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RESEARCH ARTICLE

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Cross-population analyses between cashmere, angora and non-fibre-producing goats identified signatures of divergent selection

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ABSTRACT

Angora and Cashmere goats differ in hair follicle biology and fibre traits. To explore the genetic basis of these differences, Whole Genome Sequencing (WGS) of Cashmere, Angora, and non-fibre goats were used to identify divergent selection signatures and allele frequency differences. Cross-population analyses found 5,252 variants differentially selected between Cashmere and non-fibre goats, 2,414 between Angora and non-fibre, and 326 between Cashmere and Angora. Three fibre-related genes, *COL14A1*, *FGF5*, and *CUX1*, showed divergence across all comparisons. Fisher's exact test on coding variants with high or moderate predicted phenotypic impact identified 735 significant variants in skin-expressed genes showing differing allele frequencies between Cashmere and non-fibre goats, with fewer such variants found between the other groups. These variants likely influence fibre differences among populations. Though their exact effects are unclear, this study advances understanding of fibre goat genetics.

HIGHLIGHTS

- Divergent selection analysis of Cashmere, Angora, and non-fibre-producing goats identified variants potentially linked to fibre production.
- The genes *COL14A1*, *FGF5*, and *CUX1* exhibited divergent selection across all three goat groups, highlighting their roles in fibre biology.
- Findings enhance understanding of genetic selection for fibre traits, influencing goat breeding strategies and the fibre industry.

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Angora; Cashmere; goat; cross-population analyses; extended haplotype homozygosity

Introduction

Selective breeding for fibre production has led to two main goat types: Angora and Cashmere. Angora goats, originally from Ankara, Turkey, are now bred for mohair across Europe, the Americas, and Australasia (Visser et al. 2016). Chinese Cashmere goats include several breeds, including the widely common Liaoning Cashmere breed (Jin et al. 2011), along with fine local varieties from Inner Mongolia such as the Alashan Cashmere goat (Pallotti et al. 2020). Though both were selected for fibre and phylogenetic analyses place them in the same 'long-haired breeds' cluster (Denoyelle et al. 2021), they differ markedly in hair follicle biology and fibre traits. Cashmere goats have a double coat, shedding fine underwool annually, while Angora goats have a single coat, sheared twice yearly due to low moulting (Ryder 1993). Their fibres also vary in diameter, length, and curvature (Ryder 1993; McGregor 2014). These fibre differences result from divergent selection, though the specific loci remain unknown. To address this, the present study used WGS to identify selection signatures and candidate genes potentially linked to hair follicle biology and fibre production across Cashmere, Angora, and non–fibre-producing goats.

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The supplementary materials associated with this research are available at the following link: https://doi.org/10.6084/m9.figshare.29596934
The samples generated by previous projects and used in this study are available in the NCBI Sequence Read Archive (SRA) [PRJEB37122, PRJNA338022, PRJNA387635, PRJNA399234, PRJEB4371, PRJNA158393, PRJNA378894].

Methods

Sample collection

A total of 174 WGS data were used for the study. The sample accounts for 23 Liaoning Cashmere goats, 15 Erlangshan Cashmere goats, 12 Alashan Cashmere goats, 13 Aerbasi Cashmere goats, 17 Angora goats, and 94 non fibre-producing goats (13 Boer, 15 Creole, 4 Montecristo, 12 Poitevine, 19 Saanen, 18 Alpine, 4 Leizhou, 2 Longlin, 1 Guizhou Black, 1 Jianchang Black, 1 Maguan Hornless, 1 Shannan White, 1 Xiangdong Black, 1 Yaoshan White, and 1 Yunling). All the samples were generated by previous projects (PRJEB37122, PRJNA338022, PRJNA387635, PRJNA399234, PRJEB4371, PRJNA158393, and PRJNA378894) and were retrieved from the NCBI Sequences Read Archive (SRA) (Supplementary table 1). The SRA files were downloaded to our server and converted to FASTQ. The quality of the FASTQ and adapter trimming were performed as reported in Pallotti et al. (2023) while reads alignment, variants calling and base recalibration were carried out as reported in Pallotti et al. (2025).

WGS quality control, variant calling, and sample relatedness check

The resulting VCF containing 6,376,154 variants with a global genotyping rate of 0.95, was converted to PLINK file using VCFtool (Danecek et al. 2011). None of the 174 samples were removed due to a high level of individual missing genotypes (>20%). After filtering for Minor Allele Frequency (MAF) ≥5% and genotyping rate ≥95%, 2,704,225 variants were retained. To ensure sample independence, individuals with Identity-By-Descent (IBD) PI-HAT ≥0.5 were identified using PLINK 1.9 (Purcell et al. 2007), and only samples with PI-HAT ≤0.5 were kept. Missing genotypes were imputed using Beagle v5.0 (Browning et al. 2018) with default parameters as suggested by Yang et al. (2020).

Population structure analysis

Variants with a minor allele frequency (MAF) <5% were removed and the remaining variants were pruned for Linkage Disequilibrium (LD) using the PLINK command "–indep-pairwise 1,500 150 0.1". A total of 109,544 variants and 174 samples were used for Multi-Dimensional Scaling (MDS) and admixture analyses. MDS was performed using PLINK 1.9 and visualised using ClustVis (Metsalu and Vilo 2015). ADMIXTURE (v1.23) (Alexander et al. 2009) was used for population structure analysis with K values from 3 to 12. Determination of the correct value for K and plotting were performed as reported in Pallotti et al. (2025).

Table 1. Sample grouping used for XP-EHH, fst, and θπ ratios analyses.

Group	Breed/species	*N*	Total *n* used for each group
Cashmere	Liaoning cashmere	23	63
	Erlangshan cashmere	15	
	Alashan cashmere	12	
	Aerbasi cashmere	13	
Angora	Angora	17	17
Non fibre-producing	Saanen	19	94
	Alpine	18	
	Creole	15	
	Boer	13	
	Poitevine	12	
	Leizhou Goat	4	
	Montecristo	4	
	Longlin Goat	2	
	Guizhou Black Goat	1	
	Jianchang Black Goat	1	
	Maguan Hornless Goat	1	
	Shannan White Goat	1	
	Xiangdong Black Goat	1	
	Yaoshan White Goat	1	
	Yunling Goat	1	

Cross-population analysis and identification of signatures of selection between Cashmere vs. non fibre-producing goats, Angora vs. non fibre-producing goats, Cashmere vs. Angora

To study divergent selection in Cashmere, Angora, and non-fibre-producing goats, three groups were defined as follow (Table 1): 63 Cashmere goats (Liaoning, Erlangshan, Alashan, and Aerbasi), 17 Angora, and 94 non-fibre-producing breed goats (including Saanen, Alpine, Creole, Boer, Poitevine, Leizhou Goat, Montecristo, Longlin Goat, Guizhou Black Goat, Jianchang Black Goat, Maguan Hornless Goat, Shannan White Goat, Xiangdong Black Goat, Yaoshan White Goat, and Yunling Goat). The cross-population analysis, i.e. XP-EHH (Extended Haplotype Homozygosity), Genome-wide fixation index (Fst, i.e. Weir and Cockerham's estimator) and nucleotide diversity (θπ ratios) were performed as reported in Pallotti et al. (2025).

Genomic intersections between the top 5% extreme XP-EHH values and the top 5% of extreme Fst and Θπ values were identified as specific signals of selection between the three groups. Variants were annotated using VEP (McLaren et al. 2016).

Alleles frequency distribution analysis between Cashmere, Angora, and non fibre-producing goats

Variants in coding sequences (CDS) with high (stop-gained or frameshift) or moderate (missense) predicted effects (total $N = 8{,}661$) were extracted from

the annotated VCF. To investigate whether the variants with significantly different allele frequencies between the three goat groups were potentially associated with fibre biology, their frequency distribution between the three goat groups was tested by Fisher's exact test using PLINK 1.9. The statistical threshold was set up at $p < 5.77E-06$ after applying a Bonferroni correction for multiple testing based on the number of variants tested.

Moreover, dataset from nine previous studies on genes differentially expressed (DE) during the hair follicle cycle and development in cashmere goats (Geng et al. 2013; Gao et al. 2016; Wang et al. 2017; He et al. 2020; Nocelli et al. 2020; Wang et al. 2020; Zhang et al. 2020; Wu et al. 2022; Xu et al. 2023) were collected to provide evidence of gene expression for those loci harbouring variants with significantly different allele frequencies between the fibre-producing and non-fibre-producing goat groups. A 'Gene-Expression score' (ranging from 0 to 10) was assigned to each gene based on the number of studies in which its expression was observed.

Gene-based enrichment analysis

Gene enrichment analysis was performed with the web-based tool ShinyGO (Ge et al. 2020) using the list of genes harbouring variants whose allele frequencies were significatively different between the groups.

A comprehensive flowchart of the steps applied to the full dataset is reported as Figure 1.

Results and discussion

Population structure and admixture

The MDS plot showed no distinct clusters, with the first two components explaining 18.9% of variability (Figure 2). Cross-validation errors for $K = 3$ to 12 ranged from 0.614 to 0.688, indicating $K = 3$ as most probable. The admixture plot ($K = 3$) revealed three clusters reflecting goats' productive purpose (fibre, meat, and milk) and geographic origin (Figure 3). Angora showed high admixture with meat breeds (Creole and Boer), while Cashmere formed a distinct cluster but shared genetic flow with Chinese non-fibre-producing breeds, likely due to shared geography. Milk breeds (Alpine, Poitevine, Saanen, and Montecristo) formed the most isolated cluster with minimal introgression.

Cross-population signatures of selection

Pairwise analyses highlighted divergent selection signals. Between Cashmere and non–fibre-producing goats, 5,252 significant SNPs were found, with 1,782 located in 437 genes, identifying four enriched pathways (Supplementary Tables 2A–2C). Angora vs. non-fibre-producing goats revealed 2,414 variants (664 located in 264 genes) with one enriched pathway (Supplementary Tables 3A–3C). Cashmere vs. Angora showed 326 variants (106 located in 21 genes) with no enriched pathways (Supplementary Tables 4A and 4B). Manhattan plots for these analyses are provided in Supplementary Figures 1–3.

Genes with the highest number of differentially selected variants between Cashmere and non–fibre-producing goats included *MED12L* ($N = 144$), *CP* ($N = 99$), *MCM3AP* ($N = 51$), *RFX3* ($N = 39$), and *MTARC2* ($N = 31$) (Supplementary Table 2B). These genes relate more to milk and meat production than fibre biology. For example, *MED12L* associates with reproductive biology (Zhou et al. 2021), *CP* with mammary gland function (Nakamura et al. 2006; Platonova et al. 2017), *MTARC2* with meat traits (He et al. 2024), *MCM3AP* with cattle fat thickness (Arikawa et al. 2024), and *RFX3* with fitness in wild sheep (Alipanah et al. 2024). This suggests divergent selection mostly targets milk, meat, and environmental adaptability traits, supported by pathway enrichment in serotonergic synapse, oxytocin signalling, and adherens junctions (Supplementary Table 2C). Serotonin regulates mammary involution and calcium homeostasis (Suárez-Trujillo et al. 2019; Chen et al. 2024), oxytocin affects lactation (Zhu et al. 2021), and adherens junctions maintain tissue integrity and pathogen resistance (Harris 2012; Zhang et al. 2024).

Angora vs. non-fibre-producing goats and Cashmere vs. Angora analyses showed differentially selected variants in 264 and 21 genes respectively (Supplementary Table 3A). *COL14A1* exhibited the strongest differential haplotype selection signals in both comparisons, with 34 and 39 variants differentially selected respectively (Supplementary Tables 3B and 4B). This gene is involved in hair follicle morphogenesis and cycling (anagen to catagen phases) (Gao et al. 2016; Wang et al. 2017). The adherens junction pathway was the only enriched pathway in Angora vs. non-fibre-producing goats (Supplementary Table 3C), linked to environmental adaptability.

COL14A1, *FGF5*, and *CUX1* showed divergent selection across all comparisons. *COL14A1* had 9, 34, and 39 differentially selected variants between Cashmere and

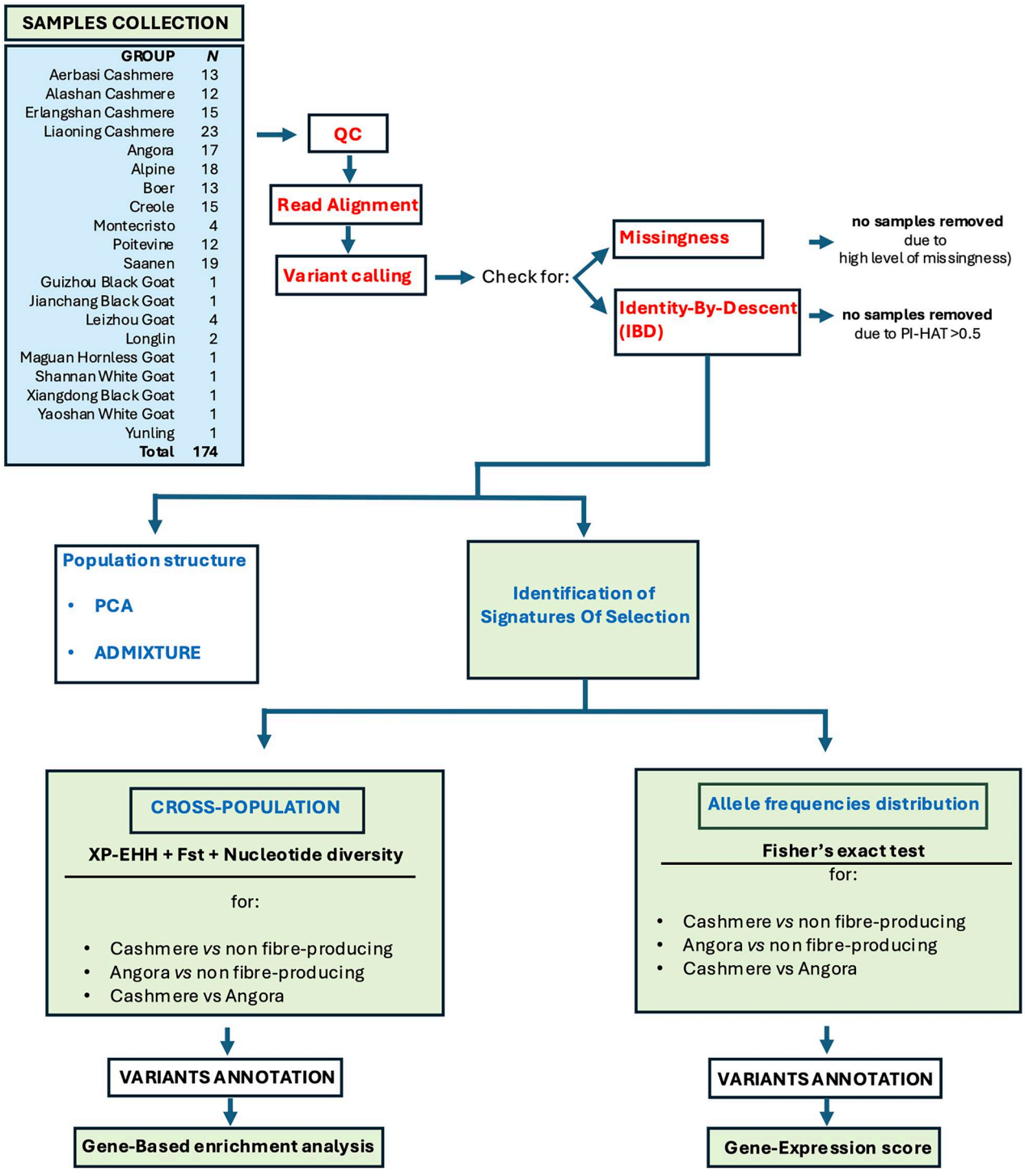

Figure 1. Flow-chart of the workflow adopted in the data processing of the full dataset. QC = Quality control.

non-fibre-producing goats, Angora and non-fibre-producing goats, and Cashmere and Angora goats, respectively. The gene is involved in hair follicle biology as discussed earlier (Gao et al. 2016; Wang et al. 2017). *CUX1* displayed 7, 11, and 6 differentially selected variants between Cashmere and non-fibre-producing goats, Angora and non-fibre-producing goats, and Cashmere and Angora goats, respectively. This gene may be essential for hair follicle biology and fibre production, as it is involved in the proliferation of dermal papilla cells (Lv et al. 2023, 2024; Zhou et al. 2023). *FGF5*, which showed two differentially selected variants

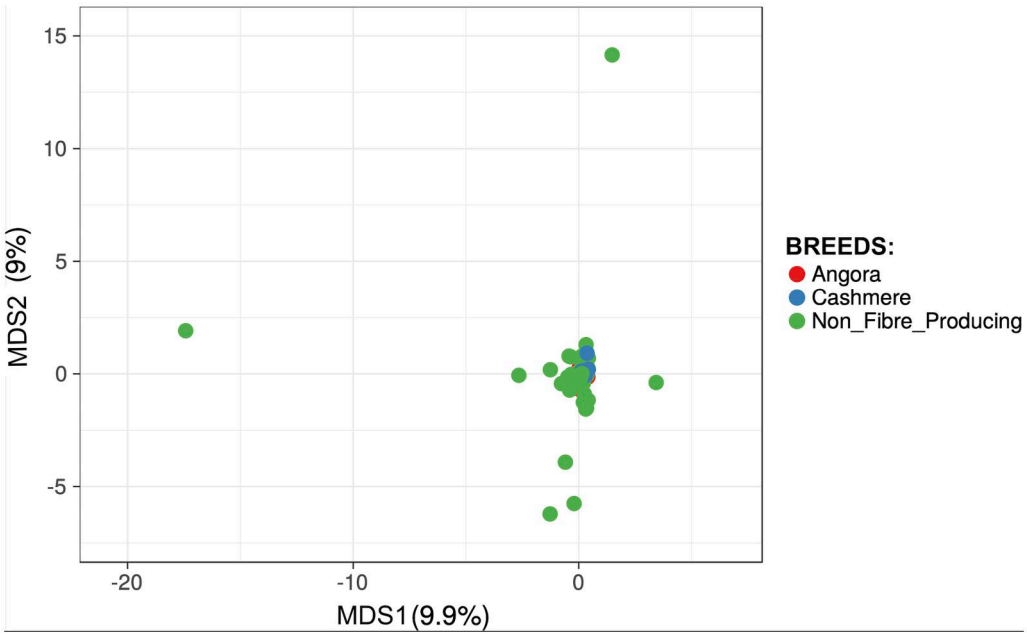

Figure 2. MDS plot for the first two dimensions, illustrating the relationships between goat populations. Each dot represents an individual sample. The x-axis displays the first dimension (MDS1), while the y-axis represents the second dimension (MDS2). The percentage of total variation explained by each axis is indicated in parentheses.

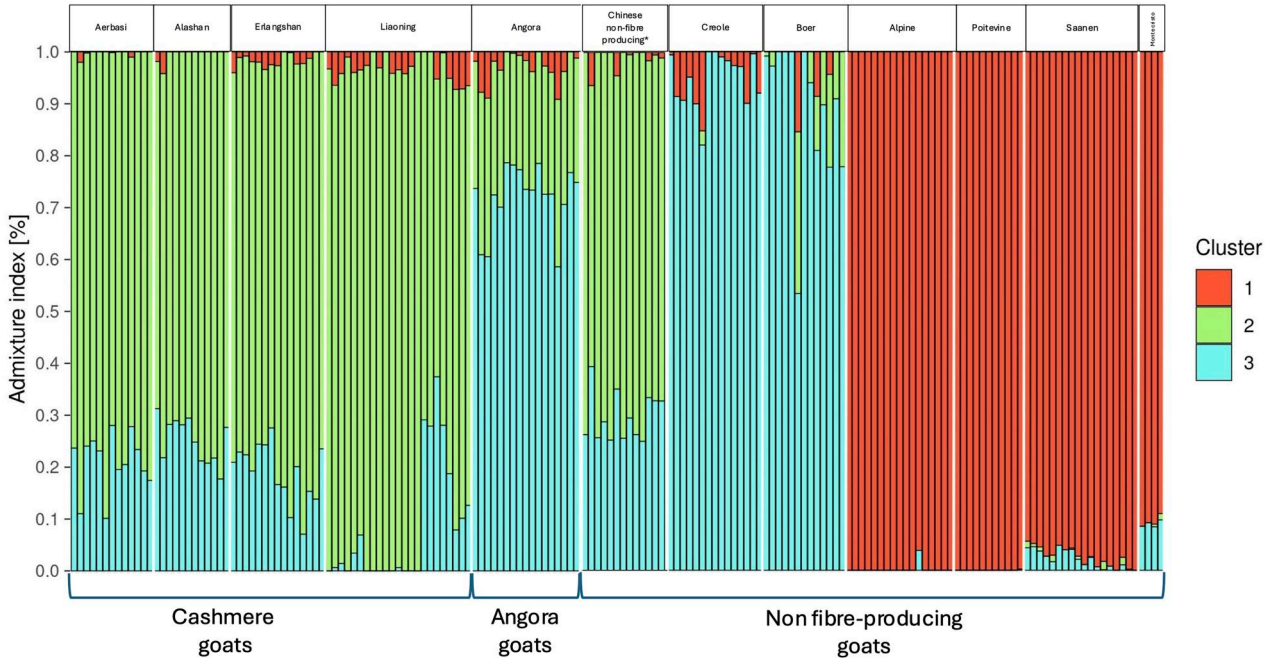

Figure 3. A) Admixture analysis plot displaying population assignments for $K = 3$. Each cluster is represented by a different colour, and each individual is represented as a vertical line divided into K coloured segments, with heights proportional to their genotype memberships in the clusters.

in each of the three comparisons, regulates hair follicle transition from anagen to catagen, affecting hair length (Pallotti et al. 2018) and cashmere growth (Li et al. 2022), though no mohair-linked variants are known.

Alleles frequency distribution analysis and gene-based enrichment analysis

Of 8,661 variants located in CDS, 595 were stop-gained or frameshift, 8,066 were missense variants.

Fisher's exact test identified 1,950 variants differing between Cashmere and non-fibre-producing goats, of which 735 were located in genes expressed in goat skin and eight enriched pathways (Supplementary Tables 5A–5C). Angora vs. non-fibre-producing goats showed 280 variants (107 located in skin genes, three pathways; Supplementary Tables 6A–6C), and Cashmere vs. Angora had 503 variants (205 skin genes, four pathways; Supplementary Tables 7A–7C).

Top 10 significant SNPs between Cashmere and non-fibre-producing goats were on *PRKDC*, *SELL*, and *F13A1* (Supplementary Table 5A), linked to fertility (Wang et al. 2021[a]), embryo implantation (Foulk et al. 2007), and desert adaptability (Yang et al. 2025), respectively.

Three of the top 10 most significative SNPs are located in *NR3C1, CD117*, and *SERPINB11* and showed different allele frequency between Angora vs. non-fibre-producing and Cashmere vs. Angora goats (Supplementary Table 6A). *NR3C1* and *CD117* are linked to puberty onset (Qin et al. 2024) and immune responses to mastitis and paratuberculosis (Cheng et al. 2021; Alonso-Hearn et al. 2019) respectively, while *SERPINB11* affects hair follicle cycling (He et al. 2020; Zhang et al. 2020). Angora and non-fibre-producing goats also showed significant differences in allele frequencies for *NDNF* and *DNAAF3*, two genes linked to hair follicle morphogenesis and cycling (He et al. 2020; Wang et al. 2020) and respiratory resistance (Enns et al. 2017), respectively.

It is also noteworthy that among the top 10 most significant variants, one (*LOC102190288*), four (*LOC102187204, LOC102179006, LOC102180556*, and *LOC102189642*), and four (*LOC102187204, LOC102179006, LOC102185708*, and *LOC102180556*) were located in uncharacterised genes (Supplementary Tables 5A, 6A, and 7A) reported to be expressed in the skin which may potentially be involved in hair follicle biology and cycling (Wang et al. 2017; He et al. 2020; Wang et al. 2020; Zhang et al. 2020).

Some enriched pathways may be related to hair follicle biology. The ECM-receptor interaction pathway, enriched in Cashmere vs. non-fibre-producing goats, relates to wool growth and bending in goats (Liu et al. 2022) and hair follicle cycle development in Cashmere goat (Wang et al. 2021[b]). Complement and coagulation cascades pathway were enriched in both Cashmere vs. non-fibre-producing (Supplementary Table 5C) and Angora vs. non-fibre-producing goats (Supplementary Table 6C), associated with high-quality brush hair formation in goat (Ji et al. 2018). The ABC transporters pathway, enriched in Cashmere vs. non-fibre-producing and Cashmere vs. Angora, is linked to the cashmere follicle cycle (Ma et al. 2024; Wu et al. 2024).

Gene expression score

Variants with the highest gene expression scores (=5) were located in *FAM171A1, IRS1, MC5R*, and *VCAN* (for Cashmere vs. non-fibre-producing; Supplementary Table 5B), *MC5R* and EPB41L3 (for Angora vs. non-fibre-producing; Supplementary Table 6B), and *IRS1*, *MC5R*, and C3 (for Cashmere vs. Angora; Supplementary Table 7B). All these genes participate in hair follicle morphogenesis and cycling (Gao et al. 2016; Wang et al. 2017; He et al. 2020; Zhang et al. 2020) and may help explain some of the differences in hair follicle biology and fibre development observed in the three goat populations studied.

Many significant variants identified through Fisher's exact test were homozygous for the reference allele, especially in Cashmere goats, suggesting an ancestral hair follicle cycle with fewer selected variants. Conversely, angora goats showed higher selection for alternative variants, possibly linked to fibre production.

Conclusion

This study presents preliminary evidence of selection signals in fibre-producing goats, but larger-scale and functional validation studies are needed.

Cross-population analyses revealed weak selection signals in Cashmere and Angora goats, while stronger signals in non-fibre-producing goats were linked to other productive traits. In contrast, allele frequency differences were found in genes potentially related to fibre biology, likely due to their expression in skin.

Despite the need for further research, these results enhance our understanding of the genetic basis of fibre production and lay a foundation for breeding strategies to improve fibre quality in Angora and Cashmere goats.

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Authors' contributions

S.P.: study conception, analysis, drafting of the manuscript; S.C.: critical review of the manuscript; C.P.: critical review of the manuscript; F.P.: critical review of the manuscript; M.A.:

critical review of the manuscript; Z.J.: critical review of the manuscript; S.H.: critical review of the manuscript; C.R.: critical review of the manuscript; financial support; V.N.: study conception, drafting of the manuscript, critical review of the manuscript.

Competing interests

The authors declare that they have no competing interests.

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