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Genetic Diversity and Phylogenetic Relationships of Seven Dairy Goat Breeds in Yogyakarta and Central Java Based on Cytochrome B Gene

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ABSTRACT

Indonesia is endowed with numerous goat breeds, including meat-type, dual-purpose, and dairy goats. Previous studies have shown that some goat breeds are at risk of extinction, while the level of extinction risk for most Indonesian dairy goat breeds remain unknown. Moreover, the characterizations of Indonesian dairy goat breeds have been dominated by phenotypic descriptions with limited molecular data analysis. This study was conducted to explore the genetic diversity and phylogenetic relationship of seven dairy goat breeds found in Yogyakarta and Central Java, which included Saanen, British Alpine, Bligon, Anglo Nubian, Toggenburg, Nigerian dwarf, and the crossbred of Anglo Nubian with PE. DNA was extracted from blood samples taken from 31 goats. A 430 bp segment of the mitochondrial cytochrome *b* (*cyt b*) gene was amplified and sequenced, followed by aligning with reference sequences obtained from GenBank and then phylogenetic and genetic diversity analyses. Phylogenetic tree constructed showed two main clades where Nigerian dwarf goat was in separate clade from other dairy breeds. Three hypervariable sites, five polymorphic sites, five number of mutations and eight number of haplotypes were found across all samples suggesting low to moderate genetic differentiation among the breeds. The overall haplotype diversity and nucleotide diversity were 0.716±0.058 and 0.00251±0.00035, respectively while genetic distances among breeds ranged from 0.0 to 0.0038. The AMOVA results showed 82.17% of genetic variation was found within breeds, while 17.83% of the genetic variation was found among breeds. The revealed low to moderate genetic diversity among seven dairy goats breeds in this study indicates a narrow genetic base and high genetic homogeneity which may reduce adaptability and increase extinction risk. The findings highlight the urgent need for structured breeding programs and increased farmers awareness to conserve genetic resources.

KEYWORDS

Cytochrome b; Dairy goats; Genetic diversity; Haplotypes; Phylogenetic analysis

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1. Introduction

Indonesia is endowed with many goat breeds, including native, imported (exotic), and cross-breeds (Suyadi et al., 2022). The total goat population in Indonesia was reported to be 15.71 million in 2024 and is scattered all over the country, with Java Island accounting for more than 67% of all goats (BPS - Statistics Indonesia, 2024). Popular exotic dairy goat breeds in Indonesia include Saanen, British Alpine, Toggenburg, Anglo Nubian, while Bligon, Sapera, and Peranakan Ettawa (PE) are local dairy breeds that were developed by crossing native Indonesian goats and exotic breeds (Sudarman, 2017; Susilorini et al., 2022). Saanen is the most popular exotic dairy goat breed in Indonesia (Sudarman, 2017; Prayitno et al., 2021), while other exotic dairy goat breeds are present in relatively low numbers and are mostly used for crossing with local goats to increase milk production (Sudarman, 2017).

Dairy goats are an important component of smallholder livestock systems in Indonesia, providing household milk, income, and employment while able to adapt in diverse agro-ecological zones (Rahmawati et al., 2022; Sujarwanta et al., 2024). Study by Rahmawati et al. (2022) showed that most of the dairy goat breed characterization studies have been dominated by phenotypic descriptions. Another study by Hartatik et al. (2015) reported that despite their economic importance and potential genetic value, Indonesian goat breeds have limited information based on their genetic diversity. Furthermore, a study by Nur et al. (2023) showed

that some breeds of goat in Indonesia are at risk of extinction, while other breeds like Saanen, Sapera, PE, and Bligon, their level of risk of extinction is not known yet. Pakpahan et al. (2023) showed that dairy goats in Indonesia are also facing the problem of uncontrolled crossbreeding for improving milk production and other traits of economic importance, and this action has led to a decrease in genetic diversity.

Some surveys show that molecular research in Indonesia has been increasing year by year, although most of the research has remained fragmented and has covered few goat breeds per study (Jiyanto et al., 2014; Susilorini et al., 2022). This creates the need to conduct comprehensive, multi-breed genetic diversity analyses of Indonesian dairy goat breeds to inform and guide conservation, crossbreeding, or genomic selection strategies. Documentation of genetic diversity and the risk of breed extinction due to genetic erosion is of great importance for the effective implementation of conservation strategies (Câmara et al., 2017; Wilson, 2021).

One of the genetic markers which has been used for genetic diversity and phylogenetic analysis is Cytochrome b (*cyt b*) gene found in mitochondrial DNA (mtDNA) (Jiyanto et al., 2014) mainly due to easy accessibility of the mtDNA genes (Owaid et al., 2023), and a high rate of evolutionary and sequence variability (Prihandini et al., 2020). Furthermore, the rate of mutation in mtDNA is likely to happen much more frequently, as it can be compared to the nuclear genes, since mtDNA has no introns and it has efficient repair mechanisms (Prihandini et al., 2020).

In connection with the above-mentioned points, the present study was conducted to explore genetic diversity and phylogenetic relationship of seven dairy goat breeds raised in Yogyakarta and Central Java, including Saanen, British Alpine, Anglo Nubian, Toggenburg, Bligon, crossbred of Anglo Nubian and PE, and Nigerian dwarf through cytochrome b gene identification. The obtained molecular information will be useful for understanding existing phylogenetic relationships and the polymorphism level in the *cyt b* gene of the dairy goat breeds in the study, thereby guiding conservation strategies and breeding programs aimed at improving the sustainability of dairy goats in these regions.

2. Materials and Methods

2.1. Study area

The study was conducted in different goat farms found in Central Java (Purworejo and Baturaden), including goat farms at Faculty of Animal Science, Universitas Gadjah Mada, and the Regional Technical Implementation Unit of the Animal Diagnostic Livestock Breeding Development Center (UPTD-BPPTDK), Department of Agriculture and Food Security, Special Region of Yogyakarta.

2.2. Sample collection

A one mL of the blood was collected from the jugular vein of a goat by using BD Vacutainer K2 EDTA tubes with a single venipuncture for all 31 goats comprising 21 Saanen, 2 Anglo Nubian, 2 Bligon, 2 British Alpine, 2 Crossbred of Anglo Nubian and PE, 1 Toggenburg, and 1 Nigerian dwarf goat. The sample size of 31 goats across seven breeds was selected purposely (Purposive sampling) to avoid selecting bloodily related animals, pregnant does in their last trimester, and underage goats (kids). The sample size selected per breed in this study was a preliminary sample, and the small number of some breeds was due to financial resource constraints and the availability of particular breeds in the area of study, although the size was still useful for the basic population genetic analyses (haplotype detection, genetic diversity indices, and pairwise distances). A small sample size carries a high risk of sampling error and unreliable genetic diversity and phylogenetic estimates; however, these risks were minimized by obtaining maximum genetic information per sample.

Before blood collection, the goats were restrained without general anesthesia or sedation, and the entire process was performed by a qualified veterinarian, as it was recommended by the ethical committee to ensure animal welfare and minimize suffering. After collecting the blood samples, they were stored at −20°C before DNA extraction at the laboratory of Animal Breeding and Genetics, Faculty of Animal Science, Universitas Gadjah Mada (UGM).

2.3. DNA extraction

DNA was extracted from blood samples of seven goat breeds in the Laboratory of Animal Genetics and Breeding, Faculty of Animal Science, UGM, using a gSYNC DNA Extraction Kit supplied by Geneaid Biotech Ltd (Geneaid Biotech Ltd., 2017), and as it was reported by Hardyta et al. (2020); Hartatik et al. (2015); Prihandini et al. (2020).

2.4. Polymerase chain reaction (PCR)

Partial sequences of the *cyt b* gene from mtDNA with 430 bp were amplified by using DNA amplification techniques with forward primer: Cytb–F (5'- ATCCGAAAGACCCACCCATT-3') and reverse primer: Cytb–R (5'- TGATGACTGTTGCCCCTCAA-

Table 1. Estimates of Evolutionary Divergence over Sequence Pairs between Groups

Breed	SA	SAFB	BLG	BRA	TGB	ANPE	AN	NGD
SA	-							
SAFB	0.0000	-						
BLG	0.0021	0.0025	-					
BRA	0.0028	0.0013	0.0038	-				
TGB	0.0017	0.0000	0.0025	0.0013	-			
ANPE	0.0021	0.0025	0.0000	0.0038	0.0025	-		
AN	0.0030	0.0013	0.0038	0.0025	0.0013	0.0037	-	
NGD	0.0017	0.0025	0.0025	0.0013	0.0038	0.0025	0.0013	-

SA = Saanen (from Yogyakarta), SAFB = Saanen from Baturraden, BLG = Bligon, BRA = British Alpine, TGB = Toggenburg, ANPE = Crossbred of Anglo Nubia and PE, AN = Anglo Nubian, NGD = Nigerian dwarf.
The number of base substitutions per site from averaging over all sequence pairs between groups are shown. Analyses were conducted using the Kimura 2-parameter model (Kimura, 1980). This analysis involved 31 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There was a total of 430 positions in the final dataset. Evolutionary analyses were conducted in MEGA11 (Tamura et al., 2021).

Table 2. Indicating genetic diversity parameters as analyzed in DnaSP V6

Parameter	Value	Description
No. of sequences	35	Total aligned DNA sequences used included 31 samples and 4 reference sequences
bp	430	Number of nucleotide positions analyzed
S	5	Sites showing variation among sequences
Eta	5	Observed number of mutations
H	8	Identified unique sequence variants
Hd	0.716±0.058	Probability of two sequence to be different
π	0.00251±0.00035	Average nucleotide differences per site

bp = Sequence length, S = Polymorphic sites, Eta = Total number of mutations, H = Number of haplotypes, Hd = Haplotype diversity, π = Nucleotide diversity.

3'). The expected PCR product size of DNA samples was 430 bp, as it was confirmed in the NCBI Prime blast. PCR was conducted following the main steps reported by Agne et al. (2009), Joshi and Deshpande (2010), and EMD Millipore (2012), which include denaturation, primer annealing, and extension.

The PCR volume was 25 μL, consisting of 12.5 μL of PCR Master Mix, 0.5 μL of Forward Primer, 0.5 μL of Reverse Primer, 9.5 μL of Sterile Water, and 2 μL of extracted mtDNA. The PCR tubes were placed into the programmed thermocycler with the following conditions: initial denaturation temperature of 95°C for 3 min, 30 cycles of denaturation temperature of 95°C for 15 s, primer annealing temperature of 55°C for 15 s, initial extension temperature of 72°C for 15 s, and final extension temperature of 72°C for 5 min for the next cycles. The PCR products were stored at 4°C prior to gel electrophoresis.

2.5. Gel electrophoresis for PCR products

The gel electrophoresis was carried out following the procedures reported by Green and Sambrook (2012) to determine the success of the DNA amplification process. A 2% agarose gel was prepared by mixing 1 g of agarose gel in 50 mL of 1× TBE buffer, while 2 μL of a 10 mg/mL solution of ethidium bromide (EtBr) was used as the fluorescent dye. The PCR product was mixed with EtBr and loaded into the gel wells along with a 100 bp DNA ladder size marker. Electrophoresis was conducted at 100 V until the front migrated sufficiently, and the DNA bands were visualized under UV illumination.

2.6. Statistical analysis

2.6.1. Assembly and alignment of nucleotides

Forward and reverse strands of multiple sequences of the *cyt b* gene were collected and assembled using Sanger Sequencing (IKU/7.2/GS-01) at the Integrated Laboratory for Research and Testing at Universitas Gadjah Mada (LPPT-UGM). The results of the *cyt b* gene sequencing were edited and compared to the 4 reference sequences from GenBank with accession numbers D84201.1, AB004074.1, NC_005044.2, and KY564254.1, by using MEGA 11 Software.

2.6.2. Phylogenetic tree and genetic distances

The phylogenetic tree was drawn by the Neighbor-joining tree (NJT) method using the MEGA 11 software, following procedures reported by Tamura et al. (2021). The NJT elaborates the phylogenetic relationships among populations from the genetic distance estimation (Owaid et al., 2023). Pairwise genetic distances among dairy goat populations were estimated using the Kimura two-parameter model algorithm found in MEGA 11 software. Also, the hypervariable sites were assessed by using MEGA 11 software after sequence alignment. A hypervariable site is the region or position in a nucleotide sequence of DNA that has a high rate of mutation or variation among a certain population of organisms (Ajibike et al., 2016).

2.6.3. Haplotyping and genetic diversity analysis

Haplotyping of the *cyt b* gene of mtDNA was performed using DnaSP v6 software (Librado and Rozas, 2009) to identify the unique combinations of genetic variations (such as SNPs) in an aligned and sequenced mtDNA. DnaSP is a software package for a comprehensive analysis of DNA polymorphic data.

2.6.4. The median-joining network analysis

Haplogroup classification of the detected haplotypes was visualized to determine the genetic relationships and evolutionary pathways among the dairy goat breeds by median-joining network (MJ) analysis performed in PopART 1.7 software (Leigh and Bryant, 2015) with default parameters.

Table 3. Haplotypes shared among seven dairy goats found in Yogyakarta and Central Java and reference breeds from *Capra hircus*.

Haplotype #	Frequency	Sequences
Hap_1	1	D84201.1-1
Hap_2	16	KY564254.1, SA1, SA2, SA3, SA4, SA5, SA18, SA19, SA22, SA35, SAFB1, SAFB2, BRA1, TGB1, AN2, NGD1
Hap_3	10	NC_005044.2, SA20, SA23, SA27, SA33, SA38, BLG1, BLG2, AN1, AN2
Hap_4	1	AB004074.1
Hap_5	2	SA7, BRA2
Hap_6	1	SA12
Hap_7	3	SA25, SA28, SA31
Hap_8	1	AN1

SA = Saanen, SAFB = Saanen from Baturraden, BRA = British Alpine, TGB = Toggenburg, AN = Anglo Nubian, NGD = Nigerian dwarf, BLG = Bligon.

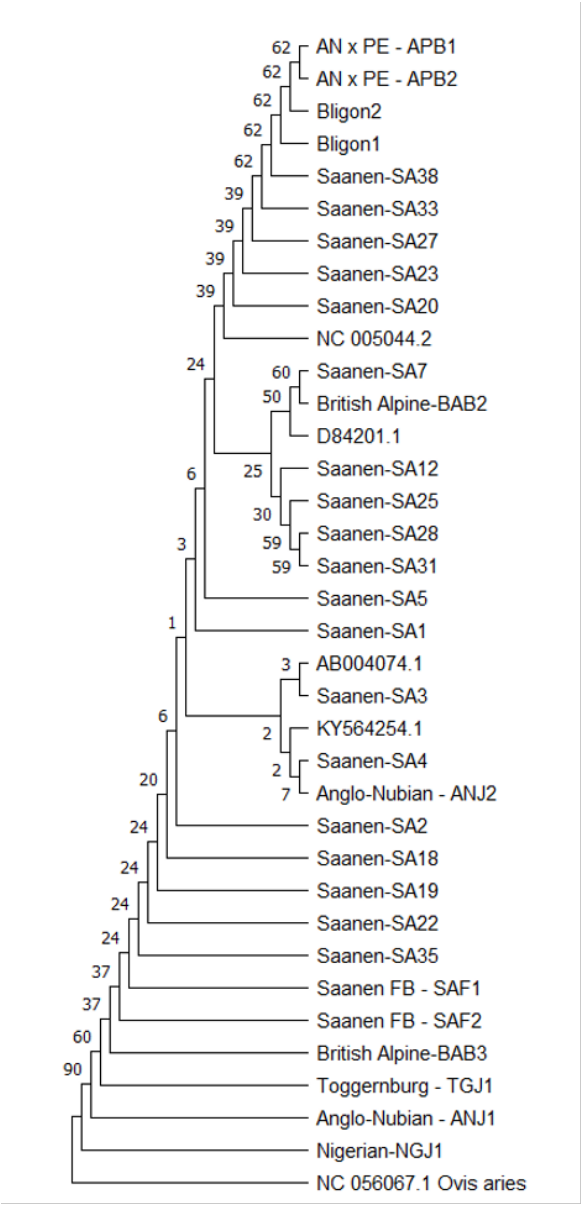

Figure 1. Phylogenetic tree of seven dairy goat breeds and reference sequences from GenBank

2.6.5. Analysis of molecular variance

Analysis of molecular variance (AMOVA) was performed to evaluate total genetic variation among and within goat breeds by using Arlequin ver 3.5.2.2 (Excoffier and Lischer, 2010) with 1000 permutations.

3. Results and Discussion

3.1. Phylogenetic tree

To ensure proper phylogenetic tree construction, the study used a GenBank sequence for Ovis aries (NC_056067.1) as an outgroup to anchor the tree and facilitate the separation of ancestral lineages among samples. The Neighbor Joining Tree (NJT), which was constructed in MEGA 11, showed two major clades. First major clade contains Saanen, British Alpine, Bligon, Anglo Nubian, Toggenburg, and Crossbred of Anglo Nubian with Peranakan Etawa, while the second major clade contains only Nigerian dwarf goat (**Figure 1**). In sub-clades, Saanen goats were found to split across multiple lineages in the tree. Sub-clade containing crossbred of Anglo Nubian and PE found to be closely with the sub-clade of Bligon and some Saanen goats. Saanen from Baturraden (Saanen FB) were found in closely sub-clades along with some Saanen from Yogyakarta and Purworejo. The Nigerian dwarf goat was found in a separate clade, far from other exotic dairy goat breeds, and is locally adapted to Indonesia. The reference sequences were found across clades containing some Saanen goats, British Alpine goats, and Anglo-Nubian goats. The Nigerian Dwarf being placed in a separate clade reflecting a distinguishable genetic signature, while Saanen, Toggenburg, British Alpine, Anglo Nubian, Bligon, and Anglo Nubian x PE crossbred to be placed in the same main clade reflects a close evolutionary relationship and possible shared maternal lineage or gene flow among the breeds.

3.2. Genetic distances

Pairwise genetic distances of seven dairy goat breeds found in Yogyakarta and Central Java were estimated by using the Kimura two-parameter model algorithm, as shown in **Table 1**. The highest genetic distances (0.0038) were observed between Nigerian dwarf against Toggenburg; Bligon against British Alpine and Anglo Nubian and British Alpine against Crossbred of Anglo Nubian and PE while the lowest genetic distances (0.0000) were observed between Saanen from Baturraden against Saanen from Yogyakarta; Bligon against crossbred of Anglo Nubian and PE; and Saanen from Baturraden against Toggenburg. This narrow genetic distance, ranging from 0.0 to 0.0038, implies a low overall divergence among the studied goat populations.

3.3. Nucleotide variations and single-nucleotide polymorphisms (SNPs) analysis

The silent mutation was found at position 24th of the Anglo Nubian goat sequence, whereby guanine changed to adenine (G>A), but the amino acid remained Threonine (**Figure 2**). A total of 3 hypervariable sites were detected at 284th, 371st, and 372nd positions in nucleotide sequences of some breeds (**Figure 3** and **Figure 4**). At position 284th, there was a missense mutation where thymine changed to cytosine (T>C) in some Saanen goats, Bligon goats, crossbreeds of Anglo Nubian × PE, and one sequence from GenBank with accession number NC_005044.2 (**Figure 3**). This missense mutation changes the amino acid from Isoleucine

Table 4. Analysis of molecular variance (AMOVA) based on mtDNA data from dairy goat breeds in the study.

SV	d.f.	SS	VC	PV	p-value
Among Population	5	3.574	0.09184 Va	17.82700	0.06061±0.00703
Within Population	23	9.737	0.42334 Vb	82.17300	
Total	28	13.310	0.51518		
Fixation Index	FST:	0.17827			

SV = Source of variation; d.f = degree of freedom; SS = Sum of squares; VC = Variance components; PV = Percentage variation, $\alpha = 0.05$.

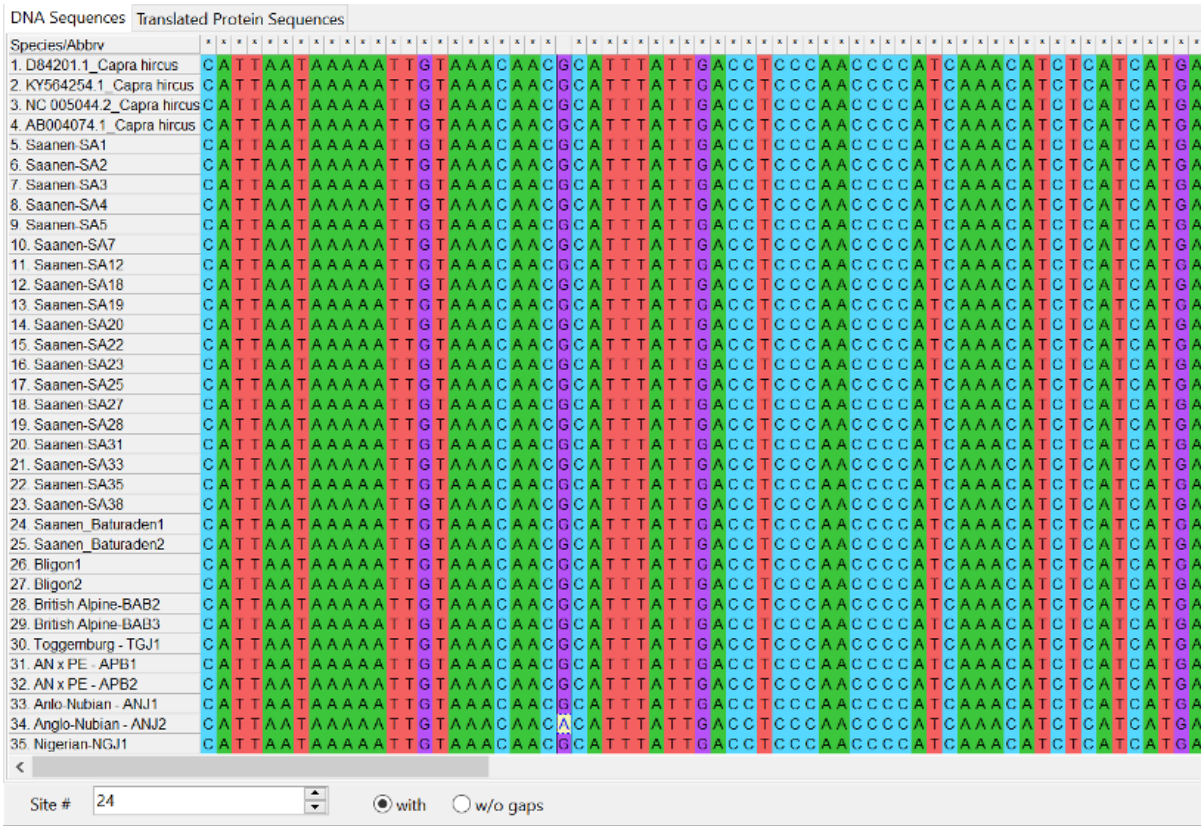

Figure 2. A silent mutation (G>A) where a base substitution did not alter the encoded amino acid was identified in the Anglo Nubian sequence at the 24th nucleotide position (highlighted in yellow) after multiple sequence alignment of *cyt b* gene fragments from seven goat breeds.

to Threonine (**Figure 5**). Another missense mutation was found at positions 371st and 372nd of some Saanen goats, British Alpine, and coincides with a mutation in the reference sequence with accession number D84201.1, where cytosine changed to thymine (C>T) (**Figure 4**). This mutation resulted in a change in the amino acid from Phenylalanine to Serine (**Figure 5**). The presence of only three hypervariable sites translated to two missense mutations and one silent mutation in the sequences with 430 bp, is an indication of limited sequence variation within the *cyt b* gene, which suggests overall mitochondrial conservation among the studied dairy goat breeds.

3.4. Haplotyping and genetic diversity analysis

The genetic diversity and haplotyping analyses were performed using *DnaSP* v6 software, including a total of 35 nucleotide sequences, comprising 31 samples from seven dairy goat breeds and 4 reference sequences from GenBank with accession numbers D84201.1, AB004074.1, NC_005044.2, and KY564254.1. The study found 5 polymorphic sites, of which 4 were in goat samples and 1 was in the reference sequence (**Table 2**). Moreover, the study found 5 mutations (Eta), of which 4 were from goat samples and 1 was found in the reference sequence. Overall haplotype diversity (Hd) and nucleotide diversity (π) were 0.716 ± 0.058 and 0.00251 ± 0.00035, respectively (**Table 2**). The moderate haplotype diversity (Hd) of 0.716 and low nucleotide diversity (π) of 0.0025 is an indication of relative homogeneous population of goat breeds with different multiple maternal origins, which combine local dual-purpose goats and exotic dairy goat breeds.

Furthermore, the study found 8 haplotypes (H) across all breeds. Out of the 8 haplotypes detected, only three haplotypes (Hap_2, Hap_3, and Hap_5) were shared by more than one population (**Table 3**). Haplotype 2 (Hap_2) was present in 15 sequences (48.39%) out of 31 samples of the dairy goats in the study and 1 sequence from GenBank, and it was found to be the most frequent haplotype.

3.5. Median joining network

The genetic relationships among 8 haplotypes that were identified in the populations of the study were analyzed by constructing Median Joining Network (MJN) using PopART software (**Figure 6**).

3.6. Analysis of molecular variance (AMOVA)

The proportion of genetic variation attributable to differences among and between populations (breeds) was analyzed using analysis of molecular variance (AMOVA) in Arlequin ver 3.5.2.2, as shown in **Table 4**. The level of genetic differentiation between two different breeds was further analyzed in RStudio software using FST values generated in Arlequin ver 3.5.2.2 as shown in **Figure 7**. The higher genetic diversity within breeds than among breeds suggests substantial gene flow and admixture among populations, reducing the degree of differentiation.

3.7. Phylogenetic tree

The results of phylogenetic tree analysis placed the seven goat breeds in the study and reference sequences into two main clades (**Figure 1**). Saanen, British Alpine, Bligon, Anglo Nubian, Toggenburg, and Crossbred of Anglo Nubian with Peranakan Etawa were placed in the same large clade with all four reference sequences. This result is in concordance with a study done by Susilorini et al. (2022), which classified goat breeds in Java into

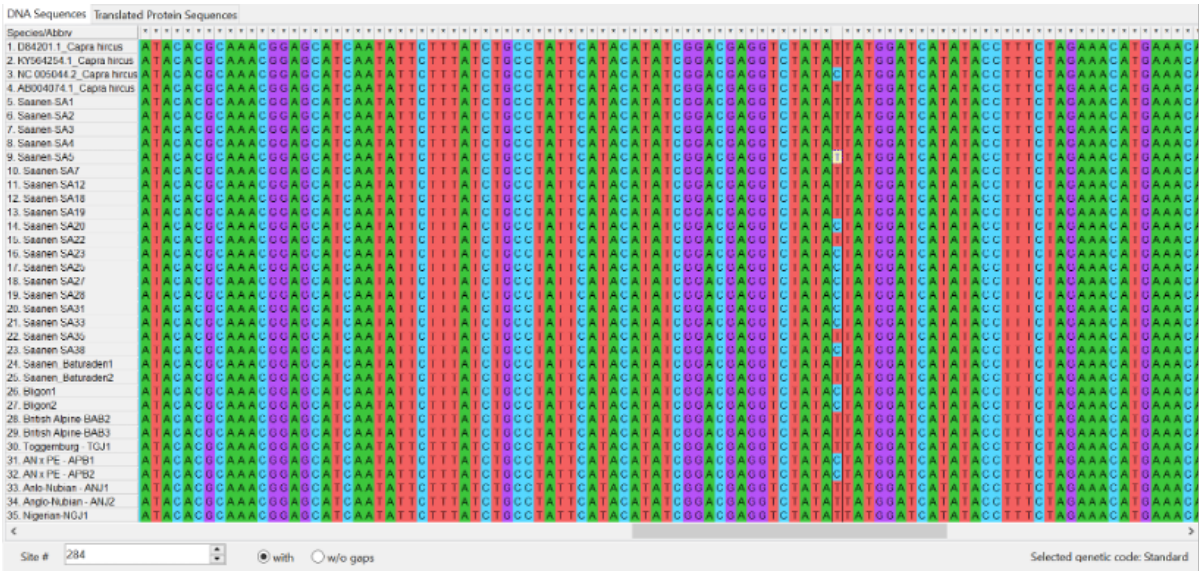

Figure 3. Showing the nucleotide hypervariability at position 284th in some sequences of Saanen, Bligon and crossbred of Anglo Nubian and PE breeds where T>C after multiple sequence alignment of *cyt b* gene fragments from seven goat breeds.

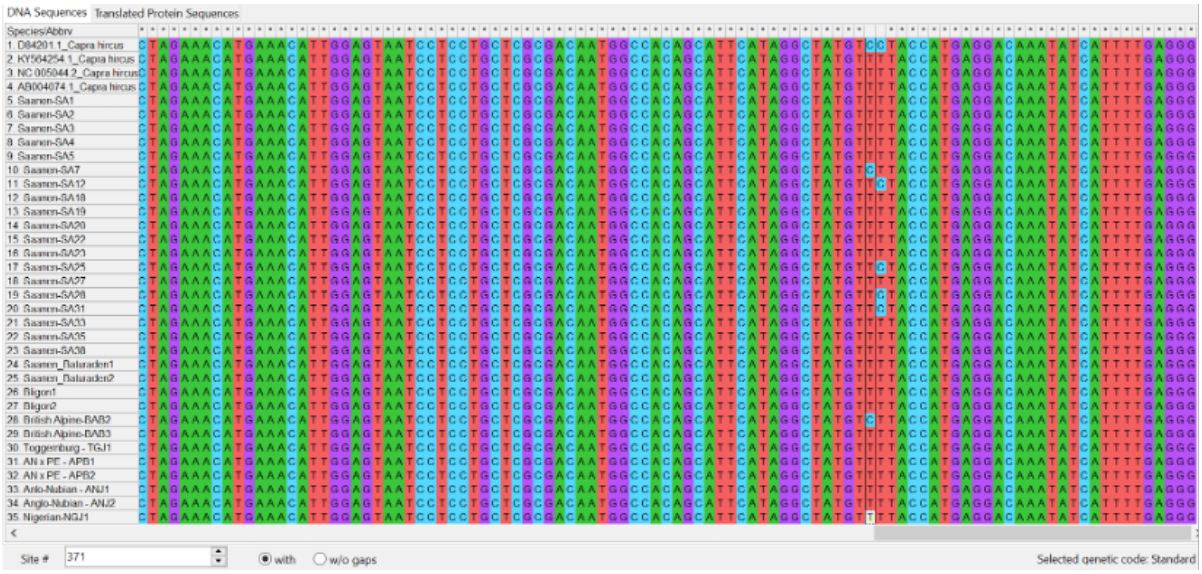

Figure 4. Showing the nucleotide hypervariability at position 371st and 372nd in some sequences of Saanen and British Alpine breeds where C>T after multiple sequence alignment of *cyt b* gene fragments from seven goat breeds.

three main clusters, with dairy goats forming a separate cluster. Within sub-clades, Saanen goats were found to split into multiple lineages, indicating mitochondrial diversity within the breed. This splitting of Saanen goats across multiple lineages could be attributed to the different maternal origins of the Saanen goat breed and crossbreeding strategies used by farmers to improve productivity, which can cause gene flow in other breeds (Tarekegn et al., 2018).

Sumarmono (2022) reported that Saanen is the most widely raised exotic dairy goat breed in Java Island; therefore, there is a possibility of the presence of uncontrolled crossbreeding with other dairy goats. Sub-clade containing crossbred of Anglo Nubian and PE found to be closely related to the sub-clade of Bligon and some Saanen goats. This is because PE and Bligon goats share mitochondrial lineage from Etawah goat (El Akbar et al., 2019; Rahmawati et al., 2022). Saanen goats from Baturraden (Saanen FB) were found in close sub-clades together with some Saanen from Yogyakarta and Purworejo. Results of the present study and previous studies categorized Saanen in one large clade of dairy goats, implying that they have a maternal relationship (Suyadi et al., 2022).

Nigerian dwarf goat was found in a separate clade relative to the other dairy goat breeds (Saanen, Toggenburg, British Alpine, Anglo-Nubian X PE crossbreeds, and Bligon). Nigerian dwarf goats are dual-purpose goats that originated from West Africa (Chiejina et al., 2009). The pattern that placed the Nigerian dwarf goat in a separate clade indicates that this breed carries a distinguishable genetic signature. This can be attributed to the historic origin of Nigerian Dwarf goats, which trace their ancestry to West African dwarf goat populations that persisted

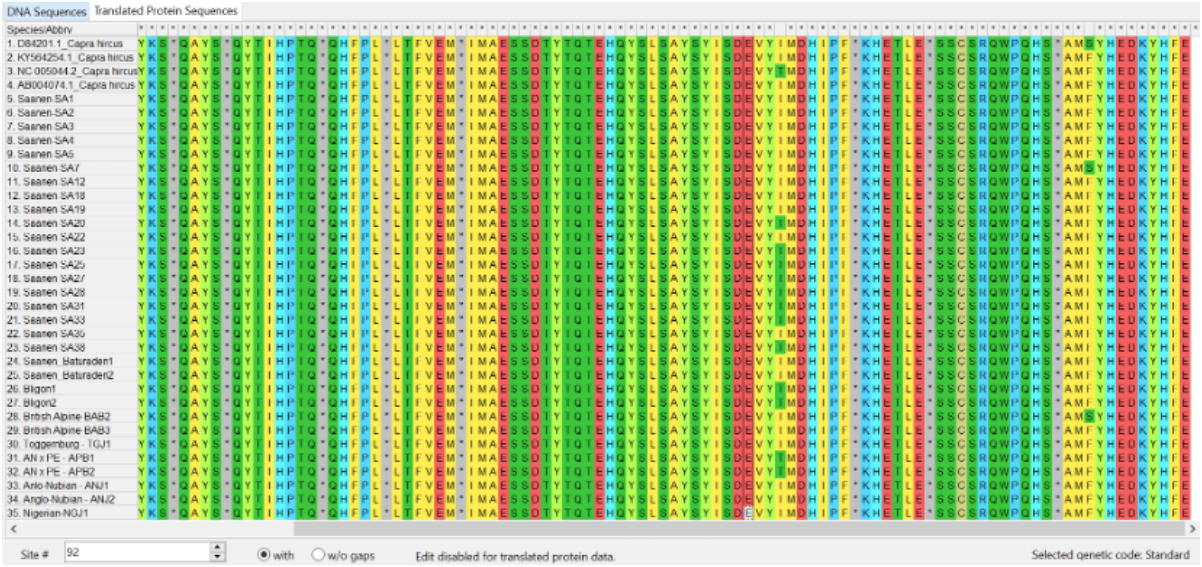

Figure 5. The missense mutation which leads to change in amino acids from Isoleucine > Threonine and Phenylalanine > Serine at positions 284th, 371st and 372nd respectively, in some sequences of Saanen, Bligon, British Alpine and Crossbred of Anglo Nubian and PE after multiple sequence alignment of *cyt b* gene fragments from seven goat breeds.

in a different geographic and breeding context from European dairy goat strains. West African dwarf goats often have mtDNA haplotypes and population structure that separate them from European and Asian dairy goats' lineages, reflecting differences in their maternal lineages (Kawaguchi et al., 2019).

Another possible reason for the Nigerian dwarf goat to be found in a separate clade is differential selection and breeding practices, which can enhance genetic separation at the breed level. Eurasian dairy breeds have been subjected to long-term intensive selection for high milk production and commercial breeding programs that might promote particular variants (Kawaguchi et al., 2019), while Nigerian dwarf goats have been managed under a small population size, adaptation to humid conditions in extensive systems (Ajibike et al., 2016). In the long run, such selective breeding regimes, combined with low gene flow from Eurasian dairy goats into Nigerian dwarf goats, can create a distinct genetic cluster. Breeding decisions and management practices taken by human beings have a direct impact on the population structure

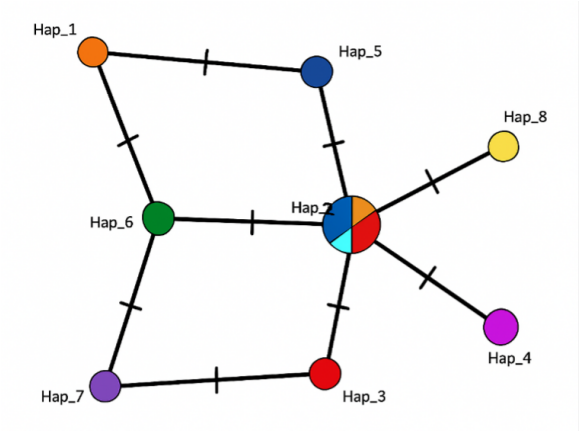

Figure 6. Median-joining network for the 8 mtDNA haplotypes of seven dairy goats in Yogyakarta and Central Java.

of the domesticated animals (Tarekegn et al., 2018). A study by Naderi et al. (2007) showed that human breeding decisions are one of the main factors that influence the clustering of breeds. Therefore, the finding of Nigerian dwarf in a separate clade is consistent with the breed's maternal origin and the breed's selection history.

Saanen, Anglo Nubian, British Alpine, and Toggenburg originated in Europe and have been domesticated in Indonesia for a long time (Stemmer et al., 2009; Norris et al., 2011; Sudarman, 2017; Praharani et al., 2019), while PE and Bligon are native to Indonesia (Rahmawati et al., 2022; Nur et al., 2023). The difference between Nigerian Dwarf and European dairy breeds (Saanen, Anglo-Nubian, British Alpine, Toggenburg), can furthermore be explained by considering their evolutionary and domestication pressures. European dairy breeds show strong signatures of selective breeding for milk production and have been reported to experience founder events associated with reduced effective population sizes due to pedigree-based management, which leads to the development of breed-specific alleles and reduced neutral diversity at some loci (Colli et al., 2018; Henkel et al., 2019). The difference between Nigerian dwarf and Indonesian crossbreeds can be attributed to the fact that Bligon and Anglo-Nubian × PE crossbreeds combine variants from native and exotic gene pools through hybridization, which might be attributed to conservation of specific variants inherited from their maternal lineages, as it was reported by Haryanto et al. (2025). The study by Xiong et al. (2023) showed that breeds raised under certain harsh conditions, such as tropical heat, high humidity, and high load of endemic parasites, develop local adaptation, which leads to the accumulation of variants that may be absent in recently introduced breeds.

3.8. Genetic distances

Pairwise genetic distances of seven dairy goat breeds raised in Yogyakarta and Central Java, which were estimated by using the Kimura two-parameter model algorithm, ranged from 0.0 to 0.0038. The highest genetic distances (0.0038) were observed between Nigerian dwarf against Toggenburg; Bligon against

British Alpine and Anglo Nubian; and British Alpine against Crossbred of Anglo Nubian and PE, while the lowest genetic distances (0.0) were observed between Saanen from Baturraden against Saanen from Yogyakarta; Bligon against crossbred of Anglo Nubian and PE; and Saanen from Baturraden against Toggenburg. These results are consistent with those reported by Pakpahan et al. (2015) which shows that some populations of Indonesian goats, such as Bligon and PE, have a very close genetic distance (0.0). Moreover, the study by Suyadi et al. (2022) showed that Indonesian goat breeds, including Bligon, PE, and their crosses, had a fairly close genetic distance, which ranged from 0.0 to 0.0040.

The current study found fairly small overall genetic distances among dairy goat breeds raised in a closely geographical environment (Yogyakarta and Central Java). This low level of genetic divergence suggests a high degree of genetic similarity, which may be attributed to gene flow due to geographical proximity, shared breeding practices, or the exchange of breeding stock among farmers in the region. The result of current study is in concordance with a study done by Wang et al. (2017) In China, which found the smallest genetic distance and relationship among groups of Chinese dairy goat breeds raised within the same geographical location.

The considerably higher genetic distances of 0.0038 between Nigerian dwarf against Toggenburg; Bligon against British Alpine and Anglo Nubian; and British Alpine against Crossbred of Anglo Nubian and PE are an indication of clear genetic differentiation, suggesting limited maternal gene flow among the populations (Batubara et al., 2012; Peng et al., 2022).

Genetic distance between Saanen goats and Bligon was relatively small (0.0021), which differs from the results reported by Suyadi et al. (2022) whereby Saanen goats had the farthest distance compared with other Indonesian goat breeds. The discrepancy may reflect differences in sampling, genetic markers used, or recent crossbreeding events in the study population that have narrowed the genetic gap between these breeds. Saanen from Baturraden showed the lowest genetic distance of 0.0 against Saanen from Yogyakarta and Toggenburg, which is attributable to shared maternal lineage and an indicator of complete genetic similarity of these populations.

De Araújo et al. (2006) reported genetic similarity between Alpine and Saanen dairy goats imported from temperate regions and their crosses in Brazil, which signifies the possibility that temperate dairy goats share a common mtDNA lineage. Furthermore, the low genetic distances that were observed in this study highlight not only the genetic closeness among breeds in the region but also raise important considerations regarding the conservation of purebred animal genetic resources.

3.9. Single-nucleotide polymorphisms (SNPs) analysis

The silent mutation was found at position 24th in the Anglo-Nubian goat, where G>A and the amino acid remained unchanged (Threonine) as shown in **Figure 2**. The silent mutation reported in the Anglo-Nubian goat has been widely reported in other studies involving dairy goats. Study by Kem Githui (2018) reported a silent mutation in Toggenburg and dual-purpose goats raised in Kenya. Although mutations are selectively neutral, they are used to trace an individual's lineage and construct a haplotype network (Hermes et al., 2020). The current study agrees with the results found by Owaid et al. (2023) which reported that most of the mutations in the *cyt b* gene are tandem mutations, with switching from a purine to a purine or a pyrimidine to a pyrimidine.

A total of 3 hypervariable sites were detected at 284th, 371st, and 372nd positions in nucleotide sequences of Saanen, Saanen Baurraden, British Alpine, Bligon, and Anglo Nubian × PE crossbreeds while absent in Nigerian Dwarf and Toggenburg goats (**Figure 3** and **Figure 4**). The current study is in concordance with the studies done by Lestari et al. (2018) and Pakpahan et al. (2016), which reported the availability of hypervariable sites in the *cyt b* gene of the Indonesian goats. The higher frequency of hypervariable sites in Saanen and British Alpine may be associated with their long history of introduction in the country, which has provided sufficient generations for mutations to accumulate under local selective pressures. The Indonesian government has coordinated various goat improvement programs by importing exotic goat breeds mainly from Australia and crossing with local breeds (Murray et al., 2011). A study by Ghanatsaman et al. (2023) showed that breeds maintained in a certain new environment for a long period of time tend to accumulate local selection signatures. Also, presence of higher hypervariable frequency in

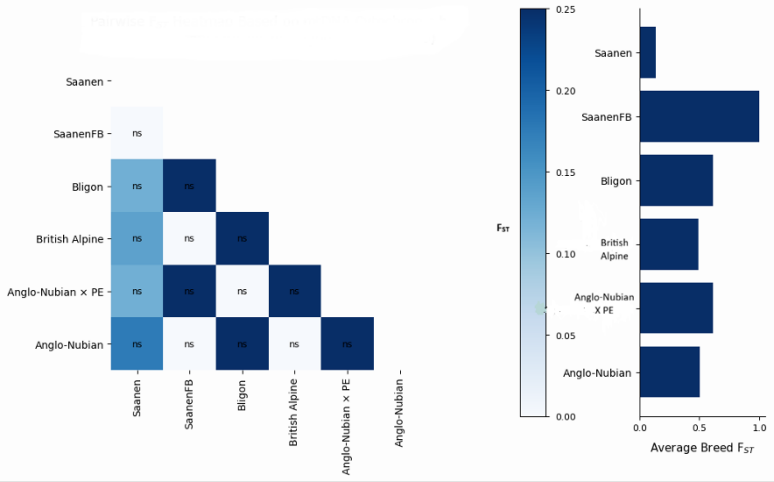

Figure 7. The triangular matrix displays pairwise genetic differentiation among the studied populations, generated using *RStudio* software. Darker shading indicates greater differentiation, while lighter shading represents lower differentiation (magnitude of FST). "ns" denotes non-significant pairwise comparisons (p>0.05). The bar plot on the right represents average breed-specific FST values calculated excluding self-comparisons.

Bligon and Anglo-Nubian × PE which are crossbreeds and native breeds to Indonesian environment, increases opportunities for the introduction of new variants from multiple parental pools, which can raise the chance of observing hypervariable sites in a sampled individual (Haryanto et al., 2025).

In contrast, the absence of the hypervariable sites in Nigerian Dwarf and Toggenburg goats could be attributable to their relatively recent introduction and smaller effective population sizes, which limit the occurrence and detection of such variants. Study by Taberlet et al. (2011) showed that breed of animal with a smaller effective size tends to have reduced genetic diversity. Moreover, the absence of hypervariable sites in these breeds could indicate a highly conserved genetic background, suggesting lower adaptation to a new environment.

At position 284th, a missense mutation involving a transition from thymine (T) to cytosine (C) was observed in some individuals of the Saanen, Bligon, and Anglo Nubian × PE crossbreeds. This missense mutation changed the amino acid from Isoleucine to Threonine. Such a shift may potentially affect protein structure or function, especially if the altered residue plays a role in electron transport within the mitochondrial membrane. Obvintseva et al. (2022) reported that isoleucine plays an important role in glucose utilization by activating glucose transporters in the intestines and muscles; therefore, the mutation can result in inefficient glucose utilization in animals.

Another missense mutation was found at positions 371st and 372nd of some sequences of Saanen goats, British Alpine, and coincides with a mutation in the reference sequence with accession number D84201.1, where C>T. This mutation resulted in a change in the amino acid from Phenylalanine to Serine. Flydal and Martinez (2013) and Li et al. (2023) reported that the major use of phenylalanine in animal species is for the biosynthesis of the enzyme phenylalanine hydroxylase, which catalyzes the hydroxylation of phenylalanine to tyrosine; therefore, a deficiency of phenylalanine hydroxylase is highly associated with a life-threatening disease such as phenylketonuria.

The detection of these hypervariable and missense mutations underscores the genetic heterogeneity within and among goat breeds in Indonesia. These findings have important implications for breed identification, phylogenetic inference, and the design of conservation strategies, particularly in safeguarding genetic resources with potentially unique mitochondrial signatures.

3.10. Haplotyping and genetic diversity

The study found 5 polymorphic sites, of which 4 were from goats' samples while 1 was found in the reference sequence (**Table 1**). Also, the study found 5 mutations (Eta), whereas 4 were from goats' samples, while 1 was found in the reference sequence. The presence of a low nucleotide variation level, which is indicated by 5 polymorphic sites and 5 mutations among 430 bp, suggests limited mutational changes in the populations of the study, which can be attributed to the small effective population size of dairy goats in Indonesia (Sudarman, 2017).

3.11. Haplotyping and genetic diversity

Furthermore, the study found that 8 haplotypes were observed in whole breeds. Availability of 8 different haplotype patterns across the sequences signifies that, despite low polymorphism shown by the population in the study, there is some degree of richness in haplotype, which is a sign of maternal lineage diversity in the mtDNA of the dairy goat breeds. The results on the number of haplotypes in the current study, which were obtained after partial sequencing of the *cyt b* gene of seven goat breeds, were still in the range of the number of haplotypes reported by Suyadi et al. (2022), which was 6 in Saanen goats and 7 in PE goats after complete sequencing of the *cyt b* gene of goats in East Java. Pakpahan et al. (2016) reported 8 haplotypes between *C. hircus* with accession number D84201 and Indonesian goats, which include PE and Bligon.

Out of the 8 haplotypes detected, only three haplotypes (Hap_2, Hap_3, and Hap_5) were shared by more than one population (**Table 3**). Haplotype 2 (Hap_2) was found in 15 sequences (48.39%) out of 31 dairy goat samples in the study and was the most frequent haplotype. A haplotype with high frequency can signify to represent maternal origin of the population in the study Prihandini et al. (2020). Saanen goats were found linked to Hap_2, Hap_3, Hap_5, Hap_6, and Hap_7. This implies that the breed has a high level of maternal genetic diversity, although this doesn't mean the breed has better productive performance than other (Fuchs et al., 2010). The results of the current study agree with the study done by Deniskova et al. (2020) The overall haplotype diversity (Hd) and nucleotide diversity (π) were 0.716 ± 0.058 and 0.00251 ± 0.00035, respectively (**Table 2**). This implies that there is a 71.6% possibility that two individuals randomly selected have different haplotypes (Fuchs et al., 2010). The Hd of 0.716 is relatively higher, insinuating that even though nucleotide changes are few, they are positioned in a way that still maintains diversity of population. These results on Hd (0.716) in the current study have a relatively close value to the Hd value (0.891) reported by Suyadi et al. (2022) on Indonesian goats. Low π value of 0.00251 signifies that there is relatively small average nucleotide variation per site, indicating the population in the study is genetically homogenous at the base pair level due to a common maternal lineage (Kartavtsev and Lee, 2006).

Low genetic diversity in dairy-goat populations is associated with reduced ability to adapt to environmental changes, including disease pressure. Studies by FAO (2010) and Gipson (2019) showed that increased homozygosity due to low genetic diversity in organisms tends to result in poor fitness and a high risk of inbreeding depression, which is directly linked to reduced fertility, compromised survival rates, and overall reduced productivity of organisms, especially under environmental stresses. Low genetic diversity in local goats raised in smallholder farms in China and Benin is reported to result in the challenges of improving traits of economic importance, such as heat tolerance and lactation persistence, due to limited selection caused by high homogeneity (Whannou et al., 2023; Lu et al., 2025).

To ensure high adaptability of dairy goats while improving dairy goat performance, different structured breeding programs have been proposed in different studies. Report by FAO (2010) showed that the combination of in-situ conservation of local animal genetic resources and scientifically guided programs can improve both adaptability and productivity. Proper animal record keeping, applying structured community-based nucleus breeding programs, controlled rotational mating schemes, baseline molecular characterization of dairy goats in an area, and implementation of genomic selection or marker-assisted selection are the promising animal breeding strategies to improve both genetic diversity and productivity (FAO, 2010; Gipson, 2019; Torres-Hernandez et al., 2022).

Study by Pakpahan et al. (2023) has shown that uncontrolled breeding due to farmers' desire to improve milk production traits has direct effects on lowering the genetic diversity of the dairy goat populations. In that context, the breeding programs that are socio-economically appropriate with clearly defined breeding

goals must be set at the farm level to ensure sustainable dairy goat production (Torres-Hernandez et al., 2022; Whannou et al., 2023).

Conservation of goat genetic resources can be strengthened through effective farm-level record keeping and controlled breeding programs, which help maintain genetic diversity within and among breeds (Toro et al., 2009). Ensuring high haplotype diversity in the breeding population is particularly important, as it reflects the presence of multiple maternal lineages and enhances the population's capacity to adapt to emerging diseases and environmental challenges (Luikart et al., 2001). In addition, maintaining high nucleotide diversity provides a broad pool of genetic variation for future selection and improvement, thereby reducing the risks of inbreeding, genetic drift, and loss of rare alleles, which are common in small and traditional production systems (FAO, 2007).

3.12. Median joining network (MJN)

The MJN revealed that haplotype 2 (Hap_2) was the most centrally connected to the other seven haplotypes. This suggests that Hap_2 is the representative of an ancestral haplotype, and through it, all other haplotypes evolved from it through mutations. Due to the presence of multiple connections originating from the Hap_2 and having a higher frequency, it is considered a genetic hub for the populations studied.

The small perpendicular bars between two haplotypes in the MJN indicate the number of mutations. From one haplotype to another, there is a single-step mutation. This indicates that the populations in studies have very low genetic divergence, which can be attributable to strong gene flow among them, possibly due to crossbreeding and uncontrolled mating. Similar results on the effect of uncontrolled mating in reducing genetic divergence in population were reported by (Fridman et al., 2014); Luikart et al. (2001); Peng et al. (2022). Furthermore, Hap_4 and Hap_8 were peripherally positioned in the MJN; these are referred to as terminal haplotypes, which signify rare or population-specific haplotypes.

3.13. Analysis of molecular variance (AMOVA)

The AMOVA results showed that 82.17% of genetic variation was found within breeds, while 17.83% of the remaining genetic variation was due to differences among breeds (**Table 4**). This indicated that there was more genetic diversity within breeds than among breeds. The higher genetic variation within breeds suggests that haplotype diversity in large part is shared within breeds rather than indicating genetic homogeneity. This result is in consonance with other studies, which found presence of higher genetic variation within breeds than among breeds (Awotunde et al., 2015; Petretto et al., 2022), and it is scientifically linked to the animal movement from one area to another for commercial purposes, which later on accelerates gene flow due to maternal lineage from different breeds coming into contacts (Awotunde et al., 2015) .

Nevertheless, the variation among breeds was not statistically significant ($p>0.05$) (**Table 4**), and the heatmap of pairwise FST values showed that the genetic differentiation among breeds was non-significant (**Figure 7**). All cells in the heatmap showed non-significance due to the fact that cytochrome b is a single, maternally inherited locus, hence has lower statistical power compared to the nuclear genome. As a result, moderate FST values may not reach statistical significance, particularly when haplotype sharing and recent admixture are present among and within the breeds. Therefore, this indicates limited maternal genetic differentiation among the studied populations. This pattern likely reflects shared maternal ancestry and extensive historical and recent gene flow resulting from unstructured breeding and frequent exchange of breeding females across production systems. Furthermore, the relatively recent development of some breeds and the generally low mitochondrial genetic diversity observed in this study may have limited the accumulation of breed-specific mtDNA variation (Floridia et al., 2025; Pegolo et al., 2025; Peng et al., 2025). Since mitochondrial DNA traces only maternal lineages, differentiation driven by nuclear genomic variation may not be fully captured, which may explain the low among-breed variance detected in the molecular variance analysis.

Additionally, the result from the current study is in concordance with the study done by Naqvi et al. (2017); and Yordanov et al. (2024) indicated low to moderate genetic differentiation among the investigated goat breeds reared in the same geographical area, possibly due to gene flow among the breeds. This structure suggests relatively weak mtDNA differentiation among breeds, implying that loss of within-breed diversity would have a strong impact on total genetic variation.

4. Conclusion

This study revealed genetic distances ranging from 0.0–0.0038, Hd of 0.716 ± 0.058 and π of 0.00251 ± 0.00035 which are considered as low to moderate genetic diversity among seven dairy goat breeds in Yogyakarta and Central Java, indicating a narrow genetic base and high genetic homogeneity, which may reduce adaptability and increase extinction risk. The presence of Saanen goats across several clades suggests genetic intermixing, likely due to uncontrolled crossbreeding and limited breeding stock. The findings highlight the urgent need for structured breeding programs and increased farmers' awareness to conserve genetic resources. This study recommends that dairy goat farmers improve pedigree record keeping and ensure controlled crossbreeding, implementation of structured community-based nucleus breeding programs, and controlled rotational mating schemes. Also, the animal breeders and other experts should conduct baseline molecular characterization of Indonesian dairy goat breeds, which will include larger sample sizes and cover a broader geographical area, while guiding farmers to utilize available genomic information for breeding purposes. Furthermore, the policymakers should formulate conducive policies geared to establishing and sustaining conservation breeding programs.

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7. Author's contribution

The authors confirm their contribution to the paper as follows: study conception and design: MM, DM; data collection: MM, DM; analysis and interpretation of results: MM, DM, DTW, AI; draft manuscript preparation: MM, DM, DTW; critical revision of the manuscript for important intellectual content: DM, DTW, AI. All authors have read and approved the final manuscript.

8. Ethics approval

This Research obtained ethical clearance from the Research Ethics Commission of the Faculty of Veterinary Medicine, Universitas Gadjah Mada with number 149/EC-FKH/int./2025.

9. Conflict of interest

The authors declare that they have no conflict of interest.

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