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# Genomic insights into the genetic underpinnings of environmental adaptation across diverse Asian goat populations

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## Abstract

# Background

Domestic goats (*Capra hircus*), domesticated approximately 10,000 years ago in the Fertile Crescent, have dispersed across Asia and adapted to an exceptionally wide range of environments. However, the genomic basis of this environmental adaptation, and the relative contributions of selection, demographic structure and introgression from wild relatives, remain incompletely characterized at continental scale.

# Results

We analyzed genome-wide 50 K SNP data (44,260 SNPs) for 930 individuals, comprising 883 domestic goats from 36 indigenous populations spanning West, Central, South, Southeast and East Asia and 47 wild caprids. Phylogenomic, PCA and ancestry analyses resolved a strong geographic structure separating wild from domestic lineages. TreeMix and f-branch statistics revealed cross-taxon gene flow, with introgression signals concentrated predominantly in East and Southeast Asian domestic groups. Population-differentiation scans (FST–π) identified 305 selected regions (48–77 per region) harboring 587 candidate genes, of which only 109 were shared by two or more regions; enrichment analyses highlighted ion transport, radiation and stress responses, and immune and signaling pathways (MAPK, calcium, AMPK, HIF-1). Landscape-genomic redundancy analysis (RDA) with eight bioclimatic variables detected 88 climate-associated outlier loci and 191 environment-associated candidate genes dominated by temperature variables, enriched for hypoxia response, angiogenesis and ion-channel activity. Only four genes (LEPR, SPIDR, TMEM18 and LOC106502445) were supported by both approaches, indicating that the two strategies capture complementary facets of local adaptation.

# Conclusions

Environmental adaptation in Asian domestic goats proceeds through a mosaic architecture that combines a small convergent core of shared selective targets with extensive region-specific responses. The candidate loci identified here, in particular the dual-supported genes, provide targets for marker-assisted breeding and for the conservation of Asian goat genetic resources.

## Background

Domestic goats (*Capra hircus*) represent one of the earliest and most economically vital livestock species domesticated by human societies, with a domestication history tracing back 9,500 to 10,500 years in the Fertile Crescent [1]. Following initial domestication, goats have undergone extensive human-mediated migration and natural selection, gradually dispersing across the Asian continent and colonizing a wide spectrum of heterogeneous ecological environments. As a pivotal livestock resource adapted to marginal and harsh habitats, Asian indigenous goat populations exhibit extraordinary phenotypic and

physiological plasticity, enabling them to thrive in divergent climatic and geographical conditions, ranging from the high-altitude hypoxic Qinghai-Tibet Plateau and frigid northern temperate zones to arid desert regions and humid tropical lowlands [2, 3]. This broad environmental adaptability, coupled with long-term geographical isolation, natural adaptive pressure, and artificial breeding selection, has fostered rich genetic diversity and unique adaptive genomic characteristics in Asian goat populations [4], making them an ideal model for exploring the molecular mechanisms of vertebrate environmental adaptation and evolutionary genomics [5].

Asia possesses the most abundant indigenous goat genetic resources worldwide, with distinct population geographical distribution and adaptive differentiation shaped by complex terrain and diverse climate gradients [4, 6, 7]. Highland goat populations in Himalayan and Qinghai-Tibet Plateau regions have evolved stable tolerance to extreme high-altitude stressors, including low oxygen partial pressure, intense ultraviolet radiation, and low annual temperatures [2, 8]. Northern Asian and temperate northern Chinese cashmere goats have formed adaptive traits against cold and dry climates, such as dense cashmere follicle development and efficient energy metabolism [2]. In contrast, southern Asian and Southeast Asian native goat exhibit strong resistance to high temperature, high humidity, and tropical parasitic diseases [3], while desert-distributed goat populations show outstanding water retention and drought tolerance [9, 10]. These population-specific adaptive phenotypes are not random phenotypic plasticity but stable heritable traits shaped by long-term genomic evolution and positive selection, which are crucial for the survival, reproduction, and ecological niche expansion of goat populations across Asia [5]. Clarifying the genetic basis of these adaptive variations is of great significance for revealing the evolutionary rules of domestic animals under environmental pressure.

With the rapid advancement of next-generation sequencing and landscape genomics technologies, research on livestock environmental adaptation has shifted from traditional phenotypic observation and physiological detection [11] to systematic exploration of genome-wide variation and selection signatures [12, 13]. Previous studies have preliminarily identified several key adaptive genes and functional pathways in specific goat populations, including genes associated with high-altitude hypoxia adaptation, cold resistance, heat tolerance, and energy metabolism [2, 3]. A small number of studies have also confirmed that adaptive introgression from wild caprid species such as markhor has accelerated the environmental adaptation process of domestic goats in specific Asian regions [8, 9]. However, most existing researches focus on single regional populations or single adaptive traits, lacking systematic cross-regional comparative genomic analysis of diverse Asian goat populations. The universal and population-specific core adaptive genetic variations across different Asian ecological zones remain unclear, and the molecular regulatory networks linking genomic variation, gene expression, and environmental adaptive phenotypes have not been fully elucidated.

In the context of global climate change and increasing livestock germplasm resource conservation demands, exploring the genomic basis of environmental adaptation in Asian goats has important theoretical and practical value [14]. On the theoretical level, cross-population genomic analysis can clarify how geographical isolation and heterogeneous environmental pressure drive genetic

differentiation and adaptive evolution of domestic goats, supplementing the evolutionary genomic theoretical system of Asian domestic animals [15]. On the practical level, indigenous goat germplasms carry elite adaptive gene resources that have been naturally screened for thousands of years. Mining these core adaptive genetic variations can provide reliable molecular markers for precision breeding, stress-resistant germplasm innovation, and efficient utilization of local goat resources [16]. Meanwhile, with the continuous impact of climate change and human activities, many local Asian goat populations are facing the risk of genetic homogenization and germplasm resource loss [4, 17], making systematic exploration and protection of their adaptive genomic characteristics increasingly urgent.

Despite the progress in goat genomic research, there are still critical research gaps in the adaptive evolution of Asian goat populations. First, most studies rely on limited population samples and fail to cover the major ecological gradient types across Asia, resulting in an incomplete understanding of the adaptive genomic landscape of Asian goats. Second, it remains unclear whether convergent adaptive phenotypes in different geographical populations are driven by convergent genomic variation or independent population-specific genetic mechanisms [5, 15]. Third, the interactive effects of natural selection, geographical migration, and genetic introgression on the formation of adaptive traits in Asian goats have not been systematically analyzed [8, 15].

To address these gaps, we present a continental-scale genomic analysis of environmental adaptation in Asian goats. We analysed Illumina goat SNP 50 K data from 883 domestic goats representing 36 populations across the five major Asian sub-regions (West, South, Central, East, and Southeast Asia), and included five wild caprid populations (Bezoar, Caucasian tur, Markhor, Mid-Asian ibex, and Siberian ibex) as evolutionary references. We first resolved the population structure and phylogeographic differentiation of Asian goats and quantified gene flow between domestic populations and their wild relatives. We then performed region-specific selection scans based on FST and nucleotide diversity (θπ) in each sub-region, and compared the candidate genes across sub-regions to distinguish convergent adaptive signals from region-specific responses. In parallel, we applied redundancy analysis (RDA), a multivariate genotype–environment association method, against eight bioclimatic variables spanning temperature and precipitation gradients to detect climate-associated genomic variation. This integrated framework allowed us to evaluate how geographical isolation, divergent environmental pressures, and wild introgression have jointly shaped the adaptive genomic landscape of Asian goats. The candidate genes and functional pathways identified here deepen our understanding of the evolutionary mechanisms underlying environmental adaptation in domestic goats and provide molecular resources for the conservation and innovative utilization of Asian indigenous goat germplasm.

## Materials and methods

# Sample collection and quality control

A total of **930 individuals** — comprising **883 domestic goats** from 36 indigenous populations and **47 wild caprids** as evolutionary references —were collected previously published goat 50 K SNP data sets [18]

(Table S1). Domestic goats spanned five Asian sub-regions: **West Asia (n = 94)** comprising three Turkish breeds (Ankara, Kil, Kilis) and one Iranian population; **South Asia (n = 439)** comprising sixteen Pakistani breeds (totalling 387 individuals) plus Bangladesh and Nepal; **Central Asia (n = 30)** comprising a single Kazakhstani population; **East Asia (n = 167)** comprising seven Chinese populations — Inner Mongolia Aarbas Cashmere, Jiangxi Guangfeng, Mongolia, Shandong Jining Grey, two Xinjiang breeds (Nanjiang and Qinggeda) and Yunnan Luoping Yellow; and **Southeast Asia (n = 153)** comprising Cambodia, Indonesia, Laos, Myanmar, Philippines and Vietnam. Wild caprids included Caucasian tur (*Capra caucasica*) from Russia and bezoar (*C. aegagrus*) from Iran in West Asia (n = 23), and markhor (*C. falconeri*) from Uzbekistan, Mid-Asian ibex (*C. sibirica/C. sakeen*) from Tajikistan, and Siberian ibex (*C. sibirica*) from Kazakhstan in Central Asia (n = 24). Sampling-site coordinates were recorded for all populations and used for downstream landscape-genomic analyses. Autosomal SNPs were retained if they had a call rate > 95%, ≥ 90% non-missing genotypes per marker and ≥ 90% non-missing genotypes per individual. After quality control, 44,260 SNPs were available for downstream analyses.

## Population Genetic Structure

An NJ tree was built from pairwise Reynolds genetic distances [19] using PHYLIP v3.68 [20] and visualized with FigTree v1.4 [21]. To examine genetic relationships, we performed principal component analysis (PCA) on identity-by-state (IBS) allele sharing in PLINK v1.9 [22] and plotted the leading components in R [23]. Prior to admixture analysis, SNPs in linkage disequilibrium were pruned using PLINK v1.9 (--indep-pairwise 50 10 0.1), removing 21,410 SNPs with pairwise $r^2 > 0.1$ across 50-SNP sliding windows. Population structure was then inferred with ADMIXTURE v1.3 [24], with the optimal number of ancestral clusters (K) selected by 6-fold cross-validation (--CV = 6), and the resulting ancestry proportions were visualized with pong [25].

## Gene flow and genomic Introgression

To infer historical gene flow among Asian domestic goats and their wild caprid relatives, we built a maximum-likelihood population graph from LD-pruned autosomal SNP allele frequencies using TreeMix v1.12 [26]. The graph was rooted with Mid-Asian ibex and Siberian ibex, and 1–6 migration edges (M) were incrementally added. For each M, model fit was quantified as the fraction of the ancestry covariance matrix explained by the inferred graph. The optimal M was defined as the value at which the explained variance reached ≥ 99.8%, beyond which additional edges contributed negligible improvement. The migration graph with the highest cumulative explained covariance at this M was retained for downstream interpretation. To formally test the gene flow events inferred by TreeMix, we computed D-statistics (ABBA-BABA tests) [27] for all relevant four-taxon (P1, P2, P3, O) quartets using Dsuite [28]. In each quartet, P1 and P2 are sister populations, P3 is a hypothesized donor, and O is an outgroup used to polarize the ABBA and BABA allele-sharing patterns. Statistical significance was assessed by weighted block jackknife resampling across the genome, with the migration weight. To localise the inferred gene flow to specific internal branches of the population graph, we additionally computed f-branch (fb)

statistics [29] in Dsuite. The fb statistic measures the excess allele sharing between each (P3) donor and each branch leading to (P1, P2), independent of the order in which other admixture events occurred. Significant fb values indicate introgression from P3 into the (P1, P2) lineage after its divergence from the rest of the tree.

## Selection Signatures

Genome-wide selection scans were performed for each of five Asian regions (Central, East, South, Southeast and West Asia) by contrasting the regional domestic goats with wild goats (bezoar) [30, 31]. After quality filtering, SNPs were scanned in sliding windows of 50 kb with a step size of 25 kb (minimum 50 SNPs per window). Nucleotide diversity (π) of each population and pairwise Weir & Cockerham weighted FST [32] between populations were calculated with VCFtools (v0.1.16) [33] and transformed into two statistics: the diversity ratio log2(π_wild/π_region) and the standardized differentiation z(FST) = (FST − mean)/SD. Adjacent candidate windows within 10 kb were merged, and genes overlapping the merged regions in the reference genome (ARS1) [34] annotation were retrieved as candidate genes. Finally, over-representation analysis of GO terms and KEGG pathways for the candidate genes was conducted with clusterProfiler (v4.x) [35], using all annotated genes as the background and applying Benjamini–Hochberg correction [36] (FDR < 0.05 considered significant); region-specificity of the selection signals was assessed by Venn intersection of the five regional candidate sets.

## Climatic correlation analysis

Bioclimatic variables were obtained from the WorldClim database (version 2.1; https://worldclim.org/data/worldclim21.html), which provides climate layers for 1970–2000 at 30 arc-second resolution in the WGS84 coordinate system [37]. Values were extracted at each sampling locality from longitude–latitude coordinates using the R packages sp and rgdal [38, 39]. To avoid collinearity, we retained the variables previously identified as most relevant to goat biogeography, focusing on indices that capture thermal and moisture variation: BIO1 (annual mean temperature), BIO5 (maximum temperature of the warmest month), BIO6 (minimum temperature of the coldest month), BIO7 (temperature annual range), BIO12 (annual precipitation), BIO13 (precipitation of the wettest month), BIO14 (precipitation of the driest month) and BIO15 (precipitation seasonality). Of these, annual mean temperature (BIO1) and annual precipitation (BIO12) were carried into the downstream association analyses.

Association analyses. Redundancy analysis (RDA) was performed with the vegan R package [40] and its built-in rda function to identify environmental predictors and quantitative traits associated with genomic diversity. RDA combines multivariate multiple regression with a principal component analysis of fitted values and displays the resulting variable relationships in two-dimensional ordination plots. Following established protocols [41–43], environmental predictors and quantitative traits were evaluated in separate models. SNPs identified by both analytical approaches at FDR < 0.05 were considered

candidate adaptive SNPs. Genes located within 100 kb upstream or downstream of the candidate SNPs were retrieved as candidate genes. Gene Ontology (GO) functional enrichment analysis was then conducted using the Metascape database [44], with significance set at $P < 0.01$.

## Results

# Population structure and phylogenetic relationships

To characterize the genetic structure of Asian goats (*Capra hircus*) and their wild relatives, we performed a phylogenomic analysis and a series of population-genomic analyses on genome-wide data covering multiple geographic groups (West, South, Southeast, Central and East Asia) together with wild taxa including the Bezoar wild goat, Markhor (*C. falconeri*), Mid-Asian, Siberian and Caucasian ibex/tur lineages (Fig. 1). A reconstructed phylogeny based on the genome-wide data resolved the samples into well-supported clades that largely corresponded to geographic and taxonomic origins (Fig. 1a). Wild taxa — the Bezoar wild goat, Markhor and the various ibex/tur lineages — formed distinct branches clearly separated from the domestic Asian populations, indicating that the dataset provides sufficient resolution to distinguish wild and domestic lineages. Principal component analysis (PCA) of all samples (Fig. 1b) revealed a pronounced separation along PC1 between the wild taxa (Bezoar wild goat, Markhor, Caucasian ibex/tur), which clustered at negative values, and the Asian domestic goats, which clustered at positive values. Among the domestic populations, samples from Southeast Asia showed the broadest dispersion along PC2, suggesting considerable internal genetic diversity that may reflect a complex or admixed demographic history. Restricting PCA to the five Asian domestic groups (Fig. 1c) recovered clear geographic substructure: South Asian goats formed a distinct cluster at low PC1 and negative PC2 values, Southeast Asian goats were distributed at intermediate-to-high PC1 values, whereas East, Central and West Asian goats clustered together at low PC1 and positive PC2 values. These results indicate substantial genetic stratification among Asian domestic goats, with South and Southeast Asian populations being the most differentiated. ADMIXTURE analysis at $K = 2–6$ (Fig. 1d) was consistent with these patterns. At the lowest K, samples were partitioned primarily into wild and domestic components; with increasing K, each wild taxon (Bezoar, Mid-Asian, Siberian and Caucasian ibex/tur, and Markhor) was progressively assigned a largely independent ancestral component, as expected for distinct taxa. Among the domestic groups, region-specific ancestry components emerged with increasing K, with South and Southeast Asian populations being differentiated at relatively low K. This is in agreement with the PCA results and suggests limited but detectable genetic admixture among Asian domestic populations against a backdrop of wild taxa that retain largely homogeneous ancestry, providing a framework for subsequent detection of gene flow and introgression between wild relatives and domestic goats.

## Gene flow and Genomic introgression

To infer the patterns and sources of gene flow among Asian domestic goats and their wild relatives, we applied TreeMix and the f-branch statistic (f_b) to the same genomic dataset (Fig. 2). We first evaluated the number of migration edges (m) to include in the TreeMix model (Fig. 2a). The mean log-likelihood L(m) (± SD) and the fraction of variance explained both increased monotonically with m (from 0 to 8), with the variance explained remaining at very high levels (> 0.9997) throughout, and the 99.8% variance threshold was used to guide model selection. The likelihood increment Δm (= L(m) − L(m − 1)) showed a prominent peak at m = 1 (Δm ≈ 18), followed by a sharp drop to near zero at m = 2 (Fig. 2b); after minor fluctuations for m = 2–5, a secondary peak was observed at m = 6 (Δm ≈ 6), before returning to near zero at m = 7–8. These results indicate that at least one migration edge is strongly supported, with a possible additional contribution around m = 6. The resulting TreeMix graph (Fig. 2c) placed the outgroup at the root with the Mid-Asian ibex at a basal position, and resolved the wild taxa (Caucasian tur, Markhor, Bezoar wild goat) and the Asian domestic groups (West, Southeast, East, Central and South Asia) into a structure consistent with the phylogeny and PCA in Fig. 1. Several migration edges (with migration weights of up to 0.5) were inferred connecting distinct wild and domestic lineages, providing direct evidence of gene flow across taxa and geographic regions. To localize introgressed branches, we computed the f-branch statistic (f_b) across all pairs of taxa (Fig. 2d). The f_b matrix was largely composed of near-zero values, but a subset of cells showed markedly elevated positive f_b (ranging from light pink to deep red on a 0–0.5 scale), concentrated predominantly in the right-hand and lower portions of the matrix, i.e., among the East and Southeast Asian domestic groups and several associated taxa. These elevated f_b signals point to specific taxon pairs as candidate sources of introgressed segments, and provide a framework for subsequent fine-scale verification of introgression sources using complementary approaches such as D-statistics and f4 statistics. Together, the model-based inference (TreeMix) and the branch-specific f_b statistic consistently support the occurrence of significant gene flow and introgression between Asian domestic goats and their wild relatives, with the strongest signals involving Southeast and East Asian domestic populations.

# Genome-wide selection scans

To identify region-specific signatures of selection in Asian domestic goats, we scanned the genome of each regional group (Central, East, South, Southeast and West Asia) against the wild reference using a combination of high F_st and a reduced π ratio (log2(π_auto/π_region)) (Fig. 3; Tables S2–S11). For each region, selected regions were defined using region-specific thresholds (log2(π_auto) ≤ approximately −1.1, an upper bound on log2(π_auto/π_region) of 0.48–1.21, and z(F_st) ≥ 2.0–2.07).

We detected a large number of selected regions in every regional group, with the most in Southeast Asia (77) and South Asia (72), followed by East Asia (56), Central Asia (52) and West Asia (48) (Tables S2, S4, S6, S8, S10). The strongest signals included a chr29 region in Central Asia (F_st = 6.66, π ratio = 2.05) harboring DDB1, TKFC, TMEM138 and TMEM216; a chr11 region in East Asia (F_st = 6.37, π ratio = 3.04) containing BRD1, ZBED4, PIM3 and IL17REL; a chr15 region in South Asia showing the highest π ratio of all (F_st = 6.80, π ratio = 7.65) encompassing MYCBP2, LMX1B, DKK1 and AHSG; a chr12 region in Southeast Asia (F_st = 4.91, π ratio = 3.16) including MYCBP2, IGF1, CLEC16A and TRPS1; and

chr13/chr12 regions in West Asia (F_st = 6.66/6.48) carrying ATP12A and RNF17. Across all groups, a total of 107, 147, 124, 112 and 97 candidate genes were annotated within the selected regions of Central, East, South, Southeast and West Asia, respectively (Tables S3, S5, S7, S9, and S11).

To determine whether selection targets were shared among regions, we compared the genes located within selected regions across the five groups (Fig. 4a; Table S12). A total of 109 genes were found to be located in the selected regions of two or more regional groups, with the highest contributions from East Asia (72), Southeast Asia (58), South Asia (51), Central Asia (38) and West Asia (35). The most pronounced overlaps were between East Asia and Southeast Asia (26 genes) and between South Asia and Southeast Asia (21 genes); additional multi-region overlaps included Central–East–West Asia (10), Central–West Asia (10) and Central–East–South Asia (8). Several genes were shared across three or four regions, including TRPS1, DKK1, CLEC16A, IGF1 and TTYH2, LMX1B, MYCBP2, OPN4, IRAK3, CAMK2A, SDHAF2 and TMEM216, indicating a set of convergent or parallel selective targets across geographically separated Asian goat populations, while the majority of selected regions remained region-specific.

Gene Ontology (GO) and KEGG enrichment analysis of these selection-associated genes recovered 40 significantly enriched terms (Fig. 4b; Table S13). The most significant terms were dominated by ion and metal transport (monoatomic ion transmembrane transporter activity, −log10P = 6.0, 12 genes; metal ion transport, 5.2; monoatomic cation transport, 5.1) involving AQP1, CACNA1A, SLC1A3, SLC30A1, VDAC3 and TTYH2, followed by responses to radiation and environmental stimuli (e.g., cellular response to radiation, −log10P = 4.2) involving DDB1, TLK2, SPIDR and OPN4, and several signaling pathways including the MAPK (3.8), calcium, AMPK and HIF-1 pathways, as well as cytokine/chemokine signaling and regulation of autophagy (involving IKBKB, CAMK2A, CCL5, CLEC16A and LEPR). Collectively, these results show that Asian domestic goats harbor extensive, partially shared selective signatures enriched for ion transport, signal transduction, stress and radiation responses, immune signaling and autophagy, supporting both region-specific and convergent adaptation to local environmental pressures and providing candidate loci for subsequent introgression and functional validation.

# Landscape genomics analyses

To link genomic variation in Asian goats to climatic gradients, we performed redundancy analysis (RDA) using eight bioclimatic variables (bio1, bio5, bio6, bio7, bio12, bio13, bio14 and bio15; Table S14) across 181 samples representing the five Asian domestic groups. Correlation among these variables followed the expected climatic structure (Fig. 5a): temperature variables were strongly positively correlated with one another (e.g., bio1–bio6, r = 0.91; bio1–bio5, r = 0.79), precipitation variables were strongly correlated (bio12–bio13, r = 0.95), whereas temperature and precipitation showed negative correlations (bio6–bio7, r = − 0.85; bio7–bio12, r = − 0.79; bio7–bio13, r = − 0.74), indicating that the variables jointly define temperature and precipitation axes.

RDA ordination of the samples against these variables (Fig. 5b–e) separated the five regional groups along the environmental gradients, with the temperature- and precipitation-associated vectors (bio1,

bio5, bio6, bio7, bio12, bio13, bio14, bio15) pointing toward the corresponding regional clusters. This indicates that climatic gradients represent a major axis of genomic differentiation among Asian goats. A total of 88 outlier loci were identified by RDA, distributed across the constrained axes (RDA1, 32; RDA2, 35; RDA3, 21; Table S15), each with a loading and a maximal correlation to a predictor climatic variable. The best-predicting variables were dominated by temperature, with bio7 (annual temperature range; 25 loci), bio5 (maximum temperature of the warmest month; 23) and bio1 (annual mean temperature; 17) contributing the most, followed by precipitation variables bio12 (11) and bio15 (9). The strongest outlier locus (snp34206-scaffold401 on chr8, RDA1, loading = − 0.20, predictor bio7, |correlation| = 0.631) exemplified the temperature-associated signal.

Mapping of the RDA outlier windows to genes yielded 191 environment-associated candidate genes (Table S16), again predominantly associated with temperature variables (bio7, 55; bio5, 50; bio1, 45) and including HERPUD2, RNF145, EBF1, CHCHD7, PLAG1, MOS and LYN as top candidates (|correlation| ≈ 0.57–0.61). Gene Ontology enrichment analysis of these genes recovered 36 significantly enriched terms (Fig. 5f; Table S17; −log10P = 2.0–3.5). The most prominent categories were circulatory system development (− log10P = 3.8, 11 genes), response to hypoxia (− log10P = 3.6, 7 genes) and other oxygen-level responses, vasculature development and angiogenesis, chemotaxis and immune signaling (regulation of leukocyte and monocyte chemotaxis, response to cytokine, response to lipopolysaccharide), voltage-gated and potassium/chloride ion channel activity, and responses to growth hormone, xenobiotics and reactive oxygen species, involving genes such as VEGFC, TGFBR3, LEPR, CA9, ADA, MTHFR, PTGS2, AGTRAP, LYN, CXCL17, KCNJ8, ABCC9, KCNH8 and CLCN6. These functions are consistent with adaptation to altitude-related hypoxia, extreme temperature and water availability across the sampled regions.

To assess the convergence between the population-differentiation–based selection scan (F_ST–π) and the environment-based approach, we compared the two gene sets (Fig. S1). Of the 109 F_ST–π selection genes and 191 RDA-associated genes, only four were recovered by both approaches: LEPR, LOC106502445, SPIDR and TMEM18. These shared genes—supported by both population differentiation and climatic association—represent the most robust candidates for local adaptation (e.g., LEPR in growth and energy metabolism, SPIDR in DNA repair/recombination, and TMEM18 in energy homeostasis). The largely complementary gene sets (105 and 187 unique to the F_ST–π and RDA approaches, respectively) indicate that the two methods capture distinct facets of adaptation, jointly providing a more complete catalogue of adaptive loci for functional validation and introgression studies.

# Discussion

In this study, we present a continental-scale genomic analysis of environmental adaptation in Asian domestic goats, integrating population structure, gene flow inference, region-specific selection scans, and genotype–environment association in a single framework based on 883 domestic goats from 36 populations spanning five major Asian sub-regions, together with five wild caprid taxa as evolutionary references. Our results resolve the phylogeographic differentiation of Asian goats, demonstrate gene

flow and introgression between domestic populations and their wild relatives, and identify extensive yet partially shared selective signatures that are enriched for ion transport, signal transduction, stress and radiation responses, immune signaling and autophagy, as well as climate-associated loci dominated by thermal gradients and enriched for circulatory and hypoxic-response functions. Notably, only four genes (LEPR, LOC106502445, SPIDR and TMEM18) were recovered by both the population-differentiation-based selection scan and the environmental association analysis, representing the most robust candidates for local adaptation.

Consistent with the known domestication and dispersal history of goats, our population-structure analyses revealed a clear separation between wild and domestic lineages and marked regional differentiation among the five Asian groups, with South Asian and Southeast Asian populations being the most differentiated (Fig. 1). The pronounced differentiation and internal diversity of South Asian (Pakistan, Bangladesh and Nepal) and Southeast Asian goats are in agreement with the deep, complex demographic histories and long-standing breed diversity of these regions, and with the broad dispersion of Southeast Asian samples along PC2 reflecting admixed demographic histories that likely accompanied human-mediated maritime dispersal. By covering the major ecological gradients across Asia in a single analysis, these results address the previously incomplete adaptive landscape that arose from studies restricted to single regional populations [2, 3], and provide a continental reference for subsequent selection and association analyses.

Our model-based inference of gene flow recovered clear signals of introgression between Asian domestic goats and their wild caprid relatives, with the strongest f-branch signals concentrated in the East and Southeast Asian domestic groups (Fig. 2). This is consistent with previous reports of wild-derived adaptive introgression in Asian goats, including markhor-derived introgression of a PAPSS2-containing region conferring high-altitude adaptability in Tibetan goats [8] and genomic evidence of ancient adaptive introgression related to desert climate in Southwest Asia [9]. Our results extend these findings by suggesting that wild-to-domestic gene flow is geographically widespread across the continent rather than limited to isolated highland or desert populations, and by highlighting East and Southeast Asia as regional hotspots of introgression. The formal validation of these gene-flow events through D-statistics and the fine-scale localization of introgressed segments represent important next steps.

The genome-wide selection scans identified abundant high-FST, low-π regions in every regional group, with the strongest differentiation in South Asia (chr15; π ratio = 7.65) and the largest number of selected regions in Southeast Asia (77). Notably, 109 genes were located in the selected regions of two or more regional groups, with the most pronounced overlaps between East and Southeast Asia (26 genes) and between South and Southeast Asia (21 genes), and including high-confidence candidates such as TRPS1, DKK1, CLEC16A, IGF1 and MYCBP2. The recurrence of the same genes in geographically separated populations provides direct evidence for convergent or parallel adaptation [45] to shared selective pressures (e.g., climate and pathogens), thereby addressing whether convergent phenotypes across Asian goat populations share a convergent genomic basis. The functional enrichment of these

selection-associated genes in ion and metal transport, responses to radiation and environmental stimuli, and MAPK, calcium, AMPK, HIF-1 and chemokine signaling, as well as in immune signaling and autophagy, is consistent with adaptation to extreme temperature, water availability, ultraviolet radiation and pathogen load across diverse ecological zones, with candidates such as AQP1, SLC transporters, CACNA1A and DDB1/TLK2/SPIDR respectively relating to water and ion homeostasis and to DNA-damage/UV responses.

The redundancy analysis anchored genomic variation to climatic gradients, separating the regional groups along temperature and precipitation axes. Temperature variables (bio7, bio5 and bio1) dominated the predictors of outlier loci, indicating that thermal gradient is a primary driver of environment-associated genomic differentiation in Asian goats. The 191 RDA-associated genes were strongly enriched for circulatory system development, response to hypoxia and decreased oxygen levels, vasculature development and angiogenesis, chemotaxis and immune signaling, and voltage-gated and potassium/chloride channel activity. These functions align with the physiological demands of the sampled environments—particularly high-altitude hypoxia (VEGFC, CA9, ADA, MTHFR), extreme temperature, and immune challenge—and echo the cold- and heat-resistance and energy-metabolism adaptations previously described in cashmere and heat-stressed goat populations [2, 3].

The modest overlap between the selection-scan and RDA gene sets (four shared genes: LEPR, LOC106502445, SPIDR and TMEM18) indicates that the two approaches capture complementary facets of adaptation: the former emphasizes population differentiation irrespective of environment, whereas the latter directly links variation to climatic gradients. That only a small number of genes are supported by both lines of evidence is expected, but the identity of these shared genes is biologically compelling—LEPR is a central regulator of growth and energy metabolism, SPIDR participates in DNA repair and recombination, and TMEM18 is implicated in energy homeostasis—making them the most trustworthy candidates for functional validation and for use as molecular markers in stress-resilient breeding programs.

Several limitations should be acknowledged. First, our analyses are based on a 50 K SNP array (44,260 autosomal SNPs), which provides limited resolution for fine-scale breakpoint localization and for capturing structural and low-frequency variants that would be accessible through whole-genome resequencing. Second, the RDA approach is correlational, and the candidate loci identified here require independent confirmation through population-genomic statistics (e.g., D-statistics for introgression) and experimental validation, including expression profiling and functional assays. Third, the unbalanced sampling across regions, particularly the small Central Asian sample size (n = 30), may reduce statistical power in that region. Finally, our inference of convergence is based on the co-occurrence of genes across selected regions; establishing truly independent versus shared-by-descent origins of these alleles will require haplotype-based analyses. Future whole-genome resequencing, combined with transcriptomic and functional experiments and denser geographic sampling, will refine the adaptive architecture and clarify how natural selection, geographical isolation and wild introgression have jointly shaped the genomic landscape of Asian goats.

In conclusion, by integrating phylogeographic, gene-flow, selection-scan and climate-association evidence at continental scale, this work demonstrates that the adaptive genomic landscape of Asian goats is shaped by the joint action of geographical isolation, divergent environmental pressures and wild introgression, and yields a catalogue of robust candidate adaptive genes—foremost among them LEPR, SPIDR and TMEM18—that provide molecular resources for the conservation and stress-resilient utilization of Asian indigenous goat germplasm.

## Conclusion

This continental-scale genomic analysis of Asian domestic goats, integrating population structure, gene-flow inference, region-specific selection scans and landscape-genomic association, reveals the adaptive architecture underlying environmental adaptation in these populations. Phylogenomic, PCA and ancestry analyses resolved clear separation between wild and domestic lineages and marked regional differentiation, with South and Southeast Asian populations being the most genetically distinct. TreeMix and f-branch statistics detected widespread wild-to-domestic introgression, with signals concentrated in East and Southeast Asia. FST–π scans identified 305 selected regions harbouring 587 candidate genes enriched for ion transport, radiation and stress responses, and immune and signaling pathways, while RDA against climatic gradients recovered 88 outlier loci and 191 environment-associated genes dominated by temperature variables and enriched for hypoxic and circulatory functions. Notably, only four genes (LEPR, SPIDR, TMEM18 and LOC106502445) were supported by both approaches, indicating that population differentiation and environmental association capture complementary facets of local adaptation. Together, these findings demonstrate that environmental adaptation in Asian goats proceeds through a mosaic architecture combining a small convergent core with extensive region-specific responses, providing robust candidate loci for marker-assisted breeding and the conservation of Asian goat genetic resources.

## Abbreviations

SNP:
Single nucleotide polymorphism
PCA:
Principal component analysis
NJ:
Neighbour-joining
ML:
Maximum likelihood
LD:
Linkage disequilibrium
IBS:
Identity-by-state
FST:

Fixation index
π:
Nucleotide diversity
RDA:
Redundancy analysis
GO:
Gene Ontology
KEGG:
Kyoto Encyclopedia of Genes and Genomes
HIF:
Hypoxia-inducible factor
MAPK:
Mitogen-activated protein kinase
AMPK:
AMP-activated protein kinase
ROS:
Reactive oxygen species
fb:
f-branch statistic

## Declarations

# Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

# Competing Interests

The authors declare no competing interests.

# Supplementary material

Table S1. Sample information of the domestic goats and wild caprids used in this study.

Table S2. Selected regions identified by the $F_{ST}$–π method in Central Asian goats.

Table S3. Candidate genes located within the selected regions in Central Asian goats.

Table S4. Selected regions identified by the FST–π method in East Asian goats.

Table S5. Candidate genes located within the selected regions in East Asian goats.

Table S6. Selected regions identified by the FST–π method in South Asian goats.

Table S7. Candidate genes located within the selected regions in South Asian goats.

Table S8. Selected regions identified by the FST–π method in Southeast Asian goats.

Table S9. Candidate genes located within the selected regions in Southeast Asian goats.

Table S10. Selected regions identified by the FST–π method in West Asian goats.

Table S11. Candidate genes located within the selected regions in West Asian goats.

Table S12. The 109 candidate genes shared by two or more regional groups.

Table S13. GO and KEGG terms identified based on the 109 candidate genes shared by two or more regional groups.

Table S14. Bioclimatic variables of the sampling localities used in the RDA analysis.

Table S15. The 88 outlier SNPs identified by RDA.

Table S16. The 191 candidate genes identified by RDA.

Table S17. GO terms identified based on the 191 candidate genes identified by RDA.

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# Author Contribution

WP, LG, LW and BS contributed equally to this work. WP and XL conceived and designed the study. WP, LG, LW, BS and TC carried out the genomic and population-genetic analyses, including population structure, gene-flow inference, selection scans and landscape-genomic association. CY, WS, BW, GL, LH and MY contributed to data curation, methodology and validation. MY supervised the project and acquired funding; XL co-supervised the project and acquired funding. WP wrote the original draft of the

manuscript. All authors revised and approved the manuscript and read and approved the final manuscript.


# Acknowledgement

Not applicable.


# Data Availability

The 50K dataset of SNPs produced in this study can be accessed in plink format on the figshare website (https://figshare.com/) via accession number: 10.6084/m9.figshare.24190413 or dir-ectly by this link: https://figshare.com/articles/dataset/PLINK_files_ped_and_map_of_wild_a-nd_domestic_goat_species/24190413. The dataset contains published data: Dryad; https://doi.org/10.5061/dryad.q1cv6;..

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# Figures

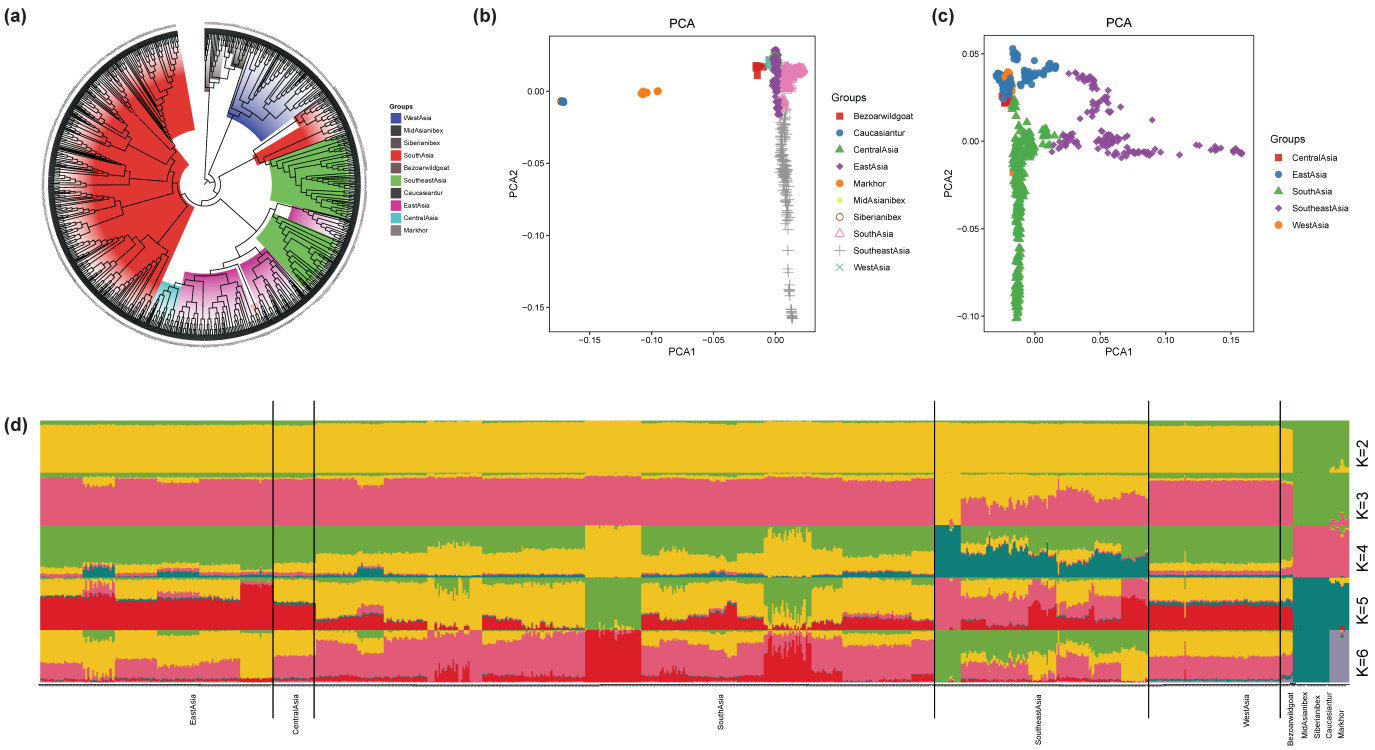
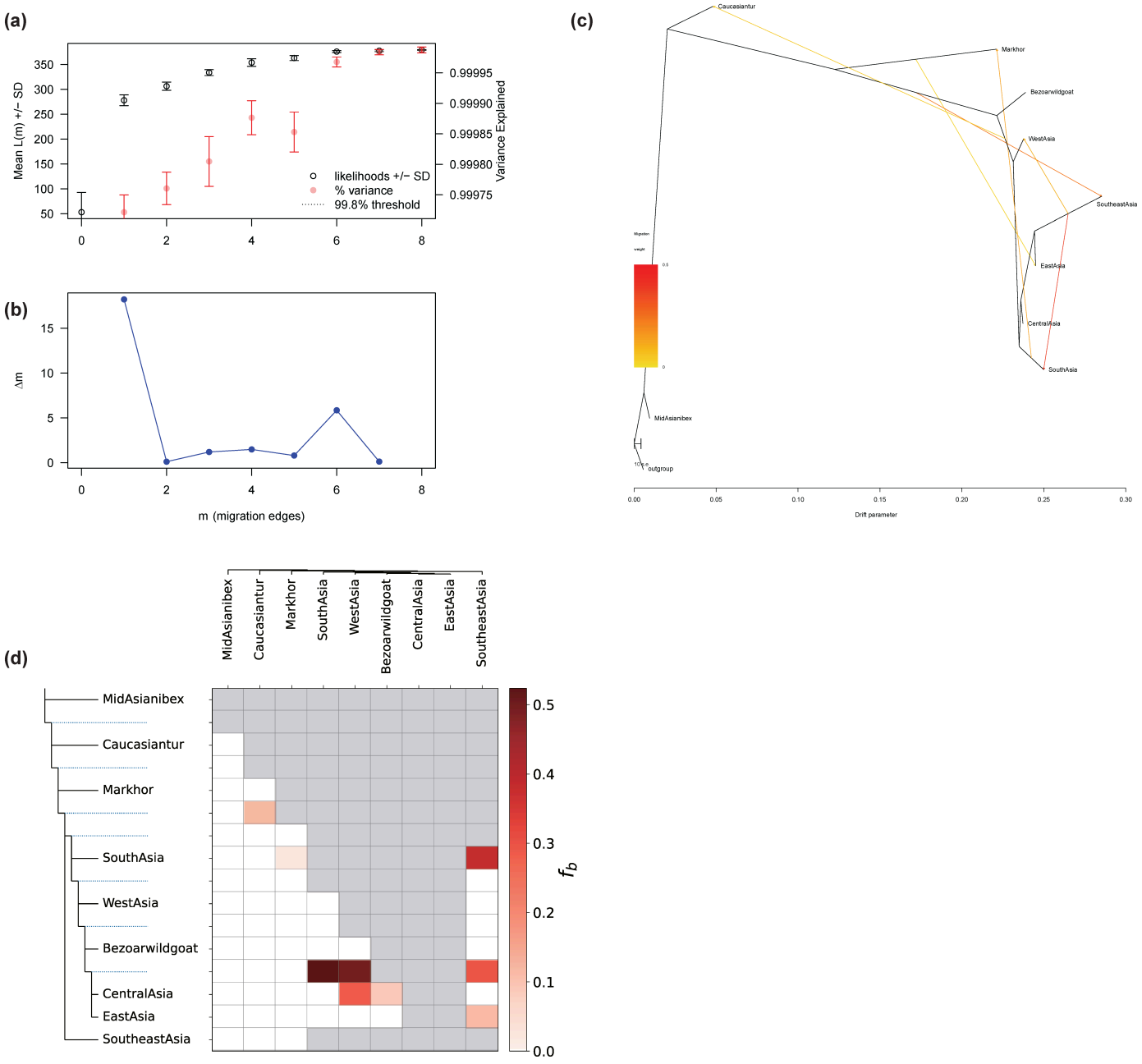



**Figure 1**

**Population structure and phylogenetic relationships of Asian goats and their wild caprid relatives.**

**(a)** Circular neighbour-joining tree of all 930 individuals (883 domestic goats from 36 Asian populations and 47 wild caprids) reconstructed from pairwise Reynolds genetic distances. Branches are coloured by group; **(b)** Principal component analysis (PCA) of the same 930 individuals based on identity-by-state allele sharing, showing PC1 versus PC2. Each point is one individual and symbols and colours denote the ten groups (legend at right); **(c)** PCA restricted to the 883 Asian domestic goats, showing the five regional groups analysed in this study; **(d)** ADMIXTURE ancestry proportions inferred from LD-pruned autosomal SNPs for K = 2–6. Each vertical bar represents one individual (one row per K) and black vertical lines separate the ten groups;




## Figure 2

**Gene flow and genomic introgression between Asian domestic goats and their wild caprid relatives.**

**(a)** Model fit of the TreeMix population graph as a function of the number of migration edges (m = 0–8). Open circles show the mean log-likelihood L(m) ± standard deviation (left axis) and red circles the fraction of the ancestry covariance matrix explained by the graph (right axis); the dotted line marks the 99.8% variance-explained threshold used to select the optimal m; **(b)** Likelihood increment Δm = L(m) − L(m − 1) for each value of m, showing a pronounced peak at m = 1 and a secondary peak at m = 6; **(c)** Maximum-likelihood TreeMix graph retained for interpretation. The graph is rooted on the outgroup (lower left) and branches are drawn in units of genetic drift (scale bar, 10 s.e. of drift); arrows denote

inferred migration edges and are coloured according to migration weight (scale bar, 0–0.5); **(d)** f-branch (f_b) statistic matrix summarising excess allele sharing between donor taxa (columns) and recipient branches of the population graph (rows); the dendrogram on the left summarises the underlying population tree. Colour scale, f_b from 0 (white) to 0.5 (dark red).

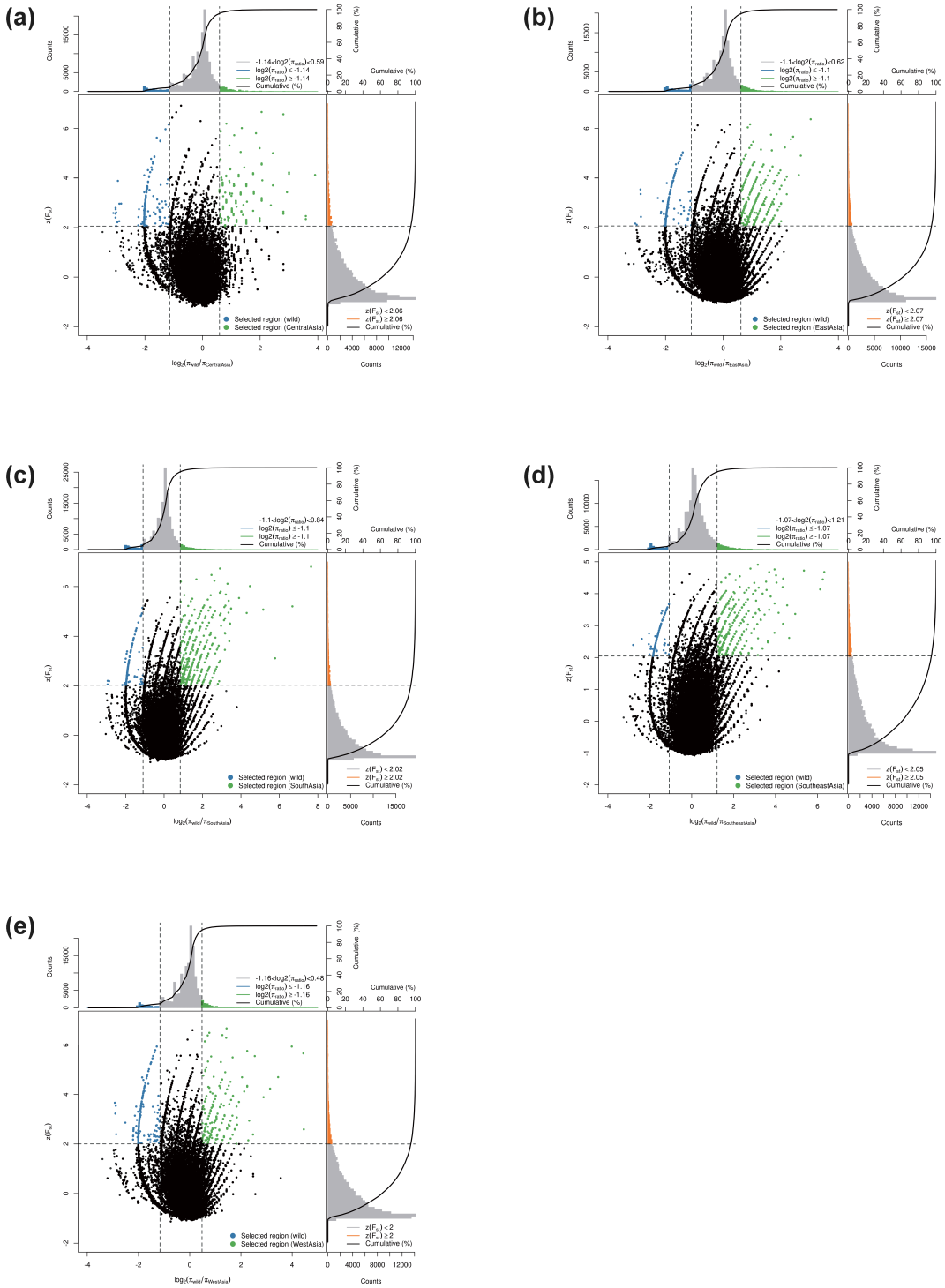
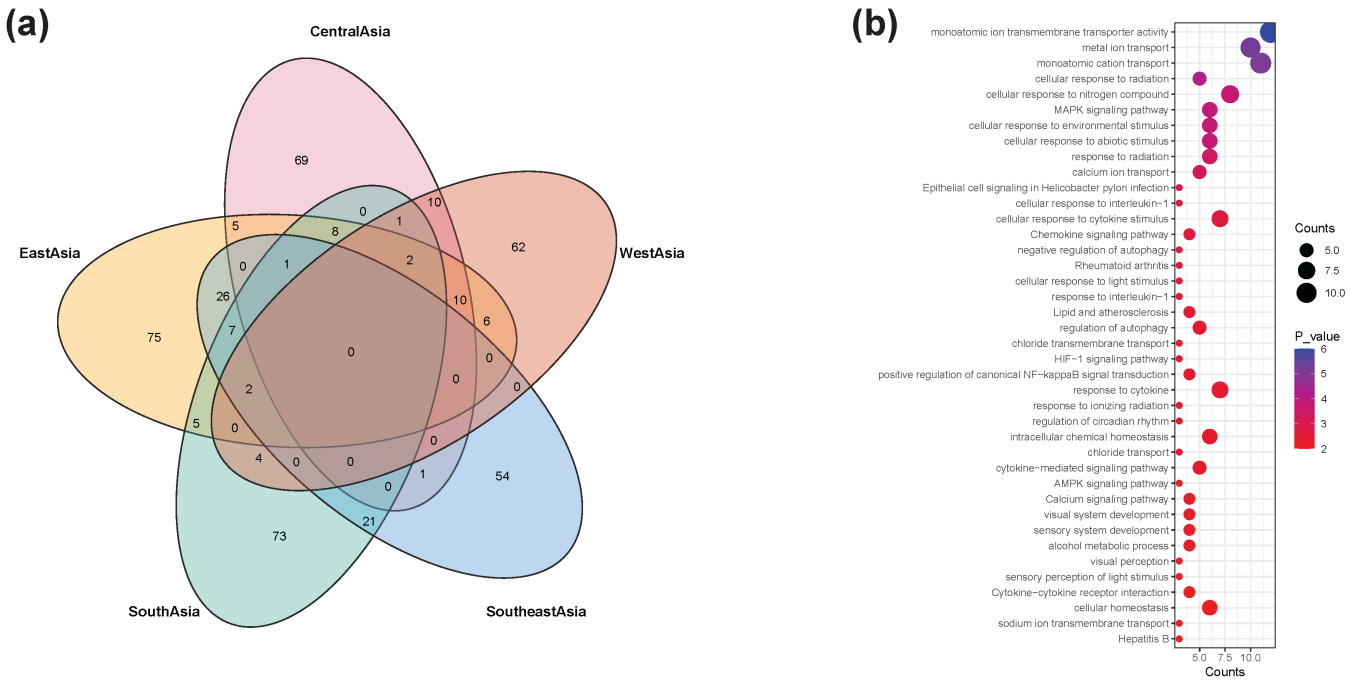



**Figure 3**

Joint distribution of the standardised genetic differentiation z(F_ST) (y axis) and the nucleotide-diversity ratio log2(π_wild/π_region) (x axis) computed by contrasting the Central (a), East (b), South (c), Southeast (d) and West Asian (e) domestic groups with the wild bezoar reference. Each point represents one 50-kb genomic window (25-kb step, ≥50 SNPs per window).

**Genome-wide $F_{ST}$–π selection scans of the five Asian domestic goat groups against the wild reference.**




## Figure 4

**Shared and functionally enriched selection targets across Asian goat groups.**

**(a)** Five-set Venn diagram of the candidate genes annotated within the selected regions of the five regional groups (Central, East, South, Southeast and West Asia). Numbers indicate the number of genes in each intersection; 109 genes were shared by two or more regional groups; **(b)** Gene Ontology (GO) and KEGG over-representation analysis of the selection-associated genes. The 40 significantly enriched terms are ranked by their enrichment significance; dot size represents the number of genes annotated to a term and dot colour represents the enrichment significance (−log10 P, colour scale at the right).

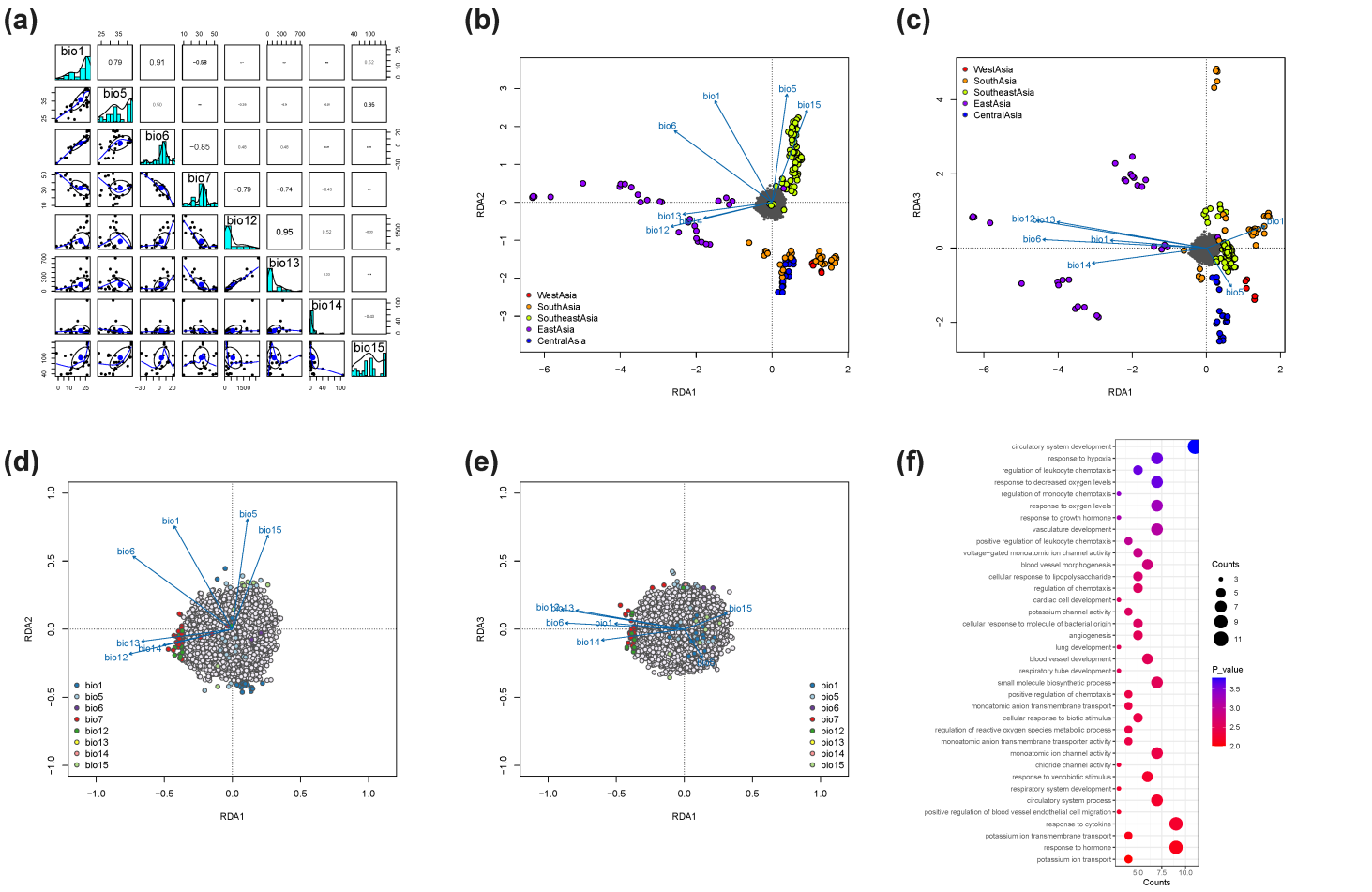



**Figure 5**

**Climatic correlates of genomic variation in Asian domestic goats.**

**(a)** Pairwise relationships among the eight bioclimatic variables (BIO1, BIO5, BIO6, BIO7, BIO12, BIO13, BIO14 and BIO15) across the 181 sampling localities with geographic coordinates. The lower triangle shows pairwise scatterplots with a fitted trend and a correlation ellipse, the diagonal shows the distribution of each variable, and the upper triangle gives the corresponding Pearson correlation coefficients; **(b, c)** Redundancy analysis (RDA) ordinations of the 181 individuals coloured by regional group, displayed as RDA1 versus RDA2 and RDA1 versus RDA3 (**c**). Bioclimatic variables are superimposed as arrows whose direction and length indicate their loadings on the constrained axes; **(d, e)** The same ordinations (RDA1 versus RDA2; RDA1 versus RDA3) with each individual coloured according to the bioclimatic variable that best explains its genomic position (legend at the lower left); individuals without a dominant single-variable association are shown in grey. Arrows and labels as in **b** and **c**; **(f)** Gene Ontology enrichment analysis of the 191 environment-associated candidate genes. The 36 significantly enriched terms are plotted against the number of genes (x axis); dot size represents the gene count and dot colour the enrichment significance (−log10 P, colour scale at the right).

# Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- TableS1S17Asiabmc.xlsx
- S1.png