <https://doi.org/10.3389/fgene.2022.774196>

35. MANDAL, A. – BANEH, H. – ROY, R. – NOTTER, D. R. (2021): Genetic diversity and population structure of Jamunapari goat in India using pedigree analysis. *Tropical Animal Health and Production*, 53(2), 21. <https://doi.org/10.1007/s11250-021-02638-1>
36. MANUNZA, A. – COZZI, P. – BOETTCHER, P. – CURIK, I. – LOOFT, C. – COLLI, L. – SÖLKNER, J. – MÉSZÁROS, G. – STELLA, A. (2025): Estimating the optimal number of samples to determine the effective population size in livestock. *Frontiers in Genetics*, 16, 1588986. <https://doi.org/10.3389/fgene.2025.1588986>
37. MDLADLA, K. – DZOMBA, E. F. – MUCHADEYI, F. C. (2018): Landscape genomics and pathway analysis to understand genetic adaptation of South African indigenous goat populations. *Heredity*, 120(4), 369–378. <https://doi.org/10.1038/s41437-017-0044-z>
38. MILANESI, M. – CAPOMACCIO, S. – VAJANA, E. – BOMBA, L. – GARCIA, J. F. – AJMONE-MARSAN, P. – COLLI, L. (2017): BITE: an R package for biodiversity analyses. <https://doi.org/10.1101/181610>
39. MUKHINA, V. – SVISHCHEVA, G. – VORONKOVA, V. – STOLPOVSKY, Y. – PISKUNOV, A. (2022): Genetic diversity, population structure and phylogeny of indigenous goats of Mongolia revealed by SNP genotyping. *Animals*, 12(3), 221. <https://doi.org/10.3390/ani12030221>
40. NANTONGO, Z. – BIRUNGI, J. – OPIYO, S. O. – SHIRIMA, G. – MUGERWA, S. – MUTAI, C. – KYALO, M. – MUNISHI, L. – AGABA, M. – MRODE, R. (2024): Genetic diversity, population structure and kinship relationships highlight the environmental influence on Uganda's indigenous goat populations. *Frontiers in Genetics*, 15, 1385611. <https://doi.org/10.3389/fgene.2024.1385611>
41. OLIVEIRA, R. R. – BRASIL, L. H. A. – DELGADO, J. V. – PEGUEZUELOS, J. – LEÓN, J. M. – GUEDES, D. G. P. – ARANDAS, J.K. G. – RIBEIRO, M. N. (2016): Genetic diversity and population structure of the Spanish Murciano–Granadina goat breed according to pedigree data. *Small Ruminant Research*, 144, 170–175. <https://doi.org/10.1016/j.smallrumres.2016.09.014>
42. ONZIMA, R. B. – UPADHYAY, M. R. – DOEKES, H. P. – BRITO, L. F. – BOSSE, M. – KANIS, E. – GROENEN, M. A. M. – CROOIJMANS, R. P.M. A. (2018): Genome-wide characterization of selection signatures and runs of homozygosity in Ugandan goat breeds. *Frontiers in Genetics*, 9, 318. <https://doi.org/10.3389/fgene.2018.00318>
43. PEGOLO, S. – BISUTTI, V. – MOTA, L. F. M. – CECCHINATO, A. – AMALFITANO, N. – Dettori, M. L. – PAZZOLA, M. – VACCA, G. M. – BITTANTE, G. (2025): Genome-wide landscape of genetic diversity, runs of homozygosity, and runs of

- heterozygosity in five Alpine and Mediterranean goat breeds. *Journal of Animal Science and Biotechnology*, 16(1), 33. <https://doi.org/10.1186/s40104-025-01155-3>
44. PEMBLETON, L. W. – COGAN, N. O. I. – FORSTER, J. W. (2013): StAMPP: an R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. *Molecular Ecology Resources*, 13(5), 946–952. <https://doi.org/10.1111/1755-0998.12129>
 45. PICKRELL, J. – PRITCHARD, J. (2012): Inference of population splits and mixtures from genome-wide allele frequency data. *Nature Proceedings*, 1–1. <https://doi.org/10.1038/npre.2012.6956.1>
 46. PURCELL, S. – NEALE, B. – TODD-BROWN, K. – THOMAS, L. – FERREIRA, M. A. – BENDER, D. – MALLER, J. – SKLAR, P. – DE BAKKER, P. I. – DALY, M. J. – SHAM, P. C. (2007): PLINK: a tool set for whole-genome association and population-based linkage analyses. *American Journal of Human Genetics*, 81(3), 559–575. <https://doi.org/10.1086/519795>
 47. R CORE TEAM. (2016): R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.R-project.org/>
 48. RASHIDI, A. – MOKHTARI, M. S. – GUTIÉRREZ, J. P. (2015): Pedigree analysis and inbreeding effects on early growth traits and greasy fleece weight in Markhoz goat. *Small Ruminant Research*, 124, 1–8. <https://doi.org/10.1016/j.smallrumres.2014.12.011>
 49. SINGH, P. – ALI, S.A. (2022): Multifunctional Role of S100 Protein Family in the Immune System: An Update. *Cells*, 11(15), 2274. <https://doi.org/10.3390/cells11152274>.
 50. TABATA, R. – KAWAGUCHI, F. – SASAZAKI, S. – YAMAMOTO, Y. – BAKHTIN, M. – KAZYMBET, P. – MELDEVEKOB, A. – SULEIMENOV, M. Z. – NISHIBORI, M. – MANNEN, H. (2019): The Eurasian Steppe is an important goat propagation route: A phylogeographic analysis using mitochondrial DNA and Y-chromosome sequences of Kazakhstani goats. *Animal Science Journal*, 90(3), 317–322. <https://doi.org/10.1111/asj.13144>
 51. WICKHAM, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York. <https://ggplot2.tidyverse.org>
 52. YANG, J. – LEE, S. H. – GODDARD, M. E. – VISSCHER, P. M. (2011): GCTA: a tool for genome-wide complex trait analysis. *American Journal of Human Genetics*, 88(1), 76–82. <https://doi.org/10.1016/j.ajhg.2010.11.011>

7. LIST OF PUBLICATIONS



UNIVERSITY of
DEBRECEN

UNIVERSITY AND NATIONAL LIBRARY
UNIVERSITY OF DEBRECEN

H-4002 Egyetem tér 1, Debrecen

Phone: +3652/410-443, email: publikaciok@lib.unideb.hu

Registry number: DEENK/309/2026.PL
Subject: PhD Publication List

Candidate: Nelly Kichamu
Doctoral School: Doctoral School of Animal Husbandry
MTMT ID: 10085144

List of publications related to the dissertation

Foreign language scientific articles in Hungarian journals (1)

1. **Kichamu, N.**, Astuti, P. K., Kusza, S.: Genetic and phenotypic basis of goat adaptability across agro-ecological zones: Implications for breeding and conservation.
*Agrártud. közl. [accepted by publisher]*2026 (1), 1-13, 2026. ISSN: 1587-1282.

Foreign language scientific articles in international journals (4)

2. **Kichamu, N.**, Astuti, P. K., Kusza, S.: Smart Solutions for Small Ruminants: The Role of Artificial Intelligence (AI) and Precision Livestock Farming in Smallholder Goat Husbandry.
AgriEngineering. 8 (3), 1-12, 2026. ISSN: 2624-7402.
DOI: <https://doi.org/10.3390/agriengineering8030103>
IF: 3 (2024)
3. **Kichamu, N.**, Wanjala, G., Dossybayev, K., Bagi, Z., Bekmanov, B., Kusza, S.: Genome-wide analysis provides insight into the genetic diversity and adaptability of Kazakhstan local goats.
Sci Rep. 15 (1), 1-15, 2025. EISSN: 2045-2322.
DOI: <http://dx.doi.org/10.1038/s41598-025-02427-8>
IF: 3.9 (2024)
4. **Kichamu, N.**, Astuti, P. K., Wanjala, G., Strausz, P., Bagi, Z., Kusza, S.: A Review on Indigenous Goats of East Africa: A Case for Conservation and Management.
Biology (Basel). 13 (6), 1-16, 2024. EISSN: 2079-7737.
DOI: <http://dx.doi.org/10.3390/biology13060419>
IF: 3.5
5. **Kichamu, N.**, Wanjala, G., Csiszter, L. T., Strausz, P., Astuti, P. K., Bagi, Z., Kusza, S.: Assessing the population structure and genetic variability of Kenyan native goats under extensive production system.
Sci. Rep. 14 (1), 1-11, 2024. EISSN: 2045-2322.
DOI: <http://dx.doi.org/10.1038/s41598-024-67374-2>
IF: 3.9





Foreign language abstracts (2)

6. **Kichamu, N.**, Wanjala, G., Astuti, P. K., Bagi, Z., Mbithi, A., Kusza, S.: Inbreeding and inbreeding dilemma in indigenous goats under extensive production systems: a review.
In: 21st Wellmann International Scientific Conference Book of abstracts / felelős kiadó Edit Mikó, szerk. Ingrid Melinda Gyalai, Szilárd Czóbel, University of Szeged Faculty of Agriculture, Hódmezővásárhely, 19, 2024. ISBN: 9789633069806
7. **Kichamu, N.**, Wanjala, G., Astuti, P. K., Kusza, S.: Estimating relatedness and inbreeding of small east african goats using pedigree.
In: Genetics and Applications: An Aspiring Interdisciplinary Journal of Genetic Research, Special edition, Book of abstracts, Institute for Genetic Engineering and Biotechnology, University of Sarajevo, Sarajevo, Bosnia and Herzegovina, 82, 2023, (eISSN 2566-431x)

List of other publications

Foreign language scientific articles in international journals (8)

8. Mkuzi, H. T., Mwakumanya, M. A., Bendzko, T., Boros, N., **Kichamu, N.**: Land Tenure, Socio-Economic Drivers, and Multi-Decadal Land Use and Land Cover Change in the Taita Hills, Kenya.
Wild. 3 (1), 1-16, 2026. ISSN: 3042-4526.
DOI: <https://doi.org/10.3390/wild3010001>
9. Wanjala, G., Bagi, Z., Gavojdian, D., Badaoui, B., Astuti, P. K., Mizeranschi, A. E., Ilisiu, E., Ohran, H., Pasic Juhas, E., Loukovitis, D., Kawęcka, A., Šveistienė, R., Becskei, Z., Strausz, P., **Kichamu, N.**, Kusza, S.: Genetic diversity and adaptability of native sheep breeds from different climatic zones.
Sci. Rep. 15 (14143), 1-13, 2025. EISSN: 2045-2322.
DOI: <http://dx.doi.org/https://doi.org/10.1038/s41598-025-97931-2>
IF: 3.9 (2024)
10. **Kichamu, N.**, Astuti, P. K., Kusza, S.: The Role of Insect-Based Feed in Mitigating Climate Change: Sustainable Solutions for Ruminant Farming.
Insects. 16 (5), 1-17, 2025. EISSN: 2075-4450.
DOI: <http://dx.doi.org/10.3390/insects16050516>
IF: 2.9 (2024)
11. Wanjala, G., **Kichamu, N.**, Csiszter, L. T., Astuti, P. K., Kusza, S.: An on-station analysis of factors affecting growth traits of Pure Red Maasai and Dorper sheep breeds under an extensive production system.
Animals (Basel). 13 (2), 1-10, 2023. ISSN: 2076-2615.
DOI: <http://dx.doi.org/10.3390/ani13020300>
IF: 2.7





12. Wanjala, G., Astuti, P. K., Bagi, Z., **Kichamu, N.**, Strausz, P., Kusza, S.: A review on the potential effects of environmental and economic factors on sheep genetic diversity: consequences of climate change.
Saudi J. Biol. Sci. 30 (1), 1-10, 2023. ISSN: 1319-562X.
DOI: <http://dx.doi.org/10.1016/j.sjbs.2022.103505>
13. Wanjala, G., Astuti, P. K., **Kichamu, N.**, Bagi, Z., Kusza, S.: Assessing Genomic Inbreeding and Homozygosity Patterns in Hungarian Merino Sheep and its Relatives.
Animal Sci. Biotechn. 56 (1), 47-52, 2023. ISSN: 1841-9364.
14. Wanjala, G., Astuti, P. K., Bagi, Z., **Kichamu, N.**, Strausz, P., Kusza, S.: Assessing the genomics structure of Dorper and White Dorper Variants, and Dorper Populations in South Africa and Hungary.
Biology (Basel). 12 (3), 1-11, 2023. EISSN: 2079-7737.
DOI: <http://dx.doi.org/10.3390/biology12030386>
IF: 3.6
15. Wanjala, G., **Kichamu, N.**, Strausz, P., Astuti, P. K., Kusza, S.: On-station comparative analysis of reproductive and survival performance between Red Maasai, Dorper, and Merino sheep breeds.
Animal. 17 (3), 1-6, 2023. ISSN: 1751-7311.
DOI: <http://dx.doi.org/10.1016/j.animal.2023.100715>
IF: 4

Foreign language conference proceedings (1)

16. Astuti, P. K., Fajardo, R., Wanjala, G., **Kichamu, N.**, Ohran, H., Badaoui, B., Bagi, Z., Kusza, S.:
Heat Stress: Can Animals be Stressed but still be Healthy?
Animal Sci. Biotechn. 56 (1), 194-202, 2023. ISSN: 1841-9364.

Foreign language abstracts (3)

17. Astuti, P. K., Pradita Iustitia, S., Alek, I., Shairah, A. R., **Kichamu, N.**, Kusza, S.: Investigating the genetics of tropical climate adaptation in Asian and African indigenous sheep.
In: Biotechnológia a Debreceni Egyetemen 2024 Szimpózium : Absztraktfüzet, Debrecen Egyetem, Debrecen, 49, 2024.
18. Astuti, P. K., Sárkány, P., Wanjala, G., **Kichamu, N.**, Kusza, S.: Genetics of coat colors and its role in climate change resiliency in sheep.
In: Genetics and Applications: An Aspiring Interdisciplinary Journal of Genetic Research, Special edition, Book of abstracts, Institute for Genetic Engineering and Biotechnology, University of Sarajevo, Sarajevo, Bosnia and Herzegovina, 40, 2023, (eISSN 2566-431X).





**UNIVERSITY of
DEBRECEN**

**UNIVERSITY AND NATIONAL LIBRARY
UNIVERSITY OF DEBRECEN**

H-4002 Egyetem tér 1, Debrecen
Phone: +3652/410-443, email: publikaciok@lib.unideb.hu

19. Wanjala, G., Astuti, P. K., **Kichamu, N.**, Kusza, S.: Eco-regional influence on genetic diversity, population structure, and signatures of selection of indigenous sheep in Kenya.
In: Biotechnológia a Debreceni Egyetemen. Fókuszban az agrár- és élelmiszerbiotechnológia
: Tudományos Szimpózium előadás összefoglalók, Debreceni Egyetem MÉK Agrár Genomikai és Biotechnológiai Központ, Debrecen, 46-47, 2021. ISBN: 9789634903512

Total IF of journals (all publications): 31,4

Total IF of journals (publications related to the dissertation): 14,3

The Candidate's publication data submitted to the Tudóstér have been validated by DEENK on the basis of the Journal Citation Report (Impact Factor) database.

19 May, 2026

