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Comprehensive genomic analysis reveals population structure and conservation priorities of Chinese indigenous goats

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Introduction: Systematic genetic and conservation prioritization analyses are critical for the effective management and preservation of Chinese indigenous goat genetic resources, thereby facilitating the sustainable development of the goat industry. However, the genetic resources of Chinese indigenous goats, which comprise numerous breeds, have not yet been subjected to such comprehensive analyses.

Methods: In this study, we conducted the first large-scale whole-genome sequencing (WGS)-based genomic analysis of 25 representative indigenous goat breeds from 20 provinces and five climatic zones across China. WGS data from 214 individuals were utilized to investigate the analyses of population structure, inbreeding coefficient, and conservation prioritization. Genetic architecture was characterized using three methods.

Results and Discussion: Our results consistently identified four distinct genetic branches—Northern & Western (NW), Eastern (EA), Southwestern (SW), and Southeastern (SE)—which exhibit a strong correlation with their geographical distributions. Furthermore, genomic inbreeding coefficient analysis revealed that breeds from the SE and SW branches displayed significantly higher inbreeding levels compared to those from the NW and EA branches. Through the assessment of gene diversity (HT) and allelic diversity (AT), we established an optimized conservation priority list for Chinese indigenous goat breeds. Incorporating population structure analysis, the top three breeds of each genetic lineage were earmarked for priority protection. The NW branch includes Xinjiang Goat, Ziwuling Black Goat, and Hexi Goat; the EA branch comprises Huanghuai Goat, Jining Grey Goat, and Southern Shaanxi White Goat; the SE branch consists of Hechuan White Goat, Xiangdong Black Goat, and Hainan Black Goat; the SW branch encompasses Guizhou Black Goat, Guishan Goat, and Luoping Yellow Goat. In summary, our study provides novel

insights into the impact of geographical barriers on the genetic relationships among Chinese indigenous goat breeds and facilitates the translation of genomic advancements into practical conservation strategies for livestock genetic resources.

KEYWORDS

conservation priority, goat, inbreeding coefficient, population structure, whole-genome sequencing

1 Introduction

China possesses highly diversified and adapted indigenous goat breeds, which are widely distributed across various climatic zones, such as Tibetan goat (TBG) in Plateau Alpine Climate Zone, Xinjiang goat (XJG) in Temperate Continental Climate Zone, Jining grey goat (JNG) in Temperate Monsoon Climate Zone, Huanghuai goat (HHG) in Subtropical Monsoon Climate Zone, Hainan Black goat (HNG) adapted to the Tropical Monsoon Climate Zone. At the same time, these indigenous breeds demonstrate unique characteristics, such as high cashmere yield of Liaoning cashmere goat (LNC) (Meng et al., 2022), disease resistance of HNG (Chen et al., 2022), superior-quality brush hair produced by Yangtze River Delta white goat (YRD) and high prolificacy of JNG. A comprehensive assessment and understanding of the population structure of indigenous goat breeds is very important for the effective management of genetic resources and the sustainable breed breeding (Asroush et al., 2018). Various types of genetic markers were used to investigate the genetic structure of Chinese goat populations. In previous studies, low density microsatellite markers were used to analyze the genetic structure of indigenous Chinese goat breeds and provide a preliminary description of the population structure of indigenous goats (Wei et al., 2014; Liu et al., 2019). Later, single nucleotide polymorphism (SNP) chips were used to analyze the genetic structure of goat breeds, which provided 45,452–537,145 SNPs of genetic variation across the whole genome of goats (Tosser-Klopp et al., 2014; Talenti et al., 2018; Berihulay et al., 2019; Islam et al., 2019; Oget et al., 2019; Wang et al., 2022; Nantongo et al., 2024). However, these studies only focused on few Chinese indigenous breeds, such as the research of the selection signatures, introgression and population structure of 36 worldwide goat breeds (including 7 Chinese breeds), analyses of the genetic diversity of 6 Chinese goat breeds, and study of the population structure of three Chinese goat breeds (Berihulay et al., 2019; Islam et al., 2020; Wang et al., 2022). With the rapid development of second-generation sequencing technology and the reduction of sequencing cost, whole-genome sequencing (WGS) data have been applied to the analysis of genetic diversity and population structure of goat (Chen et al., 2021; Li et al., 2024; Liu et al., 2024), cattle (Xu et al., 2024), pig (Zhang et al., 2022), chickens (Zhi et al., 2023) and

duck (Feng et al., 2021), providing genome-wide genetic variation at all loci and further enhancing the power of high throughput. Xiong et al. (2022) performed the genetic diversity and genetic structure analysis based on WGS data of 8 goat breeds worldwide, including 5 Chinese breeds. Li et al. (2023) researched the genetic domestication and selection signal analysis based on WGS data of 15 goat breeds from China, Nepal and Pakistan, including 9 Chinese breeds. However, systematic genetic analysis of indigenous goat breeds across China remains to be fully elucidated.

In recent decades, the conservation of indigenous animal breeds has gained increasing recognition for its importance. In 2007, the Food and Agriculture Organization (FAO) established the *Global Plan of Action for Animal Genetic Resources* (Hoffmann et al., 2011), which has since become one of the most significant frameworks guiding the conservation and sustainable use of these resources at global, regional, and national levels. Despite these international efforts, environmental factors and artificial selection have led to a reduction in the effective population size of indigenous goat breeds, with many of them now facing the risk of extinction (Wang et al., 2022; Bionda et al., 2023). Conservation and maintenance of genetic diversity is a key action for biodiversity conservation to ensure the adaptive potential of these resources to respond to environmental challenges and the sustainable animal production system (Frankham, 1995; Hogg, 2024; Kumar et al., 2024). Weitzman (Weitzman, 1992, 1993) proposed the “diversity theory” to provide quantitative indicators for the protection of endangered resources by measuring the “diversity value”. In chicken (Nguyen-Phuc and Berres, 2018), pig (Gvozdanovic et al., 2019; Zhao et al., 2021a) and cattle (Canon et al., 2001; Mateus et al., 2004; Bennewitz et al., 2006; European Cattle Genetic Diversity, 2006; Tapio et al., 2006; Medugorac et al., 2011), selected neutral molecular markers such as microsatellites were used to assess the genetic diversity and investigate conservation priority. To avoid misleading conservation assessments of breeds within a given domestic animal species when relying solely on genetic distance, both between-breed and within-breed variations must be evaluated to obtain the overall genetic diversity of a multibreed population (Caballero and Toro, 2002). Furthermore, the contribution of each breed to global diversity of multibreed should be evaluated. The software MetaPop evaluates the contribution of each breed to genetic diversity by treating the multibreed population as a metapopulation and calculating the gain

or loss of gene and allele diversity that would occur after the removal of each breed from the metapopulation (Pérez-Figueroa et al., 2008). The updated Metapop2 software (Lopez-Cortegano et al., 2019a), optimized with C++ and released in 2019, enables the effective analysis of large datasets based on WGS data. Priority conservation analyses based on DNA chip data have been performed on chickens (Gao et al., 2023a, b) and pigs (Shang et al., 2020; Zhao et al., 2021b; Zhang et al., 2023; Arias et al., 2024). For goats, priority conservation analysis was investigated based on DNA chip data for 36 goat breeds worldwide, including 7 Chinese breeds (Wang et al., 2022). However, systematic priority conservation analysis of goat breeds in China based on genome resequencing data has not been performed.

To systematically investigate population structure, inbreeding levels, and conservation priorities of Chinese indigenous goat breeds, this study collected whole-genome resequencing data from 25 representative breeds across 20 Chinese provinces. These breeds encompass diverse ecotypes and exhibit distinct phenotypic characteristics. This study provides genetic evidence to support scientific management of indigenous caprine populations and establish a foundation for developing optimal conservation strategies.

2 Materials and methods

2.1 Ethics statement

All experiments in this study involving animals were conducted according to the ethical policies and procedures approved by the Animal Care and Use Committee of the Chinese Academy of Agricultural Sciences (IAS2019-61) and the Ministry of Agriculture of the People's Republic of China.

2.2 Sample collection and whole-genome resequencing

A total of 214 individuals representing 25 indigenous goat breeds were collected in this study (Figure 1A). With an average of approximately 8.6 individuals per breed—consistent with common sample sizes of 5–7 individuals per group (Li et al., 2020; Lv et al., 2024; Yang et al., 2024)), ensuring robust estimates of genetic diversity. To ensure accurate representation of the genetic diversity within each breed, we selected individuals that had no known pedigree connections within three generations. All the data were obtained from National Germplasm Center of Domestic Animal Resources (<https://cdad-is.org.cn/>), producing a final VCF file of 13.97 GB. Through stringent filtering and quality control procedures (Plink v1.9 arguments: `-mind 0.1 -geno 0.1 -maf 0.05 -hwe 1e-5`), low-quality variants were removed, a total of 11,465,412 SNPs were retained for subsequent analysis. The chromosomal distribution of these SNPs is shown in Supplementary Figure S1. Detailed information on the Chinese indigenous goat breeds is presented in Table 1.

2.3 Principal component analysis

Principal component analysis (PCA) was performed using GCTA v1.25.3 software (Yang et al., 2011) (GCTA v1.25.3 arguments: `-make-grm` and `-grm`). This dimensionality reduction technique transforms correlated variables into a set of linearly uncorrelated principal components through orthogonal transformation. The analysis generated the first two principal components (PC1 and PC2), which were visualized using the ggplot2 package within the RStudio environment.

2.4 Neighboring tree

Neighboring tree construction was performed using Plink v1.9 software (Purcell et al., 2007) to generate a genetic distance matrix (Plink v1.9 arguments: `-distance matrix`), followed by tree building with the ape package in RStudio. The resulting phylogenetic relationships were exported in nwk format and subsequently visualized using iTOL online platform (<https://itol.embl.de/>).

2.5 Admixture analysis

Ancestral genetic composition of indigenous Chinese goat breeds was inferred using Admixture v1.3.0 (Alexander et al., 2009). Utilizing the same statistical model as Structure but implementing faster numerical optimization algorithms, Admixture achieves computationally efficient ancestry estimation. Cross-validation (CV) values were calculated for K values ranging from 2 to 7 to determine optimal population stratification, with results subsequently visualized using RStudio.

2.6 Inbreeding coefficient analysis

The inbreeding coefficient F_{HOM} was calculated using Plink v1.9 software with the `-het` command to analyze homozygous genotypes (HOM). The computation involved determining both the observed homozygous genotype frequency and the expected frequency under Hardy-Weinberg equilibrium. The calculated F_{HOM} values were visualized using violin plots generated with the ggplot2 package in RStudio, enabling systematic assessment of inbreeding distribution patterns among the studied populations.

2.7 Contribution of genetic diversity analysis

The analysis of genetic diversity contributions was performed using the MetaPop2 software (Lopez-Cortegano et al., 2019a). The software evaluates the contribution of each breed to genetic diversity by treating the multibreed population as a metapopulation and calculating the gain or loss of gene and allele diversity that would occur after the removal of each breed from the metapopulation.

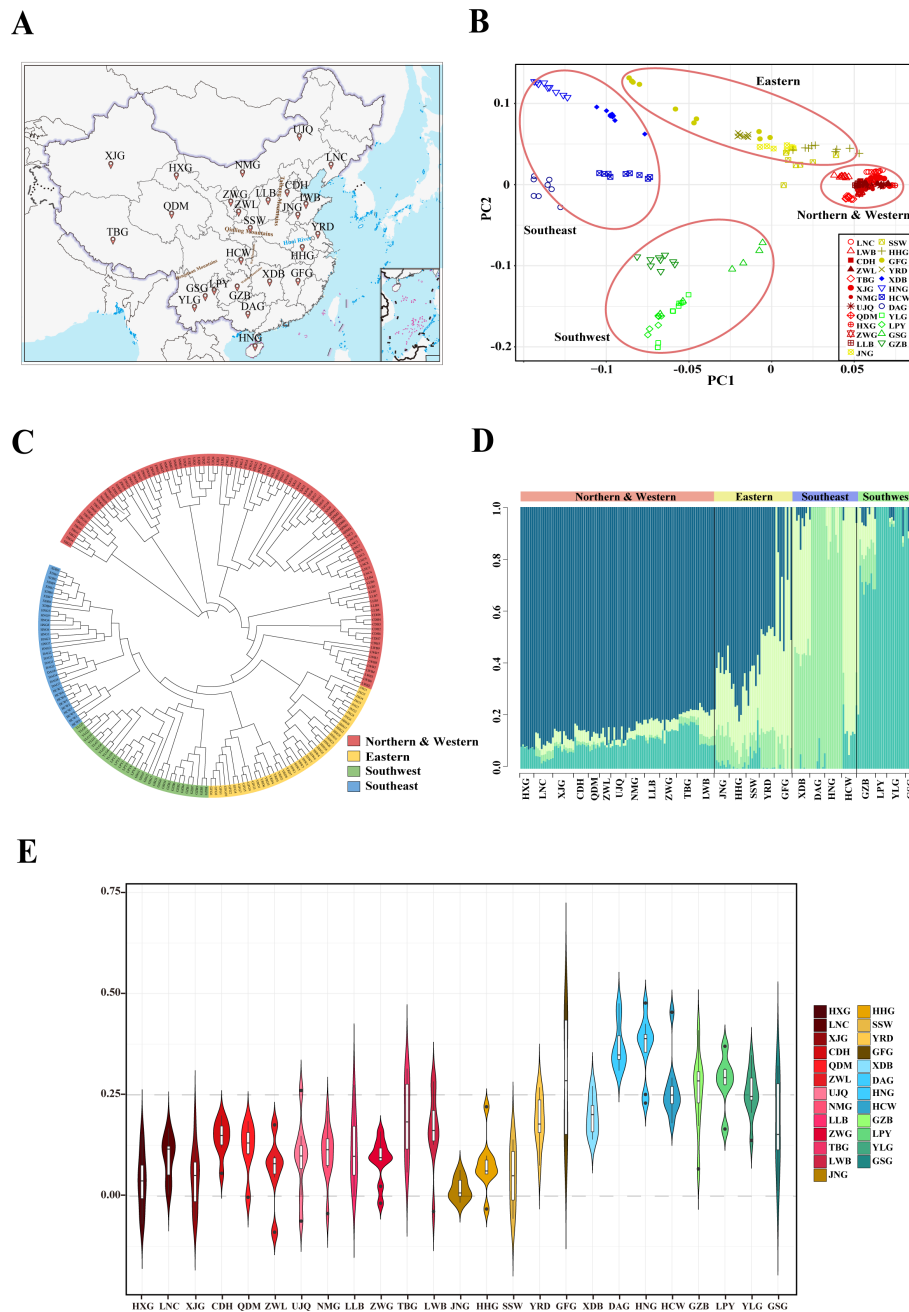


FIGURE 1 Analysis of the population structure of indigenous goat breeds in China. **(A)** Geographic distribution map of 25 indigenous goat populations. **(B)** Principal component analysis of goat populations. **(C)** Neighbor-Joining tree of goat populations. **(D)** Analysis of the genetic structure of goat populations. **(E)** Genomic inbreeding coefficient $F_{(HOM)}$ of goat population. **(B–E)** the western & northern branch is represented by red; the eastern branch is represented by yellow; the southeastern branch is represented by blue; the southwestern branch is represented by green.

(Lopez-Cortegano et al., 2019a; Gao et al., 2023a). The total gene diversity (H_T) is partitioned into the average gene diversity within breeds (H_S) and the average gene diversity between breeds (D_G). H_S is calculated as 1 minus the intra-breed co-ancestry coefficient (Nei, 1973), D_G is estimated by the average Nei’s minimum genetic distance between breeds, using the following formula:

$$H_T = H_S + D_G = (1 - \tilde{f}) + D_G$$

Where \tilde{f} represents intra-breed co-ancestry coefficient.

Similarly, the total allele diversity (AT) is divided into the average allele diversity within breeds (AS) and the average allele diversity between breeds (DA) (Caballero and Toro, 2002;

TABLE 1 Population information.

Number	Population	Abbreviation	Type	Coordinates *	Area	Size
1	Tibetan Goat	TBG	Dual-purpose (meat & cashmere)	32.50°N, 86.50°E	Tibetan	11
2	Xinjiang Goat	XJG	Dual-purpose (cashmere & meat)	41.00°N, 82.00°E	Xinjiang	11
3	Inner Mongolia Cashmere Goat	NMG	Dual-purpose (cashmere & meat)	40.80°N, 107.00°E	Inner Mongolia	10
4	Guangfeng Goat	GFG	Meat	28.45°N, 118.20°E	Jiangxi	10
5	Liaoning Cashmere Goat	LNC	Dual-purpose (cashmere & meat)	40.20°N, 122.50°E	Liaoning	10
6	Yunling Goat	YLG	Dual-purpose (meat & skin)	25.20°N, 101.50°E	Yunnan	10
7	Laiwu Black Goat	LWB	Dual-purpose (meat & cashmere)	36.20°N, 117.70°E	Shandong	9
8	Guizhou Black Goat	GZB	Dual-purpose (meat & skin)	26.85°N, 104.70°E	Guizhou	9
9	Hainan Black Goat	HNG	Meat	19.20°N, 109.70°E	Hainan	9
10	Hechuan White Goat	HCW	Dual-purpose (meat & skin)	29.98°N, 106.27°E	Chongqing	9
11	Xiangdong Black Goat	XDB	Meat	28.15°N, 113.62°E	Hunan	9
12	Huanghuai Goat	HHG	Dual-purpose (skin & meat)	33.50°N, 116.50°E	Anhui	9
13	Zhongwei Goat	ZWG	Fur (for lamb pelts)	37.52°N, 105.18°E	Ningxia	9
14	Lvliang black goat	LLB	Dual-purpose (meat & cashmere)	37.48°N, 111.10°E	Shanxi	9
15	Du an Goat	DAG	Meat	23.95°N, 107.98°E	Guangxi	8
16	Ujumqin Cashmere Goat	UJQ	Dual-purpose (cashmere & meat)	45.00°N, 117.50°E	Inner Mongolia	8
17	Chengde Hornless Goat	CDH	Meat	40.97°N, 118.00°E	Hebei	8
18	Hexi Goat	HXG	Dual-purpose (cashmere & meat)	39.50°N, 94.50°E	Gansu	8
19	Jining Grey Goat	JNG	Kid pelt	35.40°N, 116.30°E	Shandong	8
20	Yangtze River Delta White Goat	YRD	Brush wool type	31.88°N, 121.17°E	Jiangsu	8
21	Guishan Goat	GSG	Dual-purpose (dairy & meat)	24.78°N, 103.27°E	Yunnan	7
22	Southern Shaanxi White Goat	SSW	Dual-purpose (meat & skin)	32.70°N, 109.02°E	Shaanxi	7
23	Qaidam Cashmere Goat	QDM	Dual-purpose (cashmere & meat)	37.40°N, 95.00°E	Qinghai	6
24	Ziwuling Black Goat	ZWL	Purple cashmere & kid pelts	36.58°N, 107.00°E	Gansu	6
25	Luoping Yellow Goat	LPY	Primarily meat	24.90°N, 104.30°E	Yunnan	6
	Total					214

* Coordinates represent the approximate geographic centroid of each breed’s primary production area as described in official Chinese livestock breed records.

Caballero et al., 2010), using the following formula:

$$A_T = A_S + D_A = \left[\frac{1}{n} \sum_{i=1}^n \left(a_i \frac{1}{n} \sum_{j=1}^n d_{i,j} \right) \right] - 1$$

Where a_i represents the expected number of different alleles randomly chosen in the gene sample, and $d_{i,j}$ denotes the average allelic distance between subpopulations i and j .

To further simulate calculations, a synthetic pool was constructed to determine the proportion of individuals of each breed when the pool exhibits maximum gene and allele diversity (typically achieved when $N = 1000$) (Lopez-Cortegano et al., 2019a; Gao et al., 2023a). The resulting values are then standardized using Z-scores for comparability. Z-scores are used to transform data of varying magnitudes into a uniform scale. The formula for Z-score standardization involves subtracting the mean of the group from the treatment value and dividing by the standard deviation (Cheadle et al., 2003).

3 Results

3.1 Principal component analysis

We performed PCA using GCTA v1.25.3 software. The results indicated that all individuals clustered into four distinct genetic clusters (Figure 1B): the Northern & Western (NW) cluster, the Eastern (EA) cluster, the Southwestern (SW) cluster, and the Southeastern (SE) cluster. Principal Component 1 (PC1) explained 6.57% of the total genetic variance and clearly separated the NW cluster from the SE and SW clusters. Principal Component 2 (PC2) accounted for 4.93% of the genetic variance and separated the SW cluster from the other clusters (Figure 1B). The NW cluster comprised twelve breeds, including the XJG, LNG, Inner Mongolian cashmere goat (NMG), TBG, Ziwuling black goat (ZWL), Lvliang black goat (LLB), Ujumqin cashmere goat (UJQ),

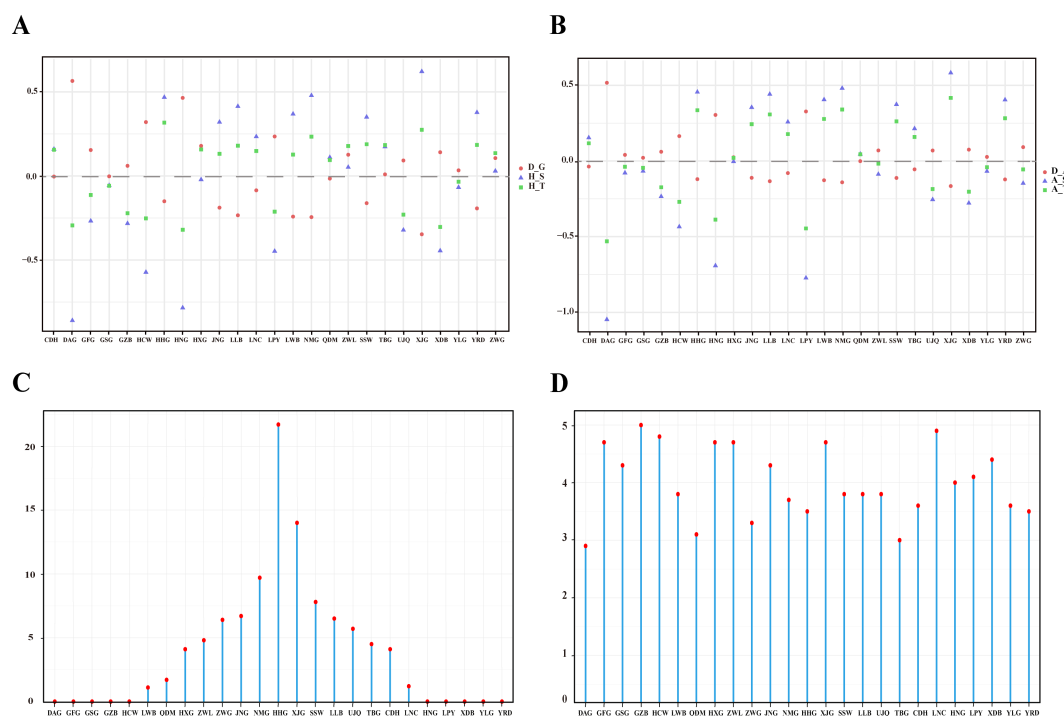


FIGURE 2 Analysis of the contribution of genetic diversity. **(A)** Contribution of indigenous goat populations to gene diversity. **(B)** Contribution of indigenous goat populations to allelic diversity. **(C)** Proportion of individuals from each breed when the population has maximum gene diversity. **(D)** Proportion of individuals from each breed when the population has maximum allelic diversity. **(A)** Loss (+) or gain (-) of gene diversity after removal of subpopulations from the metapopulation, HS is the gene diversity within-populations; DG is the gene diversity interpopulation; HT is total loss or gain gene diversity. **(B)** The loss (+) or gain (-) of allelic diversity after removing the subpopulation from metapopulation, AS is the intrapopulation allelic diversity; DA is the allelic diversity interpopulation; AT is the total loss or gain allelic diversity. **(C)** Proportion of breeds with maximum gene diversity. **(D)** Proportion of breeds with maximum allelic diversity.

Chengde hornless goat (CDH), Zhongwei goat (ZWG), Laiwu black goat (LWB), Qaidam cashmere goat (QDM), and Hexi cashmere goat (HXG). These breeds exhibited genetic overlap, reflecting their close genetic relationships. Five breeds—the HHG, JNG, YRD, Southern Shaanxi white goat (SSW), and Guangfeng goat (GFG) formed the EA cluster, showing genetic relatedness with each other. Similarly, four breeds—the Xiangdong black goat (XDB), HNG, Hechuan white goat (HCW), and Du’an goat (DAG) clustered together in the SE cluster. In contrast, the four breeds from the SW cluster namely the Guizhou black goat (GZB), Guishan goat (GSG), Luoping yellow goat (LPY), and Yunling goat (YLG), were genetically distant from the other clusters, as reflected by their position in the bottom left corner of the PCA plot.

3.2 Neighboring tree

The results demonstrated that individuals from the same breed clustered together, and all breeds were grouped into four distinct phylogenetic branches (Figure 1C), namely the NW, EA, SW, and SE branches. Interestingly, this clustering pattern, along with the breed composition of each branch, aligns with the PCA results. The breeds in the NW branch included XJG, NMG, ZWL, LNC, LWB, CDH, TBG, UJQ, QDM, HXG, ZWG, LLB. These breeds were primarily distributed across ten provinces, including Xinjiang,

Gansu, Inner Mongolia, Liaoning, Tibet, Qinghai, Ningxia, Hebei, Shanxi and Shandong, which are geographically located in Northern and Western China (Figure 1C). Similarly, the EA branch included JNG, SSW, HHG, GFG, YRD, which clustered together and were predominantly distributed in Shaanxi, Shandong, Anhui, Jiangsu, and Jiangxi provinces in eastern China. The SE branch comprised XDB, HNG, HCW, DAG, which were distributed across Hunan, Chongqing, Guangxi, and Hainan provinces in southeastern China. In contrast, the SW branch consisted of YLG, LPY, GSG, GZB, which were restricted to Yunnan and Guizhou provinces in southwestern China. Notably, we observed that certain breeds within specific branches exhibited closer genetic relationships. For instance, within the NW branch, NMG and UJQ, both distributed in Inner Mongolia, demonstrated a closer genetic affinity compared to other breeds in the same branch. Similarly, in the SW cluster, YLG, GSG, and LPY, which are all native to Yunnan Province, displayed stronger genetic connections relative to other breeds in the cluster.

3.3 Admixture analysis

The genetic compositions of Chinese indigenous goat breeds were plotted with Admixture software for $K = 2$ to $K = 7$ (Supplementary Figure S2). At $K = 4$, the model achieved the

TABLE 2 Statistics on the contribution of each breed to the genetic diversity of the population.

Population	Gene diversity/%	Allelic diversity/%	Z-gene diversity	Z-allelic diversity	Final Z-score
XJG	14	4.7	1.900	1.122	3.022
HHG	21.7	3.5	3.363	-0.801	2.561
ZWL	4.8	4.7	0.152	1.122	1.274
HXG	4.1	4.7	0.019	1.122	1.141
JNG	6.7	4.3	0.513	0.481	0.994
LNC	1.2	4.9	-0.532	1.443	0.911
GZB	0	5	-0.760	1.603	0.843
NMG	9.7	3.7	1.083	-0.481	0.602
HCW	0	4.8	-0.760	1.282	0.522
SSW	7.8	3.8	0.722	-0.321	0.401
GFG	0	4.7	-0.760	1.122	0.362
LLB	6.5	3.8	0.475	-0.321	0.154
UJQ	5.7	3.8	0.323	-0.321	0.002
XDB	0	4.4	-0.760	0.641	-0.119
GSG	0	4.3	-0.760	0.481	-0.279
LPY	0	4.1	-0.760	0.160	-0.600
CDH	4.1	3.6	0.019	-0.641	-0.622
ZWG	6.4	3.3	0.456	-1.122	-0.666
HNG	0	4	-0.760	0.000	-0.760
LWB	1.1	3.8	-0.551	-0.321	-0.872
YLG	0	3.6	-0.760	-0.641	-1.401
TBG	4.5	3	0.095	-1.603	-1.508
YRD	0	3.5	-0.760	-0.801	-1.561
QDM	1.7	3.1	-0.437	-1.443	-1.880
DAG	0	2.9	-0.760	-1.763	-2.523

lowest CV error, demonstrating the optimal population structure. In the admixture analyses, when $K = 2$, the initial partition was divided into Northern and Southern clusters; when $K = 3$, the Southern group was further separated into SE and SW cluster. When $K = 4$ (Figure 1D), the Northern cluster was further subdivided into a NW cluster and an EA cluster. The ancestral composition of the Southwest cluster exhibits a relatively homogeneous structure and serves as a contributor to the ancestral components of the Northern cluster. Furthermore, both the Southeast and Northern cluster have contributed to the ancestral component of the EA cluster.

Overall, the results of these three analyses, admixture analyses, PCA and NJ tree, consistently classified the Chinese goat breeds into four distinct genetic clusters, with identical breed composition within each cluster. This result may be closely associated with the geographical characteristics of the regions where these breeds are distributed. Specifically, the Taihang Mountains-Qinling Mountains-Hengduan Mountains distinguishes the NW branch

from the other branches, the Wuling Mountains-Wu Mountains separates the SW branch from the SE branch, and the Qinling-Huai River divides the EA branch from the SE branch.

3.4 Inbreeding coefficient analysis

To enhance our understanding of the inbreeding status of each breed, we calculated the Genomic inbreeding coefficient (F_{HOM}) (Supplementary Table S1). The F_{HOM} values across the 25 breeds ranged from 0.0165 to 0.3708, with an average of 0.1619. According to Figure 1E, the majority of breeds within the NW branch exhibited relatively low inbreeding coefficients, with an average F_{HOM} of 0.1048. Similarly, the EA branch displayed a slightly higher average F_{HOM} of 0.1238 compared to the NW branch. In contrast, the SE and SW branches demonstrated significantly higher inbreeding levels, with average F_{HOM} values of 0.2992 and 0.2436, respectively. From an individual breed perspective, the highest

inbreeding coefficient was observed in JNG ($F_{\text{HOM}}=0.0165$) from the EA branch, while the lowest inbreeding coefficient was identified in DAG ($F_{\text{HOM}}=0.3708$) from the SE branch.

3.5 Contribution of genetic diversity analysis

Genetic diversity can be assessed through both gene diversity and allele diversity metrics. According to previous studies (Caballero and Toro, 2002; Caballero et al., 2010), when quantifying the genetic diversity of domesticated animals, it is crucial to account for both within breed and between breed diversity components. The HT is partitioned into the HS and the DG. Correspondingly, the AT is divided into the AS and the DA.

To evaluate the genetic diversity contribution of each breed, the 25 indigenous breeds in this study were treated as an integrated metapopulation. The loss or gain of HT and AT was quantified by sequentially removing each breed from the metapopulation, thereby elucidating the relative contribution of each breed to the overall genetic diversity of the metapopulation (Figures 2A, B).

Furthermore, we constructed a synthetic pool comprising $N = 1000$ individuals to investigate the optimal breed proportions at which HT and AT are maximized (Figures 2C, D). The optimal breed proportions were calculated and presented in Table 2, which were subsequently standardized to generate the final Z-scores, enabling a comprehensive integration of both gene diversity and allele diversity.

The results from the Z-score for gene diversity (Table 2) show that 12 breeds contribute positively, with 9 from the NW branch, including XJG (1.9), NMG (1.083), LLB (0.475), ZWG (0.456), UJQ (0.323), ZWL (0.152), TBG (0.095), HXG (0.019), and CDH (0.019); and 3 from the EA branch, including HHG (3.363), JNG (0.513), and SSW (0.722). Among these, HHG from the EA branch (3.363) has the highest contribution to gene diversity.

The Z-score analysis of gene diversity (Table 2) reveals that 12 breeds exhibit positive contributions to gene diversity of synthetic pool. Notably, 9 of these breeds originate from the NW branch, including XJG (1.9), NMG (1.083), LLB (0.475), ZWG (0.456), UJQ (0.323), ZWL (0.152), TBG (0.095), HXG (0.019), and CDH (0.019). Additionally, three breeds stem from the EA branch, namely HHG (3.363), SSW (0.722), and JNG (0.513). Among all positively contributing breeds, HHG from the EA branch demonstrates the highest contribution to gene diversity, with a Z-score of 3.363.

The Z-score analysis of allelic diversity (Table 2) indicates that 11 breeds contribute positively to allelic diversity of synthetic pool. Specifically, four breeds originate from the NW branch, including LNC (1.443), XJG (1.122), ZWL (1.122), and HXG (1.122). Two breeds are from the EA branch, namely GFG (1.122) and JNG (0.481). Additionally, two breeds stem from the SE branch, HCW (1.282) and XDB (0.641), while three breeds belong to the SW branch, GZB (1.603), GSG (0.481), and LPY (0.16). Among these positively contributing breeds, GZB from the SW branch exhibits the highest contribution to allelic diversity, with a Z-score of 1.603. Notably, the patterns of gene diversity and allelic diversity in

Chinese goats are not entirely consistent. For example, HHG, which demonstrates the highest contribution to gene diversity, exhibits a negative contribution to allelic diversity. Conversely, GZB, which shows the highest contribution to allelic diversity, has a negative impact on gene diversity. These findings highlight the complex and potentially divergent genetic contributions of different breeds across various diversity metrics, emphasizing the importance of considering multiple dimensions of genetic variation in conservation and breeding strategies.

Combining geographic distribution characteristics and population structure analyses, we identified the top three breeds with the highest contributions within each cluster, thereby establishing a prioritized conservation list (Table 2). Specifically, the NW branch includes XJG, ZWL, and HXG; the EA branch comprises HHG, JNG, and SSW; the SE branch consists of HCW, XDB, and HNG; and the SW branch encompasses GZB, GSG, and LPY. Prioritizing the conservation of breeds with significant contributions to genetic diversity across these four clusters provides a valuable reference for establishing conservation priorities.

4 Discussion

China, a country renowned for its rich diversity of indigenous goat breeds, has recently completed the third national survey on livestock and poultry genetic resources, a comprehensive effort spanning three years. According to the National Breed List of Livestock and Poultry Genetic Resources (2024 edition) released by the National Livestock and Poultry Genetic Resources Committee (http://www.nahs.org.cn/gk/tz/202502/t20250210_452797.htm), there are 90 nationally recognized goat breeds in China, including 69 indigenous breeds. Maintaining the genetic diversity of indigenous livestock breeds is essential for developing new breeds and adapting to potential future demands in animal production (Toro et al., 2009). Concurrently, the rapid advancement of genome sequencing technologies, coupled with the corresponding reduction in costs, has led to a significant expansion of genomic data resources (Allendorf et al., 2010), systematic evaluation of genetic architecture, inbreeding levels, and conservation priorities using genomic data resources is essential for Chinese indigenous goat breeds.

Integrative analysis of PCA, NJ tree, and Admixture results revealed four distinct genetic clusters in Chinese goat populations, demonstrating strong concordance with their geographical distributions. Notably, these findings are largely consistent with the population structure analysis of Chinese goats conducted by Wei et al. (2014) using microsatellite markers. However, our study demonstrates a more accurate alignment between genetic branches and geographical distribution. For example, the LNC, located in northern China, was assigned to the NW cluster in our analysis, whereas previous studies classified it into the southern cluster, a grouping inconsistent with its geographic distribution (Wei et al., 2014). Additionally, our study provides a more coherent grouping of breeds from geographically adjacent regions. For instance, the JNG and HHG, both native to eastern China, were grouped into the

eastern cluster in our analysis, in contrast to previous research that classified them into the NW cluster, which does not reflect their true geographical distribution. These results suggest that population structure analysis based on WGS is more accurate compared to low-density microsatellite markers, owing to its comprehensive genome-wide coverage.

This study represents the first large-scale genetic analysis of Chinese indigenous goats based on WGS data. Previous studies using DNA chips and WGS data have focused on a limited number of Chinese goat breeds (Berihulay et al., 2019; Islam et al., 2019; Chang et al., 2024; Li et al., 2024; Liu et al., 2024). For example, the LNC from the north was distinctly separated from the LPY from the southwest (Islam et al., 2019), which also aligns with our results. A clear separation was observed between the JNG from the eastern and the XDB from the southeast (Liu et al., 2024), as well as between the DAG from the southeast and the JNG from the eastern (Li et al., 2024), which is in agreement with our findings. Additionally, a clear distinction was demonstrated between the GZB from the southwest and the TBG from the northwest (Chang et al., 2024), which is also consistent with our results.

Additionally, although this study includes goat samples from five distinct climate types, no significant association was observed between climate type and population structure. These findings suggest that geographical barriers (e.g., mountains) play a major role in shaping the genetic structure of indigenous goat breeds, whereas climatic factors do not appear to be determining factors. This result is consistent with findings from global studies on goat populations.

Population structure analysis demonstrated that the four genetic clusters correlate strongly with the geographical features of the regions where the breeds are distributed. Specifically, the Taihang Mountains–Qinling Mountains–Hengduan Mountains act as a natural barrier distinguishing the NW cluster from the others. This mountain system collectively forms an elongated S-shaped configuration, traversing central China along a northeast-southwest axis, consistent with the recognized role of major mountain systems in driving population divergence through physical isolation. A well-documented example is the Qinghai–Tibet Plateau, whose dramatic uplift has profoundly reshaped regional topography and facilitated allopatric divergence in adjacent areas (Zhong et al., 2022). Similarly, the Qinling Mountains, stretching over 1,500 km east-west across central China, serve as a biogeographic barrier that has driven evolutionary differentiation in numerous wildlife species between their northern and southern slopes (Yu et al., 2014; Zhong et al., 2022). Furthermore, the Hengduan Mountains separate the NW and SW clusters—a finding consistent with previous research (Wei et al., 2014). Serving as a hot spot for biodiversity and genetic variation, this region function as a significant factor in accelerated speciation (Wang et al., 2019). In parallel, the Wuling Mountains–Wu Mountains demarcate the SW and SE clusters. Stretching north–south along the central topographic axis of southern China, this range imposes a strong barrier to the distribution of various wild mammal species, leading to pronounced genetic structure within their populations (Sun et al., 2020). Finally, the Qinling Mountains–Huai River line delineates

the EA and SE clusters. This line is an east-west stretching boundary in central China, formed by the Qinling Mountains and the Huai River, which defines the natural partition between North and South China (JIA). Notably, although our study included goat samples originating from five distinct climate types, no significant association was observed between climate classification and population structure. These findings collectively suggest that major mountain ranges—rather than climatic gradients—serve as the primary drivers of genetic differentiation among indigenous Chinese goat breeds. This conclusion aligns with global patterns observed in goat populations, wherein physical barriers, rather than environmental variables, emerge as the dominant factor shaping population structure (Colli et al., 2018). Extending this perspective to neighboring regions, South Asia also possesses rich goat genetic resources. Notably, although goats from Pakistan and Bangladesh show closer genetic affinity to Chinese goats compared with those from other regions (Zhang et al., 2024), Asian goat populations can be broadly divided into three major lineages, within which South Asian (e.g., Pakistani) goats remain clearly separated from East Asian (Chinese) goats (Petretto et al., 2024). Together, these results suggest the important role of biogeography in shaping the genetic structure of goat populations.

The inbreeding coefficient (F_{HOM}) is a critical parameter that reflects the extent of inbreeding within a breed. A high inbreeding level may reduce the adaptability of the breed to indigenous environmental conditions (Hamilton and Miller, 2016; Robinson et al., 2019; Gao et al., 2023b). In this study, the analysis of the inbreeding coefficient reveals that Southern branches exhibit higher levels of inbreeding compared to Northern branches. Specifically, the inbreeding coefficients for the SW (mean $F_{\text{HOM}}=0.2436$) and SE (mean $F_{\text{HOM}}=0.2992$) branches are significantly higher than those of the NW (mean $F_{\text{HOM}}=0.1048$) and the EA (mean $F_{\text{HOM}}=0.1238$) branches. These findings are consistent with previous studies based on DNA chip and WGS data, which have identified elevated inbreeding levels in certain Chinese goat breeds (Berihulay et al., 2019; Islam et al., 2019; Zhao et al., 2024). For instance, Berihulay et al. (2019) reported that goats from the SW branch such as the LPY ($F_{\text{IS}}=0.014$), exhibited higher inbreeding coefficients than those from the NW branch, including the XJG ($F_{\text{IS}}=-0.014$). Similarly, the goats from the EA branch, such as the GFG ($F_{\text{ROH}}=0.19$), had higher inbreeding levels than those from the NW branch, such as the LNC ($F_{\text{ROH}}=0.162$) (Islam et al., 2019). Furthermore, Zhao et al. (2024) found that the inbreeding coefficient of the JNG ($F_{\text{ROH}}=0.0446$) from EA branch was higher than that of the NMG ($F_{\text{ROH}}=0.0263$) from NW branch. The elevated inbreeding levels observed in these regions may be attributed to historical breeding practices, geographical isolation, and limited gene flow. These results suggest that future breeding programs for southern goat breeds should take into account the levels of inbreeding.

The preservation of genetic diversity is a critical component of the new Global Biodiversity Framework (Lopez-Cortegano et al., 2019a, b; Hogg, 2024). Systematic research on conservation priorities is essential to ensure the effective protection of livestock genetic resources (Zhao et al., 2021b). In this study, gene and allele diversity were used to evaluate genetic diversity. Both within breeds

and between breeds diversity were considered to assess global diversity of the metapopulation, making the evaluation more appropriate for domesticated animals (Caballero and Toro, 2002). In this study, we employed large-scale WGS data of indigenous Chinese goat breeds for the first time to assess the contribution of each breed to the genetic diversity of the metapopulation. The gene diversity analysis revealed that 12 breeds made positive contributions to the HT. All of these breeds originated from the NW and EA lineages. Previous studies have shown that gene diversity is correlated with expected heterozygosity (Lacy and Ballou, 1998; Zhao et al., 2021a). The results of Wei et al. (2014) indicate that goats from the Northern and Western combined and Eastern lineages display higher expected heterozygosity, a pattern consistent with the positive contributions of NW and EA breeds to metapopulation genetic diversity observed in our study.

Researchers are committed to further optimizing conservation strategies, and previous studies have proposed that integrating genetic clustering results with conservation prioritization may generate a more accurate prioritized conservation list. In this study, we integrated the results of the four genetic clusters of indigenous Chinese goat breeds with the final Z-scores for conservation prioritization, thereby proposing an optimized recommended breed list for indigenous Chinese goats. Thus, under conditions of limited conservation funding and efforts, the recommended breed list will maximize the preservation of genetic diversity in indigenous Chinese goat breeds. While future conservation frameworks might incorporate non-genetic factors—such as socio-cultural significance and potential economic value—considerable research and development are needed before their implementation in practical breeding programs.

5 Conclusions

In this study, population structure analysis identified four distinct genetic branches among Chinese indigenous goats. Inbreeding coefficient assessment revealed significantly higher inbreeding levels in southern breeds (SE/SW) compared to northern populations (NW/EA). Genetic diversity contribution analysis enabled establishment of a prioritized conservation list, with the top three breeds identified for each branch. The integration of these genomic assessments has facilitated the development of a conservation framework and provided a scientific basis for the strategic management of the genetic resources of Chinese indigenous goats.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repository and accession number(s) can be found below: <https://figshare.com/10.6084/m9.figshare.29397095>.

Ethics statement

The animal study was approved by Animal Care and Use Committee of the Chinese Academy of Agricultural Sciences. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

YhZ: Formal Analysis, Writing – review & editing, Writing – original draft. JA: Formal Analysis, Writing – original draft. MW: Data curation, Writing – review & editing. ML: Writing – review & editing, Data curation. JL: Visualization, Writing – review & editing. ZH: Writing – review & editing, Visualization. YnZ: Writing – review & editing, Visualization. YP: Writing – review & editing. QZ: Writing – review & editing. SY: Writing – review & editing. LJ: Writing – review & editing. YM: Funding acquisition, Writing – review & editing. XH: Writing – review & editing, Project administration, Funding acquisition.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Alexander, D. H., Novembre, J., and Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* 19, 1655–1664. doi: 10.1101/gr.094052.109
- Allendorf, F. W., Hohenlohe, P. A., and Luikart, G. (2010). Genomics and the future of conservation genetics. *Nat. Rev. Genet.* 11, 697–709. doi: 10.1038/nrg2844
- Arias, K. D., Fernández, I., Gutiérrez, J. P., Bozzi, R., Álvarez, L., and Goyache, F. (2024). Characterizing local pig breeds as reservoirs for the domestic pig genetic variability worldwide via contributions to gene diversity and allelic richness. *J. Anim. Sci.* 102, skae329. doi: 10.1093/jas/skae329
- Asroush, F., Mirhoseini, S. Z., Badbarin, N., Seidavi, A., Tufarelli, V., Laudadio, V., et al. (2018). Genetic characterization of Markhoz goat breed using microsatellite markers. *Arch. Anim. Breed* 61, 469–473. doi: 10.5194/aab-61-469-2018
- Bennewitz, J., Kantanen, J., Tapio, L., Li, M. H., Kalm, E., Vilkki, J., et al. (2006). Estimation of breed contributions to present and future genetic diversity of 44 North Eurasian cattle breeds using core set diversity measures. *Genet. Selection Evol.* 38, 201–220. doi: 10.1186/1297-9686-38-2-201
- Berihulay, H., Li, Y., Liu, X., Gebreselassie, G., Islam, R., Liu, W., et al. (2019). Genetic diversity and population structure in multiple Chinese goat populations using a SNP panel. *Anim. Genet.* 50, 242–249. doi: 10.1111/age.12776
- Bionda, A., Lopreiato, V., Amato, A., Cortellari, M., Cavallo, C., Chiofalo, V., et al. (2023). Phenotypic and genomic characterization of the Comune di Sicilia goat: towards the conservation of an endangered local breed. *Anim. (Basel)* 13, 3207. doi: 10.3390/ani13203207
- Caballero, A., Rodríguez-Ramilo, S. T., Ávila, V., and Fernández, J. (2010). Management of genetic diversity of subdivided populations in conservation programmes. *Conserv. Genet.* 11, 409–419. doi: 10.1007/s10592-009-0020-0
- Caballero, A., and Toro, M. A. (2002). Analysis of genetic diversity for the management of conserved subdivided populations. *Conserv. Genet.* 3, 289–299. doi: 10.1023/A:1019956205473
- Canon, J., Alexandrino, P., Bessa, I., Carleos, C., Carretero, Y., Dunner, S., et al. (2001). Genetic diversity measures of local European beef cattle breeds for conservation purposes. *Genet. Sel Evol.* 33, 311–332. doi: 10.1186/1297-9686-33-3-311
- Chang, L., Zheng, Y., Li, S., Niu, X., Huang, S., Long, Q., et al. (2024). Identification of genomic characteristics and selective signals in Guizhou black goat. *BMC Genomics* 25, 164. doi: 10.1186/s12864-023-09954-6
- Cheadle, C., Vawter, M. P., Freed, W. J., and Becker, K. G. (2003). Analysis of microarray data using Z score transformation. *J. Mol. Diagn.* 5, 73–81. doi: 10.1016/S1525-1578(10)60455-2
- Chen, Q., Chai, Y., Zhang, W., Cheng, Y., Zhang, Z., An, Q., et al. (2022). Whole-genome sequencing reveals the genomic characteristics and selection signatures of Hainan black goat. *Genes (Basel)* 13, 1539. doi: 10.3390/genes13091539
- Chen, Q., Huang, Y., Wang, Z., Teng, S., Hanif, Q., Lei, C., et al. (2021). Whole-genome resequencing reveals diversity and selective signals in Longlin goat. *Gene* 771, 145371. doi: 10.1016/j.gene.2020.145371
- Colli, L., Milanesi, M., Talenti, A., Bertolini, F., Chen, M., Crisa, A., et al. (2018). Genome-wide SNP profiling of worldwide goat populations reveals strong partitioning of diversity and highlights post-domestication migration routes. *Genet. Sel Evol.* 50, 58. doi: 10.1186/s12711-018-0422-x
- European Cattle Genetic Diversity, C. (2006). Marker-assisted conservation of European cattle breeds: An evaluation. *Anim. Genet.* 37, 475–481. doi: 10.1111/j.1365-2052.2006.01511.x
- Feng, P., Zeng, T., Yang, H., Chen, G., Du, J., Chen, L., et al. (2021). Whole-genome resequencing provides insights into the population structure and domestication

Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fanim.2026.1739134/full#supplementary-material>

SUPPLEMENTARY FIGURE 1

Chromosome SNP density map of indigenous goats in China.

SUPPLEMENTARY FIGURE 2

Admixture analysis of indigenous Chinese goat breeds.

SUPPLEMENTARY TABLE 1

Genomic inbreeding coefficient of 25 local goat breeds.

signatures of ducks in eastern China. *BMC Genomics* 22, 401. doi: 10.1186/s12864-021-07710-2

Frankham, R. (1995). Conservation genetics. *Annu. Rev. Genet.* 29, 305–327. doi: 10.1146/annurev.ge.29.120195.001513

Gao, C., Du, W., Tian, K., Wang, K., Wang, C., Sun, G., et al. (2023a). Analysis of conservation priorities and runs of homozygosity patterns for Chinese indigenous chicken breeds. *Anim. (Basel)* 13, 599. doi: 10.3390/ani13040599

Gao, C., Wang, K., Hu, X., Lei, Y., Xu, C., Tian, Y., et al. (2023b). Conservation priority and run of homozygosity pattern assessment of global chicken genetic resources. *Poult. Sci.* 102, 103030. doi: 10.1016/j.psj.2023.103030

Gvozdanovic, K., Margeta, V., Margeta, P., Djurkin Kusec, I., Galovic, D., Dovc, P., et al. (2019). Genetic diversity of autochthonous pig breeds analyzed by microsatellite markers and mitochondrial DNA D-loop sequence polymorphism. *Anim. Biotechnol.* 30, 242–251. doi: 10.1080/10495398.2018.1478847

Hamilton, J. A., and Miller, J. M. (2016). Adaptive introgression as a resource for management and genetic conservation in a changing climate. *Conserv. Biol.* 30, 33–41. doi: 10.1111/cobi.12574

Hoffmann, I., Boerma, D., and Scherf, B. (2011). The Global Plan of Action for Animal Genetic Resources — The road to common understanding and agreement. *Livestock Sci.* 136, 7–14. doi: 10.1016/j.livsci.2010.09.002

Hogg, C. J. (2024). Translating genomic advances into biodiversity conservation. *Nat. Rev. Genet.* 25, 362–373. doi: 10.1038/s41576-023-00671-0

Islam, R., Li, Y., Liu, X., Berihulay, H., Abied, A., Gebreselassie, G., et al. (2019). Genome-wide runs of homozygosity, effective population size, and detection of positive selection signatures in six Chinese goat breeds. *Genes (Basel)* 10, 938. doi: 10.3390/genes10110938

Islam, R., Liu, Z., Li, Y., Jiang, L., and Ma, Y. (2020). Conservation assessment of the state goat farms by using SNP genotyping data. *Genes (Basel)* 11, 652. doi: 10.3390/genes11060652

Kumar, A., Aggarwal, R. A. K., and Tantia, M. S. (2024). Deciphering genetic diversity in conserved cattle bulls to achieve sustainable development goals. *Sci. Rep.* 14, 10794. doi: 10.1038/s41598-024-61542-0

Lacy, R. C., and Ballou, J. D. (1998). Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. *Evolution* 52, 900–909. doi: 10.1111/j.1558-5646.1998.tb03715.x

Li, Y., Gong, Y., Zhang, Z., Li, L., Liu, X., He, X., et al. (2023). Whole-genome sequencing reveals selection signals among Chinese, Pakistani, and Nepalese goats. *J. Genet. Genomics* 50, 362–365. doi: 10.1016/j.jgg.2023.01.010

Li, C., Wang, X., Li, H., Ahmed, Z., Luo, Y., Qin, M., et al. (2024). Whole-genome resequencing reveals diversity and selective signals in the Wuxue goat. *Anim. Genet.* 55, 575–587. doi: 10.1111/age.13437

Li, X., Yang, J., Shen, M., Xie, X. L., Liu, G. J., Xu, Y. X., et al. (2020). Whole-genome resequencing of wild and domestic sheep identifies genes associated with morphological and agronomic traits. *Nat. Commun.* 11, 2815. doi: 10.1038/s41467-020-16485-1

Liu, Z., Li, H., Luo, Y., Li, J., Sun, A., Ahmed, Z., et al. (2024). Comprehensive whole-genome resequencing unveils genetic diversity and selective signatures of the Xiangdong black goat. *Front. Genet.* 15. doi: 10.3389/fgene.2024.1326828

Liu, G., Zhao, Q., Lu, J., Sun, F., Han, X., Zhao, J., et al. (2019). Insights into the genetic diversity of indigenous goats and their conservation priorities. *Asian-Australas J. Anim. Sci.* 32, 1501–1510. doi: 10.5713/ajas.18.0737

Lopez-Cortegano, E., Perez-Figueroa, A., and Caballero, A. (2019a). metapop2: Re-implementation of software for the analysis and management of subdivided

- populations using gene and allelic diversity. *Mol. Ecol. Resour* 19, 1095–1100. doi: 10.1111/1755-0998.13015
- Lopez-Cortegano, E., Pouso, R., Labrador, A., Perez-Figueroa, A., Fernandez, J., and Caballero, A. (2019b). Optimal management of genetic diversity in subdivided populations. *Front. Genet.* 10. doi: 10.3389/fgene.2019.00843
- Lv, F. H., Wang, D. F., Zhao, S. Y., Lv, X. Y., Sun, W., Nielsen, R., et al. (2024). Deep ancestral introgressions between ovine species shape sheep genomes via argali-mediated gene flow. *Mol. Biol. Evol.* 41, msae212. doi: 10.1093/molbev/msae212
- Mateus, J. C., Eding, H., Penedo, M. C., and Rangel-Figueiredo, M. T. (2004). Contributions of Portuguese cattle breeds to genetic diversity using marker-estimated kinships. *Anim. Genet.* 35, 305–313. doi: 10.1111/j.1365-2052.2004.01168.x
- Medugorac, I., Veit-Kensch, C. E., Ramljak, J., Brka, M., Markovic, B., Stojanovic, S., et al. (2011). Conservation priorities of genetic diversity in domesticated metapopulations: a study in taurine cattle breeds. *Ecol. Evol.* 1, 408–420. doi: 10.1002/ece3.39
- Meng, Y., Zhang, B., Qin, Z., Chen, Y., Shan, X., Sun, L., et al. (2022). Stepwise method and factor scoring in multiple regression analysis of cashmere production in Liaoning cashmere goats. *Anim. (Basel)* 12, 1886. doi: 10.3390/ani12151886
- Nantongo, Z., Birungi, J., Opiyo, S. O., Shirima, G., Mugerwa, S., Mutai, C., et al. (2024). Genetic diversity, population structure and kinship relationships highlight the environmental influence on Uganda's indigenous goat populations. *Front. Genet.* 15. doi: 10.3389/fgene.2024.1385611
- Nei, M. (1973). Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci. U.S.A.* 70, 3321–3323. doi: 10.1073/pnas.70.12.3321
- Nguyen-Phuc, H., and Berres, M. E. (2018). Genetic structure in Red Junglefowl (*Gallus gallus*) populations: Strong spatial patterns in the wild ancestors of domestic chickens in a core distribution range. *Ecol. Evol.* 8, 6575–6588. doi: 10.1002/ece3.4139
- Oget, C., Servin, B., and Palhiere, I. (2019). Genetic diversity analysis of French goat populations reveals selective sweeps involved in their differentiation. *Anim. Genet.* 50, 54–63. doi: 10.1111/age.12752
- Pérez-Figueroa, A., Saura, M., Fernández, J., Toro, M. A., and Caballero, A. (2008). METAPOP—A software for the management and analysis of subdivided populations in conservation programs. *Conserv. Genet.* 10, 1097–1099. doi: 10.1007/s10592-008-9718-7
- Petretto, E., Dettori, M. L., Luigi-Sierra, M. G., Noce, A., Pazzola, M., Vacca, G. M., et al. (2024). Investigating the footprint of post-domestication dispersal on the diversity of modern European, African and Asian goats. *Genet. Sel. Evol.* 56, 55. doi: 10.1186/s12711-024-00923-5
- Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A., Bender, D., et al. (2007). PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* 81, 559–575. doi: 10.1086/519795
- Robinson, J. A., Raikkonen, J., Vucetich, L. M., Vucetich, J. A., Peterson, R. O., Lohmueller, K. E., et al. (2019). Genomic signatures of extensive inbreeding in Isle Royale wolves, a population on the threshold of extinction. *Sci. Adv.* 5, eaau0757. doi: 10.1126/sciadv.aau0757
- Shang, P., Li, W., Tan, Z., Zhang, J., Dong, S., Wang, K., et al. (2020). Population genetic analysis of ten geographically isolated Tibetan pig populations. *Anim. (Basel)* 10, 1297. doi: 10.3390/ani10081297
- Sun, J., Wen, Z., Feijó, A., Cheng, J., Wang, Y., Li, S., et al. (2020). Elevation patterns and critical environmental drivers of the taxonomic, functional, and phylogenetic diversity of small mammals in a karst mountain area. *Ecol. Evol.* 10, 10899–10911. doi: 10.1002/ece3.6750
- Talenti, A., Palhiere, I., Tortereau, F., Pagnacco, G., Stella, A., Nicolazzi, E. L., et al. (2018). Functional SNP panel for parentage assessment and assignment in worldwide goat breeds. *Genet. Sel. Evol.* 50, 55. doi: 10.1186/s12711-018-0423-9
- Tapio, I., Varv, S., Bennowitz, J., Maleviciute, J., Fimland, E., Grisli, Z., et al. (2006). Prioritization for conservation of northern European cattle breeds based on analysis of microsatellite data. *Conserv. Biol.* 20, 1768–1779. doi: 10.1111/j.1523-1739.2006.00488.x
- Toro, M. A., Fernández, J., and Caballero, A. (2009). Molecular characterization of breeds and its use in conservation. *Livestock Sci.* 120, 174–195. doi: 10.1016/j.livsci.2008.07.003
- Tosser-Klopp, G., Bardou, P., Bouchez, O., Cabau, C., Crooijmans, R., Dong, Y., et al. (2014). Design and characterization of a 52K SNP chip for goats. *PLoS One* 9, e86227. doi: 10.1371/journal.pone.0086227
- Wang, X., Li, G., Jiang, Y., Tang, J., Fan, Y., and Ren, J. (2022). Genomic insights into the conservation and population genetics of two Chinese native goat breeds. *J. Anim. Sci.* 100, skac274. doi: 10.1093/jas/skac274
- Wang, Z., Zhuang, H., Wang, M., and Pierce, N. E. (2019). *Thitarodes shambalensis* sp. nov. (Lepidoptera, Hepialidae): a new host of the caterpillar fungus *Ophiocordyceps sinensis* supported by genome-wide SNP data. *Zookeys* 885, 89–113. doi: 10.3897/zookeys.885.34638
- Wei, C., Lu, J., Xu, L., Liu, G., Wang, Z., Zhao, F., et al. (2014). Genetic structure of Chinese indigenous goats and the special geographical structure in the Southwest China as a geographic barrier driving the fragmentation of a large population. *PLoS One* 9, e94435. doi: 10.1371/journal.pone.0094435
- Weitzman, M. L. (1992). On diversity. *Q. J. Econ* 107, 363–405. doi: 10.2307/2118476
- Weitzman, M. L. (1993). What to preserve? An application of diversity theory to crane conservation. *Q. J. Econ* 108, 157–183. doi: 10.2307/2118499
- Xiong, J., Bao, J., Hu, W., Shang, M., and Zhang, L. (2022). Whole-genome resequencing reveals genetic diversity and selection characteristics of dairy goat. *Front. Genet.* 13. doi: 10.3389/fgene.2022.1044017
- Xu, L., Wang, X., Wu, J., Wang, H., Zhou, W., Liu, J., et al. (2024). Genetic variation analysis of Guanling cattle based on whole-genome resequencing. *Anim. Biosci.* 37, 2044–2053. doi: 10.5713/ab.24.0181
- Yang, J., Lee, S. H., Goddard, M. E., and Visscher, P. M. (2011). GCTA: a tool for genome-wide complex trait analysis. *Am. J. Hum. Genet.* 88, 76–82. doi: 10.1016/j.ajhg.2010.11.011
- Yang, J., Wang, D. F., Huang, J. H., Zhu, Q. H., Luo, L. Y., Lu, R., et al. (2024). Structural variant landscapes reveal convergent signatures of evolution in sheep and goats. *Genome Biol.* 25, 148. doi: 10.1186/s13059-024-03288-6
- Yu, D., Chen, M., Tang, Q., Li, X., and Liu, H. (2014). Geological events and Pliocene climate fluctuations explain the phylogeographical pattern of the cold water fish *Rhynchocypris oxycephalus* (Cypriniformes: Cyprinidae) in China. *BMC Evol. Biol.* 14, 225. doi: 10.1186/s12862-014-0225-9
- Zhang, C., Asadollahpour Nanaei, H., Jafarpour Negari, N., Amiri Roudbar, M., Amiri Ghanatsaman, Z., Niyazbekova, Z., et al. (2024). Genomic analysis uncovers novel candidate genes related to adaptation to tropical climates and milk production traits in native goats. *BMC Genomics* 25, 477. doi: 10.1186/s12864-024-10387-y
- Zhang, W., Li, X., Jiang, Y., Zhou, M., Liu, L., Su, S., et al. (2022). Genetic architecture and selection of Anhui autochthonous pig population revealed by whole genome resequencing. *Front. Genet.* 13. doi: 10.3389/fgene.2022.1022261
- Zhang, L., Zhang, S., Zhan, F., Song, M., Shang, P., Zhu, F., et al. (2023). Population genetic analysis of six Chinese indigenous pig meta-populations based on geographically isolated regions. *Anim. (Basel)* 13, 1396. doi: 10.3390/ani13081396
- Zhao, Q., Huang, C., Chen, Q., Su, Y., Zhang, Y., Wang, R., et al. (2024). Genomic inbreeding and runs of homozygosity analysis of Cashmere goat. *Anim. (Basel)* 14, 1246. doi: 10.3390/ani14081246
- Zhao, Q., Liu, H., Qadri, Q. R., Wang, Q., Pan, Y., and Su, G. (2021a). Long-term impact of conventional and optimal contribution conservation methods on genetic diversity and genetic gain in local pig breeds. *Heredity (Edinb)* 127, 546–553. doi: 10.1038/s41437-021-00484-z
- Zhao, Q. B., Lopez-Cortegano, E., Oyelami, F. O., Zhang, Z., Ma, P. P., Wang, Q. S., et al. (2021b). Conservation priorities analysis of Chinese indigenous pig breeds in the Taihu lake region. *Front. Genet.* 12. doi: 10.3389/fgene.2021.558873
- Zhi, Y., Wang, D., Zhang, K., Wang, Y., Geng, W., Chen, B., et al. (2023). Genome-wide genetic structure of Henan indigenous chicken breeds. *Anim. (Basel)* 13, 753. doi: 10.3390/ani13040753
- Zhong, H., Sun, Y., Wu, H., Li, S., Shen, Z., Yang, C., et al. (2022). Pleistocene climate and geomorphology drive the evolution and phylogeographic pattern of *Triplophysa robusta* (Kessler 1876). *Front. Genet.* 13. doi: 10.3389/fgene.2022.955382

Glossary

WGS	whole-genome sequencing	YLG	Yunling Goat
NW	Northern & Western	LWB	Laiwu Black Goat
EA	Eastern	GZB	Guizhou Black Goat
SW	Southwestern	HNG	Hainan Black Goat
SE	Southeastern	HCW	Hechuan White Goat
HT	total gene diversity	XDB	Xiangdong Black Goat
AT	total allele diversity	HHG	Huanghuai Goat
SNP	single nucleotide polymorphism	ZWG	Zhongwei Goat
PCA	Principal component analysis	LLB	Lvliang black goat
HOM	homozygous genotypes	DAG	Du an Goat
HS	average gene diversity within breeds	UJQ	Ujumqin Cashmere Goat
DG	average gene diversity between breeds	CDH	Chengde Hornless Goat
AS	average allele diversity within breeds	HXG	Hexi Goat
DA	average allele diversity between breeds	JNG	Jining Grey Goat
CV	Cross-validation	YRD	Yangtze River Delta White Goat
TBG	Tibetan Goat	GSG	Guishan Goat
XJG	Xinjiang Goat	SSW	Southern Shaanxi White Goat
NMG	Inner Mongolia Cashmere Goat	QDM	Qaidam Cashmere Goat
GFG	Guangfeng Goat	ZWL	Ziwuling Black Goat
LNC	Liaoning Cashmere Goat	LPY	Luoping Yellow Goat