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Insights into genomic diversity and population structure of Thuringian and other European goat breeds using SNP data

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Introduction

Europe represents only about 1.9% of the global goat population, but contributes 15.1% of global goat milk and 35.1% of goat cheese production, with France, Italy, and Greece among the major producers (Ruiz Morales *et al.*, 2019). In Germany, the goat population includes about 154,900 herdbook animals according to the Federal Office for Agriculture and Food (Bundesinformationszentrum Landwirtschaft, 2022), highlighting the relatively minor role of goats in the livestock sector. Most goat breeds in Germany are used for dairy production, with German Improved White, German Improved Fawn, and Thuringian goats representing the main dairy breeds (Bundesverband Deutscher Ziegenzüchter E.V., 2024). Recent statistics indicate that the European goat population has declined by over 15 % in the past decade (Eurostat, 2024), largely due to agricultural intensification and a preference for high-yielding commercial breeds, which has accelerated genetic erosion and the endangerment of local breeds (Eusebi *et al.*, 2019), including the Thuringian goat (Zentrale Dokumentation Tiergenetischer Ressourcen in Deutschland, 2025). The Thuringian goat originated in the early 20th century from crosses between local goats in Thuringia and Swiss Toggenburg goats and was officially recognized in 1935 (The Society for the Conservation of Old and Endangered Livestock Breeds, 2024). The Thuringian goat is a high-producing, medium-framed dairy breed characterized by high fertility, robustness, and frequent multiple births. Its resilience to harsh climates makes it well suited for landscape management (Bundesverband Deutscher Ziegenzüchter E.V., 2024). The average milk yield of Thuringian goat ranges from 700 to 1,000 kg per lactation, with about 3.5 % fat and 3.0 % protein (The Society for the Conservation of Old and Endangered Livestock Breeds, 2024). Despite its favourable traits, the Thuringian breed is classified as critically endangered (Category II) on the Red List of the Society for the Preservation of Old and Endangered Domestic Animal Breeds e.V. (The Society for the Conservation of Old and Endangered Livestock Breeds, 2024). The aims of this study were to characterize the genetic composition of the Thuringian goat, to evaluate its genetic relationships with other European breeds with particular emphasis on its historical ancestor, the Toggenburg goat, and to identify genomic regions under positive selection.

Materials & Methods

Dataset and quality control. Blood samples from 88 Thuringian goats were collected during routine health checks, including 84 animals from a family farm in Thuringia, Germany, and four from Tierpark Arche Warder using EDTA vacutainer tubes. Genomic DNA was extracted using the NucleoSpin Tissue Kit (Macherey-Nagel, Germany) and samples were genotyped using Axiom Caprine 60K SNP Chip. Additional genotype data from 2,397

European goats were obtained from public databases and collaborators; AdaptMap goats were genotyped with the Illumina Goat SNP50 BeadChip. After standard quality control, 1,687 animals from 39 breeds (47 populations) and 47,670 SNPs were retained for analysis. In a selection analysis step to identify breeds closely related to the Thuringian goat, a phylogenetic tree was constructed using all retained European populations by using a modified Manhattan distance. Hierarchical clustering was performed in R with *hclust*, and population relationships were visualized using *dendextend* package (Galili, 2015). Representative populations from each major branch were selected based on the lowest pairwise F_{ST} values relative to the Thuringian goat. This subset included 444 goats from eight populations representing seven breeds: Alpine (Italy), Corsican (France), Danish Landrace, Malagueña (Spain), Maltese (Italy), Saanen (Italy), Toggenburg (Switzerland), and Toggenburg (Tanzania).

Genetic diversity assessment. Genomic diversity in Thuringian goats and other European breeds was assessed by estimating observed (H_O) and expected heterozygosity (H_E), and nucleotide diversity (π) using VCFtools v0.1.15 (Danecek *et al.*, 2011). Genomic inbreeding was assessed using inbreeding coefficients based on excess of homozygosity (F_{Hom}) with VCFtools (Danecek et al., 2011).

Relatedness analysis. Pairwise population differentiation was estimated using Weir and Cockerham's fixation index (F_{ST}) with VCFtools v0.1.15 (Danecek et al., 2011, Weir and Cockerham, 1984). Population structure was explored by principal component analysis (PCA) in R using *prcomp*, and the first two components were visualized with *ggplot2* (Wickham, 2016). Ancestral relationships were inferred using unsupervised ADMIXTURE v1.3 with K values from 2 to 9, and the optimal K was chosen based on cross-validation error, using a <1% decrease threshold between successive K values (Alexander *et al.*, 2009).

RoH islands. RoH islands were identified by calculating SNP frequencies within RoH for each population and retaining SNPs in the top 1% (≥99th percentile). Adjacent high-frequency SNPs within 1 Mb on the same chromosome were merged into RoH islands. Protein-coding genes within these regions were identified using the *Capra hircus* (ARS1.112) GFF3 annotation.

Results

The Thuringian breed had the second-lowest mean MAF (26.21%), after Toggenburg (Switzerland) (Table 1). The Thuringian breed showed the lowest observed heterozygosity (36.7%) (Table 1). In contrast, the highest H_O values were detected in Malagueña (Spain) and Saanen (Italy), both exceeding 41.9%. Expected heterozygosity (H_E) followed a similar trend, with the lowest value again in Thuringian goats (35.4%) and the highest in Malagueña (41.69%; Table 1). The average nucleotide diversity ranged from 6.42×10^{-6} in Thuringian to 8.22×10^{-6} in Saanen (Italy) goats, with Thuringian showing the lowest genetic variation among the populations (Table 1). Thuringian goats showed the second highest inbreeding level (F_{Hom} = 18.2%), with values ranging from 4.1% in Saanen (Italy) to 19.2% in Toggenburg (Switzerland). Thuringian goats showed relatively moderate differentiation from all other European breeds, with values ranging from 0.107 (Thuringian vs. Alpine) to 0.165 (Thuringian vs. Maltese), including marked differentiation from the two Toggenburg populations, 0.132 and 0.141 for Toggenburg populations from Switzerland and Tanzanian, respectively. The first two principal components explained approximately 9.5% of the total genetic variance. Thuringian goats and the eight selected populations formed distinct clusters. Thuringian goats clustered closely with Saanen (Italy), Toggenburg (Switzerland), and Alpine (Italy) populations. (Figure 1). In ADMIXTURE analysis and across all K-values, Thuringian breed consistently showed a largely homogeneous genetic background with minimal evidence

of admixture. At K = 4, Thuringian (Germany), Landrace (Denmark), and Alpine (Italy) breeds were mostly assigned to distinct ancestral clusters. Toggenburg (Tanzania) showed higher Landrace ancestry and lower Thuringian ancestry than Toggenburg (Switzerland).

Table 1: Genetic diversity metrics of Thuringian and selected European goat populations.

Breed	Country	N[1]	MAF[2] (%)	H_O[3] (%)	H_E[4] (%)	π[5]	F_{Hom}[6]
Thuringian	Germany	87	26.21	36.66	35.44	6.42×10^{-6}	0.182
Alpine	Italy	159	32.14	40.99	40.92	8.02×10^{-6}	0.061
Corsican	France	30	31.49	40.57	40.91	8.03×10^{-6}	0.074
Landrace	Denmark	120	29.53	37.30	38.56	7.45×10^{-6}	0.154
Malagueña	Spain	42	32.58	41.94	41.69	8.18×10^{-6}	0.041
Maltese	Italy	16	28.47	36.72	38.94	7.51×10^{-6}	0.176
Saanen	Italy	24	32.13	41.99	41.67	8.22×10^{-6}	0.041
Toggenburg	Switzerland	31	26.10	37.11	36.53	6.72×10^{-6}	0.192
Toggenburg	Tanzania	22	29.66	38.79	39.56	7.57×10^{-6}	0.121

[1]sample size, [2]average minor allele frequency, [3]observed heterozygosity, [4]expected heterozygosity
[5]average nucleotide diversity, [6]genomic inbreeding coefficient

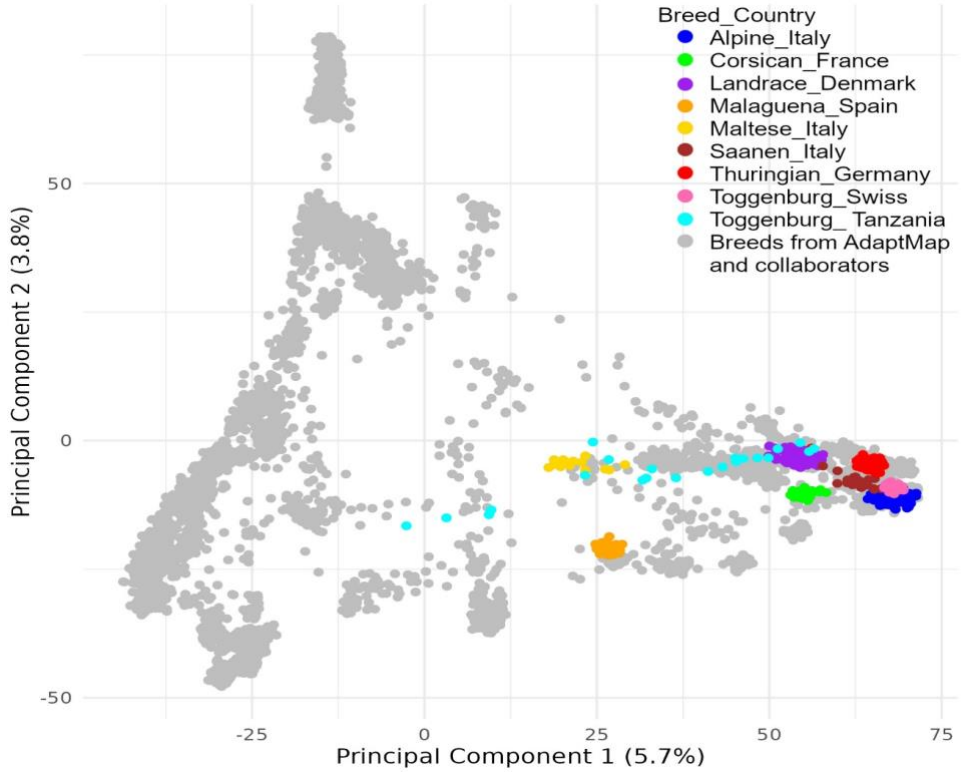

Figure 1: Principal components plot of global goat breeds from AdaptMap and collaborators (grey) with the Thuringian goat and eight selected populations highlighted: Alpine (Italy), Corsican (France), Landrace (Denmark), Malagueña (Spain), Maltese (Italy), Saanen (Italy), Toggenburg (Switzerland), and Toggenburg (Tanzania).

A total of 140 genes were identified within ten run of homozygosity (RoH) islands in Thuringian goats, many of which are associated with essential cellular processes. Notable examples include *fat storage inducing transmembrane protein 2* (*FITM2*, chromosome 13), involved in lipid metabolism; *Complement C5* (*C5*, chromosome 8), linked to immune and inflammatory responses; *Gametocyte Specific Factor 1-Like* (*GTSF1L*, chromosome 13), related to gametogenesis; and *MYB Proto-Oncogene Like 2* (*MYBL2*, chromosome 13), a regulator of cell cycle progression and differentiation.

Discussion

Thuringian goats show the lowest observed and expected heterozygosity and nucleotide diversity among the analyzed breeds, indicating limited genetic variability, which is consistent with their small population size (~1,800–1,850 herdbook animals in 2023) (Gesellschaft Zur Erhaltung Alter Und Gefährdeter Haustierrassen E.V. (Geh), 2025). In contrast, large populations such as Saanen and Alpine goats exhibit the highest nucleotide diversity. Thuringian goats exhibit high excess homozygosity, indicating substantial inbreeding and reduced genetic diversity, consistent with their endangered status. The moderate genetic relationship between Thuringian goats and Toggenburg populations, with a closer affinity to Swiss than Tanzanian Toggenburg, may reflect the historical use of Swiss Toggenburg goats in the development of the Thuringian breed. In PCA, Thuringian goats show close genetic clustering with Alpine, Saanen, and Swiss Toggenburg breeds, likely due to shared geography, dairy oriented selection, and adaptation to higher altitudes. Across all K values, admixture analysis indicates that Thuringian goats are genetically distinct; at K = 4, they contribute approximately 20% ancestry to Swiss Toggenburg and about 10% to Tanzanian Toggenburg populations. Consequently, the data provide no strong evidence for a direct ancestral relationship between Thuringian goats and the analyzed Toggenburg populations. In Thuringian goats, several positional candidate genes detected under selection may influence not only milk production but also overall fitness and resilience of the breed, thereby indirectly supporting milk performance.

Conclusions

Thuringian goats exhibit moderate genetic relationships with other European dairy breeds, particularly Alpine, Italian Saanen, and Swiss Toggenburg, supporting a history of shared ancestry. Despite these relationships, Thuringian goats remain a genetically distinct and largely homogeneous breed, highlighting the importance of continued conservation efforts by breeders and breed associations. Furthermore, the detected selection signatures indicate that functionally relevant loci are associated with milk production, immunity, fertility, and overall resilience, reflecting both the adaptive capacity and productive performance of the breed.

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