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NELLY KICHAMU

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Doctoral School of Animal Science

Head of doctoral school:

Prof. Dr. István Komlósi, D.Sc.

Professor

Supervisor:

Prof. Dr. Szilvia Kusza, D.Sc.

Professor

**Population Structure and Genetic Characterization of Indigenous
Goat Breeds from Different Climatic Zones as A Climate Change and
Adaptation Mechanism**

Nelly Kichamu

Doctoral candidate

Debrecen

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

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Written by **Nelly Kichamu**, certified Agribusiness (M.Sc.)

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Dissertation supervisor: **Prof. Dr. Szilvia Kusza, D.Sc.**

The official opponents of the dissertation:

Dr.

Dr.

The evaluation board:

Chairperson: Dr... ..

Members: Dr.

Dr.

Dr.

Dr.

The date and venue of the dissertation defense: Debrecen.....2026

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LIST OF ABBREVIATIONS AND ACRONYMS

A2 (HSPA2)	Heat shock protein family A (HSP70) member 2
ADAMTSL3	ADAMTS like 3
AEN	Apoptosis enhancing nuclease
ATP1A1	ATPase Na ⁺ /K ⁺ transporting subunit alpha 1
ASIP	Agouti signaling protein
AQP3	Aquaporin 3 (Gill blood group)
BAW	Banat White goat
B4GAT1	Beta-1,4-glucuronyltransferase 1
BTNL2	Butyrophilin like 2
CENPJ	Centromere protein J
CD58	CD58 molecule
CHI1	Chitinase 1
CNOT2	CCR4–NOT transcription complex subunit 2
CHMP5	Charged multivesicular body protein 5
DAB	Local goat population from Darbazo village
DBSK	Domaća Balkanska Šarena Koza goat
DENND1A	DENN domain containing 1A
DIP2C	DIP2 disco interacting protein 2 homolog C
DLG1	Disc large scaffold protein 1
DNAJC5	DnaJ heat shock protein family member C5
EDNRB	Endothelin receptor type B
ENO1	Enolase 1 (Alpha)
ERBB2	Erb-B2 receptor tyrosine kinase 2
FAO	Food and agriculture organization
FAOSTAT	Food and agriculture organization statistical database
FGF2	Fibroblast growth factor 2
F _{IS}	Inbreeding coefficient
F _{IT}	Total inbreeding coefficient
GAL	Galla goat
GNAI3	Guanine nucleotide binding protein alpha inhibiting polypeptide 3
H _E	Expected heterozygosity
HLA	Human leukocyte antigen
H _O	Observed heterozygosity
HOXC12	Homeobox C12
HOXC13	Homeobox C13
HSP70	Heat shock protein 70
HUN	Old Hungarian Native goat
HYAL1	Hyaluronoglucosaminidase 1
HYAL3	Hyaluronoglucosaminidase 3
IFNLR1	Interferon lambda receptor 1
IGSF3	Immunoglobulin superfamily member 3
IL10RB	Interleukin 10 receptor subunit beta
ISG20	Interferon stimulated exonuclease gene 20
KEF	Keffa goat
KENS	Local goat population from Kenes village
KOSS	Local goat population from Kosseit village
KPNA4	Karyopherin subunit alpha 4

KUN	Local goat population from Kundyzydy village
MEA	Maasai East African goat
MRPL46	Mitochondrial ribosomal protein L46
MRPS11	Mitochondrial ribosomal protein S11
MST1	Macrophage stimulating 1
MTOR	Mechanistic target of rapamycin kinase
Ne	Effective population size
NFX1	Nuclear transcription factor, x-box binding 1
NPBWR2	Neuropeptides B/W receptor type 2
NTRK3	Neurotrophic receptor tyrosine kinase 3
NOL6	Nucleolar protein 6
OPRL1	Opioid related nociceptin receptor 1
PARP4	Poly(ADP-Ribose) polymerase family member 4
PCK	Phosphoenolpyruvate carboxykinase
PGLYRP3	Peptidoglycan recognition protein 3
PHIN	Philippine Native Antipas Cotabato group
PLCB1	Phospholipase C beta 1
PP1R36	Protein phosphatase 1 regulatory subunit 36
PPP4R3B	Protein phosphatase 4 regulatory subunit 3B
PRPF6	Pre-mRNA processing factor 6
PTPRR	Protein tyrosine phosphatase receptor type R
PWT	Pare White goat
RGS19	Regulator of G-Protein signaling 19
RNF17	Ring finger protein 17
ROH	Runs of homozygosity
SAMD10	Sterile alpha motif domain containing 10
S100	S100 calcium binding protein family
SEA	Small East African goat
SHOK	Local goat population from Shokpar village
SLC6A2	Solute carrier family 6 member 2
SLC7A11	Solute carrier family 7 member 11
SOX18	SRY-box transcription factor 18
TCEA2	Transcription elongation factor A2
TENM3	Teneurin trans membrane protein 3
UBAP2	Ubiquitin associated protein 2
UBE2R2	Ubiquitin conjugating enzyme E2 R2
UCKL1	Uridine-cytidine kinase like 1
UGT2A2	UDP glucuronosyltransferase family 2 member A2
USH	Local goat population from Ushterek village
WG	Woyto-Guji goat
YBP	Years before present
YPEL	Yippee-like protein
ZNF512B	Zinc finger protein 512B

1. INTRODUCTION

1.1 Research background

Modern agricultural activities are highly shaped by the adverse effects of climate change. Prevalence of disease outbreaks, poor and insufficient water supplies, and unfavorable weather patterns are just a few of the variables that have a direct and indirect impact on agricultural production and the environment. The severity of heat waves and changing rainfall patterns poses a threat to the existence of both human beings and natural ecosystems. Even in the short run, the sustainability of the social and ecological systems is still questionable under such conditions. These predicaments are worsened by the constantly growing population, especially in emerging nations.

The overwhelming decline in biological diversity has become a reality, with direct implications for food security. The disruption in agricultural production and its supply chains is increasing, especially in developed countries, while becoming worse in developing countries. Therefore, agricultural production should be able to adapt fast and efficiently to provide high-quality and sustainable food for people. And because of this, the future output will only be dominated by those breeds that are able to withstand such demanding conditions. The well-being and survival of many populations depend on the continuous availability and supply of animal-based protein sources. Considering the aforementioned circumstances and challenges, among the viable species will be the earliest domesticated animals, specifically the native goats.

From economic, nutritional, and cultural perspectives, goats have been one of the most significant domestic animal species to human beings for over 10,000 years. Initially, these goats were domesticated in Southwest Asia, and then spread to other parts of the world, including Europe and Africa, where they now inhabit different environments. Goats are important in almost all African and various Asian cultures. Their small body size, high reproductive rate, and short gestation interval render them suitable, especially for households with limited resources and women who frequently own and care for them. Currently, there exists a number of native goat breeds across Europe, Asia, and Africa dominating various agro-ecological and socio-economic settings. These goats provide high-quality, nutritious meat, milk, and fiber at a low expense. Besides, they thrive well in marginal lands where crops or other large ruminants cannot survive or produce effectively, utilize the available natural resources,

and are a source of diversified food, including high-quality meat (chevon) and dairy products.

The level of adaptability of goats to various agro-ecological zones is also a highly valuable trait, particularly in the current climate change era. However, the genetic diversity of these indigenous goats have been compromised by the following activities, indiscriminate crossbreeding with exotic commercial breeds intensified by technological limitations, inadequate conservation management systems, production systems employed, human induced intensive selection, insufficient funding for effective breed conservation programs especially in developing countries, and a lack of structured breeding management systems that have often failed to control or monitor crossbreeding practices leading to the dilution of unique local genetic traits. As a result, some indigenous populations are now endangered, thus threatening their loss of valuable genetic resources and traditional agricultural heritage that is hard to reverse. This condition not only impacts local biodiversity but also presents a considerable threat to global biodiversity conservation initiatives. The continued decline of these indigenous populations makes it challenging for them to foster climate resilience, promote sustainable agriculture, and conserve the genetic resources, all of which are important for adapting to ever-changing environments.

However, knowledge of the genetic diversity and population structure is essential for the preservation and protection of these goats, particularly those with small populations. Understanding their basis of adaptability is also important before it can be effectively utilized as a resource. Therefore, the population structure and genetic diversity of these goat breeds across different environmental conditions provide an excellent foundation for this research and promise rapid progress to their genetic makeup and to fully leverage their adaptive potential.

1.2 Research aim

This doctoral study aimed at assessing the population structure and genetic characterization of indigenous goat breeds from different climatic zones for climate change and adaptation mechanisms under the following objectives:

- i. To perform genetic characterization of Kenyan indigenous goat breeds using pedigree information.

- ii. To evaluate the genomic characteristics of African, Asian, and European native goat breeds.
- iii. To establish the genomic relationships between African, Asian, and European native goats.
- iv. To identify the signature selection that underpins the adaptation of this goat population.

2. LITERATURE REVIEW

2.1 Overview of livestock production

Livestock production forms an essential element of the global agricultural system. About 40% of total agricultural output value comes from livestock, which also contributes to more than 50% of the agricultural gross domestic product (GDP) in developing countries (FAO, 2023a; IFAD, 2023). The sector also provides for the livelihoods of about 1.3 billion people globally and uses approximately 2.5 billion hectares of land, which accounts for 50% of the total land under agricultural production. Their products, including meat, milk, and blood, contribute to over 18% of worldwide caloric consumption and account for around 40% of animal-based dietary protein, thus serving as an important function in mitigating nutrient deficits that cannot be obtained in plant-based protein (FAO, 2023a).

The increasing demand for consumption of animal-based protein, which is projected to reach 47.9 Mt over the next decade, coupled with the annual per capita consumption projected to increase by 0.9 kg per capita/year for the edible retail weight equivalent by 2034. These projections majorly drive the transformation of the livestock sector due to an ever-growing population, rural-urban migration, changes in lifestyles, increased disposable income, and consumer perception on food preferences (OECD/FAO, 2025). Furthermore, the expansion of fast-food stores, increasing consumption of convenient processed foods, and the growing consumer health concerns also contributes to the transformation in livestock sectors (FAO, 2024). Following the aforementioned importance, there is need for conservation and sustainable use of indigenous livestock, especially the indigenous goat genetic resources found worldwide. They are among the species best suited to address this demand and adapt to local environments, showing resilience to diseases, especially under current climate fluctuations, making them important for food security and sustainable livelihoods in their native regions.

2.2 Replacement of lost genetic diversity in indigenous populations

Indigenous goat populations have developed unique mechanisms since their initial domestication in the Fertile Crescent of the Near East. These mechanisms have enabled them to thrive in their local environments, including adaptability and disease resistance, allowing them to produce and reproduce well in harsh environments where

international breeds often cannot endure (BASHIRU and OSENI, 2025). If we allow them to become extinct, we may end up losing the important genetic resource that is needed for future agricultural production and rural livelihoods, especially in the current climate change regime. Therefore, there is a need to conserve these populations for the betterment of the country's cultural heritage and biodiversity, as well as to ensure that future generations have access to these essential genetic resources (NYAMUSHAMBA et al., 2017).

Most of indigenous populations are predictably small in number, which encourages the use of all available animals for subsequent breeding, thereby subjecting them to the risk of extinction. Breeders must therefore exercise great caution when managing genetic diversity of these populations, as it is irreplaceable once lost. Managing genetic diversity can be achieved through implementation of proper breeding programs, developing and strengthening community-based conservation initiatives, and establishing gene banks that can help maintain and preserve these populations for future livestock improvement and sustainable agricultural development (ABU, 2021).

Although the advancement of modern technologies has tried to improve breed performance and disease resistance in these populations, they cannot fully substitute for the lost diversity that is natural in these indigenous breeds. These advancements only provide tools to characterize, utilize, and access animal genetic resources for food security and production enhancement, but not for restoring the lost diversity. Especially the genetic diversity lost through reduction in effective population size (N_e), known as bottleneck effects, cannot be recovered even if the population size increases at a later stage (KUKUČKOVÁ et al., 2018). Since the overall N_e over generations is calculated using the harmonic mean of population sizes, meaning that generations with the fewer breeding individuals reduces the overall N_e due to increased genetic drift (MANUNZA et al., 2025).

As a result, breeding programs must be carefully planned to avoid genetic bottlenecks by maintaining sufficiently large populations over time to ensure a stable N_e throughout the generations. Furthermore, it is recommended to maintain the largest number of animals in generation zero (founder flock), as the original population contains a full range of genetic diversity that must be conserved, despite ongoing mutations.

However, if the founder population is small, breeding programs should be tailored in a way that the founder populations are not related and are non-inbred, this

will ensure the population maintains a pure gene pool while preventing the buildup of harmful genetic alleles, which can affect the overall health of the population, including reduced fertility, poor growth rate, and low productivity (WILLI et al., 2022). However, it is not easy to achieve this, especially if the founder population has been small throughout the generations or if the pedigree information is incomplete or unavailable, making it challenging to avoid mating among relatives.

Generally, it is preferable to start breeding from all existing individuals rather than expanding from a small subset. Proper and complete record-keeping, organized mating systems, and periodic introduction of unrelated individuals from other populations (CAO et al., 2020). These approaches will help to maximize the retention of genetic diversity and reduce the risk of inbreeding depression, thus securing the adaptive potential and sustainability of indigenous breeds.

2.3 Global goat population and their significance

After the process of domestication in the Near East (ZHENG et al., 2020), goats (*Capra hircus*) continued to play a vital role in the livelihood of many people. FAOSTAT (2024) noted an increasing trend of the global goat population, ranging from 754 million in 2000 to 1,185.52 million (1.19 billion) heads in 2024 (Figure 1). This trend clearly indicates their growing importance in the overall livestock sector. From the statistics, we see that most of the global goat population comes from Asia, with approximately 595 million head accounting for 50.08% of the global share, with India and China accounting for most of this production, followed by Africa, with 533.7 million (44.94 %), with Ethiopia and Nigeria having the highest population. America, Europe, and Oceania maintain significant or relatively small populations at 39.6 million (3.33%), 13.77 million (1.16%), and 5.6 million (0.49 %), respectively, with Brazil and Australia producing the most (Figure 2A & B). This increase in goat population, by nearly 57.6 % in the past two decades, highlights the unique adaptive traits they contain, especially the increase by 119 % in Africa, which justifies their strong adaptation to arid and semi-arid environments, as most of these populations are found in these regions of Africa. Furthermore, the 31% increase trend observed in Asia suggests their suitability across diverse production systems despite land size constraints. About 13.5% growth in the goat population in America signifies their important role in export market development, mainly in industrialized countries.

Generally, the increasing trend positions goats as a vital livestock investment with great potential to alleviate poverty, particularly in developing countries (KICHAMU et al., 2024a). These goats represent a feasible sector in the face of climate change, given their constant supply of high-quality and healthy products that help meet food security and income generation, especially for rural families. Besides, goats are important for the growth of international trade and export markets, mainly in industrialized countries. They also contribute to about 17% of the world's animal protein and 38% of the dairy production in developing countries (UTAAKER et al., 2021). All these benefits demonstrate how goats are important in creating sustainable, inclusive, and climate-resilient food systems, capable of meeting future environmental and population challenges.

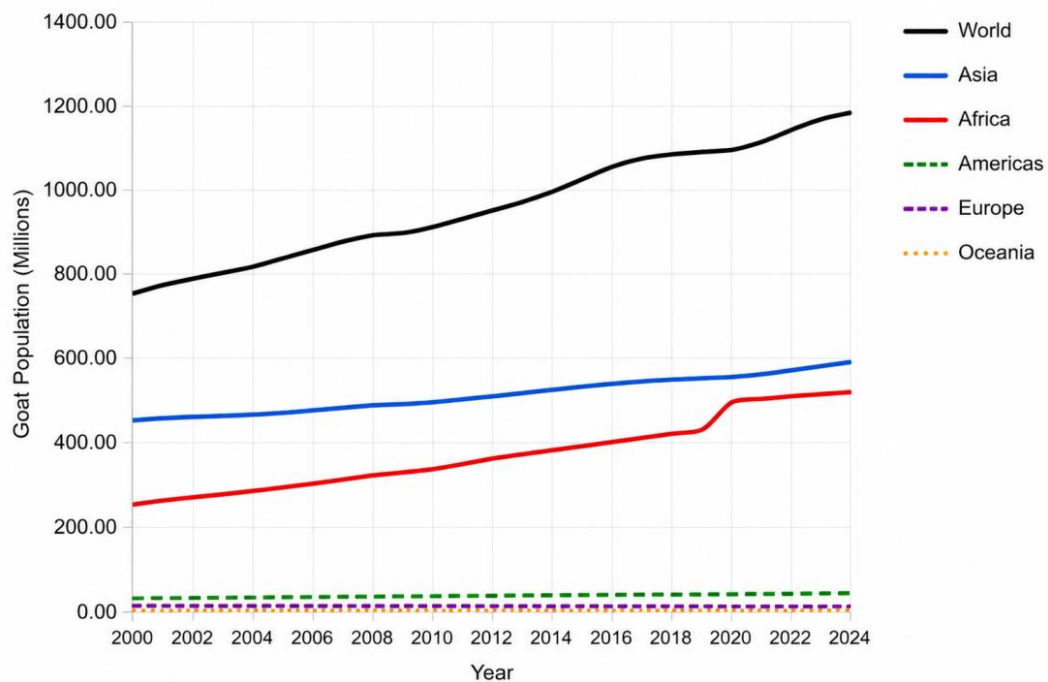


Figure 1. Global goat population trend (2000-2024) (FAOSTAT, 2024)

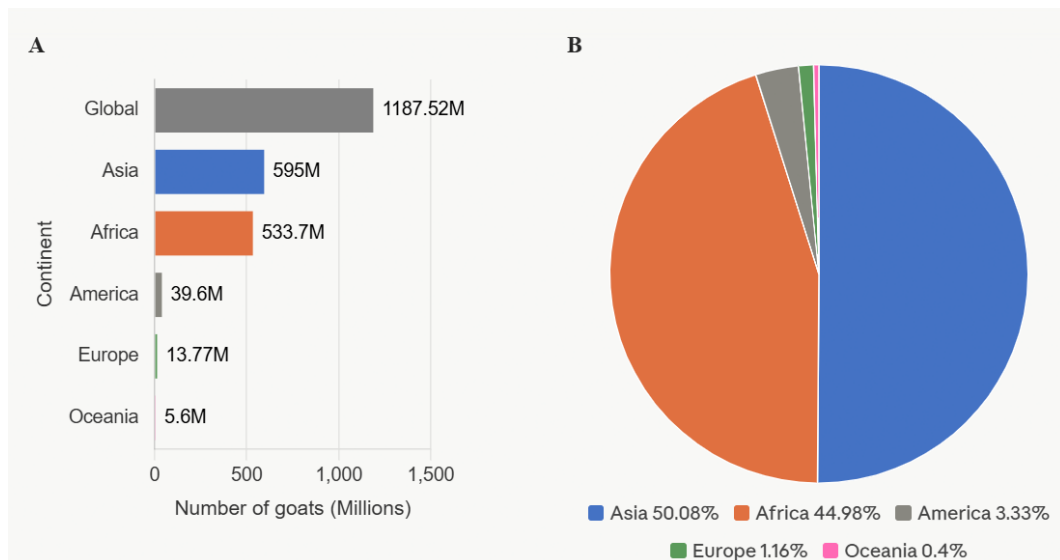


Figure 2. Statistics of global goat population; (A) Current goat population per continent in millions and (B) Total percentage share of goats per continent (FAOSTAT, 2024)

Indigenous goats are therefore defined as those breeds that are local to the region in which they exist or to the specific areas they are raised (MONAU et al., 2020). This implies that they survive, reproduce, and produce in that environment, regardless of its condition, including arid and marginal fields, mountainous or valleys, unsuitable for agricultural production or for large ruminant production (KERVEN, 2024). Survival of these goats in such harsh and variable environments is necessitated by the unique physiological and genetic features they possess including efficient utilization of water and feeds, tolerance to heat and drought and ability to continue producing under the feed scarcity era, the presence of morphological adaptations including short body, glossy hair for heat dissipation, light body weight for more effortless movement over the rough, hilly and rocky terrain, and variation in coat color that can reflect sunlight (JOY et al., 2020).

These traits help indigenous goats to survive where other livestock can not, making them a highly resilient and cost-effective enterprise, especially for resource-constrained and rural farmers. Moreover, the investment and management cost for these goats is low, and they can produce various products, including meat, milk, skin, cashmere, and manure. They are capable of converting low-quality pasture into valuable animal products; all these features enhance their importance for sustainable livelihood assets, especially in traditional production systems (CHENG et al., 2022). Besides, they

also multiply very fast with a short gestation period of 5 months, while resuming mating shortly after kidding, depending on the breed characteristics and communal management practices. This reproductive pattern allows for more frequent breeding, potentially resulting in three successful kidding within two years under good management. This enables rapid reproduction, faster increase in flock size, steady supply of products, quicker returns on investment and continuous income opportunities for smallholder and resource-scarce farmers (RUVUGA and MALEKO, 2023).

Beyond the economic benefits, chevon is becoming more popular for its nutritional value, characterized as lean with less fat and more protein content, as compared to other livestock meats, which correspond with global dietary trends of favoring healthier sources of animal protein (GAWAT et al., 2023). These features and their significance to the economic and socio-cultural activities highlight the necessity for sustainable utilization and the development of conservation strategies aimed at protecting the indigenous goat genetic resource.

2.4 The origin and domestication of goats

Goats (*Capra hircus*) are among the earliest domesticated livestock species that played a considerable historical and cultural role in various communities. They descended from their ancestor, the wild bezoar ibex (*Capra aegagrus*), which inhabited the mountainous regions of Southwest Asia (TABERLET et al., 2011). Studies on goats' archaeological and genetic evidence indicate that their domestication took place in the Fertile Crescent between 10,000 and 11,000 years ago during the early agricultural period, mainly around Ganj Dareh (Iran) and Çayönü (Turkey) (NADERI et al., 2008; PENG et al., 2022; TIAN et al., 2021).

Domestication was made possible by the mutual relationship goats had with human beings, the adaptation mechanisms, a manageable social behavior, and steady supply of nutritious meat, milk, and skin to human beings (ZHENG et al., 2020). After the domestication process, they spread rapidly across Europe, Africa, and South Asia through human migration and trade routes (PETRETTO et al., 2024). There are several arguments about goat domestication. For instance, DALY et al. (2018) argue that goats were domesticated independently from a number of wild populations, resulting in genetically and geographically distinct breeds, an indication that each ancestor produced a distinct lineage characterized by unique traits. Besides, large-scale mitochondrial

DNA (mtDNA) analyses suggest that the initial domestication of goats occurred in Eastern Anatolia and the Zagros Mountains (NADERI et al., 2008), with the current studies indicating that the domestication took place along the Inner Asian mountain corridor during the bronze and iron ages (HERMES et al., 2020).

Other studies argue that domestication process involved multiple maternal origins across the Near East, which gave rise to six divergent mtDNA haplogroups (including A, B, C, D, F, and G) (NOMURA et al., 2013). Furthermore, the use of multiple sequentially Markovian coalescent (MSMC) by ZHENG et al. (2020) on demographic modeling of the goat domestication reported that the split between modern Asian and European goat populations may be a sign that domestication occurred earlier than the estimated timeline. These findings challenge the traditional view that domestication occurred before 10,000 years before present (YBP), raising the possibility of an earlier and more complex domestication process.

2.4.1 The wild goat (*Capra aegagrus*)

The bezoar wild goat (*Capra aegagrus*) belongs to the family Bovidae, genus *Capra*. This family has 8 species and 11 subspecies—the *Capra aegagrus* has 4 subspecies, including *Capra aegagrus aegagrus*, which are distributed in Afghanistan, Armenia, Azerbaijan, Lebanon (extinct), Russia (Eastern Caucasus), Turkey, Georgia, and Iran. The *Capra aegagrus blithy*, which are found in Pakistan, Iran, Iraq, and Turkmenistan, *Capra aegagrus chialtanensis* found in Pakistan, and *Capra aegagrus cretica* found in Greece (WEINBERG and AMBARLI, 2020). From the mentioned subspecies, *Capra aegagrus* is considered the ancestor of the current domestic goat (*Capra hircus*) and is regarded as the most important species in the early history of animal domestication. These goats inhabited the dry rocky mountain ranges and shrubs around the Middle East and Central Asia. Despite them inhabiting the rocky and dry regions, they are also termed as forest species often found in the middle of the mountains (AHMED et al., 2016).

Archaeological and genetic evidence confirms that domestic goats emerged directly from wild bezoar populations, which were gradually tamed for their milk, meat, and hides by human beings, but in some areas, interbreeding still exists between wild and domestic populations (NADERI et al., 2008). This bezoar goat is a medium-sized, hoofed animal that moves easily in the mountain, steep, and rocky terrain. Mature bucks can weigh up to 80 kg with long and backward-curving horns, which can exceed one

meter in length and form an elegant spiral (NADERI et al., 2008) (Figure 3). The breed has a short and coarse coat, typically grayish brown in color with lighter underparts; they have a dark beard and a dorsal stripe along the spine. Besides, the bezoar does are smaller in size with short horns and light in color (AMININASAB et al., 2023). They feed primarily on shrubs, pasture, and leaves and are highly fast climbers that seek safety on mountain cliffs whenever they are threatened by predators like leopards, wolves, or eagles (AHMED et al., 2016).

The International Union for Conservation of Nature (IUCN) has currently classified the wild bezoar goats as at risk of extinction, with declining populations in many countries due to illegal poaching for meat and trophies which is commonly practices in Iran and Armenia, the loss of habitat due do environmental degradation, and steep competition from other domestic livestock thus leading to isolation and reduction in this wild goat populations (WEINBERG and AMBARLI, 2020). However, in countries where conservation programs are enforced, such as in Iran's protected areas and Armenia's Khosrov forest reserve, populations have shown some recovery.



Figure 3. The bezoar wild goat (*Capra aegagrus*) (NADERI et al., 2008)

2.5 Identification of ancestral-descendant or lineage of goats

The ancestral lineage, also known as the ancestral-descendant line, is a genetic family of a given population that can be traced back over generations. It is used to understand the history of species domestication, breed formation, and genetic differentiation among livestock populations (TORO et al., 2011). Ancestral descendant is essential in identifying the maternal or paternal origins while tracking genetic diversity within and between the populations (TORO et al., 2011). Various studies have

identified six lineages or ancestral descendant of domesticated goats spread across the world through multiple routes at different time periods. For instance, study by COLLI et al. (2015) on whole mitochondrial genome discovered various groups of haplogroups including (A1-A7, B1, C1a, D1 and G), PENG et al. (2022) also identified six mtDNA lineages (A, B, C, D, F, G) by using 4,189 sequences where haplotype A was dominant across the globe, B had some sub-lineages including B1 (Asia, Africa, Middle East, Europe) and B2 (China and Mongolia) while C was seen in Asian and European goat populations.

The study on mitochondrial DNA Hypervariable Region I (mtDNA HVI) analysis of Philippine and Indonesian goats observed two haplogroups, including A and B, where haplogroup B was more common in Indonesian goats. In contrast, both A and B were observed in Philippine goats (MASUKO et al., 2025). Besides, YI et al. (2022) reported six haplogroups (including A, B, C, D, F, and G), where haplogroup A was found in all the study populations across the globe, haplotype B was divided into sub-groups, including B1 and B2, where B2 was mainly observed in Chinese and Mongolian goats. Haplotype C was observed in the Asian and European population; haplogroups D and G were found in Northern China, Qinghai-Tibet, African, and the Middle East goat populations. Lastly, haplogroup F was very rare and only observed in Sicilian populations. From these findings, it is concluded that the origin or lineage of the wild goat is Asia, but not the other parts of the world.

After domestication, these goats later dispersed into Europe via two primary routes, including the Danube river corridor and the Mediterranean coast (FERNÁNDEZ et al., 2006). The Neolithic agro-pastoral communities introduced goats to Greece and Bulgaria around 6500 YBP, then subsequent expansions into Northern Europe by 5500 YBP and eventually Scandinavia and the British countries in 4000 YBP (FERNÁNDEZ et al., 2006). Before this, at around 9000-10,500 YBP, agricultural settlers had already transported goats and other livestock like cattle, pigs, and sheep to Cyprus, which marked one of the earliest maritime dispersals of domestic animals (PETRETTO, 2023).

From Cyprus, they spread across the Mediterranean basin to Greece by 8500–9000 YBP, Italy in 7600-8100 YBP, the Iberian Peninsula in 7300-7700 YBP, and to North Africa by 7000 YBP (SILVA et al., 2022). Genetic studies confirm that these European goats are descended from the Near East wild goat populations. However, they have undergone a significant loss of diversity due to the founder effects during their expansion to the western side (COLLI et al., 2018). In Africa, these goats were first

introduced to North Africa around 7000 YBP, which happened through the migrations to the Levant via the Sinai Peninsula or by maritime routes across the Mediterranean (PETRETTO et al., 2024). This dispersal of goats coincided with the African humid period which occurred between 9000 and 5000 YBP, during the late Pleistocene to Holocene epochs when much of Northern Africa, including the Sahara, it was experiencing increased rainfall, leading to sufficient pasture growth, the emergence of more rivers and lakes, and increased vegetation that supported several ecosystems and human pastoral communities (BRIERLEY et al., 2018).

Later, around 4000 YBP, the occurrence of drought and desertification in the Saharan region, which led to tsetse fly infestations in the area, caused these pastoralists to move southward into the Sahel, the Upper White Nile region, and Kenya (BENJAMINSEN et al., 2019). Genetic and archaeological studies confirm that these movements introduced goats to sub-Saharan Africa, where they became an integral part of agro pastoral communities (TAREKEGN et al., 2021) and by 2000 YBP, the Iron Age communities reached southern Africa, where they started cultivating crops while keeping sheep and goats. The interactions of these pastoral communities with the local hunter-gatherer in these regions led to the emergence of the Khoikhoi pastoralist, which was evidenced by the presence of livestock remains in archaeological sites (LANDER and RUSSELL, 2018).

The dispersal of goats into Asia occurred through two primary routes, including the southern route that passed through Khyber into the Indian subcontinent, followed by their distribution to Southeast Asia through both land and water transport (PENG et al., 2022). These dispersal routes have also been confirmed by some genetic studies; for instance, YONEZAWA et al. (2026) reported genetic relationships between Indian goat populations and Southwest Asian ancestral goat lineages, suggesting historical migration and gene flow from regions such as Mesopotamia into South Asia. The spread of these goats across South Arabia, East Africa, and South Asia was highly facilitated by the Indian Ocean trade networks in 4000 BP (YONEZAWA et al., 2026).

By 3500 BP, the northern route, which passed through the Eurasian steppe that connected the Fertile Crescent region with Mongolia and North China, was developed (TAYLOR et al., 2021). Therefore, ancient DNA studies show that steppe pastoralists transported goats Eastwards during their migrations, with distinct genetic signatures appearing in Chinese Bronze Age populations (HERMES et al., 2020).

2.6 Genetic diversity of indigenous goats

Genetic diversity is the distribution of alleles and variation of genotypes within and among populations, which involves inbreeding coefficients and differences in populations (RAMOROKA et al., 2025). Genetic diversity forms a fundamental pillar of animal and crop diversification, as every living organism acquires distinct genetic characteristics that are influenced by specific natural ecosystems, environmental conditions, and socio-economic factors. The population structure, tailored to particular conditions, is essential for effective genetic conservation. Collectively, these unique traits contribute to the species diversity found on earth, forming the foundation for adaptation, survival, and sustainable development in changing environments (AKIS et al., 2014; SALGOTRA and CHAUHAN, 2023).

Understanding the genetic diversity helps in establishing a breeding program geared towards maximizing the N_e , reducing the inbreeding rate, and preserving heterozygosity within a given population (MANUNZA et al., 2025; WANJALA et al., 2025). These are essential genetic factors needed to enhance critical economic traits, including fertility, growth rate, resistance to disease, and general adaptability. Some of the recommended practices that can influence genetic improvement and guarantee the sustainability of goat populations include maintaining an ideal ratio of breeding bucks to does and closely monitoring the replacement rates (KICHAMU et al., 2024b).

Indigenous goats, therefore, have been known to be adaptable and hardy livestock species that are reared in diverse environmental conditions and geographical locations across the globe. These regions range from arid, semi-arid, desert, and glacial to mountainous and steep landscapes (KICHAMU et al., 2024a). However, their population structure has been changed over generations through natural and artificial selection processes, which have differentiated them from their wild bezoar ibex (DALY et al., 2021). While classification of these goats based on traditional systems recognizes about 136 distinct goat breeds (DUBEUF and BOYAZOGLU, 2009), the recent genomic studies suggest that there are over 570 genetically distinct goat populations in the world (FAO, 2023b). However, their genetic potential is being compromised through various activities, as discussed below.

2.7 Factors affecting genetic diversity in indigenous goats

A number of genetic, demographic, environmental, management, and geographic factors have played a role in shaping the population structure of indigenous goats. Each of these factors significantly influences their genetic diversity, productivity, and sustainable adaptability.

2.7.1 Genetic factors

2.7.1.1 Selective breeding and mating systems

Selective breeding is mating individuals with desirable traits to enhance the prevalence of those traits within a population. The process involves choosing animals based on their genetic attributes to improve their characteristics, mainly for economic, cultural, or social purposes (VAN EENENNAAM, 2025). On the other hand, mating systems are organized strategies used in joining animals for reproduction. These factors may influence the genetic diversity, inbreeding levels, and the effectiveness of selective breeding programs in a population (ÇELİK et al., 2024).

Selective breeding and mating systems can adversely affect the genetic structure of a population. For instance, practices like controlled mating, where breeders intentionally select breeding animals based on the desired features, assortative mating, where farmers select breeding animals based on similarity in phenotypes or genotypes, and crossbreeding, where they join animals from different breeds to enhance their heterosis (ÇELİK et al., 2024; VAN EENENNAAM, 2025). These practices can change the allelic frequencies and heterozygosity levels within the population, thereby affecting essential traits related to growth, fertility, adaptability, and disease resistance. Selective breeding can reduce the genetic diversity, as alleles that are not linked to selection objectives may be lost over generations.

This reduction may lead to inbreeding and genetic bottlenecks, which later increase homozygosity and the risk of inbreeding depression that affects the fitness traits related to reproduction, immunity, and adaptability (HOBAN et al., 2023). For instance, studies of Chinese indigenous goats observed reduced genetic diversity and increased inbreeding in Bohuai goats, which were subjected to intensive selection (ZHANG et al., 2025). Besides, ONZIMA et al. (2018) observed high levels of inbreeding in Boer goats due to intensive selection for fast growth traits compared to Ugandan indigenous goats. These findings support the conclusion that when goats are subjected to intensive selection, their genetic diversity is reduced while the inbreeding

levels increase, which consequently affects the overall genetic health of the population. The current advancement in genomics has enabled a more precise selection by incorporating genomic diversity measures, which helps in balancing genetic gain with long-term sustainability (PANIGRAHI et al., 2025).

2.7.1.2 Mutation

Mutation occurs typically when the DNA sequence of a gene or chromosome is altered. This alteration later introduces new alleles into an individual that were not present in their parental lineage, such small changes, like a single base pair mutation, or more significant chromosomal changes involving multiple base pairs. The introduced new variants into the populations are ones that cause genetic diversity as they are produced by mutations (DURLAND and AHMADIAN-MOGHADAM, 2022). For instance, CHEN et al. (2024) utilized whole-genome sequencing of the human genome and determined that the average mutation rate was 2.1×10^{-8} per nucleotide per generation. Although most mutations are thought to be neutral, some beneficial changes have also been reported. For instance, the presence of the *MUC6* gene through EDNRB mutations has been reported to play an important role in adaptations and resistance, including high-altitude tolerance and disease resistance (NELSON et al., 2020).

Some studies suggest that native livestock breeds may carry a higher load of deleterious mutations of approximately 1.3 – 1.8 times that observed in commercial breeds, likely due to historical bottlenecks and reduced effective population size. Nevertheless, artificial selection has limited efficacy in purging mildly deleterious alleles, especially those linked to health, growth, and reproductive performance (BOSSE et al., 2018). Considering that mutation is a fundamental source of unique genetic variability that supports adaptation, this scenario underscores the necessity for balanced conservation measures that would manage genetic diversity while safeguarding mutation-derived diversity.

2.7.1.3 Genetic drift and bottleneck events

Genetic drift is a change in evolutionary mechanism that arises due to natural selection. This natural selection can lead to random change or modification in allele frequencies within a given population (LYNCH et al., 2016). This process dominates in those breeds with small population size and isolated populations. In this scenario, some

events may lead to loss or fixation of alleles, thus causing a reduction in genetic diversity. For example, a report by FAO (2023b) shows that approximately 27 % of all characterized livestock species are classified as being at risk of extinction or already extinct. In addition, several studies on indigenous goat populations have reported a low N_e (< 50) (BERG et al., 2020; LIU et al., 2025; KICHAMU et al., 2024b), suggesting a risk of genetic erosion in these populations.

The bottleneck event is where there is a reduction in N_e for at least one generation due to natural events like outbreaks of particular diseases, severe climatic events (droughts or floods), and human-induced activities (bush clearing for crop production) (LUCENA-PEREZ et al., 2021). Then, if this outbreak occurs, those populations that survive may not represent the genetic diversity of the original population. Studies on the genetic diversity of native goats have reported that reductions in population size over generations increase genetic drift and linkage disequilibrium, thus decreasing genetic diversity (WHANNOU et al., 2023; MANUNZA et al., 2023; GEBRESELEASH et al., 2024; LE et al., 2024). Looking at these findings, some strategies need to be put in place to aid in the conservation of these study goat populations to ensure their sustainability. Therefore, understanding and avoiding the impacts of genetic drift and bottleneck events in goat populations is vital for conserving their diversity and adaptive potential.

2.7.1.4 Migration and admixture

Migration and admixture are important processes in genetics and evolutionary biology. These factors play a role in shaping the genetic composition of populations. Migration is simply the movement of individuals within and out of a given population (COLLI et al., 2018), these movements may introduce new alleles leading to admixed populations. For instance, PENG et al. (2022), on their study discovered that trade and migration route in Southwest China contributed to gene flow across Asian goat populations, additionally, studies on the genetic landscape of populations along the Silk Road have shown that the ancient migration routes facilitated gene flow and admixture events thus shaping the adaptive mechanisms that are seen in the modern goat populations (MEZZAVILLA et al., 2014). Therefore, to manage the level of gene flow in the population, there is a need to include genetic markers in conservation programs.

2.7.2 Demographic factors

Demographic factors, including age, sex ratio, reproduction rate, generation interval, and population size, determine the changes in goat populations over time. They influence their genetic diversity, population structure, N_e , genetic drift, and inbreeding levels, thereby determining how well a population can survive and adapt to changing environments (MANUNZA et al., 2023). Population size, particularly N_e , has a substantial impact on the rate of genetic drift and inbreeding. For instance, NANTONGO et al. (2024) observed three distinct groups in Uganda's indigenous goats, which corresponded to different agro-ecological zones, each of these populations also showed demographic features shaped by both the surrounding environment and management practices applied by farmers. For example, Mubende goat breeds raised in warm and humid central and southwestern regions of Uganda had larger body sizes compared to other populations. The large body size signifies their adaptive mechanism to the local environments.

Further, studies on genetic variability of Kenyan indigenous goats (Galla and Small East African (SEA)) using pedigree data reported an average generation intervals of 3.8 and 4.4 years for Galla and SEA goats, respectively, along with increasing inbreeding rate of approximately 0.04 and 0.05 per generation, coupled with small effective population sizes suggest the influence of demographic factors on genetic diversity in a given population (KICHAMU et al., 2024b).

Sex ratio and breeding structure also play a bigger role in shaping the genetic makeup of a population. For instance, the use of considerably fewer bucks rather than does can lead to a decline in N_e and increases relatedness within the flock, which eventually results in loss of genetic diversity (QUAN et al., 2025). Some management practices, including culling and replacement, further shape the demographic patterns of a population by determining how often new animals and new genes are introduced into a population. Therefore, understanding these demographic factors alongside genetic information is essential for developing sustainable breeding and conservation programs that protect the genetic diversity and strengthen adaptability in goat populations.

2.7.3 Environmental factors

Climate change is currently a global problem affecting the entire agricultural sector. These changes come along with adverse effects, including heat waves, droughts,

and heavy rainfalls, which directly influence the physiology, behavior, and genetic makeup of livestock populations (WANJALA et al., 2023). Climate change can shape the physical habitat for living things. For instance, heavy rains with flooding can disrupt traditional migration routes and destroy habitats, which later affects gene flow into or between populations. This decrease in gene flow later influences the genetic diversity, thus lowering the adaptive potential within the populations (CORTELLARI et al., 2021). Besides, harsh environmental conditions like extreme drought affect the quality and quantity of livestock feeds and introduce new diseases into the region, which directly affect the survival and reproductive potential of livestock. For instance, LIU et al. (2025) reports on the effect of drought on livestock pasture, which has changed the population structure due to inadequate feed. These studies conclude that environmental factors influence the genetic diversity and population structure of goats through modification of their adaptability, productivity, and survival mechanisms in varied agro-ecological zones.

To address this, it is recommended to design a breeding and conservation program tailored towards maximizing productivity while maintaining adaptive genetic diversity. This enhances the genetic diversity; one needs to understand the population structure.

2.7.4 Geographical factors

Geographic isolation is essential for the genetic diversity of livestock. When species are isolated, gene flow between and among populations is limited. This isolation is brought about by natural barriers like mountains and rivers, or human-imposed activities like farming practices and habitat fragmentation. These activities create obstacles that restrict the movement of animals from one area to another (DAR and RAHMAN, 2024).

Isolated populations evolve independently from each other, resulting in the development of unique genetic traits tailored to their specific environments, ultimately enhancing their adaptive capabilities. For instance, CARDOSO et al. (2018) observed that insular goats from Iceland and Madagascar exhibited a higher degree of homozygosity due to geographic isolation from their continental counterparts. Additionally, COLLI et al. (2018) on genome-wide SNP profiling of worldwide goat

populations, reported on how geographical isolation affected the genetic makeup of global goat populations due to distinct gene pools across different continents.

These barriers allow for the development of independent traits that are useful in local environment adaptation. Over time, these adaptive features become more pronounced, resulting in the emergence of distinct breeds with different morphological features, such as body size (short or tall), coat color, skin color, and resistance to local diseases, and other traits that enhance their survival and productivity in specific climates or terrains (BERTOLINI et al., 2018; SERRANITO et al., 2021). Therefore, understanding these factors by combining both genomic and ecological data can aid in designing practical breeding, conservation, and sustainable utilization programs that maintain genetic diversity, foster adaptability, and enhance production in diverse agro ecosystems for the indigenous goat breeds.

2.7.5 Estimation of genetic diversity and population structure of goats

Molecular markers and pedigree data are the major information or tools used to assess the genetic variation and structure in animal populations (TORO et al., 2009; KOPPS et al., 2015). Due to inaccuracies in pedigree recording, the development of various molecular tools has eased ways to assess population structure and genetic diversity while addressing pedigree inaccuracies, despite being cost-effective for smallholder farmers (TOSSER-KLOPP et al., 2014). In molecular markers, the following parameters are used to evaluate the genetic diversity in a population. These parameters include the observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficients (F_{IS}), and allelic distribution (SARAVANAN et al., 2021).

H_E is expected based on actual frequency and Hardy-Weinberg Equilibrium (HWE)-calculated genotype frequency. H_O is usually expressed as a ratio (PUNURU et al., 2025). Heterozygosity is a crucial way to measure genetic diversity as it shows the average frequency across all loci while minimizing the effect of rare alleles in the population (PUNURU et al., 2025). Therefore, comparing H_E and H_O helps to identify significant changes in populations. When H_O values are less than H_E , it means the presence of recent population bottlenecks or intensive selection pressure within the population (SARAVANAN et al., 2021; KARDOS, 2023). Various studies have reported variation in genetic diversity and inbreeding coefficient across goat populations (Table 1). Results from SNP data showed low heterozygosity values (0.32 - 0.43) as compared

to microsatellite studies (0.45 - 0.68). The African goat populations (Tanzania, Uganda, and Kenya) record high diversity ($H_O > 0.45$), as compared to international breeds.

F_{IS} values are generally positive, indicating some levels of inbreeding, except in highly outbred populations. The high levels of within-population genetic diversity are likely due to low selection pressure, large population size, and introduction of new alleles into the population. In contrast, others reported low levels of genetic diversity, likely due to intensive selection, geographical isolation, or the management system.

Table 1. Genetic diversity of various goat breeds in different countries

Country	Studied breeds	Molecular markers	H_O	H_E	F_{IS}	Reference
Algeria	Arabia, M'Zabite	18 microsatellites	0,47	0,5	0,06	GAOUAR et al. (2021)
China	Various indigenous	CaprineSNP50 Beadchip	0,355	0,351	-	ZHONG et al. (2023)
Ethiopia	Arsi-Bale, Woyto-Guji	Goat SNP50K	0,38	0,39	0,03	TAREKEGN et al. (2023)
Greece	Skopelos, Eghori	Goat SNP50K	0,4	0,41	0,024	FARMAKI et al. (2019)
Iran	Markhoz, Raeini	30 microsatellites	0,55	0,58	0,052	ASROUSH et al. (2018)
Laos	Indigenous	30 microsatellites	0,3	0,34	0,11	LE et al. (2024)
Nepal	Khari, Terai	15 microsatellites	0,48	0,51	0,059	GORKHALI et al. (2021)
Nigeria	West African Dwarf	20 microsatellites	0,53	0,57	0,07	ADEBAMBO et al. (2020)
Northern Peru	Creole	GGPGoat70k	0,41	0,41	0,01	CORREDOR et al. (2024)
Pakistan	Beetal, Teddy	SNP50K array	0,37	0,38	0,026	KUMAR et al. (2018)
South Africa	Indigenous Veld goats	CaprineSNP50 Beadchip	0,32	0,33	0,22	MDLADLA et al. (2018)
Tanzania	Small East	8	0,66	0,68	-	NGULUMA et

Country	Studied breeds	Molecular markers	H_O	H_E	F_{IS}	Reference
	African	microsatellites				al. (2018)
Uganda	Mubende,	15	0,46	0,51	-	NANTONGO et
	Kigezi	microsatellites				al. (2024)

Besides, pedigree analysis remains valuable in estimating the generation interval and identifying influential ancestors if the records are complete and accurate (OLIVEIRA et al., 2016; GIPSON, 2019). N_e is defined as the number of an idealized population expected to produce the exact value of a given genetic makeup as that in the population under study (FEDORCA et al., 2024). It is an important concept used to understand evolutionary and conservation biology and livestock breeding programs (WAPLE, 2025). N_e measures and monitors the extent of within-population genetic diversity, including inbreeding and genetic drift (WRIGHT, 1931).

To assess the N_e demographic, pedigree, and genomic data can be used (WANG et al., 2025). For demographic information, calculation of N_e is done based on the expected change in inbreeding coefficient per generation (ΔF), while considering the number of breeding bucks and does, as well as the variance in family size. When using the pedigree data, N_e is calculated from the inbreeding coefficients over generations using ΔF as the basis (MANUNZA et al., 2025). Traditionally, pedigree has been considered effective in estimating N_e in livestock. However, reliable estimates of N_e depend on the completeness of the pedigree (WANG et al., 2021). Current FAO guidelines recommend maintaining $N_e \geq 50 - 100$ for short-term sustainability ($\Delta F < 1\%$ per generation) and $N_e \geq 100 - 500$ animals for long-term genetic conservation (FAO, 1998).

For genomic data, three primary methods are employed to estimate N_e including: (i) method that considers change in ΔF reflecting the rate of genetic drift, (ii) coancestry rate measuring the increase in genetic relatedness among individuals over time and (iii) degree of linkage disequilibrium (LD) between neutral loci providing the insights into historical and contemporary structure and population size (MANUNZA et al., 2025). NADACHOWSKA-BRZYSKA et al. (2022) present various statistical methods used in assessing recent and historical N_e from genomic data.

Assessment of inbreeding has evolved significantly with the advent of genomic tools. While pedigree-based inbreeding coefficients (FPED) remain helpful for many,

genomic measures such as runs of homozygosity (ROH) and Wright's F -statistics provide an accurate assessment (PERIPOLLI et al., 2017). The use of F -statistics, including the individual inbreeding relative to the subpopulation (F_{IS}) the variation within the subpopulation (F_{ST}), and the individual inbreeding relative to the total population (F_{IT}) (WEIR and GOUDET, 2017), offers a broader understanding of population structure.

The use of Bayesian clustering, particularly the STRUCTURE (PORRAS-HURTADO et al., 2013) and ADMIXTURE (ALEXANDER et al., 2009), are essential tools in visualizing population structure. These methods assign individuals to their respective genetic clusters without prior population information and enable the detection of admixture and gene flow within populations.

ROH methods are commonly used to assess both recent and historical inbreeding based on the stretch length. The length and distribution of ROH segments provide essential information; for instance, a long ROH indicates recent inbreeding of within five generations or less, while a short ROH suggests the ancient inbreeding, probably sharing a common ancestry (BÉRÉNOS and HOFFMAN, 2025). Studies on goat breeds using high-density SNP arrays have reported that goats that have undergone intensive selection often exhibit higher ROH-based inbreeding coefficients ($F_{ROH} = 0.08 - 0.15$) as compared to indigenous populations ($F_{ROH} 0.03 - 0.08$) (ZHAN et al., 2025; KICHAMU et al., 2025).

2.8 Signature selection in goats

The identification of regions under selection is a key principle in theoretical and applied evolutionary genetics. Signature selection provides information on evolutionary processes that are involved in shaping the genomes, as well as physical and functional information about genes (RODRIGUES et al., 2025). The process of domestication, followed by breed formation and selection for traits of economic importance, led to development of various goat breeds adapted to a range of environments with unique genetic and phenotypic features. Besides, the varied geographic landscapes, such as rocky, mountainous, and valley, coupled with selection processes, both natural and human-induced, have contributed to specific changes in genomic regions that control particular traits, including body conformation, productivity, and disease resistance (SARAVANAN et al., 2021; AKHATAYEVA et al., 2025).

These selections can be positive, negative, or a balanced selection. Positive selection occurs when a particular mutation leads to a trait of benefit, such as adaptability or survival (SARAVANAN et al., 2021; TIAN et al., 2025). The region where mutations occur later forms a haplotype block due to changes in allele frequencies of genetic variants (ÁLVAREZ-ANTONIO et al., 2021). These changes in allele frequency from positive selection create footprints on the genome called selection signatures. When significant variants are removed from the population, along with neutral variations linked to them, it is then referred to as negative selection (RAPAPORT et al., 2021).

The current ongoing climate change poses a significant threat to global agricultural production. It is projected that by 2050, global temperatures will rise by 1.5 to 2°C (KLIMENKO et al., 2025). These changes will affect productivity and survival rates of various livestock species due to heat stress and the spread of different diseases (WANJALA et al., 2023). Indigenous goats, which have evolved through natural selection, have developed adaptive mechanisms to withstand these extreme environmental conditions, thus making them a crucial climate-resilient breed (UTAAKER et al., 2021; PARSAD et al., 2025). The advances in genomics have revealed signature selection on various genes linked to thermo tolerance, immune response, metabolic adaptation, and coat color modulation (Table 2).

These genes represent a signature by which indigenous goats adapt to their environments while adjusting their physiological and biological functions to deal with challenging conditions. For instance, genes that are associated with thermotolerance assist in the efficient management of thermoregulation and heat stress resistance, while those related to immunity can enhance goats' resistance towards pathogens and parasites common in harsh environments. Similarly, those genes responsible for metabolic adaptation help in supporting efficient utilization of energy, especially under feed scarcity, while the coat colour genes may influence solar radiation absorption and protection. Therefore, understanding the genetic background not only sheds light on evolutionary history but also provides significant markers for selective breeding programs that are targeted at enhancing the resilience and productivity of the goat population.

Table 2. Candidate genes for adaptation and immune response in some indigenous goats

Breed	Country	Method	Candidate gene	Function	References
Aberegalle	Ethiopia	Whole-Genome Sequencing	<i>PPP4R3B</i> , <i>UGT2A2</i>	Regulate lipid metabolism and energy homeostasis	BERIHULAY et al. (2019)
Barki	Egypt	Caprine and ovine 50K SNP Beadchip	Multiple genes (<i>FGF2</i> , <i>GNAI3</i> , <i>PLCB1</i>)	Thermotolerance, energy and digestive metabolism, nervous and autoimmune response	ABOUL-NAGA et al. (2025)
Begiat	Ethiopia	Whole-Genome Sequencing	Multiple genes (<i>SLC6A2</i> , <i>SLC7A11</i>)	Immune response and adaptation	GEBRESELEAS E et al. (2024)
Galla	Kenya	Illumina GoatSNP50 Bead Chip	<i>HYAL1</i> , <i>HYAL3</i> , <i>MST1</i> , <i>PCK</i>	Immunity regulation, adaptation	WAINEINA et al. (2022); KAMIDI et al. (2023)
Galla	Kenya	mtDNA D-loop and HSP70 gene	<i>HSP70</i>	Thermoregulatory role in testes (spermatogenesis)	MASILA et al. (2024)
Indigenous breeds	Various climatic regions	Whole-Genome Sequencing	Various genes (<i>ASIP</i> , <i>DENND1A</i> , <i>DLG1</i>)	Coat color, feed intake, immune response, heat tolerance	PENG et al. (2024)
Karamoja	Uganda	Illumina GoatSNP50 Bead Chip	<i>KPNA4</i> (<i>CHI1</i>), <i>MTOR</i>	Heat shock	ONZIMA et al. (2018)
Kigezi	Uganda	Illumina GoatSNP50 Bead Chip	<i>IL10RB</i> , <i>IFNLR1</i>	Immunity regulation	ONZIMA et al. (2018)
Mubende	Uganda	Illumina GoatSNP50 Bead Chip	<i>PPP1R36</i> , <i>A2(HSPA2)</i>	Heat shock protein, heat stress	ONZIMA et al. (2018)

Breed	Country	Method	Candidate gene	Function	References
SEA	Uganda	Illumina GoatSNP50 Bead Chip	<i>ERBB2</i> & <i>ENO1</i>	Immunity regulation	ONZIMA et al. (2018)

2.9 Different indigenous goat breeds used in the present dissertation

This doctoral research used indigenous goat breeds from Europe, Asia, and Africa. These goats were defined as ecotypes or populations originating from and adapted to the agro-ecological conditions of their respective countries, with unique morphological, productive, and genetic traits developed through generations of low-input smallholder systems, without a specific population census. The study acknowledges their essential contribution to rural livelihoods and agricultural systems. These populations present distinct adaptation mechanisms to various environmental conditions, making them significant genetic resources for sustainable livestock production and enhancing resilience to climatic changes. In this section, we describe these study populations individually.

2.9.1 Breeds from Africa

Galla. The Galla goat (Figure 4A), also known as the large-white Somali, Digodi, Marebo, Borana, Benadir, and Gigwain, depending on the region or tribe it is raised in. There are two types of Galla goats: those that are raised for meat production, called the Degyir, and those that are raised for milk, the Degeun. The breed originated from the Arabian Peninsula but is currently distributed in most of the arid and semi-arid regions of Kenya, Ethiopia, Djibouti, Eritrea, and Somalia (MUTINDI et al., 2022). Galla goats are highly adaptable to harsh environmental conditions. This adaptation is made possible by their long, strong legs and tall body structure, strong jaw and teeth, and white coat color with black skin (SILA et al., 2021).

Small East African (SEA). The SEA (Figure 4B) is a diverse group of goats that are characterized by variable types, conformations, and body sizes. According to DAGRIS (2018), the breed is known by different local names depending on the community producing them. These goats belong to the short-eared and small-horned breed group. They present themselves in various coat colors and patterns with fine coat

hair, short, and the skin color is black, with a height between 60-65 cm at the withers. They are distributed widely across various environments in Kenya, Tanzania, Uganda, and extending southward through central Africa to Zaire, Angola, and Northern Namibia. The SEA breed is primarily raised under extensive production systems, is hardy, and is mainly raised for meat rather than milk. Although highly prolific, hardy, and adaptable to the local environment, they are considered to be less profitable by breeders, as they typically reach a market weight of only 20 kg at the age of two years, with a three-month weaning weight at 8-10 kg and age at first kidding between 14-17 months (SAFARI et al., 2011). This delay is caused by the production system and management they are exposed to, which are constrained by feed scarcity, with mild breeding seasonality aligned to rainy periods.

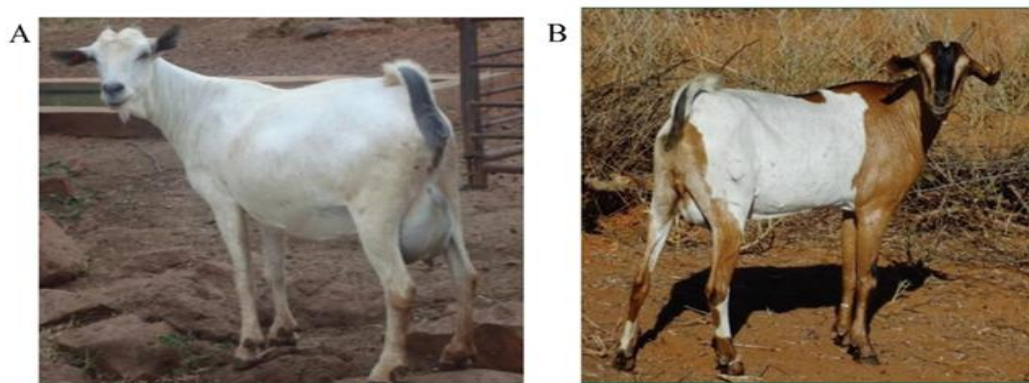


Figure 4. Kenyan native goats; (A) Galla and (B) Small East African (KICHAMU et al., 2024b)

Pare White. The Pare White goats (PWT) are among the goat populations grouped in the SEA strains. The breed is mainly found in the pastoral and agro pastoral communities of Kilimanjaro, Arusha, and Manyara districts located in the Northern part of Tanzania. PWT are predominantly white in color, with long legs (Figure 5A). The breed is said to be having the most significant body weight (29.8 ± 0.50 kg), heart girth (72.3 ± 0.51 cm), height at wither (61.4 ± 0.43 cm), body length (53.9 ± 0.51) and rump height (63.4 ± 0.60 cm) as compared to other native breed in the country (MSEMWA and MBAGA, 2018). They are mainly kept for meat, but some get milk for home consumption.

Maasai East African goat. The Maasai East Africa (Maasai AE) breeds are primarily raised in the Maasai steppe region of Northern Tanzania. They also belong to

the SEA group. They present themselves in various colors, including black, grey, multicolored, white, and reddish-brown. They are small in size, as mature ones weigh between 25.83 and 30.34 kg (Figure 5B) (HYERA et al., 2018).

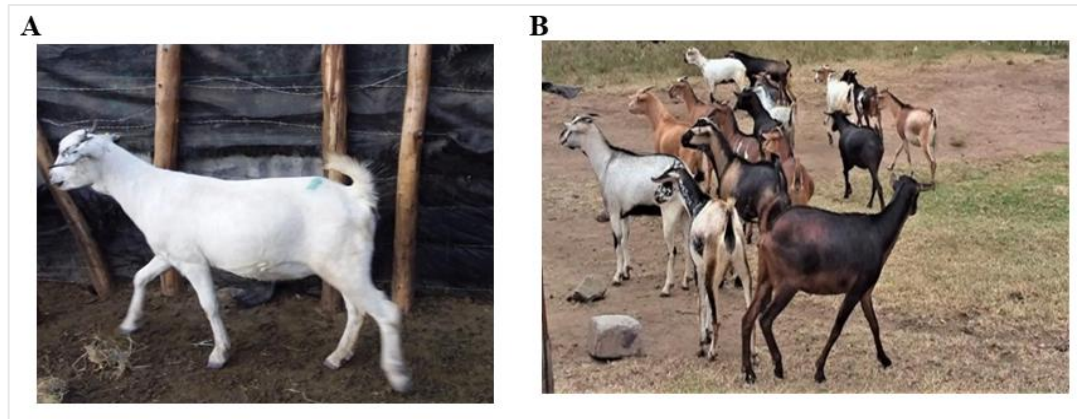


Figure 5. Tanzanian native goats; (A) Pare White goat and (B) Maasai EA. Photo taken by Nelly Kichamu

Keffa goat. Keffa goats (Figure 6A) are found in the Keffa zone of Ethiopia and belong to a small East African family with no exact data on population size. They are relatively smaller in size, as they weigh approximately 2.78 kg at birth and an average of 9 kg at the weaning stage in between 90-120 days. They are hardy and resistant to harsh conditions and some diseases (TEREFE et al., 2022). The breed presents itself in a range of colors, including white, brown, and mixed. They are mainly kept for meat.

Woyto-Guji goat. Woyto-Guji goats (Figure 6B) are found in the Northern and Southern regions of Ethiopia, with no available data for population size. They are brown, black, multi, or red in color with a shiny, smooth coat and a small head with a straight or concave facial profile, the coat color is often marked with a black or brown stripe along the back, on the underside, or on the front of the legs, and is mainly kept for meat production (MULUNEH and TADESSE, 2022; FEREJA, 2016).

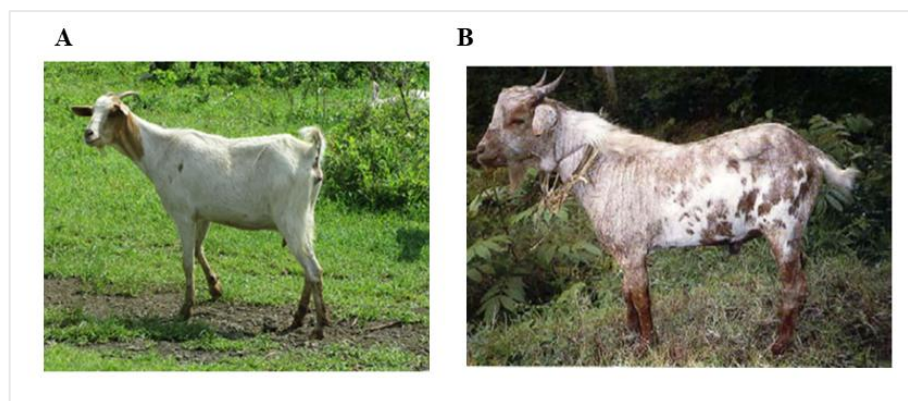


Figure 6. Ethiopian native goats; (A) Mature Keffa doe and (B) Woyto-Guji buck (FEREJA, 2016)

2.9.2 Breeds from Asia

Philippine Native Antipas Cotabato group. Philippine Native Antipas Cotabato group (PHIN) (Figure 7) traces its origins to the Indo-Malay Katjang breed, and is known for its well-built, small body size, and is predominantly raised in smallholder settings for meat (PHILIPPINE STATISTICS AUTHORITY, 2024). The breeds are known locally as Kambing (*Filipino* and *Tagalog*), Kanding (*Binisaya* and *Hiligaynon*), and Kalding (*Ilocano*). Adults weigh around 20 kg, with an average carcass weight of 8 kg. These goats reach puberty as early as five months (DEPARTMENT OF AGRICULTURE – BUREAU OF AGRICULTURAL STATISTICS, 2018). However, they produce a low milk volume, averaging 0.3 kg per day, and have a short lactation period of 187 days. The kidding rate is about 81%. The Philippine Native goats are presented as uncharacterized ecotypes with no exact breed population numbers. They exist in a variety of colors, and the major ones are black-brown, red, and some have mixed colors of brown, black, reddish brown, and have a solid color of white (BONDOC et al., 2002).



Figure 7. Philippine Native Antipas Cotabato group. Photo taken by Roland Fajardo

Native goats from Kazakhstan. The local goat populations in Kazakhstan have not been characterized, as they are named after the location or community from which they originate, rather than having a specific breed name (Prof Bakhytzhan Bekmanov, personal communication). For instance, Kundyzydy, Darbaza, Shokpar, Ushterek, Kenes, and Kosseit represent villages (Figure 8). They are named based on their breeding regions and are referred to as ecotypes.

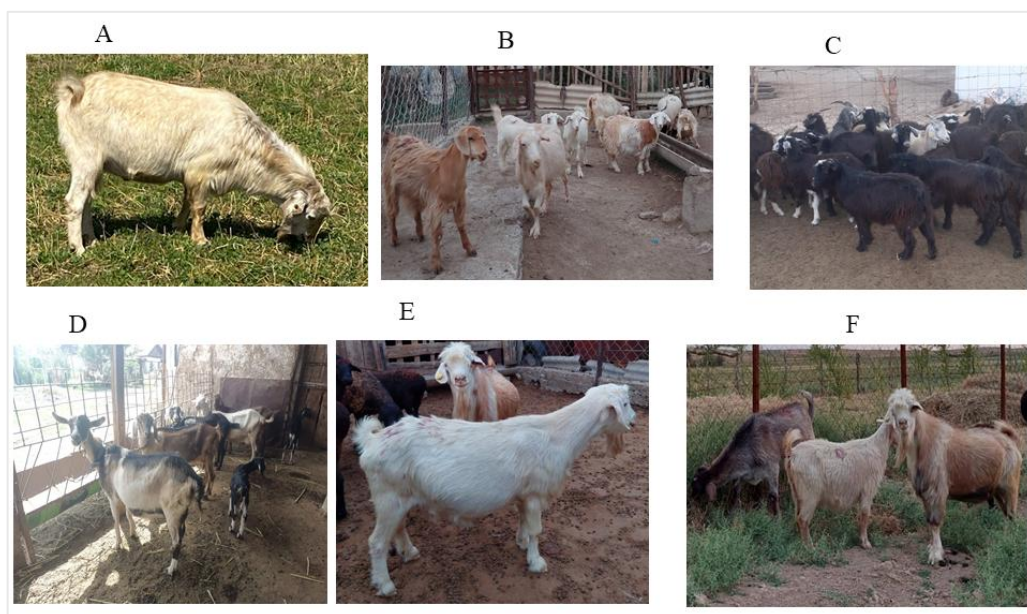


Figure 8. Kazakh native goat populations; (A) Darbaza, (B) Kenes, (C) Kosseit, (D) Shokpar, (E) Ushterek, and (F) Kundyzydy. Photo taken by Dr. Kairat Dossybayev

2.9.3 Breeds from Europe

Banat White. Banat White (BWT) is an indigenous goat breed in Romania. The breed performs much better, but it is among those breeds listed as an endangered species in the genetic conservation program. The population is very small, with a census of less than 1000 purebred does, reared in 5 farms. The BWT are generally white in color (Figure 9), produce 370-400 kg of milk per lactation period, and are highly prolific, with an average reproduction rate of 200–225% (VOIA et al., 2010).



Figure 9. Romanian native goats, Banat White breed. Photo taken by Dr. Dinu Gavojdian

Domaća Balkanska Šarena Koza. Domaća Balkanska Šarena Koza (DBSK) is an indigenous breed in Bosnia and Herzegovina (Figure 10). It was developed under poor breeding conditions on barren, rocky, and inaccessible terrains, which have agile, easy mobility, modesty, and resilience with no exact breed population. The breed has long, dense, coarse, and shiny hair, which is most often multicolored. However, it can occasionally be in solid-colored (brown, black, or gray) (FEDERAL MINISTRY OF AGRICULTURE, WATER MANAGEMENT AND FORESTRY, 2018). The breed has a small head with horns, mature females weigh up to 40 kg, while bucks weigh between 40 and 60 kg, but under good management, they can reach 70 kg. The breed is kept for milk production with a lactation period lasting between 150 and 250 days, while producing approximately 100 to 250 liters of milk per lactation, and is hardy (ŠAKIĆ et al., 2011).



Figure 10. Bosnia and Herzegovina native goats, Domaća Balkanska Šarena Koza breed. Photo taken by Dr. Husein Ohran

Old Hungarian Native (Magyar parlagi kecske). The Old Hungarian Native (HUN) is a Hungarian breed that was developed in the Carpathian basin, partly bearing the outward stamps of goats that came to Hungary during the period of the great migrations. The phenotypic characterization of the breed is still underway. The dominant feature is that the hair length of the adult animals is at least 10 cm, which covers the entire body (with curly locks) and the body part behind the arch of the ribs (rough-legged) (Figure 11). These features are inherited from their ancestors. Except for

the brown body with dark back strap, they present themselves in various colors. They were either horned or polled. The horned males have outward-curved horns. Their age at first mating ranges from 7 to 12 months, and they can produce milk. However, the primary goal is not high milk yield production but to conserve their adaptive genes; there is no large-scale production of this breed in the country, and no comprehensive public list of current population and breeding sites exists due to their small-scale and decentralized nature in production (Hungarian Sheep and Goat Breeders Association, 2025).



Figure 11. Hungarian native goats, Old Hungarian Native breed. Photo from the Hungarian sheep and goat breeders association (MJKSZ, <https://mjksz.com/tenyesztes/fajtak/magyar-parlagi-kecske-old-hungarian-goat-hungarian-plain-goat>)

3. MATERIALS AND METHODS

3.1 Ethics statement

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

3.2 Genetic characterization of Kenyan native goat breeds using pedigree

3.2.1 Animal populations and data for pedigree analysis

Pedigree information on Galla and SEA (Figure 3A and B) was obtained from the national livestock registry maintained by the Kenya Stud Book (KSB), which involved 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. The following information were used, individual animal identification number (Animal_ID), doe number (Mother_ID), buck number (Father_ID), date of birth, and animal sex. Animals were raised under an extensive management system and selection of the breeding flock was based on physical observations, specifically body size and growth rate.

3.3 Genetic characterization of European, Asian, and African goats using molecular data

3.3.1 Breed/populations and sample collection regions

For this doctoral research, 372 samples were obtained from 16 different indigenous goat populations or breeds (Table 3), collected in three continents, including Africa, Asia, and Europe (Figure 12). Majority of the study populations were ecotypes without pedigree information and lacked proper characterization. To minimize the kinship bias, unrelated goats were selected from distinct populations, based on farmer reports confirming no shared parents.

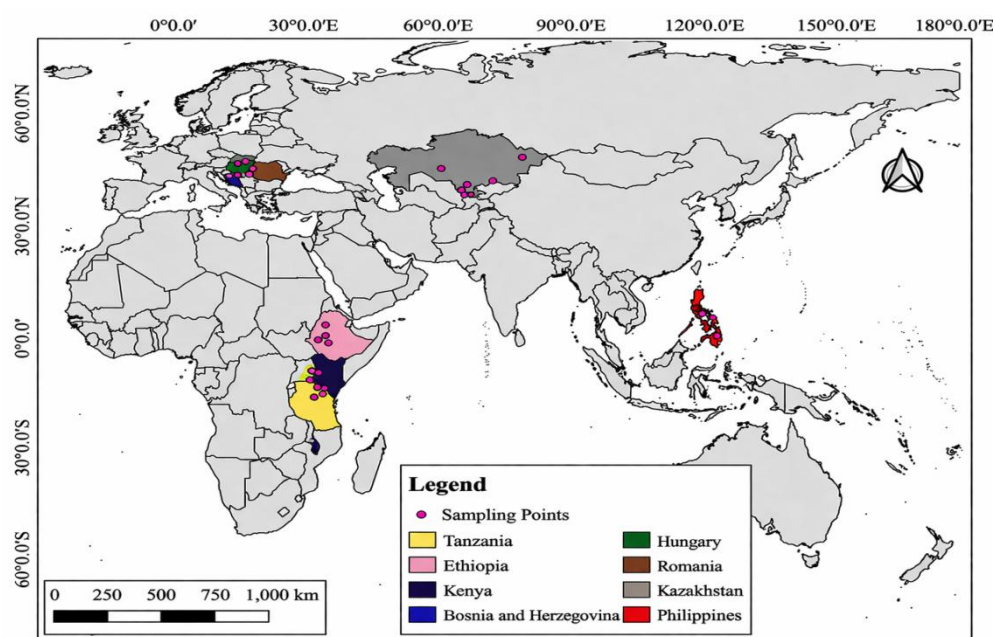


Figure 12. Map of blood collection points for the local study goat population mapped with QGIS (QUANTUM GIS DEVELOPMENT TEAM, 2015)

Table 3. Breed name or village, 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 EA	MEA	25
Hungary	Europe	Old Hungarian Native	HUN	40
Romania		Banat White	BAW	12
Bosnia-Herzegovina		Domaća Balkanska Šarena Koza	DBSK	20
Philippines	Asia	Philippine Native Antipas Cotabato group	PHIN	25
Kazakhstan		Local goat population from Darbaza village	DAB	20
		Local goat population from Kenes village	KENS	20
		Local goat population	KOSS	20

Country	Continent	Breed name	Breed code	Numbers
		from Kosseit village		
		Local goat population from Shokpar village	SHOK	20
		Local goat population from Ushterek village	USH	20
		Local goat population from Kundyzdy village	KUN	20
Total				372

3.3.2 Sample collection and genotyping

Blood samples were collected from the jugular vein of the goats using Vacutainer tubes 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, then sent to the NEOGEN Company in Scotland for genotyping using the CaprineSNP70K Bead Chip array (Illumina, USA). The 70K bead chip contains more than 70,000 evenly distributed SNP-targeting probes, which allows adequate SNP density for assessment of genetic diversity, population structure, and signatures of selection (INTERNATIONAL GOAT GENOME CONSORTIUM, 2018). The whole process from DNA isolation to variant call was performed by the genotyping company.

3.3.3 Quality control

The genotyped data were then subjected to quality control (QC) using the PLINK version 1.9 (PURCELL et al., 2007). This was done to ensure high-quality data and reliability of the analyses. Standard QC procedures were applied to both the individual and SNP levels. Before QC, the study had a total of 372 goat samples, each with 64,264 autosomal SNPs after removing the sex chromosomes. The sex chromosome SNPs were removed to avoid biases from their different inheritance patterns in males and females. First, the raw genotypes were converted to the binary PLINK format (.bed, .bim, .fam) after this the following threshold was applied for QC, all individuals with more than 10% missing genotypes were excluded using the --mind 0.1 command, SNPs with a call rate of below 95% were removed using the --geno 0.05 filters, this ensured that only individuals with high-quality genotypes were retained.

Then the SNPs with minor allele frequency (MAF) < 0.01 were excluded using --maf 0.01, which allowed for the elimination of rare variants that might have limited statistical power.

In order to detect potential genotyping errors in the data, the HWE test was performed on control samples. From this, all the variants with significant deviations from HWE ($p < 1 \times 10^{-6}$) were removed using the --hwe 1e-6 flag, all animals with first-line relations (parent-offspring and sibling-sibling) using --king-cutoff 0.177 were also excluded. Besides this, all the SNPs at linkage disequilibrium (LD) were pruned using the --indep-pairwise 50 5 0.2 flag and options.

During the quality control process, the following exclusions were made: 2,000 variants were removed due to missing genotype data (--geno), one individual was removed due to high number of missing genotypes rate exceeding the QC threshold (--mind 0.1), 3,575 variants were removed due to MAF (MAF < 0.01) --hwe: 2,086 variants removed due to the HWE test, 5,484 variants were identified and excluded during LD pruning using --indep-pairwise 50 5 0.2. The remaining SNPs for analysis of genetic diversity and population structure were 51,119 and 371 samples with an average call rate of 0.97.

3.4 Statistical analysis

3.4.1 Genetic characterization of Kenyan native goat breeds using pedigree

ENDOG software version 4.8 (GUTIERREZ and GOYACHE, 2005) was used to assess various parameters in the studied goat population. The software allows for the assessment of genetic variability and changes in the population. In this study, the following parameters were assessed: pedigree completeness, generation interval (GI), inbreeding coefficient (F), average relatedness (AR), effective population size (N_e), and effective number of founders (f_e) and effective number of ancestors (f_a).

3.4.1.1 Estimating pedigree completeness

The pedigree completeness is the number of complete generations known (GOYACHE et al., 2003). This was done to determine the accuracy of pedigree information for each individual using the following parameters: (a) Number of maximum traced generations (MG), which is the number of generations separating the progeny from its most distant known ancestor along each path, (b) Complete generation

equivalent (EqG) calculated as the most distant generation for which all ancestors could be determined, (c) Number of complete generations (CG) which is the number of generations n , between the individual and the furthest generation when both generation ancestors are known (GOYACHE et al., 2003). Pedigree completeness was then calculated as follows:

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

Where n is the number of generations separating the individual from each known ancestor (GINJA et al., 2017).

3.4.1.2 Estimation of generation interval (GI)

GI is the average age of parents at the birth of offspring that are subsequently used for breeding (CASTRO-VÁSQUEZ et al., 2023). Understanding of GI of a given breed helps in making selection decision on which animal to use for breeding; primarily, animals with shorter GI are more likely to pass on their important traits to the next generation more rapidly, thereby contributing to quicker genetic improvement (HONG et al., 2024). Therefore, the GI 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:

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

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

F is the level of relationship between two individuals, this was calculated by applying the formula proposed by BIJMA and WOOLLIAMS (2000), where inbreeding rates per year ($\Delta F/y$) and per generation ($\Delta F/g$) were derived by regressing F values on the year of birth or EqG, respectively. The AR refers to the probability that any offspring randomly selected originates from a specific animal in the pedigree data (GUTIÉRREZ and GOYACHE, 2005). AR can be used in place of or in addition to inbreeding to help in predicting the long-term inbreeding in a population. Therefore, AR helps in maintaining genetic variability in a population by mating animals with low AR values (RASHIDI et al., 2015). This coefficient was also computed by adopting the method described by BERNARDES et al. (2016).

3.4.1.4 Estimation of effective population size (N_e)

N_e is the number of individuals in an ideal population that would result in the same rate of genetic diversity as that observed in the actual population being studied; it is inversely proportional to the increasing rate of inbreeding (MANUNZA et al., 2025). N_e was calculated by regressing individual inbreeding on the mean MG, mean CG, and mean EqG. This method was chosen as it is used when there is a likelihood of inadequate pedigree data and was done to approximate the lower, higher, and actual bounds of N_e (BARROS et al., 2011). Besides, the individual change in inbreeding ΔF_i was calculated using the formula defined by GOYACHE et al. (2003).

$$\Delta F_i = 1 - \frac{E_q G_i - 1}{\sqrt{1 - F_i}}$$

Where F_i and $E_q G_i$ are the coefficient of inbreeding and equivalent complete generation for the individual I , respectively. The coefficients of individual increase in inbreeding were averaged, and the realized effective population size was estimated as follows.

$$NeF = 1/2\Delta F$$

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

These parameters were assessed to characterize the genetic variability of the population and to trace gene origin for individuals whose pedigrees include both parents. The f_e is the number of animals that, if mating is done randomly, would produce the same level of genetic variation as that in the study population. This parameter considered those individuals with known parentage. The calculation was performed by summing up the number of progenies of each founder in the population (BERNARDES et al., 2016).

$$f_e = \frac{1}{\sum_{k=1}^f q_k^2}$$

Where f was the number of founders and q_k presented the genetic contribution of the k^{th} founder to the reference population.

The genetic contribution of ancestors (f) to the reference population (whether founders or not), as well as their expected marginal contribution to the gene pool, were assessed by calculating the likelihood that an offspring inherits an allele from a specific ancestor using the formula proposed by BOICHARD et al. (1997). While the f_a defined as the minimum number of ancestors, not necessarily founders, that explains the

complete genetic diversity of the current population. This was computed based on the marginal contribution of each ancestor using the following formula:

$$f_a = \frac{1}{\sum_{j=1}^a q_j^2}$$

Where q_j is the marginal contribution of an ancestor j , i.e., the genetic contribution made by an ancestor that is not explained by other ancestors chosen previously (BOICHARD et al., 1997).

3.4.2 Statistical analysis using molecular data from CaprineSNP70K Bead Chip

3.4.2.1 Analysis of within-population genetic diversity

Observed and expected counts of autosomal homozygous genotypes were computed for each sample to estimate genetic diversity. H_O for each population was calculated from genotype frequencies across populations. Five inbreeding coefficient estimates were derived using PLINK v1.9 (PURCELL et al., 2007). The first, method-of-moments estimator (F_{hom}), quantified deviations from expected homozygosity under the HWE, indicating overall inbreeding levels. Individual genomic inbreeding coefficients based on ROH (F_{ROH}) were then estimated using the detectRUNS package (BISCARINI et al., 2019) in R (R CORE TEAM, 2016). This approach measures the proportion of the genome covered by homozygous segments, thereby capturing both recent and ancient inbreeding events.

Three additional genomic inbreeding measures, including F_{hat1} (the standard relationship variance minus), F_{hat2} (measures the sum of ratios), and F_{hat3} (the correlation between uniting gametes), were computed in PLINK using the --ibc flag, following the framework established in the GCTA software (YANG et al., 2011). F_{hat1} estimates inbreeding based on deviations in genotype variance from expected values, F_{hat2} quantifies the excess of homozygosity, and F_{hat3} represents the correlation between alleles inherited from both parents, consistent with WRIGHT's (1931) concept of inbreeding.

ROH were identified using the consecutive runs method implemented in detectRUNS without LD pruning. 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 F_{ROH} was then summarized both per length category and for each population. The overall mean values were computed by averaging all populations included in the dataset.

The N_e of each population or breed was assessed using two methods, including the historic N_e , which was estimated using the LD-based method in the SNeP software version 1.11 (BARBATO et al., 2020). LD was measured using r^2 , which is the squared correlation coefficient between pairs of SNPs. The rate of decline in N_e was estimated between each pair of consecutive reported generations and for the overall distribution of generations. To compare the current and historic N_e , the GONE software was used while setting default parameters (COOMBS et al., 2012). Results from SNeP and GONE were then visualized in R with ggplot2 (WICKHAM, 2016).

3.4.2.2 Population structure and relationship between the studied goat populations

Genomic relatedness among the study goat populations was assessed using a Neighbor-Net phylogenetic network, constructed from Reynolds' pairwise genetic distances F_{ST} and visualized in SplitsTree v4 (HUSON and BRYANT, 2006). The F_{ST} matrix was calculated using the StAMPP package (PEMBLETON et al., 2013). The StAMPP package allows analysis of biallelic SNP data and estimates population differentiation under the assumption of random mating within populations and determines the level of differentiation between populations.

Population structure was further assessed using Principal Component Analysis (PCA), performed in PLINK v2.0 (CHANG et al., 2015) and visualized using Tidyverse package (Wickham, 2017) implemented in the R package (R CORE TEAM, 2016). PCA was chosen as it is capable of reducing dimensions and visualizing genetic variation, on the assumption of linear independence between components. In addition, proportions of ancestry membership were estimated using ADMIXTURE v1.3 (ALEXANDER et al., 2015) using the LD-pruned dataset. The number of clusters (K) was set from 1 to 20, and the optimal K value was determined based on the lowest cross-validation (CV) error. Admixture bar plots were then visualized using the BITE v2 package (MILANESI et al., 2017) in the R package (R CORE TEAM, 2016).

To further refine the reconstruction of evolutionary history, the gene flow events among populations were assessed using the maximum likelihood approach implemented in TreeMix v1.13 (PICKRELL and PRITCHARD, 2012). Because TreeMix requires

specifying the number of migration edges (m) a priori, we first ran the analysis with $m = 5$ and then incrementally increased m by one in subsequent runs. The final value of m was chosen when the variance explained reached approximately 99.8%, as indicated by PICKRELL and PRITCHARD (2012).

3.4.2.3 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). eROHi refers to those genomic regions with high levels of ROH in a given population, also known as ROH hotspots (CRISCIONE et al., 2025). It is used to identify genomic regions that may have undergone recent positive selection based on the frequency and overlap of ROH across individuals within a population. Those regions with a high amount of individuals shared overlapping ROHs are then considered as ROH islands, which reflects selection that favors a specific allele (ZHAO et al., 2006).

In this study, the eROHi was assessed using the output files generated from ROH above. The genomic regions were then classified as eROHi if they met the following criteria: (i) the SNPs within the region appeared in ROH segments of more than 70% of individuals in the population, and (ii) the region contained at least three SNPs to be considered a reliable selection signal. Additionally, in order to identify the most statistically significant loci in the analysis, the genome-wide threshold was set at the top 1% of log p-values; this ensured that only strong selection signatures were selected, as well as reducing the false positives.

To complement eROHi results, iHS test was done basically to detect the ongoing selection sweeps within the populations. The calculation of iHS then compares the extent of haplotype homozygosity that surrounds the ancestral and derived alleles at each SNP, following the assumption that regions under recent positive selection typically show extended haplotype homozygosity (EHH) around the favored allele. The iHS method was assessed using the Rehh package (GAUTIER and VITALIS, 2012; SZPIECH et al., 2014) implemented in R software. A specific genomic region was considered a potential candidate region if it exceeded the top 0.01% of the F_{ST} values. Genes located within 250 kilobases upstream and downstream of each candidate

selection region were identified and annotated using BioMart (DURINCK et al., 2005) based on the *Capra hircus* reference genome ARS1 from the Ensembl database (HUBBARD et al., 2002). The biological functions of the identified genes were further interpreted using published scientific literature. Since the selection-signature analyses were performed at the genomic-region and candidate-gene levels, rather than as a functional variant-effect analysis of individual SNPs, the SNPs were not classified into intronic, exonic, synonymous, or non-synonymous categories and their relative proportions were not calculated.

4. RESULTS

4.1 Genetic variability of Kenyan native goat breeds using pedigree records

4.1.1 The quality of pedigree information

The quality of pedigree information is important in achieving accurate results, especially when assessing the F in a given population. For this study, 7,384 indigenous goats from Kenya were analyzed, including 5,222 Galla and 2,162 SEA breeds, respectively. From the results, the maximum generation for the Galla and SEA breeds in terms of completeness was 14.6 and 14.5, respectively. With the following percentages of pedigree completeness in first, second, third, and fourth generations for the studied goat breeds being 98.09%, 85.44%, 69.00%, 47.34%, and 96.99%, 84.86%, 62.9%, 44.3%, respectively. As the generation increased to the current one, the pedigree information increased, as shown in Figure 13A and B, similar pattern was reported by RASHID et al. (2015) in Markhoz goats. This trend may arise possible due to lack of parental information in the earlier generations.

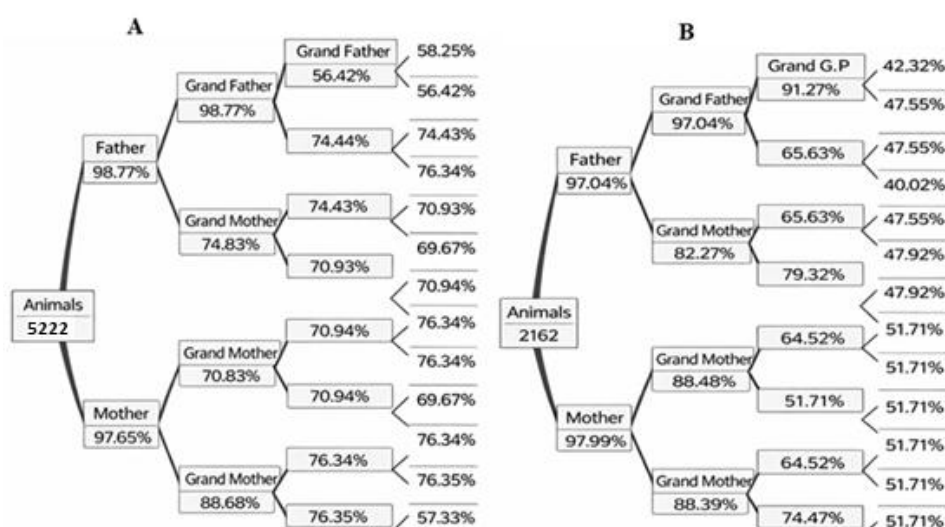


Figure 13. Pedigree structure for Kenyan goat; (A) Galla and (B) SEA goats

4.1.2 Pedigree-based genetic diversity for complete (CG) and maximum generation (MG)

Pedigree-based genetic diversity for Galla and SEA goats recorded a steady increase in inbreeding and average relatedness towards the current generations, although the rate of change varied between the two breeds (Tables 4 and 5). The average F and

AR for Galla and SEA breeds were 0.46 and 0.18, and 0.44 and 0.47, respectively. Lower *F* values (0.24) were reported in Indian Jamunapari goats (MANDAL et al., 2021) and Iranian Adani goats (JOEZY-SHEKALGORABI et al., 2017); which were due to periodic introduction of external bucks that were only allowed to serve for 3 years and strictly limited to 20 does per year, as well as incomplete pedigree records as most of the individuals lacked either the buck or doe information.

The average increase in inbreeding per generation for Galla and SEA breeds was 0.04 and 0.05, respectively. These rates clearly lie within the 1% increase per generation limit set by FAO for assessing breeds classified as threatened with extinction (FAO, 1998). The increase may arise from the breeding program that encouraged mating between related individuals in the population.

Ne was consistently low in both breeds, indicating a small number of individuals contributed genetically to the population. In Galla goats, *Ne* 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, *Ne* 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 *Ne* values indicate the presence of a strong genetic drift and a small number of founders in both breeds, with SEA goats demonstrating even lower *Ne* 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 *Ne*. In general, these results indicate the narrow genetic base in these breeds due to increased *F*, *AR*, with alarming small *Ne*, suggesting that these populations had few ancestors which makes them more susceptible to further loss in genetic diversity.

Table 4. Population parameters for maximum and complete generations for Galla 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	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

Maximum generation (MG)							Complete generation (CG)					
G	No	F%	% Inbred	F for inbred	AR	Ne	No	F%	% Inbred	F for inbred	AR	Ne
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 5. 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.

4.1.3 Generation intervals (GI)

From the results, Galla goats recorded a shorter generation interval (3.83 years) than SEA goats (4.39 years), while the average parental age at the birth of offspring was also lower in Galla goats (3.94 years) than in SEA goats (4.56 years). These differences suggest earlier use of Galla parents in the breeding population and a faster turnover of breeding animals, although farmer management decisions can also strongly 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 GI 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.

Based on the four pathways, the Galla breed had the longest GI in the buck–son pathway (6.44 years), followed by buck–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.

These results indicate that Galla goats have shorter GI and lower parental ages at the birth of breeding offspring compared to SEA goats. This implies a faster turnover of breeding animals in the Galla breed, which may support quicker genetic progress if structured selection is applied. Contrary to this, the longer GI and high values of parent ages in SEA goats suggest a slower rate of genetic improvement and reduced selection response. These differences are likely due to breed-specific management practices, replacement decisions, reproductive performance, and longevity of breeding animals.

Table 6. Generation interval and average age of parent at birth of offspring in four different pathways for Galla and SEA

Generation interval in years					Average age of the parent at the birth of offspring (years)			
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	1,0211	3.94 $\pm$ 0.02	4,182	4.56 $\pm$ 0.04

4.1.4 Effective number of founders (f_e) and ancestors (f_a)

Parameters in the origin of the gene in a population reveal clear differences in the structure of the two breeds. Galla goats had a higher total number in the pedigree (5,222 animals) than the SEA breed (2,162 animals) (Table 7). A high number of individuals had both parents with known records in both breeds, with Galla recording 5,100 animals and 2,096 in SEA, indicating an overall good pedigree completeness in the current generation. However, Galla recorded a higher number of individuals with one or both parents unknown, reflecting some missing pedigree records in the early generation before later improvements in data recording.

The Galla breed had a large f ($f = 99$) as compared to SEA goats ($f = 61$), suggesting a broader initial genetic base in the Galla population. Despite this, both breeds reported a very small f_e with Galla (7) and SEA (2). These small numbers show that despite having many founders in the pedigree, only a few contributed to the genetic composition of the current populations. Similar results were observed in the f_a , where Galla recorded ($f_a = 7$) and SEA ($f_a = 2$), which led to the f_a/f_e ratio equal to 1 in both breeds.

The genetic contributions were evident when looking into the number of ancestors, explaining 50% of genetic variability. Only three ancestors contributed to half of the genetic variability in Galla goats, while in SEA, only one ancestor contributed. This small number of ancestors reflects the use of specific breeding animals, an indication of an intense founder bottleneck.

The f_e/f ratios further confirm this pattern, with low values observed in Galla (0.07) and SEA (0.03), findings that show only a very small percentage of founders contributed meaningfully to the current population. A similar f_a/f_e ratio was reported by OLIVEIRA et al. (2016) in Spanish Musiano-Granadina goats. While a higher ratio of 7.10 was reported by RASHIDI et al. (2015) in Iranian Markhoz breed, showing a considerable genetic bottleneck due to the lack of transfer of the alleles to subsequent generations, posing a risk to the original genetic diversity. Results from this study reflects the presence of intensive selection or the use of few breeding animals for a longer period and therefore, highlights the vulnerability of these breeds to further loss of genetic diversity.

Table 7. Proportion of ancestral contributions for Galla and SEA breeds

Parameters	Galla	SEA
Total number of animals	5,222	2,162
Animals with both parents known	51,00	2,096
Animals with one unknown parent	99.5	65
Animals with unknown parents	122	66
Number of founders (f)	99	61
The effective number of founders (f_e)	7	2
The effective number of ancestors (f_a)	7	2
The number of ancestors explains 50% of the genetic variability	3	1
Ratio f_e/f	0.07	0.03
Ratio f_a/f_e	1	1

4.2 Within-population genetic diversity of European, Asian, and African samples based on genetic markers

From the study, the genetic diversity and inbreeding coefficients varied across the goat populations (Table 8). To evaluate the genetic diversity within populations, H_O was used. From the results, the mean H_O across the population was between 0.34 ± 0.03 (PHIN) and 0.441 ± 0.01 (SHOK), with most goat populations recording between 0.36 ± 0.03 and 0.44 ± 0.01 values, indicating medium genetic diversity. Following the H_O interpretations by KANAKA et al. (2023); the $H_O > 0.5$ mean high genetic diversity, values between $H_O \approx 0.2 - 0.5$ mean medium genetic diversity, and values below $H_O < \sim 0.2$ mean low genetic diversity in a population.

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). Demonstrating that majority of these populations retained a significant degree of ancestral genetic makeup despite some being subjected to unregulated breeding methods. However, if proper measures are not taken into account, their genetic diversity may be compromised due to inbreeding and genetic drift.

Inbreeding levels were assessed using various methods, including F_{hom} , F_{ROH} , F_{hat1} , F_{hat2} , and F_{hat3} . 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. In contrast, some African populations, MEA (-0.01 ± 0.03) and WG (0.000 ± 0.02), recorded minimal and negative F_{hom} values, an indication of low inbreeding or possibility of outbreeding.

Further inbreeding estimates (F_{hat1} , F_{hat2} , and F_{hat3}) supports these patterns, with PHIN populations recording the highest inbreeding values across all the methods ($F_{hat1} = 0.232$, $F_{hat2} = 0.274$, $F_{hat3} = 0.274$), possibly due to its distinct geographic isolation or small effective population size, as evidenced by LEON-APODACA et al. (2024). Similar findings were also reported in other goat studies where the controlled gene flow increased homozygosity levels in geographically isolated or island populations, thereby intensifying the risk of inbreeding and inbreeding depression (LI et al., 2022; PEGOLO et al., 2025). Furthermore, significantly low levels of genetic diversity within the SHOK, KENS and HUN populations were observed, aligning with population structure analyses that showed historical admixture and gene flow. These differences in inbreeding values highlight the effects of breed management history and population structure on genetic diversity.

The F_{ROH} (Figure 14A), further emphasizes this variability in inbreeding, with KOSS (0.094), SEA (0.070), and PHIN (0.062) goat populations having the highest values, suggesting that these populations were subjected to recent inbreeding or have a narrow genetic base, thereby calling for conservation measures to safeguard them. On the other hand, SHOK (0.008) and WG (0.007) populations showed the lowest F_{ROH} values, a sign of relatively higher genetic diversity. In general, these findings show the

presence of moderate genetic diversity and variation in inbreeding levels across the studied indigenous goat populations. And therefore, populations like PHIN and KOSS with high inbreeding coefficients and high levels of homozygosity values should be given priority in any available conservation and sustainable breeding measures to preserve their genetic potential and ensure long-term population viability.

The ROH analysis identified clear differentiation patterns across the studied goat populations, a reflection of variation in their demographic history and inbreeding levels. From the results, the highest count of ROH was observed in the shortest length categories (0-12 Mb) (Figure 14B). The dormancy of short-run ROH suggests past population bottlenecks associated with either domestication, breed formation, or population establishment, as also reported in Chinese and Italian goat breeds (HUANG et al., 2024; PEGOLO et al., 2025). PHIN and KOSS populations showed high ROH counts across all length classes, which is consistent with their high inbreeding coefficients and N_e reductions. These results are comparable to those found in closed populations with limited gene flow (BERTOLINI et al., 2018; ONZIMA et al., 2018; THOMAS et al., 2023; HUANG et al., 2024). DAB population's ROH pattern suggested a recent inbreeding event, aligning with observations from other native goats where closed breeding or mating among relatives heightened long ROH (PEGOLO et al., 2025).

Furthermore, the WG, GAL and SEA showed moderate ROH counts, which is consistent with larger N_e or well-planned breeding systems that limit mating among closely related individuals; as also reported in global goat diversification studies (CHESSARI et al., 2024). In the current study, although very long ROH (>48 Mb) were rare, their presence in a few individuals (e.g., PHIN, DAB and KOSS) indicated that some individuals in those populations were subject to recent inbreeding.

Table 8. Summary statistics of observed heterozygosity and 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	0.10 ± 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

FID	H_o	F_{hom}	F_{hat1}	F_{hat2}	F_{hat3}
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

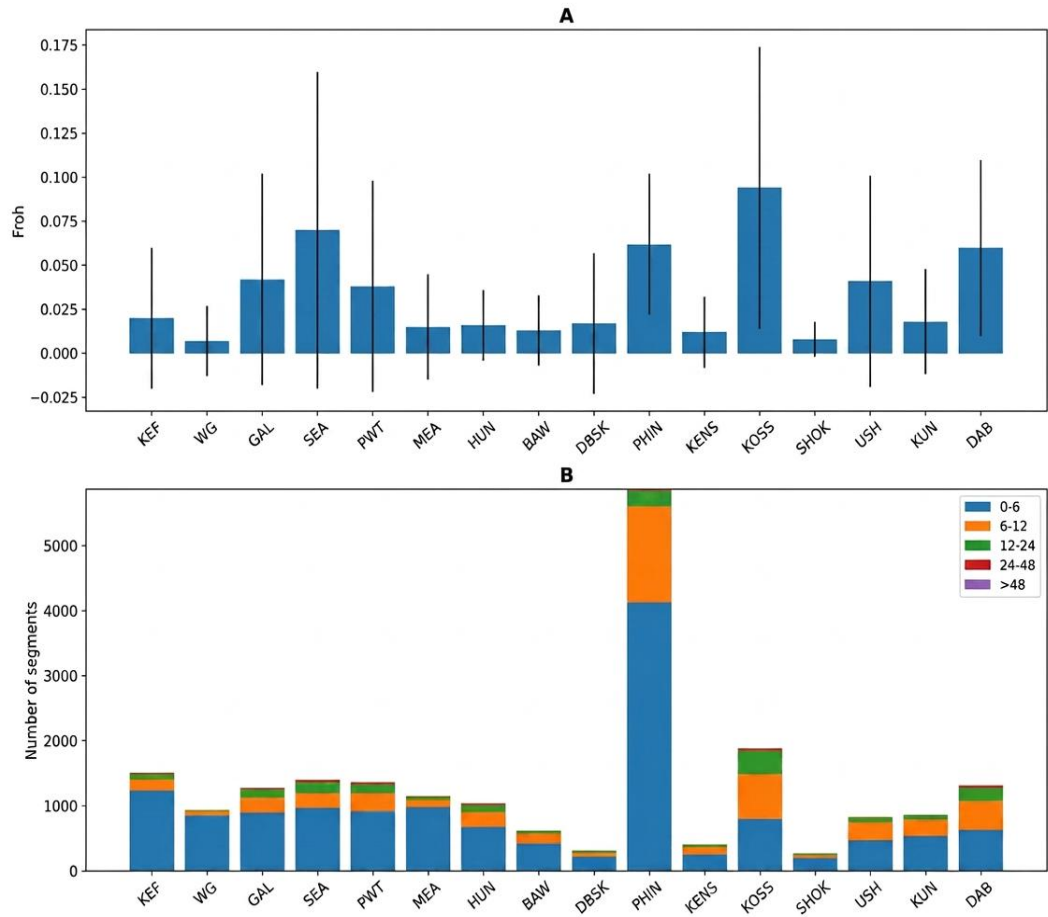


Figure 14. ROH Analysis results; (A) Inbreeding coefficients based on runs of homozygosity (F_{ROH}) and (B) The ROH class by length

4.3 Interpopulation relationships and population structure

To establish the genomic relationships between African, Asian, and European native goats, the inter-population relationships were assessed using the following methods: the Neighbor-Net joining tree was constructed based on Reynold genetic distances using the SplitTree software v4 and the gene flow events among populations using the maximum likelihood approach implemented in TreeMix v1.13. Neighbor- Net joining tree (Figure 15) divided the populations into four major groups based on the geographical origin and historical migrations, including the African, European, Central Asia (Kazakhstan), and Southeast Asia (Philippines) populations separately. This pattern shows a clear continental stratification resulting from a mix of historical migratory events and breeding practices particular to a given location, for example, the presence of ancient Silk Road dispersals (HERMES et al. 2020), the colonial-era translocations, and region-specific breeding practices, including selective mating and breed standardization policies in specific countries. Similar results were reported in other goat studies (BELAY et al., 2024; ZHANG et al., 2025) where study populations were clustered basing on their geographical regions.

However, the Philippines population (Southeast Asia) positioned itself very far from others, meaning a greater differentiation. This distinct position of the Philippines may be due to the geographic isolation and the presence of historical bottlenecks, as the country is located in Southeast Asia and contains numerous islands. Besides, this country is believed to have never been associated with other Asian countries (LARENA et al., 2021).

Interestingly, the Ushterek population from Kazakhstan (Central Asia) clustered closer to European breeds, suggesting some historical admixture or shared ancestry lines where some demographic events, such as migrations during the expansion of Russian Empire into Central Asia, introducing the European livestock breeds and through trade, may have shaped the genomic architecture of this goat population. This was expected considering the domestication history of goats in the Fertile Crescent around 10,000 years ago and their subsequent dispersal across Europe, Asia, and Africa, which established a continent-wide gene pool shaped by post-domestication migration and admixture (COLLI et al., 2018; PETRETTO et al., 2024). Additionally, the Eurasian Steppe, including Kazakhstan, acted as a major dispersal corridor, facilitating gene flow and shared ancestry among goat populations over time (TABATA et al., 2019).

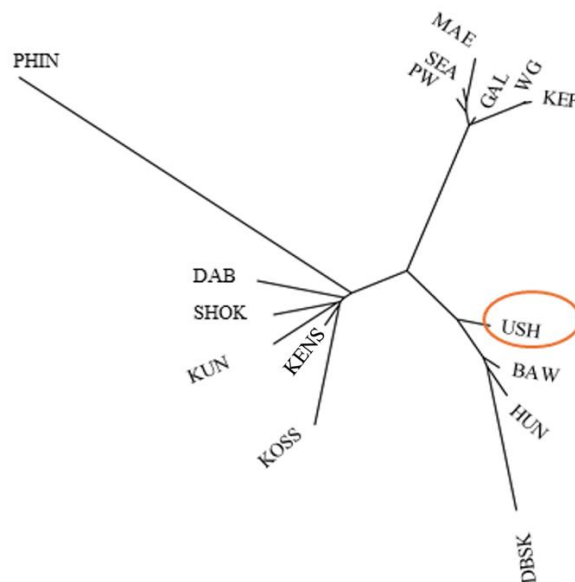
Gene flow events among populations using the maximum likelihood approach implemented in TreeMix v1.13. TreeMix analysis was done to understand the population relationships and potential gene flow among the studied goat populations. From the results, the model fit, which was measured from the log-likelihood, increased sharply with the number of migration edges before diminishing (Figure 16A). The change in log-likelihood stabilized after the fifth migration edge (Figure 16B), indicating that the optimal balance between model complexity and explanatory power was five migration events ($m = 5$). The maximum-likelihood TreeMix (Figure 16C) showed a clear split in these populations into five migration events of historical gene flow. The colored arrows represent gene flow between populations, with sharp colors showing higher levels of migration events ($m = 5$).

From the observation, the pattern of the TreeMix aligned with results from the neighbor-joining tree analyses, where goat populations were clustered according to their geographic location and the history of the breed. The first migration edge, which runs from the GAL population to the PWT, MEA, SEA, WG, and KEF breeds, suggests a significant gene flow within the African populations. GAL breed functions as a genetic link connecting the African goat populations. This trend aligns with the shared boundaries and regular transboundary livestock migrations in pursuit of water and grazing fields during arid periods. Besides the extensive spread and popularity of the GAL goat throughout East Africa, its key function in influencing the genetic makeup of neighboring breeds is underscored. This observation is consistent with previous studies that reported a weak population structure and extensive admixture among African indigenous goats (BENJELLOUN et al., 2015; ONZIMA et al., 2018). A pattern driven by pastoral production systems and shared livestock markets in Africa, where frequent livestock movement and cross-borders promote interbreeding and gene flow across regions (MDLADLA et al., 2018). Consequently, the GAL populations retain a shared ancestral polymorphism while also contributing genetic material to neighboring goat populations.

The DAB and KUN populations in Kazakhstan formed a tight genetic cluster, indicating a close genetic relationship. This genetic link may arise if both populations are from the neighboring villages or communities, which is the case for this study population, where the production system in this country is a predominantly traditional pastoralism system that encourages communal grazing and periodic livestock movements in search of pasture and water (KICHAMU et al., 2025). As this happens, it

allows neighboring flocks to interact and breed freely. Consequently, the high level of gene flow between neighboring populations contributes to their reduced genetic differentiation and their significant genetic similarity.

The BAW, USH, DBSK, and HUN populations clustered on a branch that connects through a few migration events. This clustering typically happens if the populations have a shared ancestry due to historical gene flow. Sharing of ancestors is possible as the countries are adjacent to each other and might have some common shared activities that contributed to this clustering. The PHIN population diverged earlier from different clusters, indicating a distinct genetic makeup as compared to the other populations. Finally, SHOK, KENS, and KOSS showed short migration edges, which highlight the ongoing genetic admixture within these populations.



The circled red part represents the Kazakhstan population that grouped into European goats

Figure 15. Neighbor network based on distance matrix from pairwise F_{ST} values

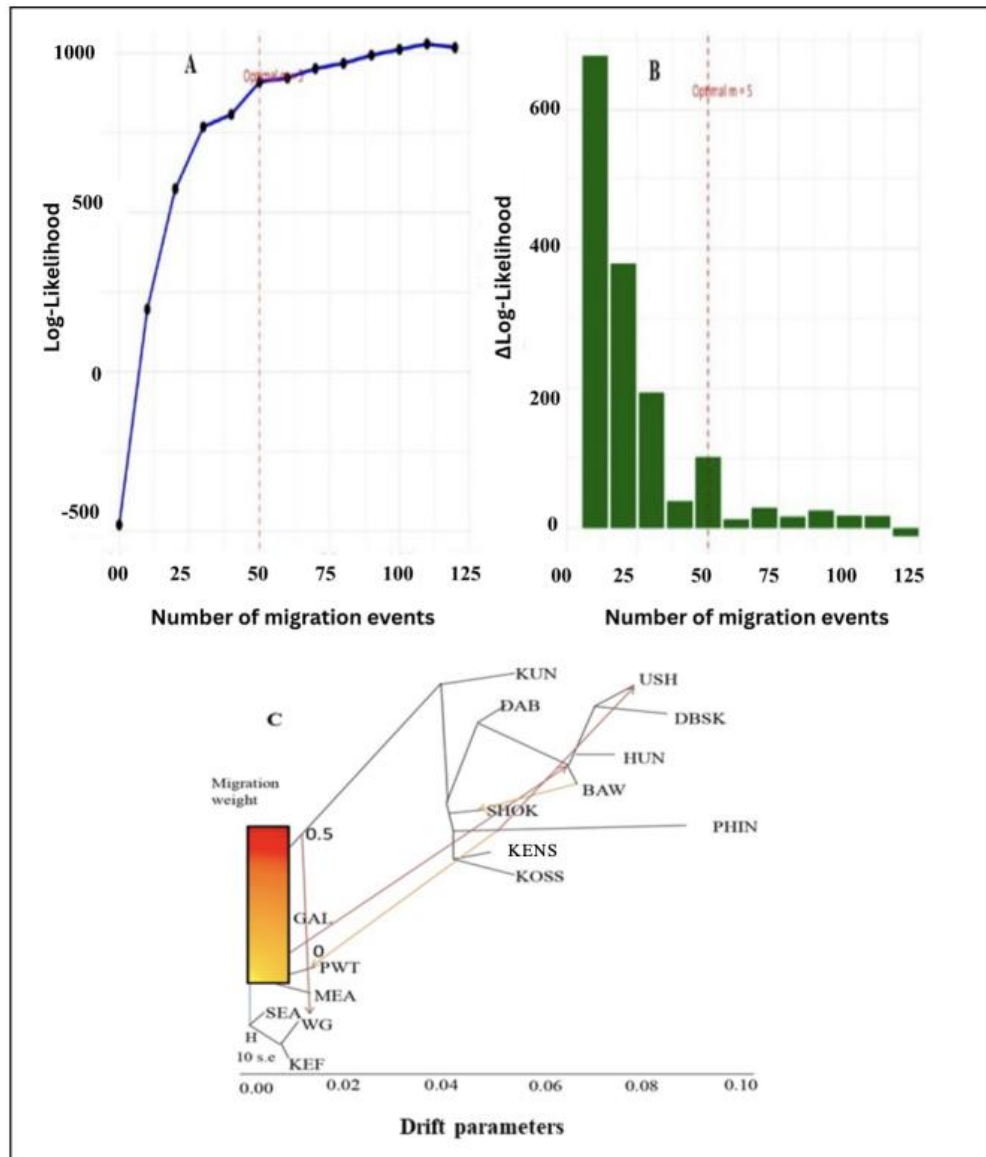


Figure 16. Population structure for studied goats; (A) Change in log likelihood and number of migration events, (B) Inferred maximum likelihood population graph, and (C) TreeMix showing the migration edges of study goats

Further, the interpopulation relationships were assessed using PCA (Figure 17). The PCA presented a similar pattern to that of neighbor-joining trees, where four distinct clusters were also formed based on the continent they are on. For instance, breeds from Africa (Kenya, Ethiopia, and Tanzania) clustered together as observed in the European breeds. Besides, the Kazakh population also clustered together, except for the Ushterek population, which moved towards the European population. The PC1 explained 25.66 % of all the variation. In comparison, PC2 explained 16.64% of the total variation, where the largest principal component (PC1) separated the African

population from those of Central Asian populations (Kazakhstan) and Southeast Asian (Philippines), while PC2 separated the European population from Southeast and some Central Asian populations.

The presence of clear continental stratification may result from a mix of historical migratory events and breeding practices particular to a given location, for example, the presence of ancient Silk Road dispersals (HERMES et al., 2020), the colonial-era translocations, and region-specific breeding practices, including selective mating and breed standardization policies. Similar results were reported in other goat studies (BELAY et al., 2024; ZHANG et al., 2025).

Co-ancestry analysis was also evaluated using ADMIXTURE software while applying $K = 1$ to $K = 20$. The population structure corresponding to the optimal K value is presented in Figure 18A, while Figure 18B displays optimal K with the lowest cross-validation error at $K = 10$. From our results, we observed four distinct patterns based on the continents, with some populations showing high levels of admixture, for instance the GAL, MEA, PWT, SEA populations from Africa were similar but highly admixed as compared to the Ethiopian breeds WG and KEF. This result suggested some gene flow in the population, arising from production system used in these countries as most of the goats farming is majorly done by smallholding and pastoral communities with lack of structured breeding program and communal grazing system thus encouraging intermixing of livestock from different communities (KICHAMU et al., 2024a).

Besides, the European populations (HUN, DBSK, BAW) also showed a similar pattern but less admixed, indicating some levels of homogeneity. This observation may arise due to the system of production used in the area, including closed breeding, selection for specific production traits such as milk yield or cashmere (intensive selection), and established legislation and policies on breed standards in Europe, which may have restricted the introduction of new genes into these populations. The Kazakhstan population (KEN, KOSS, KUN, SHOK, USH, DAB) also formed a distinct pattern of mixed ancestry. The PHIN exhibited a single coancestry, an observation similar to those reported in the PCA, an indication of genetically distinct ancestry.

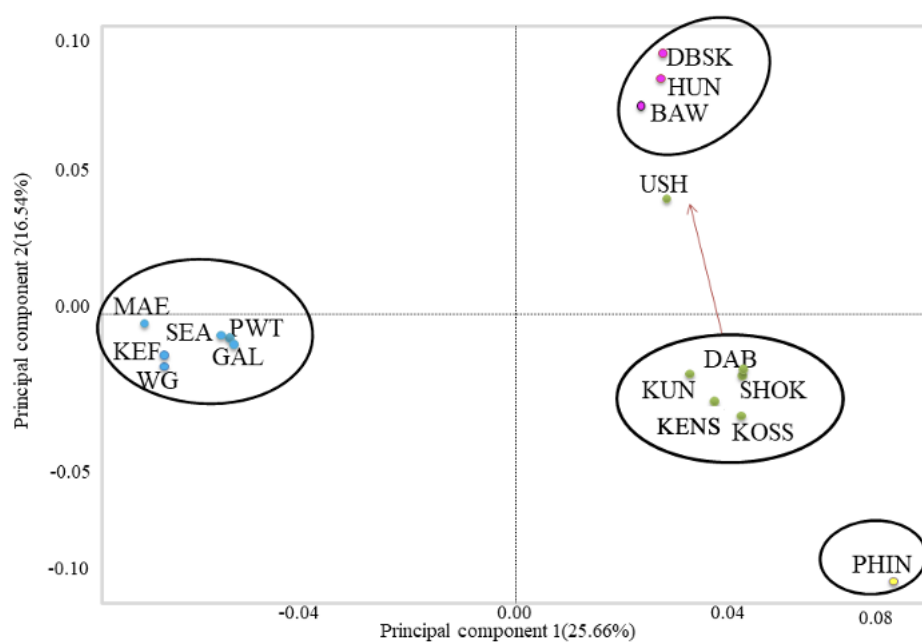


Figure 17. Population structure for the studied goat populations by principal component analysis (PCA)

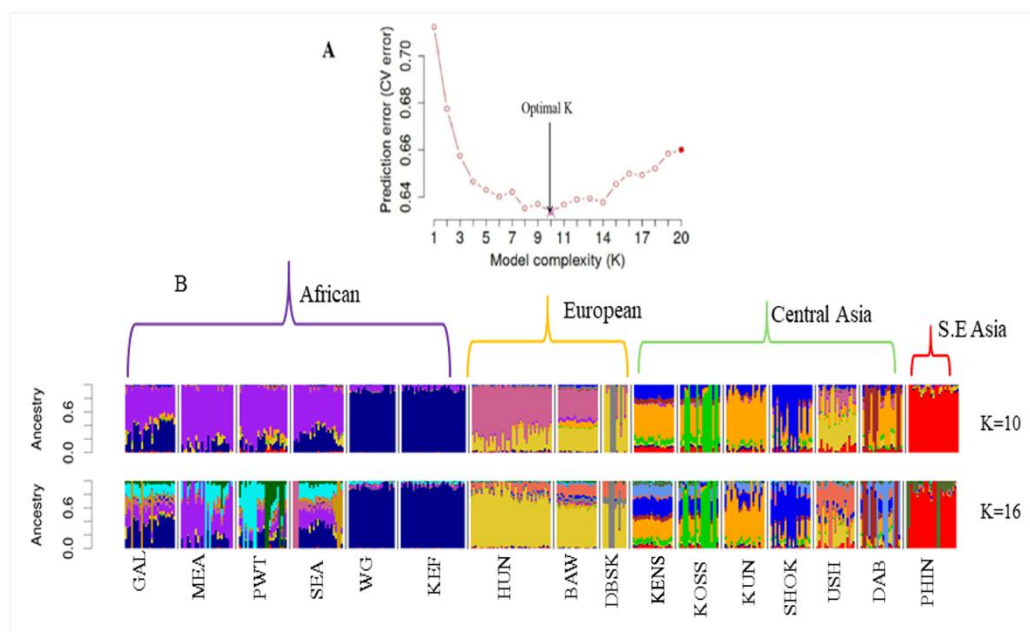


Figure 18. Ancestry structure for studied goat populations; (A) Cross-validation error plot and (B) Admixture analysis plot

4.3.1 Effective population size (N_e)

N_e was assessed to understand the recent and ancient demographic history of the studied goat populations. The SNeP results showed a declining trend in N_e across all populations (Figure 19A). A finding consistent with those observed in global patterns of genetic erosion in domestic species (BARBATO et al., 2020; COOMBS et al., 2012), these estimates may be influenced by underlying population structure and admixture, which can bias demographic inference by creating composite signals of gene flow and changes in population size.

The BAW and HUN of Europe, GAL, MEA, PWT, SEA from Africa, and KENS from Kazakhstan maintained relatively higher N_e values at the initial generation (generation 1) 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 19B) 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 these 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.

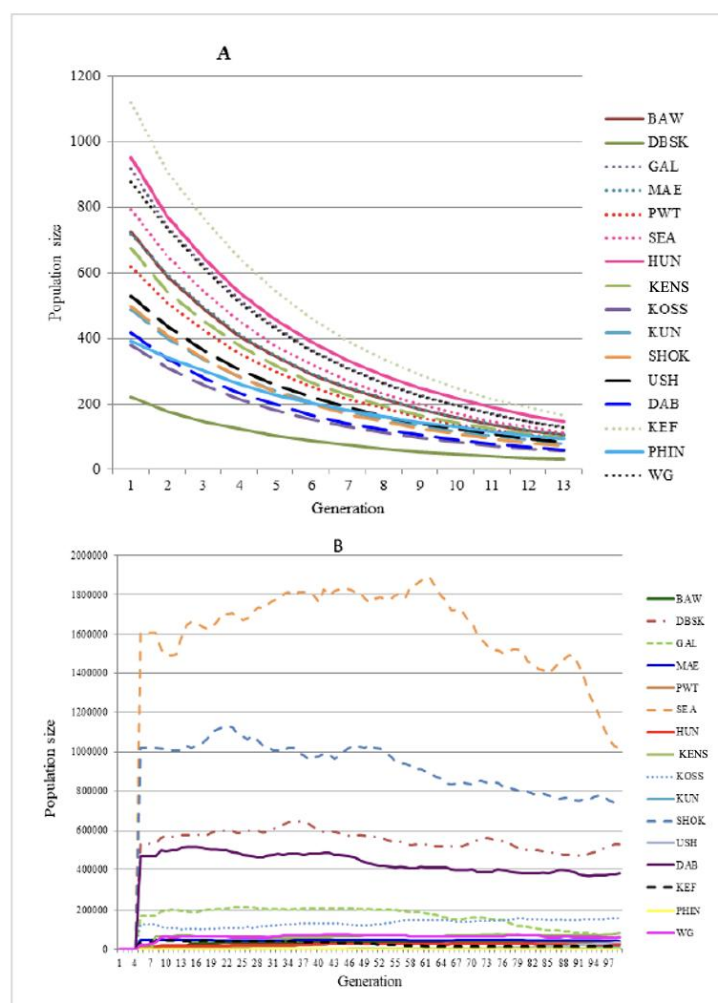


Figure 19. Historical and detailed N_e using GONE software; (A) Effective population sizes (N_e) and (B) Recent N_e estimated with SNeP for studied goats

4.4 Identification of signatures of selection for resistance and adaptation

To investigate the genomic signatures of positive selection in indigenous goat populations from Europe, Kazakhstan, Africa, and the Philippines, two complementary methods were used, the eROHi and iHS. The use of these two methods ensured that the results are credible as they capture varied evolutionary contexts and selection periods. From the results, 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; most of them were 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). Figures 20 - 24 visualise the mannhatan plots showing the signals per chromosome and Tables S1 to S4 show all the genes by both methods. These tables therefore present candidate genes located in or near the detected selection regions, but they do not represent a functional SNP-effect classification.

Moreover, there was no overlap in candidate genes observed between the two methods. This case underscores the importance of using different techniques, as each of them captures specific, selective events. Among these genes 14 of them (Figure 25) were identified as important gene 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*).

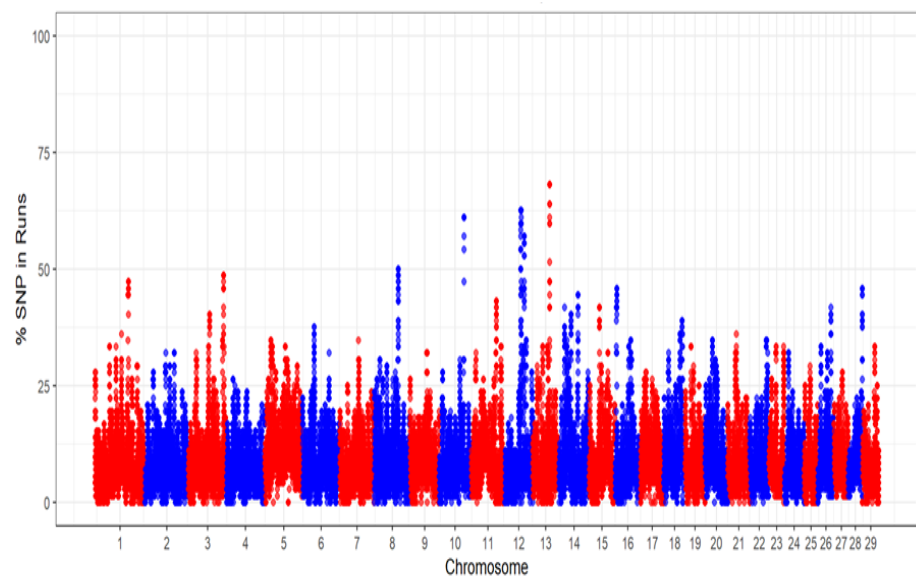


Figure 20. Manhattan plots based on eROHi showing SNPs percentage per chromosome runs for European goats

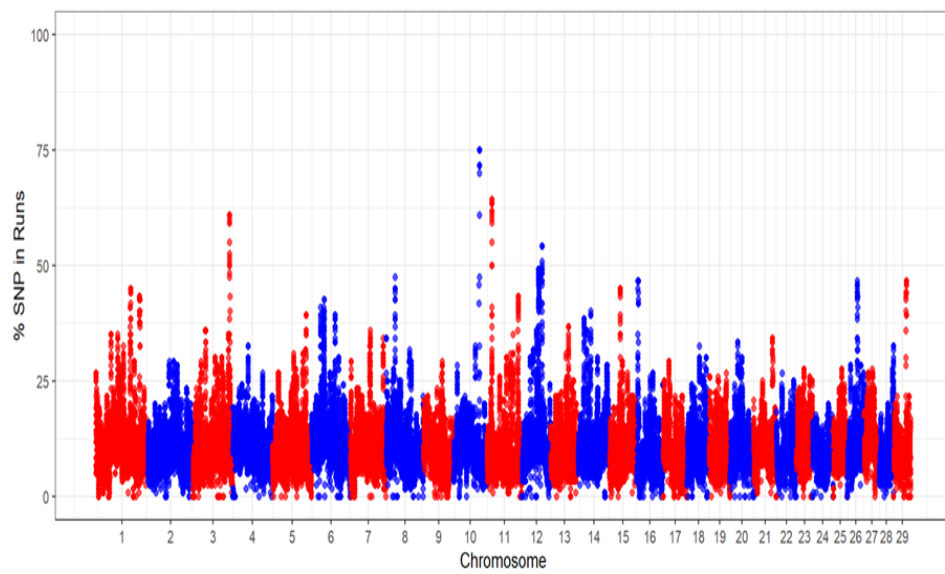


Figure 21. Manhattan plots based on eROHi showing the SNPs percentage per chromosome runs for Kazakhstan goats

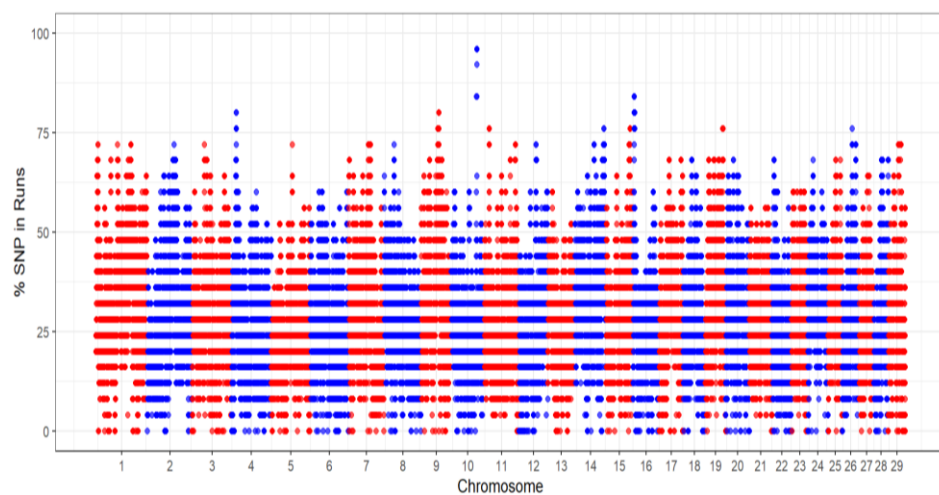


Figure 22. Manhattan plots based on eROHi showing SNPs percentage per chromosome runs for Philippine goats

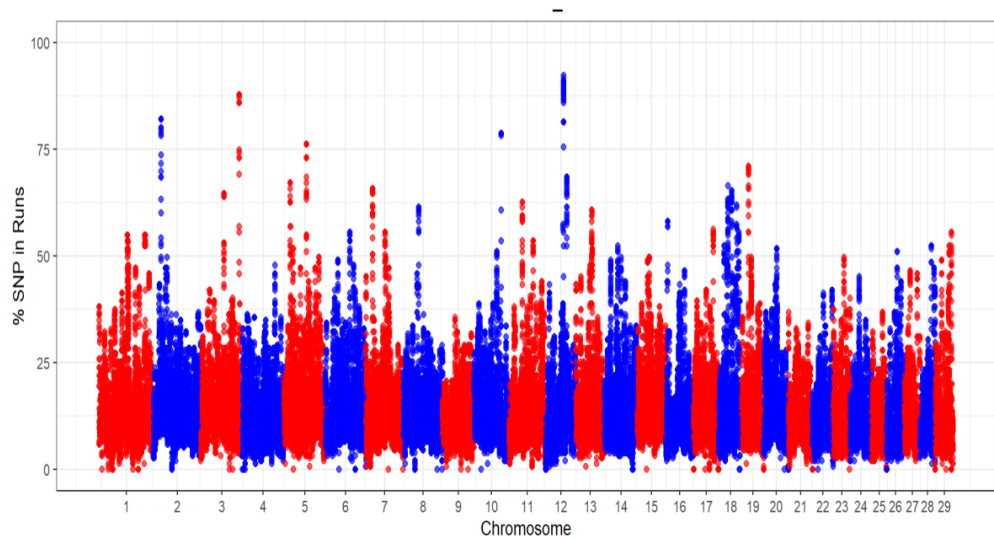


Figure 23. Manhattan plots based on eROHI showing the SNPs percentage per chromosome runs for African goats

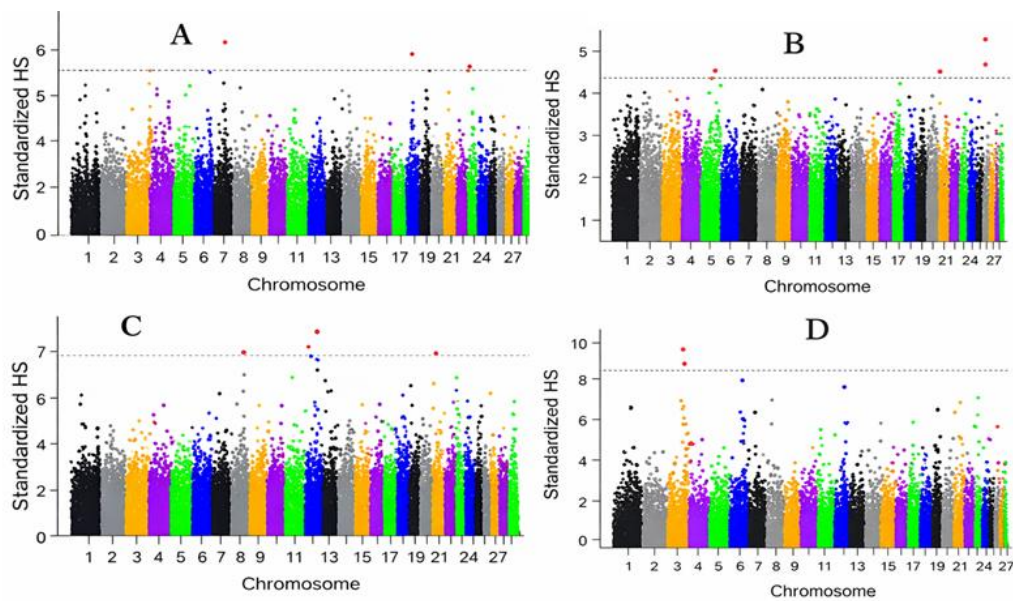


Figure 24. Manhattan plot based on standardized iHS per clustered population; A) African populations, B) Philippine populations, C) European Populations, and D) Kazakh populations

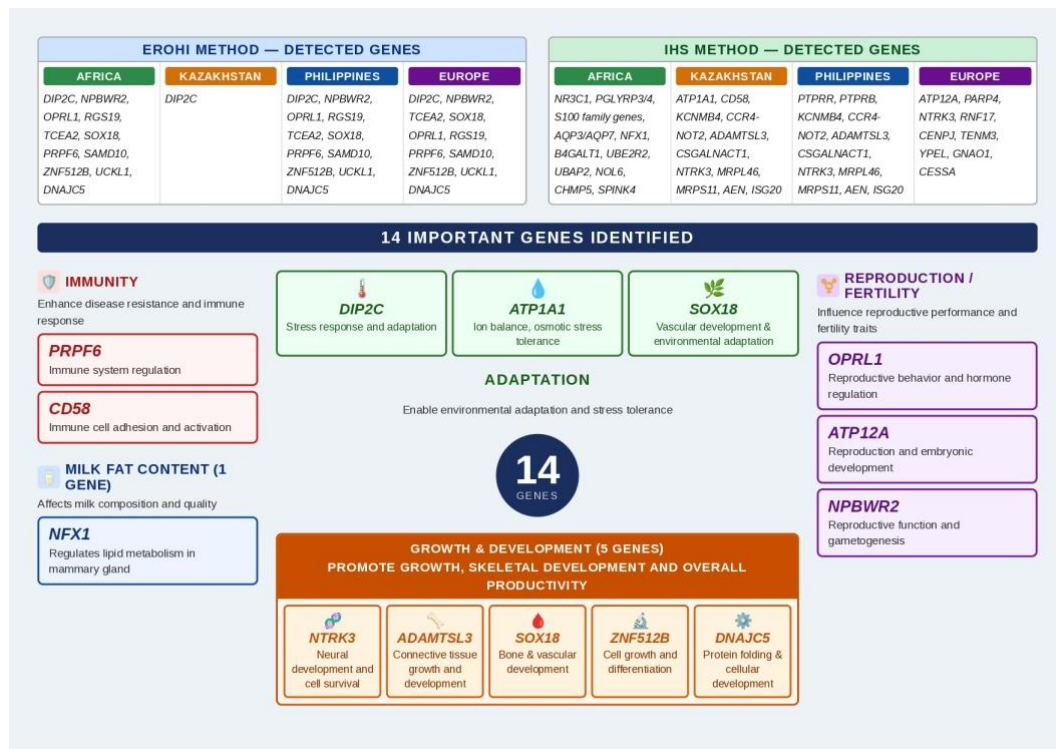


Figure 25. Signatures of positive selection mapped by the eROHi and iHS methods for all the goat populations

The identified candidate genes have been reported to be involved in key biological functions in goats, which reveal a mixture of selective pressures acting on indigenous goats across ecological gradients. For instance, the *DIP2C* gene which was detected in all the study populations, is linked to cellular osmoregulation and ion transport, the gene have been associated with heat stress responses in cattle and has been linked to stress-related adaptation and tissue management (ELAYADETH-MEETHAL et al., 2021). Their identification in our study suggests that indigenous goats from Africa, Asia, and Europe may have undergone selection for enhanced ion transport efficiency as a physiological adaptation to heat and water stress conditions.

SOX18 gene is linked to vascular development and thermoregulation (WANG et al., 2021; JIA et al., 2024), a process that is vital for maintaining homeostasis in hot environments. The gene helps to regulate blood vessel endothelium and lymphatic vasculature differentiation through activation of Prox1 transcription (FRANÇOIS et al., 2008). In our study, *SOX18* was detected in African and Philippine goat populations, where their living condition is characterized by high-temperature of humid, tropical and semi-arid environments. Its identification under putative selection suggests that these

indigenous goats may have undergone adaptive evolution in the *SOX18*-regulated vascular and thermoregulatory pathways as a response to this intensive heat stress.

PRPF6, which is a pre-mRNA-processing factor that plays a role in regulating the splicing and expression of multiple transcripts, including immune-related genes (SONG et al., 2020), was expressed in European, African and Philippine goat populations. Given that variation in splicing machinery can reshape immune-gene repertoires and inflammatory responses, the recurrent signal at *PRPF6* in these geographically diverse populations may indicate convergent selection for robust immune regulation under different disease and management regimes. These putative signature selections in my study may suggest local adaptation to pathogens, especially in the region prone to disease infestation, findings that were also reported in other tropical goat breeds where immune-related genes showed a positive selection (ONZIMA et al., 2018; BAENYI et al., 2020).

The identification of reproductive-related genes (*OPRL1*, *ATP12A*, *NPBWR2* and *PRPF6*) may reflect selection for fertility and reproductive efficiency under harsh environments where breeding opportunities are insufficient. *OPRL1* gene helps in modulating the hypothalamic pituitary–gonadal axis and has been linked to the regulation of reproductive hormones in sheep and goats (CONSTANTIN et al., 2018). *NPBWR2* helps in modulating the neuroendocrine regulation of energy balance, stress response and reproduction (TIAN et al., 2025). *ATP12A*, a gene expressed in ruminant spermatozoa, where it regulates acrosomal pH, which is critical for sperm function and fertility (FAVIA et al., 2022). In this study, the *OPRL1* and *NPBWR2* gene were detected in European, African and Philippine populations, indicating that the gene may contribute to the neuroendocrine control of reproduction in varied breeding management practices, such as intensive, seasonal and year-round mating systems. This suggests selection in optimizing metabolic efficiency and reproductive output under nutritional stress environments and potentially be a valuable genetic marker to be involved in the breeding program especially for the regions whose fertility is the key factor to livestock breeding.

Additionally, in the European population, *NTRK3* and *NFX1* were also detected, which is linked to developmental signaling pathways associated to growth-related traits (NILSSON et al., 2009) and milk production traits (AMININASAB et al., 2023), respectively. *NTRK3* which modulates pituitary gonadotrophic development and early follicular growth, this gene may contribute to both neurobehavioral performance and

growth- or reproduction-related traits under intensive or semi-intensive management systems (NILSSON et al., 2009).

The *ADAMTSL3* has been associated with skeletal growth and body size in livestock species (LIU et al., 2021; PENG et al., 2024) and was detected in Philippine populations in this study. This may reflect local selection in this population for a fast growth rate under the specific management systems and production environments encountered in the Philippines, where larger body size could confer advantages in meat production and environmental resilience. Therefore, selection at this locus may have contributed to morphological adaptation to the local production environment in this population.

Specific to Kazakh populations, *ATP1A1*, which helps to encode the $\alpha 1$ subunit of the Na^+/K^+ -ATPase, and an important process in maintaining ion gradients and cellular homeostasis under high temperature conditions (ELAYADETH-MEETHAL et al., 2021). In addition to it, *CD58* and members of the *S100* family genes which helps to encode the T-cell co-stimulatory molecule (LFA-3) responsible for facilitating T-cell activation in adaptive immune responses and defense against pathogens in sheep and cattle (CROSBY et al., 2004) were also detected. The *S100* family genes of calcium-binding proteins are well-characterized mediators of innate immunity, inflammation and antimicrobial responses (SINGH et al., 2022). In goats, these genes are up regulated in mammary and other epithelial tissues during mastitis infection and stress (TSUGAMI et al., 2022). The presence of this gene in the Kazakh population supports the idea that this gene contributes to adaptation to extreme temperature and limited water availability of arid climate in that region. Moreover, with the topographical condition and the extensive grazing system with frequent pathogen infestation, suggests the adaptive refinement of immune recognition and inflammatory regulation in this environment of this breed.

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

Pedigree-based analyses showed an increase in inbreeding across generations for both breeds, with *F*% reaching 0.79 in Galla and 0.85 in SEA by the most current generations, with consistently low *Ne* ranging from 5.19 and 4.75 in GAL and 2 to 6 in SEA with only 7 and 2 effective founders, respectively. Genomic analyses similarly

reflected reduced genetic diversity, with H_O of 0.393 in Galla and 0.385 in SEA, and positive inbreeding coefficients across all SNP-based inbreeding measures (F_{ROH} : 0.042 in Galla and 0.070 in SEA), with dominance of short ROH segments (0–12 Mb) in both breeds, suggest that the observed inbreeding was largely from ancient origin.

Both methods show that these breeds are experiencing significant inbreeding rooted primarily in ancient population bottlenecks, compounded by small founder populations and low effective population sizes observed in pedigree results. The findings between pedigree and genomic methods validates these findings and underscores an urgent need for conservation and genetic management strategies including rotational mating schemes and cryopreservation of germplasm to prevent further genetic erosion within this breed (KICHAMU et al., 2024b). Despite these, pedigree-based method is only able to capture inbreeding that only occurred on recorded generations (MELKA and SCHENKEL 2010), and there inbreeding coefficients values only reflect relationships traceable within the available pedigree depth, systematically underestimating true inbreeding when founder generations are unknown. Therefore, proper and complete records are required as well as inclusion of genomic data.

5. CONCLUSIONS AND RECOMMENDATIONS

5.1 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.

5.2 RECOMMENDATIONS

For the pedigree results, the study recommends improved and consistent pedigree record keeping, as incomplete records affect the accuracy of the pedigree analysis. To promote conservation and sustainable use of indigenous goat genetic resources, the study proposes the adoption of various strategies. This strategy involves prioritizing those populations with high inbreeding rates and low genetic diversity, like the PHIN, in any conservation and genetic enhancement project. These programs should adopt various measures, including avoidance of crossbreeding and preventing inbreeding through rotational mating systems with unrelated individuals, to improve the genetic diversity while conserving their important adaptive features.

All the investigated populations relied exclusively on *in situ* conservation, which still exposes the population to genetic erosion; therefore, complementing *in situ* with *ex situ* cryobanking using identified SNP markers for elite founders is necessary, and to strengthen this implementation, it is important to promote knowledge transfer mechanisms between researchers and farmers for these indigenous populations. These will help protect the genetic resource for future breeding and conservation initiatives. It is also important to promote the development and enhancement of community-based breeding programs so that local farmers, breeders, and pastoralists have the opportunity to manage these breeds in a sustainable way using their indigenous knowledge.

Training and extension programs can also be improved to help farmers and breeders better understand how to manage genetic diversity and the long-term importance of maintaining this genetic diversity. For the declining effective population

sizes, it is paramount that the rate of gene flow between the populations is well monitored, especially in those with small populations. Monitoring can be done through the periodic introduction of an external breeding buck or exchange of genetic material within the same breed from a different flock to help maintain diversity without affecting their genetic make-up.

Genomic information from this study should be incorporated into the breeding and conservation program, especially the identified signatures, which should be used to design a breeding program that balances productivity with adaptability. The breeding objectives should be well designed to ensure important traits related to resilience, disease resistance, and heat tolerance are well prioritized to ensure that indigenous goats remain productive under challenging environments and production systems.

Development of policies that encourage the establishment of national frameworks and databases for the conservation of these goats' genetic resources, as well as the enhancement of collaborations among relevant institutions, including research institutions, government agencies, private bodies, and local communities, to ensure the sustainable management of these valuable genetic resources.

For cross-border admixture, the neighbouring countries should develop a joint breed registry, standardized animal identification protocols, and genomic-based border screening to monitor and regulate the movement of breeding stock across shared pastoral corridors. These should be coordinated through relevant regional stakeholders, to enable systematic documentation of cross-border gene flow, facilitate evidence-based decisions on permissible breed exchanges, and prevent the uncontrolled erosion of breed-specific genetic diversity for future generations.

Future research should therefore consider expanding the sampling regions and numbers; incorporate some details, such as climate and environmental data, to help assess the correlation between environmental variables and genetic patterns to explain the local adaptation mechanisms in detail and consider studying breed-specific genetic and phenotypic characterization. To precisely characterize the specific European breed introgression into the Ushterek Kazakh population, future studies should consider employing breed-specific reference panels and local ancestry inference analyses. Additionally, future research should extract individual pedigree inbreeding coefficients for the genotyped Galla and SEA animals by matching animal IDs across the pedigree and genomic datasets, to enable a direct comparison between pedigree-derived and genomic inbreeding estimates.

These findings provide essential insights for designing sustainable breeding and conservation strategies that aim at balancing productivity with conservation of genetic diversity to ensure a sustainable use of indigenous goat breeds globally.

6. 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.

7. 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.

8. SUMMARY

Indigenous goats are essential to many livelihoods, yet they face significant challenges, including indiscriminate crossbreeding, habitat destruction, and disease prevalence, harsh environments, traditional production systems, and sociocultural contexts which have shaped their genetic diversity. However, these factors, combined with the increasing effects of climate change, influence their genetic diversity, which remains critical for their adaptation and long-term survival under increasing environmental stresses. The present doctoral research employed pedigree and molecular data to understand their genetic make-up.

For objective one, the study assessed population structure and genetic diversity of Kenyan Galla and Small East African (SEA) goats using pedigree information. A total of 7,384 animals, 5,222 of the Galla and 2,162 of the SEA breeds, born between the years 1983 and 2022, were utilized. To assess various parameters, ENDOG software was used. For objectives 2 to 4, the study aimed to understand the population structure, genetic diversity, and adaptive mechanisms of the indigenous goat population in selected countries of Asia, Africa, and Europe. A total of 372 goats were genotyped using the CaprineSNP70K Bead Chip array with 51,119 SNP markers.

For pedigree analysis, both Galla and SEA goat breeds had similarly deep but partially incomplete pedigrees (14.6 and 14.5 generations traced, with only 6 and 5 complete, respectively), shorter generation intervals in Galla and long in SEA (3.84 and 4.4 years, respectively), and low rates of inbreeding (0.04 and 0.05 per generation, respectively). Despite these, both breeds showed critically small effective population sizes ($N_e \approx 5$), a f_a/f_e ratio of 1.00, and a disproportionate contribution to genetic variability by very few ancestors (3 for Galla, 1 for SEA), underscoring the need for breed-specific management to conserve diversity and mitigate inbreeding.

For genomic analysis, the H_o was moderate in all the study populations, ranging from 0.34 in Philippine goats to 0.441 in Shokpar (Kazakhstan), with the inbreeding coefficients varying such that Philippine Native Antipas Cotabato recorded the highest inbreeding across all the measures and relatively low levels of heterozygosity, whereas Shokpar, Kenes (Kazakhstan), and Old Hungarian Native populations showed higher heterozygosity and lower inbreeding coefficients. The distribution of ROH revealed that most populations had a high frequency of short run segments (0–24 Mb), suggesting ancient inbreeding and a history of population bottlenecks, while population structure analyses identified four major genetic clusters reflecting geographic origins and

historical gene flow, with high levels of admixture observed in some African populations which may be due to cross boarder livestock movement, trade interactions, and crossbreeding among herds across regions. The observed decline in effective population sizes in all the study populations highlights the risk of genetic drift and loss in genetic diversity, which calls for attention for designing proper conservation and breeding programs geared towards sustaining the genetic health by balancing productivity and genetic diversity conservation to ensure the sustainability of indigenous goat breeds globally.

The study identified important candidate genes related to immunity (*PRPF6*, *DIP2C*, and *CD58*), adaptation (*DIP2C*, *ATP1A1*), reproduction (*OPRL1*, *DIP2C*, and *ATP12A*), milk fat content (*NFX1*) and growth and development (*NTRK2*, *ADAMTSL3*, and *SOX18*), which provides a valuable insight into the genetic mechanisms underlying economically and biologically important traits in this indigenous populations, offering useful markers for future breeding, conservation, and improvement programs aimed at enhancing productivity, resilience, and long-term sustainability of indigenous goat populations.

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10. LIST OF PUBLICATIONS



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Doctoral School: Doctoral School of Animal Husbandry
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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.

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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.
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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.
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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.
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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.
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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.
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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.
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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., Pradipta Iustitia, S., Alek, I., Shairah, A. R., **Kichamu, N.**, Kusza, S.: Investigating the genetics of tropical climate adaptation in Asian and African indigenous sheep.
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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).





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19 May, 2026



11. STATEMENTS

DECLARATIONS

I wrote this thesis in the framework of the University Of Debrecen Doctoral School of Animal Science for the purpose of obtaining a doctoral degree (Ph.D.) at the University of Debrecen.

Debrecen, 03 June 2026.



Nelly Kichamu

PhD candidate

DECLARATION

I hereby certify that the doctoral candidate **Nelly Kichamu** has carried out her work under my supervision within the framework of the Doctoral School of Animal Science, University of Debrecen. Between 2022 and 2026, the candidate has made a decisive contribution to the results of the thesis through his/her independent creative work, and the thesis is the candidate's independent work. I recommend that the thesis be accepted.

Debrecen, 03 June 2026.



Prof. Dr. Szilvia Kusza

Supervisor

12. ACKNOWLEDGEMENT

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13. ANNEXES

Appendix Table S1. Genes identified by both eROHI and iHS methods that could be under selection for adaptation in European indigenous goats

Gene	Chr	ensembl_gene_id	start_posit ion	end_positio n	eRO HI	iHS
<i>DIP2C</i>	13	ENSCHIG00000024387	45929488	46232588		
<i>NPBWR2</i>	13	ENSCHIG00000003852	53094654	53095664		
<i>OPRL1</i>	13	ENSCHIG00000024097	53100703	53107883		
<i>LKAAEAR1</i>	13	ENSCHIG00000022007	53114038	53114819		
<i>RGS19</i>	13	ENSCHIG00000004921	53121591	53123855		
<i>ATP12A</i>	12	ENSCHIG00000023218	50084768	50105547		
<i>RNF17</i>	12	ENSCHIG00000026716	50114390	50230030		
<i>CENPJ</i>	12	ENSCHIG00000004741	50233625,	50273619		
<i>PARP4</i>	12	ENSCHIG00000016066	50291042	50357417		
<i>NTRK3</i>	12	ENSCHIG00000010670	18130059	18546956		

Appendix Table S2. Genes identified by both eROHI and iHS methods that could be under selection for adaptation in Kazakhstan indigenous goats

Gene	Chr	ensembl_gene_id	start_position	end_position	eROHI	iHS
<i>YPEL</i>	27	ENSCHIG00000027005	28366964	28368961		
<i>TENM3</i>	27	ENSCHIG00000011185	31756132	31951634		
<i>ATP1A1</i>	3	ENSCHIG00000017191	93611650	93645306		
<i>CD58</i>	3	ENSCHIG00000022779	93782057	93828732		
<i>IGSF3</i>	3	ENSCHIG00000003902	93835785	938357854118		
<i>LELP1</i>	3	ENSCHIG00000001135	102923551	102923862		
<i>PGLYRP3</i>	3	ENSCHIG00000014425	103016474	103027592		
<i>PGLYRP4</i>	3	ENSCHIG00000023048	103036240	103051776		
<i>S100A9</i>	3	ENSCHIG00000016845	103060350	103062557		
<i>S100A12</i>	3	ENSCHIG00000012846	103073976	103074689		
<i>S100A8</i>	3	ENSCHIG00000026621	103093034	103095285		
<i>S100A7A</i>	3	ENSCHIG00000021789	103132447	103135381		
<i>S100A5</i>	3	ENSCHIG00000025911	103318019	103325852		
<i>S100A6</i>	3	ENSCHIG00000020688	103320703	103321327		
<i>S100A4</i>	3	ENSCHIG00000025367	103329512	103331035		
<i>S100A3</i>	3	ENSCHIG00000019122	103333674	103334421		
<i>S100A2</i>	3	ENSCHIG00000012385	103343230	103345451		
<i>DIP2C</i>	13	ENSCHIG00000024387	45929488	46232588		
<i>TENM3</i>	27	ENSCHIG00000011185	31756132	31951634		
<i>ATP1A1</i>	3	ENSCHIG00000017191	93611650	93645306		
<i>CD58</i>	3	ENSCHIG00000022779	93782057	93828732		
<i>IGSF3</i>	3	ENSCHIG00000003902	93835785	938357854118		
<i>LELP1</i>	3	ENSCHIG00000001135	102923551	102923862		
<i>PGLYRP3</i>	3	ENSCHIG00000014425	103016474	103027592		
<i>PGLYRP4</i>	3	ENSCHIG00000023048	103036240	103051776		
<i>S100A9</i>	3	ENSCHIG00000016845	103060350	103062557		
<i>S100A12</i>	3	3,ENSCHIG00000012846	103073976	103074689		
<i>S100A8</i>	3	,ENSCHIG00000026621	103093034	103095285		
<i>S100A7A</i>	3	ENSCHIG00000021789	103132447	103135381		
<i>S100A5</i>	3	ENSCHIG00000025911	103318019	103325852		

Gene	Chr	ensembl_gene_id	start_position	end_position	eROHI	iHS
S100A6	3	ENSCHIG000000020688	103320703	103321327		
S100A4	3	ENSCHIG000000025367	103329512	103331035		
S100A3	3	ENSCHIG000000019122	103333674	103334421		
S100A2	3	ENSCHIG000000012385	103343230	103345451		
DIP2C	13	ENSCHIG000000024387	45929488	46232588		

Appendix Table S3. Genes identified by both eROHI and iHS methods that could be under selection for adaptation in Philippine Native Antipas Cotabato goats

Gene	Chr	ensembl_gene_id	start_position	end_position	eROHI	iHS
<i>LTN1</i>	1	ENSCHIG000000017704	5551885	5606928		
<i>N6AMT1</i>	1	ENSCHIG000000016325	5624441	5651137		
<i>IMPG2</i>	1	ENSCHIG000000010277	45488451	45559633		
<i>SENPF</i>	1	ENSCHIG000000007729	45562538	45708401		
<i>TRMT10C</i>	1	ENSCHIG000000021446	45728081	45730881		
<i>PCNP</i>	1	ENSCHIG000000008043	45741144	45754120		
<i>ZBTB11</i>	1	ENSCHIG000000025095	45767913	45794388		
<i>RPL24</i>	1	ENSCHIG000000011680	45797490	45802486		
<i>CEP97</i>	1	ENSCHIG000000026482	45816279	45834769		
<i>NXPE3</i>	1	ENSCHIG000000019375	45862455	45911976		
<i>NFKBIZ</i>	1	ENSCHIG000000026427	45938828	45949946		
<i>CD86</i>	1	ENSCHIG000000016051	66200321	66262282		
<i>PPM1L</i>	1	ENSCHIG000000003416	105948229	106149989		
<i>ARL14</i>	1	ENSCHIG000000006468	106359940	106360518		
<i>BACE2</i>	1	ENSCHIG000000019839	140945578	141050286		
<i>VPS13C</i>	10	ENSCHIG000000021131	54902081	55081678		
<i>BIRC6</i>	11	ENSCHIG000000008751	14814450	15023548		
<i>TTC27</i>	11	ENSCHIG000000017374	15041613	15221433		
<i>LAPTM4A</i>	11	ENSCHIG000000022265	78515941	78533518		
<i>MATN3</i>	11	ENSCHIG000000018061	78543717	78561211		
<i>WDR35</i>	11	ENSCHIG000000006588	78567431	78620141		
<i>DENND1A</i>	11	ENSCHIG000000018070	94031929	94571672		
<i>CRYL1</i>	12	ENSCHIG000000020031	50765029	50829850		
<i>IFT88</i>	12	ENSCHIG000000020831	50842409	50907442		
<i>DIP2C</i>	13	ENSCHIG000000024387	45929488	46232588		
<i>COLEC10</i>	14	ENSCHIG000000014341	36906247	36966467		
<i>MAL2</i>	14	ENSCHIG000000017255	37054383	37083018		
<i>CCN3</i>	14	ENSCHIG000000020448	37205127	37212946		
<i>FABP12</i>	14	ENSCHIG000000023180	37319293	37328968		
<i>BPNT2</i>	14	ENSCHIG000000012443	58184581	58205608		
<i>PENK</i>	14	ENSCHIG000000023682	58526799	58531160		
<i>SDR16C5</i>	14	ENSCHIG000000020829	58634887	58651036		
<i>CHCHD7</i>	14	ENSCHIG000000013735	58699255	58702030		
<i>PLAG1</i>	14	ENSCHIG000000000623	58705530	58750468		
<i>MED4</i>	14	ENSCHIG000000014408	84213113	84213919		
<i>ADGRB3</i>	14	ENSCHIG000000014726	89095126	89785548		
<i>CNTN5</i>	15	ENSCHIG000000008692	73020289	73673681		
<i>RASSF5</i>	16	ENSCHIG000000020279	3646158	3719466		
<i>EIF2D</i>	16	ENSCHIG000000009380	3724413	3773755		
<i>DYRK3</i>	16	ENSCHIG000000019691	3780466	3789601		
<i>MAPKAPK2</i>	16	ENSCHIG000000026966	3826017	3874426		
<i>IL10</i>	16	ENSCHIG000000016979	3911733	3916213		
<i>IL19</i>	16	ENSCHIG000000025398	3990218	3995728		
<i>IL20</i>	16	ENSCHIG000000012522	4014668	4017657		

Gene	Chr	ensembl_gene_id	start_position	end_position	eROHI	iHS
IL24	16	ENSCHIG00000020998	4044059	4048938		
PIGR	16	ENSCHIG00000012705	4080424	4111314		
CR2	16	ENSCHIG00000024144	4811829	4861822		
CFH	16	ENSCHIG00000020774	5043000	5340821		
BRIP1	19	ENSCHIG00000015958	10852459	11034487		
NLGN2	19	ENSCHIG00000021280	26899903	26909530		
SPEM1	19	ENSCHIG00000023917	26911724	26912958		
SPEM2	19	ENSCHIG00000016697	26915295	26917125		
TMEM102	19	ENSCHIG00000014552	26924586	26926214		
FGF11	19	ENSCHIG00000007435	26928324	26931791		
CHRNB1	19	ENSCHIG00000014506	26933821	26942030		
ZBTB4	19	ENSCHIG00000008943	26946227	26950411		
POLR2A	19	ENSCHIG00000027173	26963534	26984357		
TNFSF12	19	ENSCHIG00000000561	27022567	27029946		
TNFSF13	19	ENSCHIG00000019003	27031650	27033491		
SENP3	19	ENSCHIG00000013302	27036049	27044939		
EIF4A1	19	ENSCHIG00000022153	27044917	27052117		
CD68	19	ENSCHIG00000023275	27048898	27053282		
MPDU1	19	ENSCHIG00000019131	27055203	27057983		
SOX15	19	ENSCHIG00000023104	27058791	27060151		
FXR2	19	ENSCHIG00000004007	27062218	27074796		
TP53	19	ENSCHIG00000025000	27115062	27119231		
WRAP53	19	ENSCHIG00000015730	27128624	27140297		
EFNB3	19	ENSCHIG00000027243	27142261	27146139		
DNAH2	19	ENSCHIG00000018276	27159932	27258078		
KDM6B	19	ENSCHIG00000017251	27271216	27279167		
TMEM88	19	ENSCHIG00000017315	27280796	27281386		
NAA38	19	ENSCHIG00000023618	27282423	27283177		
CYB5D1	19	ENSCHIG00000012741	27283814	27285252		
CHD3	19	ENSCHIG00000016737	27309869	27329583		
RNF227	19	ENSCHIG00000009394	27332688	27333337		
KCNAB3	19	ENSCHIG00000011995	27339323	27345597		
TRAPPC1	19	ENSCHIG00000013736	27346350	27347501		
CNTROB	19	ENSCHIG00000023991	27348737	27362472		
GUCY2D	19	ENSCHIG00000014967	27398191	27410090		
ALOX15B	19	ENSCHIG00000018610	27431401	27441932		
ALOX12B	19	ENSCHIG00000022813	27455260	27466250		
ALOXE3	19	ENSCHIG00000023588	27475122	27496753		
KRT14	19	ENSCHIG00000014749	41438964	41443106		
ATP6V0A1	19	ENSCHIG00000023886	42203714	42253663		
GH1	19	ENSCHIG00000011515	47734601	47769393		
CD79B	19	ENSCHIG00000016944	47749691	47752572		
SCN4A	19	ENSCHIG00000021518	47759118	47790226		
TIMP2	19	ENSCHIG00000024986	52667742	52723737		
CEP295NL	19	ENSCHIG00000011109	52693008	52694043		
USP36	19	ENSCHIG00000022760	52731153	52761521		
CYTH1	19	ENSCHIG00000018152	52774315	52854871		
DNAH17	19	ENSCHIG00000026163	52897938	52994842		
PGS1	19	ENSCHIG00000025453	52940412	53030476		
SOCS3	19	ENSCHIG00000011290	53047025	53047714		
SEPTIN9	19	ENSCHIG00000026942	53704072	53886331		
SEC14L1	19	ENSCHIG00000017729	53917976	53964284		
MGAT5B	19	ENSCHIG00000017785	54116939	54183008		
MFSD11	19	ENSCHIG00000025495	54225493	54255542		
SRSF2	19	ENSCHIG00000017001	54256679	54257574		

Gene	Chr	ensembl_gene_id	start_position	end_position	eROHI	iHS
<i>METTL23</i>	19	ENSCHIG00000003411	54260110	54264873		
<i>JMJD6</i>	19	ENSCHIG00000022054	54265565	54272298		
<i>MXRA7</i>	19	ENSCHIG00000009258	54278114	54308250		
<i>ST6GALNAC1</i>	19	ENSCHIG00000025600	54342504	54360205		
<i>NCKAP5</i>	2	ENSCHIG00000026101	71385431	72099649		
<i>RING1</i>	23	ENSCHIG00000015685	41282859	41287581		
<i>HSD17B8</i>	23	ENSCHIG00000017839	41289772	41291617		
<i>SLC39A7</i>	23	ENSCHIG00000024209	41291198	41295435		
<i>RXRB</i>	23	ENSCHIG00000010266	41296211	41301684		
<i>COL11A2</i>	23	ENSCHIG00000012269	41304154	41331925		
<i>HLA-DOA</i>	23	ENSCHIG00000014302	41361172	41367073		
<i>BRD2</i>	23	ENSCHIG00000013946	41390898	41399125		
<i>HLA-DMA</i>	23	ENSCHIG00000009464	41415870	41420259		
<i>HLA-DMB</i>	23	ENSCHIG00000026519	41430666	41440428		
<i>PSMB9</i>	23	ENSCHIG00000021513	41490176	41496621		
<i>TAP1</i>	23	ENSCHIG00000021983	41497225	41505487		
<i>AZGP1</i>	25	ENSCHIG00000009096	37326191	37330418		
<i>CUTC</i>	26	ENSCHIG00000003099	30928069	30961169		
<i>COX15</i>	26	ENSCHIG00000020850	30961472	30978246		
<i>ENTPD7</i>	26	ENSCHIG00000010544	30987712	31020033		
<i>SLC25A28</i>	26	ENSCHIG00000012444	31038722	31050152		
<i>NKX2-3</i>	26	ENSCHIG00000017672	31110370	31112925		
<i>GOT1</i>	26	ENSCHIG00000024327	31202588	31226427		
<i>MICU3</i>	27	ENSCHIG00000018526	25371031	25449457		
<i>ZDHHC2</i>	27	ENSCHIG00000012145	25477009	25538216		
<i>CNOT7</i>	27	ENSCHIG00000011886	25549202	25560951		
<i>VPS37A</i>	27	ENSCHIG00000014767	25562969	25597741		
<i>JAM3</i>	29	ENSCHIG00000010160	32279041	32314450		
<i>IGSF9B</i>	29	ENSCHIG00000020701	32406949	32449503		
<i>SPATA19</i>	29	ENSCHIG00000022538	32482825	32488593		
<i>KANK4</i>	3	ENSCHIG00000026610	37593162	37665561		
<i>USP1</i>	3	ENSCHIG00000015997	37796228	37805114		
<i>DOCK7</i>	3	ENSCHIG00000022741	37808445	37967395		
<i>SLAMF1</i>	3	ENSCHIG00000009511	110920402	110963644		
<i>LY9</i>	3	ENSCHIG00000015987	111216026	111243671		
<i>SLAMF7</i>	3	ENSCHIG00000021635	111319875	111328760		
<i>F11R</i>	3	ENSCHIG00000021162	111639204	111663588		
<i>OR6B1</i>	4	ENSCHIG00000009347	13409404	13410336		
<i>TCAF1</i>	4	ENSCHIG00000007610	13539370	13570010		
<i>TAS2R41</i>	4	ENSCHIG00000003306	13718114	13719049		
<i>TAS2R60</i>	4	ENSCHIG00000005346	13746731	13747684		
<i>EPHA1</i>	4	ENSCHIG00000021379	13791462	13806647		
<i>ZYX</i>	4	ENSCHIG00000006679	13807709	13815641		
<i>FAM131B</i>	4	ENSCHIG00000024536	13848174	13852281		
<i>CLCN1</i>	4	ENSCHIG00000021249	13856693	13893468		
<i>CASP2</i>	4	ENSCHIG00000017936	13900234	13916056		
<i>TMEM139</i>	4	ENSCHIG00000008369	13916357	13919937		
<i>GSTK1</i>	4	ENSCHIG00000020481	13938960	13944220		
<i>TAS2R40</i>	4	ENSCHIG00000013838	13962549	13963565		
<i>LRRN3</i>	4	ENSCHIG00000012067	63013801	63015927		
<i>IGIP</i>	7	ENSCHIG00000007518	59183771	59183932		
<i>PURA</i>	7	ENSCHIG00000009332	59197293	59198261		
<i>AFF4</i>	7	ENSCHIG00000015153	65962272	66010261		
<i>LEAP2</i>	7	ENSCHIG00000006437	66016949	66017708		
<i>UQCRCQ</i>	7	ENSCHIG00000017488	66022668	66023553		

Gene	Chr	ensembl_gene_id	start_position	end_position	eROHI	iHS
<i>GDF9</i>	7	ENSCHIG00000008167	66025761	66028245		
<i>NFIB</i>	8	ENSCHIG00000012253	29737003	29990995		
<i>SYNCRIP</i>	9	ENSCHIG00000024654	51069839	51094949		
<i>SNX14</i>	9	ENSCHIG00000017765	51113060	51184727		
<i>NT5E</i>	9	ENSCHIG00000010651	51193306	51257341		
<i>PTPRK</i>	9	ENSCHIG00000012147	53316339	53933686		
<i>IFNGR1</i>	9	ENSCHIG00000013778	62193789	62220406		
<i>ADAMTSL3</i>	21	ENSCHIG00000016050	23559190	23931341		
<i>SH3GL3</i>	21	ENSCHIG00000016013	23944408	24053516		
<i>CSGALNACT1</i>	27	ENSCHIG00000024893	7386261	7747003		
<i>INTS10</i>	27	ENSCHIG00000000076	7777730	7808698		
<i>HGSNAT</i>	27	ENSCHIG00000000180	7816593	7848495		
<i>POMK</i>	27	ENSCHIG00000011543	7857207	7866977		
<i>FNTA</i>	27	ENSCHIG00000011734	7876697	7900233		
<i>HOOK3</i>	27	ENSCHIG00000016259	7933812	8013230		
<i>SFRP1</i>	27	ENSCHIG00000014291	9355584	9395676		
<i>SNRPD2</i>	27	ENSCHIG00000016476	9464654	9465138		
<i>ZMAT4</i>	27	ENSCHIG00000022017	9653174	10021888		
<i>PTPRR</i>	5	ENSCHIG00000022880	42098970	42381066		
<i>PTPRB</i>	5	ENSCHIG00000018145	42379313	42499339		
<i>KCNMB4</i>	5	ENSCHIG00000008910	42531818	42605823		
<i>CNOT2</i>	5	ENSCHIG00000021610	42620332	42700916		
<i>MXRA7</i>	19	ENSCHIG00000009258	54278114	54308250		
<i>ST6GALNAC1</i>	19	ENSCHIG00000025600	54342504	54360205		
<i>NCKAP5</i>	2	ENSCHIG00000026101	71385431	72099649		
<i>RING1</i>	23	ENSCHIG00000015685	41282859	41287581		
<i>HSD17B8</i>	23	ENSCHIG00000017839	41289772	41291617		
<i>SLC39A7</i>	23	ENSCHIG00000024209	41291198	41295435		
<i>RXRΒ</i>	23	ENSCHIG00000010266	41296211	41301684		
<i>COL11A2</i>	23	ENSCHIG00000012269	41304154	41331925		
<i>HLA-DOA</i>	23	ENSCHIG00000014302	41361172	41367073		
<i>BRD2</i>	23	ENSCHIG00000013946	41390898	41399125		
<i>HLA-DMA</i>	23	ENSCHIG00000009464	41415870	41420259		
<i>HLA-DMB</i>	23	ENSCHIG00000026519	41430666	41440428		
<i>PSMB9</i>	23	ENSCHIG00000021513	41490176	41496621		
<i>TAP1</i>	23	ENSCHIG00000021983	41497225	41505487		
<i>AZGP1</i>	25	ENSCHIG00000009096	37326191	37330418		
<i>CUTC</i>	26	ENSCHIG00000003099	30928069	30961169		
<i>COX15</i>	26	ENSCHIG00000020850	30961472	30978246		
<i>ENTPD7</i>	26	ENSCHIG00000010544	30987712	31020033		
<i>SLC25A28</i>	26	ENSCHIG00000012444	31038722	31050152		
<i>NKX2-3</i>	26	ENSCHIG00000017672	31110370	31112925		
<i>GOT1</i>	26	ENSCHIG00000024327	31202588	31226427		
<i>MICU3</i>	27	ENSCHIG00000018526	25371031	25449457		
<i>ZDHHC2</i>	27	ENSCHIG00000012145	25477009	25538216		
<i>CNOT7</i>	27	ENSCHIG00000011886	25549202	25560951		
<i>VPS37A</i>	27	ENSCHIG00000014767	25562969	25597741		
<i>JAM3</i>	29	ENSCHIG00000010160	32279041	32314450		
<i>IGSF9B</i>	29	ENSCHIG00000020701	32406949	32449503		
<i>SPATA19</i>	29	ENSCHIG00000022538	32482825	32488593		
<i>KANK4</i>	3	ENSCHIG00000026610	37593162	37665561		
<i>USP1</i>	3	ENSCHIG00000015997	37796228	37805114		
<i>DOCK7</i>	3	ENSCHIG00000022741	37808445	37967395		
<i>SLAMF1</i>	3	ENSCHIG00000009511	110920402	110963644		
<i>LY9</i>	3	ENSCHIG00000015987	111216026	111243671		

Gene	Chr	ensembl_gene_id	start_position	end_position	eROHI	iHS
<i>SLAMF7</i>	3	ENSGHIG000000021635	111319875	111328760		
<i>F11R</i>	3	ENSGHIG000000021162	111639204	111663588		
<i>OR6B1</i>	4	ENSGHIG000000009347	13409404	13410336		
<i>TCAF1</i>	4	ENSGHIG000000007610	13539370	13570010		
<i>TAS2R41</i>	4	ENSGHIG000000003306	13718114	13719049		
<i>TAS2R60</i>	4	ENSGHIG000000005346	13746731	13747684		
<i>EPHA1</i>	4	ENSGHIG000000021379	13791462	13806647		
<i>ZYX</i>	4	ENSGHIG000000006679	13807709	13815641		
<i>FAM131B</i>	4	ENSGHIG000000024536	13848174	13852281		
<i>CLCN1</i>	4	ENSGHIG000000021249	13856693	13893468		
<i>CASP2</i>	4	ENSGHIG000000017936	13900234	13916056		
<i>TMEM139</i>	4	ENSGHIG000000008369	13916357	13919937		
<i>GSTK1</i>	4	ENSGHIG000000020481	13938960	13944220		
<i>TAS2R40</i>	4	ENSGHIG000000013838	13962549	13963565		
<i>LRRN3</i>	4	ENSGHIG000000012067	63013801	63015927		
<i>IGIP</i>	7	ENSGHIG000000007518	59183771	59183932		
<i>PURA</i>	7	ENSGHIG000000009332	59197293	59198261		
<i>AFF4</i>	7	ENSGHIG000000015153	65962272	66010261		
<i>LEAP2</i>	7	ENSGHIG000000006437	66016949	66017708		
<i>UQCRQ</i>	7	ENSGHIG000000017488	66022668	66023553		
<i>GDF9</i>	7	ENSGHIG000000008167	66025761	66028245		
<i>NFIB</i>	8	ENSGHIG000000012253	29737003	29990995		
<i>SYNCRIP</i>	9	ENSGHIG000000024654	51069839	51094949		
<i>SNX14</i>	9	ENSGHIG000000017765	51113060	51184727		
<i>NT5E</i>	9	ENSGHIG000000010651	51193306	51257341		
<i>PTPRK</i>	9	ENSGHIG000000012147	53316339	53933686		
<i>IFNGR1</i>	9	ENSGHIG000000013778	62193789	62220406		
<i>ADAMTSL3</i>	21	ENSGHIG000000016050	23559190	23931341		
<i>SH3GL3</i>	21	ENSGHIG000000016013	23944408	24053516		
<i>CSGALNACT1</i>	27	ENSGHIG000000024893	7386261	7747003		
<i>INTS10</i>	27	ENSGHIG000000000076	7777730	7808698		
<i>HGSNAT</i>	27	ENSGHIG000000000180	7816593	7848495		
<i>POMK</i>	27	ENSGHIG000000011543	7857207	7866977		
<i>FNTA</i>	27	ENSGHIG000000011734	7876697	7900233		
<i>HOOK3</i>	27	ENSGHIG000000016259	7933812	8013230		
<i>SFRP1</i>	27	ENSGHIG000000014291	9355584	9395676		
<i>SNRPD2</i>	27	ENSGHIG000000016476	9464654	9465138		
<i>ZMAT4</i>	27	ENSGHIG000000022017	9653174	10021888		
<i>PTPRR</i>	5	ENSGHIG000000022880	42098970	42381066		
<i>PTPRB</i>	5	ENSGHIG000000018145	42379313	42499339		
<i>KCNMB4</i>	5	ENSGHIG000000008910	42531818	42605823		
<i>CNOT2</i>	5	ENSGHIG000000021610	42620332	42700916		

Appendix Table S4. Genes identified by both eROHI and iHS methods that could be under selection for adaptation in African native goats

Gene	Chr	Ensembl ID	Start Position	End position	eROHI	iHS
<i>GNAO1</i>	18	ENSCHIG00000017883	25631854	25810789		
<i>CES5A</i>	18	ENSCHIG00000022885	26052029	26078928		
<i>BTNL2</i>	23	ENSCHIG00000020377	23313039	23326040		
<i>HLA-DRA</i>	23	ENSCHIG00000013201	23345617	23350010		
<i>DRB3</i>	23	ENSCHIG00000015976	23451944	23470477		
<i>CAHI-DQA2</i>	23	ENSCHIG00000010572	23557436	23568336		
<i>NR3C1</i>	7	ENSCHIG00000016782	56060015	56169881		
<i>ALAMF6</i>	3	ENSCHIG00000024954	110752497	110775276		
<i>CD84</i>	3	ENSCHIG00000020076	110806993	110847683		
<i>SLAMF1</i>	3	ENSCHIG00000009511	110920402	110963644		
<i>LY9</i>	3	ENSCHIG00000015987	111216026	111243671		
<i>KITLG</i>	5	ENSCHIG00000025211	17951263	18151736		
<i>NUP37</i>	5	ENSCHIG00000014565	64565822	64616711		
<i>PARBP</i>	5	ENSCHIG00000023012	64621561	64687303		
<i>PMCH</i>	5	ENSCHIG00000015954	64685250	64688807		
<i>IGFI</i>	5	ENSCHIG00000018863	64865221	64942529		
<i>PSPCI</i>	12	ENSCHIG00000016708	50435835	50484710		
<i>ZMYM5</i>	12	ENSCHIG00000022250	50495391	50512494		
<i>ZMYM2</i>	12	ENSCHIG00000011031	50561124	50625311		