Animal 20 (2026) 101732

Contents lists available at ScienceDirect

Animal
The international journal of animal biosciences

Spatio-temporal genomics of goats: recent evolution, adaptation, and future vulnerability

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ARTICLE INFO

Article history:
Received 26 September 2025
Revised 28 November 2025
Accepted 1 December 2025
Available online 8 December 2025

Keywords:
Biodiversity
Capra hircus
Genomic offset
Landscape genomics
Local breeds

ABSTRACT

Italy hosts a rich biodiversity of local goat breeds, shaped by its wide variety of climates, landscapes, and traditional farming systems, making the preservation of these locally adapted populations critical for maintaining genetic resources. This study aimed to explore the genomic biodiversity of Italian goats, track recent temporal changes through comparison with samples collected about two decades ago, and investigate the genomic mechanisms underlying environmental adaptation, as well as identify hotspots of possible climatic vulnerability. Demographic data over the last 15 years show that only five breeds are currently considered not at risk of extinction according to FAO criteria, while 22 breeds are classified as critical or formally extinct (no registered animals in 2024). Medium-density single-nucleotide polymorphism (**SNP**) data from 685 goats representing 31 populations were analysed for population structure, genomic background, and genetic diversity. Comparison with historical samples revealed changes over time, exemplified by Bianca Monticellana and Capestrina, which now display a highly similar and uniform genetic background and higher inbreeding. Genomic analyses revealed a clear separation between northern and central-southern breeds, with northern populations exhibiting more distinct genomic backgrounds while central-southern populations are generally more admixed. Landscape genomic analyses were conducted on a subset of 693 goats from 32 populations, using latent factor mixed model and partial redundancy analysis approaches together with present and projected (SSPs 2–4.5 and 5–8.5, 2080–2100) climatic variables from WorldClim 2.1. A total of 468 SNPs were identified as putatively adaptive, including five detected by both methods, encompassing genes such as *KPNA1*, *PARP9*, and *LRP8*. Genomic offset analyses highlighted vulnerable areas in the northern fringes of the Alpine region, the eastern Po Valley (unsampled due to limited presence of local goat populations), and the Murgia-Gargano region of Apulia, home to the Garganica breed. Overall, these results reveal the impact of breeding practices and environmental pressures on Italian goat genomes, provide insights into adaptive genetic variation of goat species, and identify populations and regions at greatest risk, emphasising the need for targeted conservation and management strategies to preserve this unique component of livestock biodiversity.

Implications

Italy harbours 47 local goat breeds, shaped by its numerous environments and centuries of farming traditions. This study presents a comprehensive genomic analysis of this biodiversity, introducing a novel temporal approach: by comparing historical and recent samples within demographic, historical, and sociocultural contexts, we provide new insights into breed evolution, genetic diversity, and population structure. Integrating landscape genomics, we identify genomic regions underlying adaptation in goat species and highlight populations and geographic areas vulnerable to future climate change, defining conservation priorities. Overall, these findings support preserving locally adapted breeds and the maintenance of biodiversity under climatic and anthropogenic pressures.

Introduction

Meeting the growing global demand for food and animal products while preserving biodiversity and ecosystem resilience is a major challenge for modern agriculture (van Dijk et al., 2021). In this context, small ruminants—and goats in particular—play a critical role in sustainable livestock systems. As one of the earliest

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https://doi.org/10.1016/j.animal.2025.101732
1751-7311/

domesticated species (Crepaldi et al., 2024), goats are now reared across a wide range of environmental conditions and production systems, from high-input dairy farms to low-input, extensive settings. Their exceptional adaptability, hardiness, and ability to thrive on scarce resources make them particularly valuable in marginal areas and resource-limited regions, where they often represent a primary source of food, income, and livelihood security for rural communities (Clutton-Brock, 1999; Bertaglia et al., 2007; Silanikove and Koluman, 2015; Sejian et al., 2020; Nair et al., 2021).

Italy offers a unique case study for investigating goat biodiversity and environmental adaptation. The country hosts 48 officially recognised local goat breeds, managed by the Italian Sheep and Goat Breeders Association (Asso.Na.Pa., https://www.assonapa.it), and many ecotypes still unrecognised, shaped by centuries of agro-pastoral practices, diverse ecological zones, and regional selection pressures. This genetic richness is matched by a mosaic of landscapes—from alpine valleys to Mediterranean coasts—and a variety of traditional management systems that reflect both environmental constraints and cultural heritage (Bigi and Zanon, 2020; Cortellari et al., 2021a; 2021b). These breeds, often raised in extensive or low-input systems, have developed distinct adaptive traits that allow them to survive, reproduce, and remain productive under sub-optimal or highly variable conditions (FAO, 2015b). Furthermore, the strong link between local breeds and their territories contributes to landscape management, prevents land abandonment, and supports traditional economies based on high-quality niche products (LPP et al., 2010; Leroy et al., 2018; Hall, 2019).

Understanding the genomic basis of adaptation in these breeds is crucial for designing future-oriented breeding and conservation strategies (Nienaber and Hahn, 2007; Nardone et al., 2010). The development of affordable genotyping technologies and the availability of dense single-nucleotide polymorphism (**SNP**) arrays and whole genome sequencing data have opened new opportunities to explore the genetic structure of livestock populations and to identify loci under selection (Jones and Wilson, 2022; Ajmone-Marsan et al., 2023). International initiatives, such as the Italian Goat Consortium (Nicoloso et al., 2015; Cortellari et al., 2021b), AdaptMap (Stella et al., 2018), and VarGoats (Denoyelle et al., 2021b), have significantly contributed to the generation of large-scale genomic datasets that support such analyses. In addition, CHEESR (2017–2021) and SHEEP&GOAT (2021–2025) are two national projects funded under the National Rural Development Plan (PSRN, submeasure 10.2), coordinated by Asso.Na.Pa. in collaboration with several academic and research institutions. These initiatives were developed to enhance Italian sheep and goat biodiversity, production, and health, also through the introduction of genomic tools in the sector.

Among the tools enabled by large-scale genomic datasets, landscape genomics provides a robust framework to investigate how environmental factors influence genetic variation across space. This approach combines genome-wide data with high-resolution environmental variables to detect signatures of local adaptation, typically through genotype–environment association (**GEA**) methods or spatially explicit models (Joost et al., 2007; Rellstab et al., 2015). The identification of candidate adaptive loci or genomic regions under selection enables researchers not only to understand evolutionary processes but also to support the development of informed breeding, conservation, and management strategies.

In this context, the concept of genomic offset (**g.o.**) has emerged as a key tool for assessing vulnerability to climate change. Genomic offset quantifies the predicted mismatch between the current genomic composition of populations and the allele frequencies that would be theoretically optimal under future climatic conditions. It provides a quantitative measure of adaptive distance, helping identify populations that may face greater challenges in maintaining fitness as their environments shift. This information is especially useful for prioritising conservation actions, such as *in situ* preservation, targeted gene flow, or climate-informed breed management (Capblancq et al., 2020; Rellstab et al., 2021; Ahrens et al., 2023).

While identifying the genomic signatures of adaptation is essential, it is equally important to monitor how livestock populations change over time in response to both environmental and human-driven forces. Local animal populations are not fixed entities—they are constantly shaped by climatic variability, political shifts, economic pressures, and breeder decisions (Tisdell, 2003; FAO, 2007; Cao et al., 2021; Martyniuk, 2021). As such, preserving their genetic resources requires not only a snapshot of current diversity but also a temporal perspective that captures how genetic structure and relationships have evolved. Monitoring these changes through genomic analyses provides critical insight into the balance between maintaining breed identity and adapting to new challenges. This is particularly relevant for understanding the relationships among populations, identifying cases of introgression or fragmentation, and evaluating how well current management practices support the long-term viability and distinctiveness of each breed (Berry and Spangler, 2023; Nayak et al., 2024). Taken together, these approaches offer the opportunity to move beyond static assessments of genetic resources and towards a more dynamic and predictive understanding of livestock diversity.

Within this framework, the present study provides an updated and comprehensive characterisation of the genetic diversity and structure of Italian goat populations, using newly generated SNP data for 31 breeds. It incorporates a temporal comparison between individuals sampled approximately 20 years ago and those sampled more recently, offering insight into how the genomic makeup of these populations has changed over time. In parallel, it applies landscape genomics approaches to explore genotype–environment relationships and estimate genomic offset under projected climate scenarios. Owing to the remarkable diversity of local breeds reared in extensive systems and the wide range of climatic conditions, Italy represents an exceptional natural laboratory for investigating livestock genomic adaptation, giving this study a broader relevance beyond the national context. By integrating genomic, environmental, and temporal dimensions, this work contributes to a deeper understanding of how Italian goat populations are responding to ongoing challenges and provides a knowledge base for their effective conservation and climate-resilient management.

Material and methods

Demographic data

Census data were obtained from Asso.Na.Pa. and comprised the number of officially registered farms and live animals recorded on December 31st of each year from 2010 to 2024.

For each breed, the proportional change in farm and animal numbers was calculated as the difference between the values recorded in 2024 and those recorded in 2010; for breeds officially recognised after 2010, the first year of recognition was used as the baseline. The annual growth rate was estimated from the logarithmic difference in animal numbers between two consecutive censuses, standardised by the time interval in years, excluding years with zero registrations (FAO, 2013). For 2024, the expected rate of inbreeding increase (ΔF) was computed as $1/(2^{*}N_e)$, where N_e represents the effective population size, estimated using Wright's formula (Wright, 1931; FAO, 2013).

Risk status for each breed was then determined according to the FAO criteria (FAO, 2013), which criteria into account the number of breeding females and males, total population size, growth rate, and ΔF (Fig. 1).

Sampling

A total of 5 888 goats from 34 Italian breeds were sampled using nasal swabs and genotyped with the GoatSNP60 or GoatSNP65 v2/v3 BeadChips (Illumina Inc., San Diego, CA). Specifically, 5 584 samples from 30 populations were collected within the CHEESR and SHEEP&GOAT projects, 232 samples from 16 breeds were obtained within the Agritech project, and data for the 72 Comune di Sicilia/Mascaruna (**CCS**) goats were retrieved from Bionda et al. (2023) and Floridia et al. (2025) (Supplementary Table S1).

For most breeds, the sampling strategy involved the collection of 11–60 animals registered in the herd book, with one male and two unrelated (according to pedigree data and indications of the breeder) females selected per farm. In some breeds, such as Camosciata delle Alpi (**CTP**) and Saanen (**SNN**)—where the sampling was also intended to support the development of genomic breeding values—additional related and unrelated individuals were collected for further analyses.

Dataset and quality control

As mentioned above, the sampling of SNN and CTP goats followed different criteria compared to other breeds, for example by including relatives and French and Dutch bucks used for artificial insemination in Italy. For this reason, we preselected these breeds, only retaining Italian animals that were enrolled in the main section of the herd book and, for males, with positive parentage verification. The resulting dataset comprised 2 793 goats from 34 different populations (Table 1 and Supplementary Table S1).

Quality control was performed using PLINK v1.9 (Purcell et al., 2007), filtering out SNPs located on sex chromosomes and those with a call rate below 95%. Individuals with more than 5% missing genotypes or identified as closely related (based on Mendelian errors, detected using an in-house script) were also excluded. Furthermore, SNPs with a minor allele frequency (**MAF**) below 0.1% and those in linkage disequilibrium (**LD**) were pruned using the *-indep-pairwise* 50 10 0.5 option in PLINK. To prevent over- or underrepresentation of certain breeds, we excluded populations with fewer than eight animals (Jonica, Cilentana Fulva, and Cilentana Nera), and subsampled the remaining breeds to a maximum of 27 individuals (corresponding to the dataset's breed size median), using the *bite.representative.sampling* function from the BITEV2 R package (Milanesi et al., 2017). The final dataset included 685 goats from 31 populations and 46 878 SNPs.

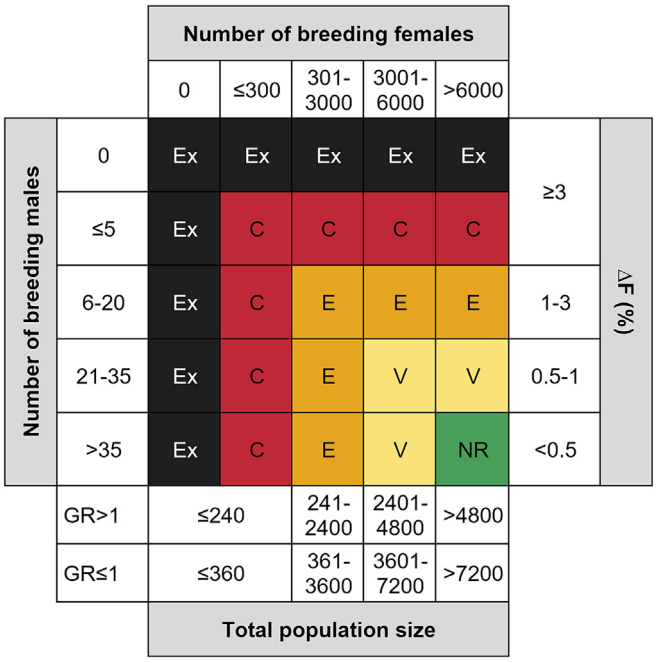

Fig. 1. Criteria for the definition of breed risk categories according to FAO. For each goat breed, the risk category was assigned based on the least favourable parameter. Abbreviations: GR = Growth rate; ΔF = Inbreeding rate; NR = Not at risk; V = Vulnerable; E = Endangered; C = Critical; Ex = Extinct.

Population structure and phylogenomic relationships

A multidimensional scaling analysis was conducted with PLINK using the number of dimensions equal to the number of individuals. A further dimensionality reduction to better visualize both local and global relationships was performed by applying PHATE (Moon et al., 2019) using the first 20 principal components (**PCs**) from the multidimensional scaling, with the following parameters: knn = 31, decay = 100, and gamma = 0.

Reynolds distances among populations were calculated using an in-house script and used to generate a NeighbourNet with SplitsTree (Huson and Bryant, 2006), which was plotted with phangorn and tangle R packages (Schliep et al., 2017; 2025). Bootstrapped identity-by-state (**IBS**) distances among individuals were computed with PHYLIP (Felsenstein, 1989), and the related tree was visualised using the ggtree R package (Xu et al., 2022). TreeMix (Pickrell and Pritchard, 2012) was run, allowing 0–10 migration events. Additionally, we computed f3 statistics.

Ancestral genomic components were inferred with ADMIXTURE v1.3 (Alexander and Lange, 2011), testing ten models for a number of clusters (**K**) from 2 to 25. The best-fitting model was selected as the one with the median five-fold cross-validation (**cv**) error across all runs. For each K, the run with the lowest cv was plotted.

After phasing the dataset (pruned for MAF but not for LD) with Beagle v4.1 (Browning and Browning, 2007), identity-by-descent (**IBD**)–based haplotype sharing was analysed using RefinedIBD v3.1 (Browning and Browning, 2013) with default parameters. We computed the pairwise median of shared segments between individuals from different populations, assigning a value of 0 in the absence of shared haplotypes. The top 5% longest haplotype sharing values were visualised using the circlize R package (Gu et al., 2014).

Genomic diversity analyses were carried out on the unphased dataset, without breed size balancing or LD pruning (Meyermans et al., 2020), including 2 458 individuals and 48 573 SNPs. Observed and expected heterozygosity (**Ho** and **He**) and McQuillan's inbreeding coefficient based on runs of homozygosity ($\mathbf{F_{ROH}}$) were estimated (McQuillan et al., 2008). ROHs were detected with PLINK v1.9 using the following parameters: *-homozyg-gap* 500, *-homozyg-kb* 1000, *-homozyg-window-het* 0, *-homozyg-window-missing* 2. The minimum number of SNPs required to define both a ROH and the window size (*-homozyg-snp* and *-homozyg-window-snp*, respectively) was estimated to be 42 according to the *L* parameter (Meyermans et al., 2020). Density parameter (*-homozyg-density*) was set as 55, corresponding to the lowest value that maximised genome coverage, which under these conditions reached 98.2% (Meyermans et al., 2020).

Effective population size (N_e) based on LD was estimated using SNeP v1.1 (Barbato et al., 2015), analysing SNPs at 280 Kb to 20 Mb distance and applying Sved & Feldman recombination rate modifier (Sved and Feldman, 1973). N_e was also estimated using GONE v1.0 (Santiago et al., 2020) with default settings. While SNeP estimates N_e based on the decay of LD (r^2) as a function of SNP distance, GONE models the temporal evolution of LD across generations using the δ^2 parameter (r^2 weighted by the product of allele variances). We applied both methods to account for the

Table 1
Dataset composition and main results of genomic biodiversity analysis on Italian goat breeds.

Breed Code	Breed Name	N. raw	N. QC	N. balanced	He	Ho	F_{ROH}	Ne (SNeP)	Ne (GONE)
AET	Argentata dell'Etna	29	28	27	0.407	0.406	0.023 ± 0.045	35	411
BDL	Bionda dell'Adamello	29	29	27	0.396	0.389	0.051 ± 0.052	32	233
BNM	Bianca Monticellana	29	27	27	0.349	0.355	0.113 ± 0.053	30	340
CAP	Capestrina	18	17	17	0.369	0.373	0.083 ± 0.079	19	173
CCR	Ciociara Grigia	12	12	12	0.396	0.403	0.039 ± 0.042	13	120
CCS	Comune di Sicilia/ Mascaruna	72	66	27	0.406	0.403	0.043 ± 0.072	29	133
CPS	Capestrina	60	57	27	0.410	0.403	0.028 ± 0.04	34	470
CTN	Cilentana Nera	28	27	27	0.409	0.415	0.011 ± 0.012	35	918
CTP	Camosciata delle Alpi	1 097 (3 202)*	916	27	0.414	0.408	0.047 ± 0.033	33	323
DRP	Di Potenza	33	31	27	0.410	0.404	0.035 ± 0.052	31	160
DRT	Di Teramo	11	9	9	0.383	0.407	0.033 ± 0.032	8	32
FDM	Fulva dei Monti Picentini	17	14	14	0.365	0.387	0.071 ± 0.046	14	61
FNS	Frisa Valtellinese	25	23	23	0.378	0.381	0.054 ± 0.037	26	117
GRG	Girgentana	25	25	25	0.351	0.339	0.133 ± 0.089	27	117
GRM	Campobasso Grigia Molisana	9	9	9	0.387	0.409	0.028 ± 0.041	9	50
GRN	Garganica	127	122	27	0.408	0.391	0.057 ± 0.06	31	199
LRN	Lariana/ Di Livo	21	21	21	0.398	0.405	0.013 ± 0.017	26	506
MCH	Pezzata Mochena	20	18	18	0.393	0.410	0.022 ± 0.022	21	173
MLT	Maltese	32	30	27	0.384	0.374	0.088 ± 0.077	30	147
MSN	Messinese	65	61	27	0.414	0.409	0.019 ± 0.029	35	1 526
NCT	Nicastrese	155	149	27	0.413	0.408	0.025 ± 0.034	34	465
NPT	Napoletana	9	8	8	0.345	0.370	0.106 ± 0.098	7	32
ORB	Orobica	29	27	27	0.343	0.344	0.094 ± 0.031	33	220
RCN	Roccaverano	21	19	19	0.408	0.414	0.027 ± 0.04	22	233
RCR	Rustica di Calabria	63	61	27	0.412	0.404	0.028 ± 0.039	34	529
RSM	Rossa Mediterranea/ Derivata di Siria	36	33	27	0.409	0.403	0.038 ± 0.039	32	173
SNN	Saanen	536 (1 540)*	451	27	0.415	0.410	0.049 ± 0.037	28	123
SRR	Sarda	118	117	27	0.414	0.404	0.03 ± 0.039	34	490
VLD	Valdostana	20	19	19	0.366	0.378	0.056 ± 0.015	23	213
VLS	Vallesana	18	17	17	0.359	0.356	0.112 ± 0.084	18	76
VRZ	Verzaschese	15	15	15	0.377	0.378	0.057 ± 0.054	17	138

Cilentana Fulva, Cilentana Grigia, and Jonica were excluded because, after quality control and exclusion of relatives, less than eight individuals were retained.
Abbreviations: N. raw = Number of individuals before quality control; N. QC = Number of individuals after quality control; N. balanced = Number of individuals after breed size balancing; He = Expected heterozygosis; Ho = Observed heterozygosis; F_{ROH} = Inbreeding based on runs of homozygosity; N_e = Genomic effective population size, calculated with SNeP or GONE software.
* For Camosciata delle Alpi and Saanen, the number of individuals before prescreening (see main text) is reported in parentheses.

known differences in N_e estimates that arise from variation in population structure and demographic history (Kidner et al., 2021; Becker et al., 2024) and to facilitate comparison with other studies that implemented only one of the two approaches.

Comparison with older data

The balanced dataset described above was compared with data of goats sampled in 1995–2010, including the publicly available Italian Goat Consortium (**IGC2**) dataset (Cortellari et al., 2021b), which includes 1 071 samples genotyped with the GoatSNP50 BeadChip (Illumina Inc., San Diego, CA), and newly generated data from the Agritech project for Orobica (**ORB**, n = 42), Bionda dell'Adamello (**BDL**, n = 37), Verzaschese (**NVE**, n = 25), Lariana (**LRN**, n = 38), SNN (n = 17), and CTP (n = 23) goats born between 1995 and 2010, genotyped with the GoatSNP65 BeadChip (Illumina Inc., San Diego, CA).

Samples from the Bezoar, Montecristo, and Maltese × Sarda populations from IGC2 were excluded, whereas Maltese sampled in Sardinia or elsewhere, as well as Rossa Mediterranea and Derivata di Siria, were merged, as they are different denominations for the same breed. After merging the datasets, we applied the same quality control, filtering, and breed size balancing procedures described above, resulting in a final dataset of 46 807 SNPs and 1 358 goats from 37 breeds: 22 breeds were included in both the "present" and "older", nine only in the present one, and six only in the older one (Supplementary Table S1).

The following analyses were then repeated, focusing on comparisons between contemporary and historical samples of the same breeds: multidimensional scaling, ADMIXTURE (testing up to 27 K), and F_{ROH} estimation.

Landscape genomics

Dataset and quality control

For the landscape genomics analysis, only recent animals with geographic coordinates were considered. SNN and CTP goats were excluded due to their rearing in intensive or semi-intensive systems, making them less exposed to environmental pressures. The resulting dataset included 1 159 animals from 32 breeds.

Quality control followed the same approach as above: excluding SNPs and individuals with low call rates, closely related individuals, and sex chromosome SNPs, along with pruning for MAF and LD. Additionally, to avoid population structure bias, the seven overrepresented breeds (Nicastrese, Comune di Sicilia, Dell'Aspromonte, Garganica, Messinese, Rustica di Calabria, and Sarda) were reduced to a maximum of 35 individuals, selected based on geographic distribution, ensuring at least one individual per farm. The final dataset comprised 693 animals and 46 255 SNPs (Supplementary Table S1).

Climatic variables

Environmental data were obtained from the WorldClim v2.1 database at a 30-second resolution (~1 km^2), covering the period 1970–2000. We extracted elevation and the average values of 19 bioclimatic variables (Fick and Hijmans, 2017) described in Supplementary Table S2. Additionally, monthly data on precipitation, minimum temperature and maximum temperatures were used to calculate median seasonal values, considering December, January, and February for winter season; March, April and May for spring season; June, July, and August for summer season, and September, October and November for autumn season. Environ-

mental data were assigned to each sample using the *extract* function from the raster R package (Hijmans, 2025).

To avoid collinearity, a subset of environmental variables was selected (Rellstab et al., 2015): the *exclude* function from usdm R package (Naimi et al., 2014) was applied to recursively exclude variables with a variance inflaction factor (**VIF**) > 5; subsequently, *findCorrelation* function from caret R package (Kuhn, 2008) was applied to exclude the least number of variables so that the maximum Pearson correlation coefficient was 0.75.

Projections of the environmental variables were retrieved at a resolution of 30 s from WorldClim v2.1 for the period 2081–2100 and referred to the global climate model ACESS-CM2 (Bi et al., 2020; Petrie et al., 2021), and the shared socio-economic pathways (**SSP**) 2–4.5 (moderate climate change) and 5–8.5 (severe climate change) (Meinshausen et al., 2020).

Population structure

A multidimensional scaling (**MDS**) analysis was performed using PLINK v1.9 as previously described. Additionally, ancestral population structure was inferred using the *snmf* function of the LEA R package (Frichot and François, 2015), running 30 replicates for K values from 1 to 25. Cross-entropy (**ce**) was calculated for each replicate and K value. The best-fitting K was defined as the one with the lowest median ce. Inspired by the parsimony principle (Coelho et al., 2019), which favours the simplest model that adequately explains the data, we also identified the most parsimonious value of K as follows: i) We used the *calculate.fda* function from the doremi R package (Mongin et al., 2025) to model the ce values as a function of K and to compute its first derivative (i.e., f'(K)); ii) we calculated the absolute difference between the derivative at each K and the derivative at the best-fitting K (i.e., $|\Delta f'(K)|$), representing the rate at which ce approached its minimum; and iii) we selected the lowest K among those with $|\Delta f'(K)|$ less than or equal to the third quartile of the $|\Delta f'(K)|$ distribution as the most parsimonious value. This criterion identifies the smallest K that achieves a near-optimal improvement rate, consistent with the parsimony principle.

Genotype-environment associations

To identify SNPs associated with selected focal environmental variables, we combined two complementary genotype–environment association (GEA) approaches: univariate latent factor mixed model (**LFMM**) and multivariate partial redundancy analysis (**pRDA**).

Introduced by Frichot et al. (2013), LFMM is a Bayesian univariate mixed models that account for neutral population structure by incorporating a user-defined number of latent factors as random effects, inferred simultaneously with genomic–environmental associations using a Markov Chain Monte Carlo algorithm, while environmental predictors are modelled as fixed effects. In the present study, LFMM was conducted using the lfmm R package v2.0 (Jumentier, 2021). The *lfmm_ridge* function estimated regularised effect sizes using a number of latent factors equal to the most parsimonious K. The *lfmm_test* function produced *P*-values for each genotype–environment association, calibrated using the genomic control method. These *P*-values were then transformed into q-values using the qvalue R package (Storey et al., 2025); an FDR < 0.05 was set as the significance threshold.

Partial redundancy analysis is a constrained ordination method that models multivariate linear relationships between genotype and environment by constructing canonical axes through PCA on fitted genetic values constrained by environmental predictors. Unlike standard redundancy analysis (**RDA**), pRDA incorporates neutral genetic structure as a conditioning variable, improving robustness under isolation by distance or low dispersal and reducing spurious associations caused by spatial autocorrelation or population structure (Capblancq and Forester, 2021). Here, partial redundancy analysis was performed with the *rda* function from the vegan R package (Oksanen et al., 2025), using the latent score matrix from LFMM as a covariate (conditioning matrix). Since the *anova.cca* function is not optimized for large genomic datasets, we were unable to run it due to computational constraints. Therefore, we selected significant axes based on explained variance, following approaches used in similar studies (Capblancq and Forester, 2021; Kebede et al., 2024; Francisco et al., 2025; Omondi et al., 2025). Specifically, we retained the minimal number of axes required to capture at least 70% of the cumulative constrained variance, with each axis explaining at least 10%. SNPs were deemed significant if their score exceeded the mean by at least 3 SDs on at least one of the significant canonical axes.

Genes located within ±26.6 kb of these SNPs were identified, 26.6 kb being half of the average gap between consecutive analysed SNPs. Gene ontology (**GO**) enrichment analysis was carried out using GeneCodis v4 (Garcia-Moreno et al., 2022), comparing these genes to a background set including all genes associated with all SNPs available in the GEA dataset. GO terms were assigned according to the *Bos taurus* annotation, as it is the closest reference species. A significant threshold was set to 0.05 after Benjamini-Hochberg correction.

Local genomic offset

To estimate individual local genomic offset (**g.o.**) metrics, we first calculated a current Adaptive Index (**AI**), which reflects the relationship between putatively adaptive genetic variation and present-day environmental conditions. We performed an RDA using only the SNPs identified as candidates in previous GEAs as the response matrix, and the standardised environmental variables used for GEAs as the explanatory matrix. Significant RDA axes were determined using the *anova.cca* function with 999 permutations and a significance threshold of $P < 0.01$.

For each of the spatial pixels in the study area (i.e., Italy) and significant RDA axis, the current AI was computed as: $ev * \sum_{i=1}^{n} b_i a_i$, where a_i is the loading of environmental variable i on the selected RDA axis, b_i is the standardised value of that variable at the pixel, and ev is the variance explained by the RDA axis. All pixel-level environmental maps were standardised with the same centre and scale factor as the present individual-level matrix.

To evaluate whether individuals could be grouped based on similar AI values, we applied K-means clustering to individual AI scores. On ten random subsamples of 10 000 pixels, we applied *KMeans_rcpp*, testing 2–10 models, and *silhouette_of_cluster* functions from ClusterR package (Mouselimis, 2024), and selected the number of clusters consistently associated with the highest silhouette score.

Next, we predicted future AI values using climate projections under two alternative SSPs. Each environmental variable was weighted according to its loading from the initial RDA, thus reflecting its contribution to SNP-environment associations under current conditions, and the future AI was calculated following the same procedure as for the current AI, but using the future values of standardised environmental variables.

Local g.o. was then computed as the Euclidean distance between the current and future AI values for each pixel across the study area. To test whether the two climate change scenarios or individual groups of individuals were associated with different average local genomic offsets, we performed Kruskal-Wallis and Dunn test through *kruskal_test* and *dunn_test* functions from rstatix

(Kassambara, 2023), after assessing normality and variance homogeneity with Shapiro and Levene tests, respectively.

To evaluate whether loci with stronger environmental associations exerted greater influence on g.o. estimates, we repeated the RDA using SNP-specific weights derived from their association *P*-values. For each RDA axis, two-sided *P*-values were computed from the standardised SNP loadings. Each SNP was assigned the minimum *P*-value observed across axes and given a weight equal to the inverse of that value. To avoid extreme leverage, weights exceeding the 99th percentile were capped, and all weights were normalised. Each SNP column in the genotype matrix was multiplied by the square root of its corresponding weight. The resulting weighted RDA model was then compared with the unweighted model to assess how SNP weighting affected g.o. estimates.

To identify potential spatial outliers (i.e., individuals with significantly different g.o. values compared to their neighbours) and/or local clusters (i.e., groups of geographically close individuals with consistently higher or lower offset), we evaluated the local spatial autocorrelation of g.o. values. Specifically, the rgeoda's (Li and Anselin, 2025) *local_moran* function was used to calculate local Moran's I statistics based on individual genomic offsets (averaged across the two climate scenarios), using spatial weights derived from the *knn_weights* function across a range of K values from 2 to 100. Significance was determined using 999 conditional permutations, with *P*-values adjusted using the Benjamini–Hochberg method. A threshold of 0.01 was used to identify statistically significant results.

Results

Census data

Census data reveal that over the past 15 years (2010–2024), the number of registered goat farms has steadily declined, with an overall reduction of 32%. In contrast, the number of registered animals exhibited a more variable trend: an initial decline of 16% between 2012 and 2014 was followed by a 40% increase up to 2018, and then a subsequent decline of 23% in the last four years.

A similar pattern was observed when focusing solely on breeds under conservation programmes (Fig. 2A). Although the number of farms decreased by 28%, the total number of registered animals increased by 5% compared to 2010, despite a downward trend in the past five years. However, notable differences emerged among individual breeds (Supplementary Figure S1). For instance, Alpina, Jonica, Maltese, Rossa Mediterranea, and Valdostana showed a consistent decline over the entire period. In contrast, breeds such as Cilentana Grigia, Di Potenza, Di Teramo, Grigia Valle Lanzo Fiurina, Nicastrese, and Pomellata showed an overall increasing trend. An

Fig. 2. Trends in animal and farm registration for Italian goat breeds under conservation (A) and selection (B) programmes.

interesting case is the Girgentana breed, which experienced a sharp decline in both animals and farms in 2017–2018; while the number of farms then stabilised, the number of animals peaked abruptly in 2019 before slowly returning to 2018 levels. Similarly, the Garfagnana breed saw a marked increase between 2012 and 2013, after which farm numbers remained stable, but animal numbers declined. It is worth noting that nine local breeds were newly recognised during the study period. However, no registrations were reported in 2024 for ten breeds, suggesting a possible extinction risk.

A different scenario emerged for the three breeds under selection programmes (Fig. 2B). The Sarda goat maintained a relatively stable number of farms and showed an overall positive trend in animal numbers—despite a recent decline. However, given the limited number of registered bucks, the Sarda was reclassified as "breed under conservation programme" in 2025. In contrast, both Saanen and Camosciata delle Alpi experienced a negative trend in farm numbers and, especially after 2018, in animal numbers as well. Compared to 2010, Camosciata delle Alpi lost 37% of farms and 30% of animals, while Saanen suffered losses of 60 and 64%, respectively.

Estimates of census-based effective population size (N_e), often used to assess extinction risk, indicated that 21 breeds (45%) had N_e < 50, representing a short-term risk of extinction, including ten with N_e equal to 0. Another 16 breeds (34%) had N_e values between 50 and 500, indicating a long-term risk, while 10 breeds (21%) had N_e > 500, including five with values exceeding 1 000 (Table 2).

ΔF values could not be calculated for the 10 breeds with no registrations in 2024. Among the remaining breeds, ΔF was below 0.5% for 22 breeds, between 0.5 and 1% for four breeds, between 1 and 3% for three breeds, and above 3% for Valdostana and Passeirer Gebirgziege (Table 2).

According to the FAO criteria (FAO, 2013), only five breeds (11%) are currently not at risk of extinction: Camosciata delle Alpi, Aspromontana, Messinese, Nicastrese, and Rustica di Calabria. Five breeds, including the Sarda goat—which, despite being the largest Italian breed, had only 32 registered bucks in 2024—are classified as vulnerable. Alarmingly, 15 breeds (32%) are considered endangered, 12 (26%) are critical, and the 10 breeds with no registrations in 2024 should be formally regarded as extinct (Table 2).

Italian goat population biodiversity

The population structure inferred from the multidimensional scaling analysis (Fig. 3A) revealed a clear north-to-south separation of Italian goat populations along PC1, which accounted for 3.52% of total genetic variation. PC2 distinguished Bianca Monticellana (**BNM**) and Capestrina (**CAP**) from other populations, with some overlap from Ciociara Grigia (**CCR**). PC3 further isolated the Orobica (ORB) population and, to a lesser extent, the Girgentana (**GRG**).

The PHATE analysis provided a smoother representation of geographic gradients. While PC1 still reflected the north–south divide, PC2 distinguished central breeds (BNM, CAP, CCR) and partially separated insular (Sicilian, Sardinian, and Maltese) populations (Fig. 3B).

The two main branches of the NeighbourNetwork based on Reynolds' genetic distances separated northern and southern populations, with the Di Teramo (**DRT**) and the Pezzata Mochena (**MCH**) being the most central breeds. Further grouping could be observed, mostly connecting breeds with similar geographical origin (Fig. 3C). Individual IBS distances (Fig. 3D) showed that most individuals grouped with their respective populations along a geographic continuum. Notable exceptions included genetic intermixing among: Sicilian breeds Argentata dell'Etna (**AET**) and Messinese (**MSN**); the central Italian breeds BNM, CAP, and CCR; and the southern breeds Cilentana Nera (**CTN**), Di Potenza (**DRP**), and Garganica (**GRN**). Moreover, some MSN individuals clustered near the Comune di Sicilia/Mascaruna (CCS); three Roccavrano (**RCN**) were near Bionda dell'Adamello (BDL); and a few Lariana (LRN) goats grouped with northern breeds such as ORB, Frisa Valtellinese (**FNS**) and Verzaschese (VRZ). Additionally, several DRP individuals were positioned between Napoletana (**NPT**) and Rustica di Calabria (**RCR**).

Treemix identified one main migration event connecting the RCN to the Sarda (**SRR**) population (Supplementary Figure S2). f3 statistics confirmed significant admixture from BNM to CAP and from both to CCR; from GRG to Aspromontana (**CPS**); from ORB and FNS or VRZ to LRN; and from Maltese (**MLT**) to MSN (Supplementary Table S3).

Haplotype sharing analysis (Fig. 4A) highlighted substantial sharing between BNM and CAP, confirming their close genetic relationship. Other sharing events, typically involving shorter haplotypes, were mainly restricted to geographically proximate populations. Only one case of sharing with a cosmopolitan breed was detected, between RCN and CTP.

Admixture analysis supported these findings. At K = 2, a clear north–south ancestry gradient was observed. At K = 3 and 4, distinct clusters emerged for BNM-CAP and ORB (Supplementary Figure S3). The lowest median cross-validation error was observed at K = 16 (Fig. 4B), but it should be noticed that cv for K 15–17 were all very close (Supplementary Figure S4). At this resolution, most of the northern populations displayed defined, breed-specific ancestries, while most southern populations shared a common ancestral component –here referred to as the "Mediterranean component"– with varying degrees of introgression. Three northern populations exhibited a composite background: the VRZ was mainly composed by FNS and MCH; similarly, the LRN displayed shared ancestry with multiple northern populations. When, at K = 17, a cluster was identified for VRZ, it also appeared as the predominant component in LRN and as an introgressing component in some FNS; in this model, the MCH cluster disappeared, and the breed appeared mainly related to BDL, with relevant portions also from the Mediterranean component and VRZ. A different pattern was instead found for the RCN, where most individuals showed clear introgression from the specialised dairy breed CTP. CAP and BNM had nearly identical profiles, which separated from neighboring breeds. Among southern populations, FDM, GRG, MLT, and SRR formed unique clusters, with signs of reciprocal introgression between the latter two. GRN and CCS also formed specific clusters, though with substantial individual variation. All the other populations displayed a similar admixed pattern, with the Mediterranean component largely dominating the background, with contributions from other southern populations' clusters. In particular, MSN, AET, RCR, and NCT shared a very similar background, with evident sharing with CCS, GRG, SRR, and MLT in addition to the Mediterranean component. In contrast, the FDM cluster was present in other breeds from Campania (CTN and NPT, the latter obtaining its cluster at K = 17, despite the limited sample size), whereas GRN and BNM clusters in breeds from central Italy (GRM and CCR). Interestingly, the background of DRT shared ancestry also with MCH and CTP, whereas the GRG cluster was particularly evident in CPS, consistent with other results.

Inbreeding, estimated via ROH, varied considerably among populations (Table 1). F_{ROH} ranged from 1.1 ± 1.2% in CTN to 13.3 ± 8.9% in GRG, with an average value across all the individuals of 4.6 ± 4.5%. Differences in the distribution of ROH length classes reflected contrasting demographic histories. Populations such as GRG, NPT, and Vallesana (**VLS**) exhibited high F_{ROH} values predominantly due to long ROH (>16 Mb), indicative of recent inbreeding. In contrast, ORB and BNM showed elevated inbreeding, but spread across all ROH classes. Some populations with moderate overall

Table 2
Main results on census data analysis for Italian goat breeds.

Breed	N. farms (2024)	ΔFarms	N. animals (2024)	ΔAnimals	Growth Rate	N_e	ΔF	Risk
North-western Italy								
ALPINA	6	−138 (−95.8%)	1	−609 (−99.8%)	0.70	0		Ex
BIONDA DELL'ADAMELLO	63	−48 (−43.2%)	1 501	−522 (−25.8%)	0.98	384	0.13	E
CAMOSCIATA DELLE ALPI	208	−121 (−36.8%)	7 900	−3 341 (−29.7%)	0.98	942	0.05	NR
FRISA VALTELLINESE	43	−29 (−40.3%)	1 561	223 (16.7%)	1.02	385	0.13	E
GRIGIA VALLE LANZO FIURINA	42	40 (2 000%)	756	752 (18 800%)	2.35	214	0.23	E
LARIANA O DI LIVO	15	−52 (−77.6%)	736	−896 (−54.9%)	0.97	122	0.41	E
MANTELLATA POSTERIORE	3	0 (0%)*	0	0 (NaN%)*		0		Ex
OROBICA O DI VAL GEROLA	98	19 (24.1%)	3 036	1 079 (55.1%)	1.04	677	0.07	E
ROCCAVERANO	32	−8 (−20%)	1 570	711 (82.8%)	1.05	437	0.11	E
SAANEN	114	−167 (−59.4%)	4 472	−7 907 (−63.9%)	0.93	314	0.16	V
SEMPIONE	3	0 (0%)	27	11 (68.8%)	1.08	7	6.75	C
VALDOSTANA	6	−199 (−97.1%)	13	−1 674 (−99.2%)	0.74	4	13.54	C
VALLESANA	17	0 (0%)	410	265 (182.8%)	1.09	154	0.32	E
VERZASCHESE	8	−23 (−74.2%)	609	−317 (−34.2%)	0.98	132	0.38	E
North-eastern Italy								
PASSEIRER GEBIRGZIEGE	0	−1 (−100%)*	0	−1 (−100%)*	1.00	0		Ex
PEZZATA MOCHENA	26	6 (30%)	229	117 (104.5%)	1.09	49	1.02	C
Central Italy								
BIANCA MONTICELLANA	12	−21 (−63.6%)	512	−543 (−51.5%)	0.98	92	0.55	E
CAPESTRINA	18	−23 (−56.1%)	291	−125 (−30%)	0.99	39	1.29	C
CIOCIARA GRIGIA	12	−16 (−57.1%)	142	−199 (−58.4%)	0.97	47	1.06	C
DI MONTECRISTO	0	−1 (−100%)*	0	−4 (−100%)*	0.94	0		Ex
GARFAGNANA	18	10 (125%)	165	−78 (−32.1%)	1.28	34	1.47	C
Southern Italy								
CAMPOBASSO GRIGIA MOLISANA	3	−2 (−40%)	119	−126 (−51.4%)	0.99	23	2.19	C
CILENTANA FULVA	8	−3 (−27.3%)	362	160 (79.2%)	1.06	76	0.66	E
CILENTANA GRIGIA	11	4 (57.1%)	55	27 (96.4%)	1.10	38	1.33	C
CILENTANA NERA	40	1 (2.6%)	1 649	590 (55.7%)	1.04	344	0.15	E
DELL'ASPROMONTE	113	−39 (−25.7%)	13 597	−1 682 (−11%)	1.02	2 753	0.02	NR
DI BENEVENTO VALFORTORINA	6	5 (500%)*	27	26 (2 600%)*	1.68	19	2.68	C
DI POTENZA	59	51 (637.5%)	3 189	3 065 (2471.8%)	1.30	672	0.07	V
DI TERAMO	4	3 (300%)	128	127 (12 700%)	1.53	59	0.85	C
FULVA DEGLI ALBURNI	1	0 (0%)*	0	0 (NaN%)*		0		Ex
FULVA DEI MONTI PICENTINI	0	−1 (−100%)*	0	0 (NaN%)*		0		Ex
GARGANICA	44	13 (41.9%)	3 983	2 282 (134.2%)	1.10	760	0.07	V
GRIGIA DEGLI ALBURNI	0	−1 (−100%)*	0	0 (NaN%)*		0		Ex
GRIGIA DEI MONTI PICENTINI	0	−1 (−100%)*	0	0 (NaN%)*		0		Ex
JONICA	3	−13 (−81.2%)	18	−817 (−97.8%)	0.80	0		Ex
NAPOLETANA	2	0 (0%)	83	43 (107.5%)	1.67	29	1.73	C
NICASTRESE	72	29 (67.4%)	6 316	3 589 (131.6%)	1.07	1 118	0.04	NR
POMELLATA	4	3 (300%)	59	57 (2 850%)	1.36	18	2.73	C
RUSTICA DI CALABRIA	97	1 (1%)	11 166	772 (7.4%)	1.01	2 388	0.02	NR
SCREZIATA	1	0 (0%)*	0	0 (NaN%)*		0		Ex
Isles								
ARGENTATA DELL'ETNA	110	51 (86.4%)	2 910	1 035 (55.2%)	1.04	1 241	0.04	E
GIRGENTANA	20	−25 (−55.6%)	768	−704 (−47.8%)	1.00	190	0.26	E
MALTESE	34	−56 (−62.2%)	643	−2 384 (−78.8%)	0.97	66	0.76	E
MESSINESE	114	−5 (−4.2%)	7 097	−675 (−8.7%)	1.00	1 869	0.03	NR
ROSSA MEDITERRANEA	18	−43 (−70.5%)	780	−1 847 (−70.3%)	0.93	126	0.4	E
SARDA**	129	−5 (−3.7%)	14 930	2 582 (20.9%)	1.02	128	0.39	V
SARDA PRIMITIVA	57	16 (39%)	4 478	1 228 (37.8%)	1.03	958	0.05	V

Abbreviations: ΔFarms/Animals = Absolute and percentage difference in the number of registered farms/animals from 2010 (or year of recognition) to 2024; N_e = census-based effective population size; ΔF = census-based inbreeding rate; FAO extinction risk categories: NR = Not at risk; V = Vulnerable; E = Endangered; C = Critical; Ex = Extinct.
* Breeds that were recognized after 2010. For these breeds, ΔFarms and ΔAnimals refers to the difference between the recognition year and 2024.
** Breeds under selection programmes; all other breeds are under conservation programmes. It should be noted that the Sarda breed has been reclassified as "breed under conservation programme" in 2025.

inbreeding, such as AET and CCS, still harboured individuals with signs of recent consanguinity. The specialised dairy breeds SNN and CTP showed moderate F_{ROH} values with uniform ROH distributions.

Effective population size (N_e) estimates obtained from SNeP and GONE varied in absolute values (8–38 for SNeP and 34–1 142 for GONE). however, ranking of the populations was largely superimposable, with a few exceptions, such as the LRN, which positioned among the breeds with the highest N_e only using GONE software (Table 1) likely due to its complex genomic background, which involves ancient and recent admixture with other northern breeds, leading to bias in N_e estimation with both methods. Considering the most recent generations, NPT and DRP had the lowest N_e values, while MSN had the highest. Temporal N_e trajectories from GONE (Supplementary Figure S5) revealed breed-specific dynamics that aligned with ROH-based inbreeding trends. For example, DRT

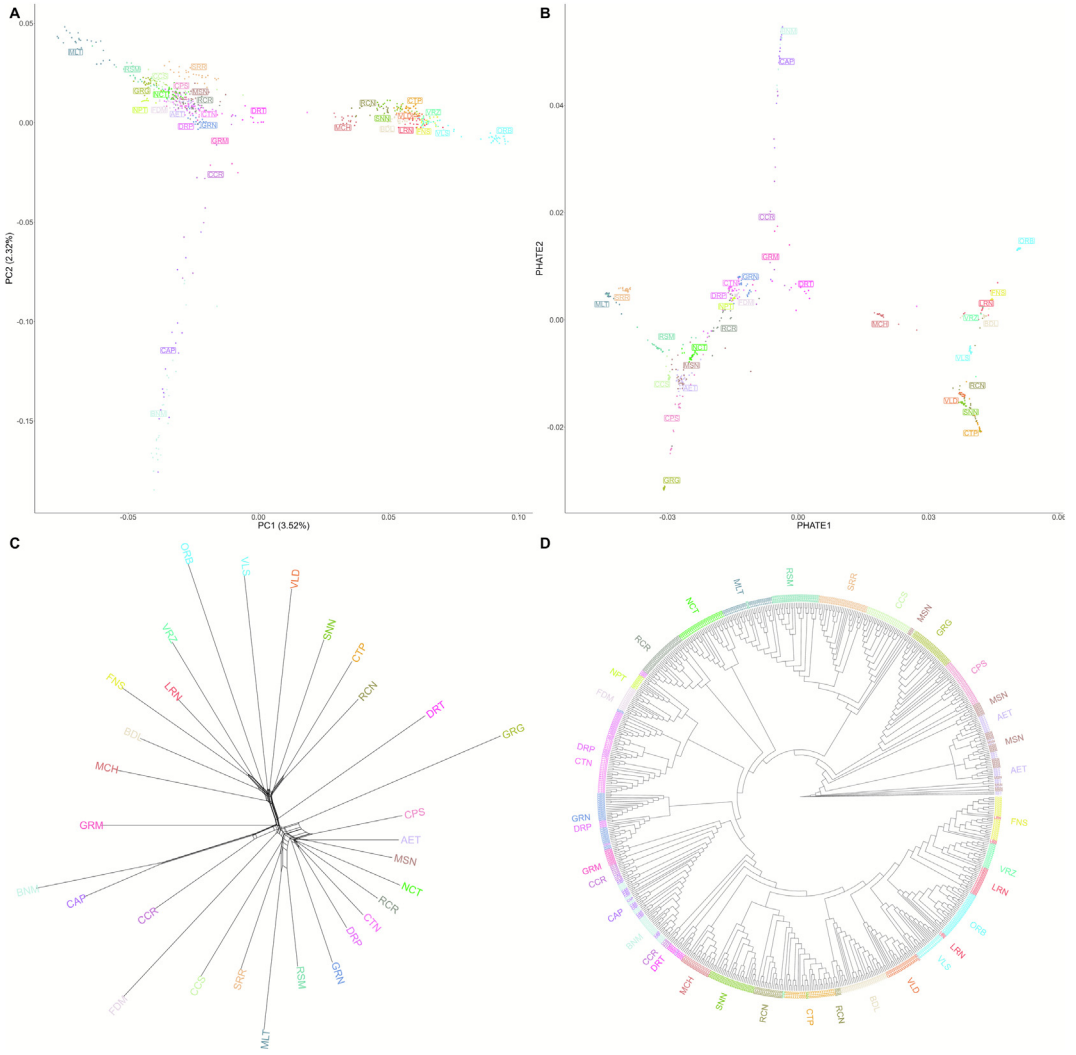

Fig. 3. Genetic population structure of Italian goat breeds. First two principal components (PCs) of multidimensional scaling analysis (A) and Potential of Heat-diffusion for Affinity-based Trajectory Embedding (PHATE) (B). Each point corresponds to a subject, and points are coloured by breed. Reynold distance-based NeighbourNetwork (C) and individual identity-by-state dendrogram (D). Breed codes are defined in Table 1.

showed N_e values much higher than all the other populations up to about four generations ago, when a sharp decline occurred, whereas ORB experienced a long-term decline beginning ~65 generations ago, followed by partial recovery and stabilisation ~40 generations ago.

Comparison with older samples

The MDS plot (Fig. 5A) obtained from the merged dataset closely mirrored the one based on contemporary samples alone, showing a clear south-to-north geographic gradient along PC1 and primarily distinguishing BNM and CAP along PC2. Notably, individuals from the same population consistently clustered together regardless of sampling period, indicating strong temporal continuity and preservation of population identity over time.

Admixture analysis identified K = 22 as the best-fitting model (Fig. 5B and Supplementary Figure S6). In line with the MDS results, most populations showed minimal differences between historical and contemporary samples. Notably, we observed that, in addition to the Mediterranean component, two other clusters were largely present in Southern and Central breeds, respectively: one maximized in certain NCT individuals, and another prevailing in both MCH and IGC Val Passiria (**VPSold**) backgrounds, with the latter breed also exhibiting contributions from BRZ, BDL, and the Mediterranean component. Some notable differences emerged between older and contemporary populations for certain breeds. Compared to historical samples, current BNM and CAP individuals displayed greater genetic uniformity, with higher Q-values for their characteristic ancestral component, while the opposite was true for Rossa Mediterranea (**RSM**). To a lesser extent, SRR also exhibited increased introgression from MLT. The LRN population remained highly admixed across timepoints but showed more evident introgression from FNS in recent samples. The most marked changes were observed in CCR and DRT: while a distinct ancestral component was evident in part of the older individuals, contemporary samples exhibited a more admixed genetic background. Interestingly, two separate clusters were primarily associated with the MLT population and were present in both time periods; these clusters appeared to align with sampling location, distinguishing goats from Calabria or Sicily *vs* those from Sardinia, reflecting differentiation due to geographic isolation and consequent genetic drift.

Inbreeding levels, measured by F_{ROH}, changed over time in several populations (Fig. 5C). A few breeds showed a reduction in F_{ROH}, i.e., CTP, NCT, VLD, RNC, and DRT, which all previously exhibited elevated levels of recent inbreeding. Conversely, several populations showed an increase in F_{ROH}, especially BNM, CAP, and GRG.

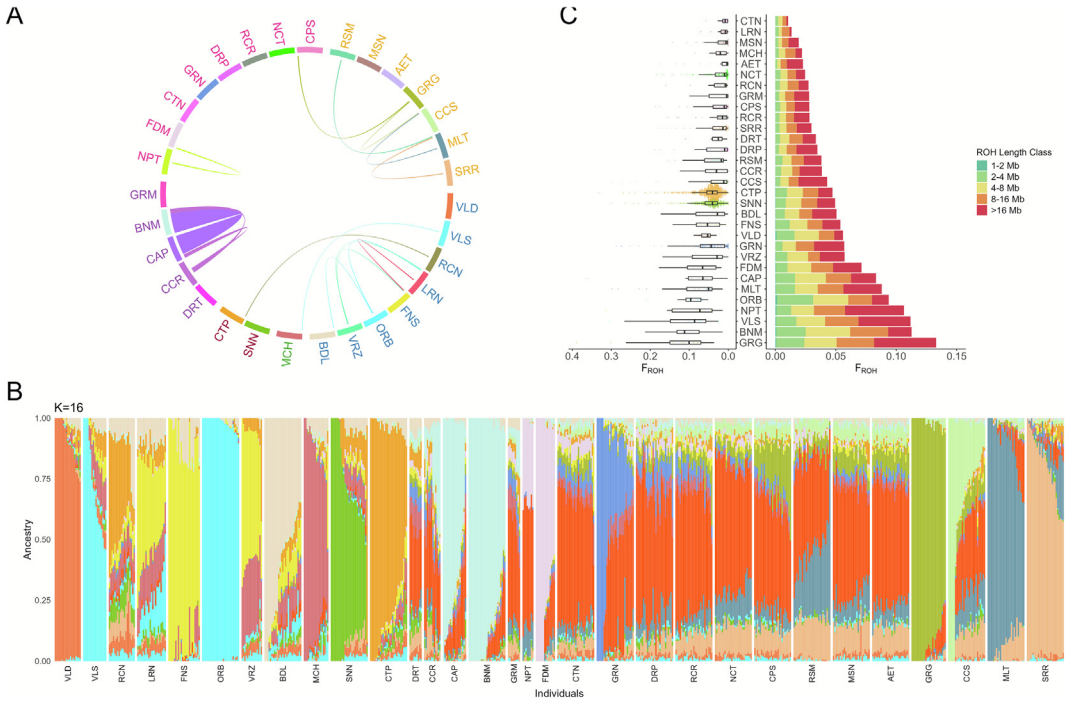

Fig. 4. Genomic background and diversity of Italian goat breeds. (A) Identity-by-descent (IBD) haplotype sharing, showing the top 5% longest segments shared among breeds; breed names are coloured by microregion of origin. (B) Admixture analysis with the best-fitting model (K = 16). Each bar represents an individual, and each colour indicates the proportion of ancestry assigned to a specific cluster. Breeds are ordered geographically. (C) Inbreeding estimated from runs of homozygosity (F_{ROH}), shown at the individual level (boxplot, left) and as breed averages (barplot, right). In the barplot, colours represent the contribution of different ROH length classes, and breeds are ordered by average total F_{ROH}. Breed codes are defined in Table 1.

Among them, GRG also increased in F_{ROH} associated with long ROH, and so did, for example, VLS, whereas this was minimal for BNM and CAP, despite the overall F_{ROH} increase of 4.5–6%.

Landscape genomics

Genomic structure

The 693 goats, belonging to 32 breeds, selected for the GEA dataset mainly represented populations from the Alpine region, central–southern Italy, as well as Sicily and Sardinia (Fig. 6A). No samples were available from the central–northern regions, where the number of goat farms is generally low, particularly when excluding specialised dairy breeds. In this area, the main local breed is the Garfagnina, which unfortunately was not included in the present dataset. This breed registered 165 animals in 2024 and, according to our analyses, presents an admixed genomic background, mainly composed of the Mediterranean component and the cluster related to MCH and VPSold, consistent with previous findings (Cortellari et al., 2021b; Somenzi et al., 2022).

The plot obtained from the first two components of the multidimensional scaling was largely consistent with that from the dataset used for biodiversity analysis. The primary differentiation was observed along PC1, separating northern from southern populations, whereas PC2 distinguished BNM, CAP, and partly CCR breeds (Supplementary Figure S7A). According to the median ce values across Ks (Supplementary Figure S7B), the sNMF analyses indicated K = 13 as the best-fitting model (lowest ce), and K = 7 as the most parsimonious solution. At K = 13, most central–southern breeds shared a predominant ancestral component (the "Mediterranean component"), whereas most northern breeds displayed a distinctive background (Supplementary Figure S7C). At K = 7, only a few breeds remained clearly distinct (FNS, GRG, MLT, ORB, BNM–CAP, and VLD–VLS), while all others showed an admixed background (Supplementary Figure S7D).

Environmental data

Pruning of the environmental matrix for collinearity resulted in the identification of a subset of seven variables used for the GEA analysis, as reported in Table 3 and Supplementary Figure S8. This subset included variables related to both precipitation (prec_autumn, prec_spring), temperature (tmax_summer, BIO8-Mean temperature of wettest quarter), and their daily or seasonal variation (BIO3-Isothermality, BIO4-Temperature seasonality, BIO15-Precipitation seasonality).

Genotype–environment associations

LFMM analysis was performed using seven latent factors, corresponding to the number of K inferred as the most parsimonious solution in the sNMF analysis. At a 0.05 FDR threshold, six SNPs were significantly associated with environmental variables: four with BIO8, one with prec_spring, and one with a combination of BIO4, BIO8, and tmax_summer (Table 4 and Supplementary Figure S9). The partial redundancy analysis model had an adjusted R^2 of 1.8%. Based on the screeplot and explained variance, the first four canonical axes were considered significant (Fig. 6B). RDA1 (39.5% of variance explained) was mainly driven by BIO4, tmax_summer, and BIO15 (scores = 0.71, −0.52, −0.45, respectively). RDA2 (13.7%) was driven by BIO3 (−0.65); RDA3 (12.6%) by BIO15, BIO8, and prec_spring (0.60, −0.49, 0.47); and RDA4 (10.2%) by tmax_summer and prec_spring (0.87, 0.55).

In total, we identified 111, 107, 134, and 116 SNPs with outlier loadings across the four axes, corresponding to 467 unique outlier SNPs (Supplementary Table S4). Notably, five of the six SNPs identified with LFMM were also recovered among the partial redundancy analysis outliers (Fig. 6C).

Three genes were identified within the windows surrounding consensus SNPs: *KPNA1*, *PARP9*, and *LRP8*. In addition, the consensus SNP on chromosome 24 was located in close proximity to, but not within, the *MC4R* gene.

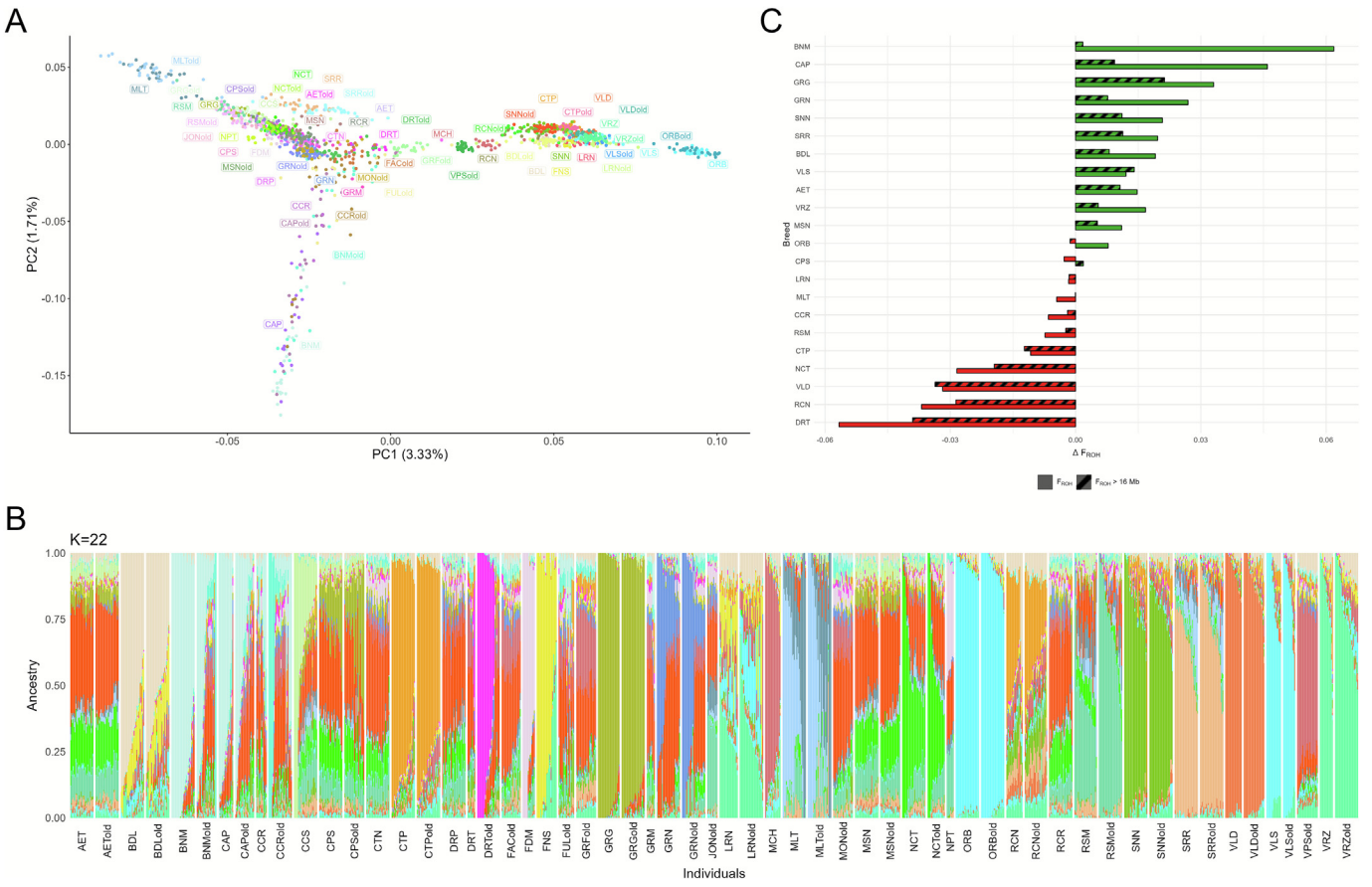

Fig. 5. Comparison of recent samples with goats sampled 20 years ago. (A) First two principal components (PCs) of multidimensional scaling analysis; open points represent older samples and filled points represent samples from the current dataset. (B) Admixture analysis with the best-fitting model with 22 clusters (K). (C) Differences in runs of homozygosity-based inbreeding (F_{ROH}) between individuals of the same breed from the older and current dataset, including both overall F_{ROH} and the component associated with recent inbreeding (ROH > 16 Mb). Codes including 'old' refer to the older dataset. Codes for breed only present in the older dataset: FACold = Facciuta della Valnerina; FULold = Fulva del Lazio; GRFold = Garfagnana; JONold = Jonica; MONold = Capra di Montefalcone; VPSold = Capra della Val Passiria. All other breed codes are defined in Table 1.

Considering all 468 SNPs detected by either LFMM or pRDA, we identified 284 associated genes (Supplementary Table S5). When analysing all genes together, no significant GO terms were detected. In contrast, focusing only on the subsets of genes associated with individual pRDA axes revealed five significant terms for RDA1-related genes and 52 for RDA4-related genes (Supplementary Table S6).

Genomic offset

Given the low number of consensus SNPs, we used the union of SNPs detected by either LFMM or pRDA for genomic offset (g.o.) estimation. An adaptively enriched RDA was performed using these SNPs and the standardised present-day environmental matrix, yielding an adjusted R^2 of 9.8%. Based on permutation tests, all seven canonical axes were retained for g.o. calculation (Table 5).

For each pixel of the Italian map, we calculated a present adaptive index (AI), which allowed us to identify two main adaptive groups: Group 1, covering northern and central-eastern Italy, and Group 2, encompassing southern and central-western Italy as well as the islands (Fig. 7A). Notably, when single-axis adaptive indexes were inspected individually (Supplementary Figure S10), the distribution appeared to be mainly driven by the south-to-north gradient of RDA1 (since AI was weighted by the explained variance of each axis). However, most of the other axes showed distinct values strongly associated with altitude, with higher or lower values along the Alps and Apennines. From a climatic perspective, Group 2 was characterized by higher and more stable annual temperatures, but lower and more seasonally variable precipitation (Fig. 7B). With the exception of CCR, all breeds were assigned to a single group (Table 6). The Euclidean distance between present and future AIs was used to calculate a local g.o. for each pixel under both the moderate (SSP 2–4.5) and severe (SSP 5–8.5) projected climate scenarios. Under the moderate scenario, g.o. values ranged from 0.06 to 1.22 (mean ± SD: 0.23 ± 0.11), with higher values observed in some Alpine areas along the northern borders of Italy, in eastern Veneto/Friuli-Venezia Giulia, and in a pronounced hotspot in the eastern Po Valley. In contrast, the southernmost part of Italy and Sicily showed lower values (Fig. 8A). In this scenario, g.o. was most strongly correlated with BIO8 (r = –0.56) and, to a lesser extent, with tmax_summer (r = 0.23) (Supplementary Figure S11). Since only a few breeds were located in areas with the highest g.o. values, the populations with the highest average g.o. were all from southern or insular Italy: AET, Cilentana Fulva (**CTF**), and SRR (Table 6). When adaptive groups were compared, they were significantly different, with Group 2 showing slightly higher values (0.21 ± 0.07) than Group 1 (0.19 ± 0.08) (*P*-value = 4.56×10^{-8}, Fig. 8B). As expected, under the severe scenario, g.o. values ranged from 0.09 to 1.39 (mean ± SD: 0.43 ± 0.16), significantly higher than in the moderate scenario. Areas with high g.o. under the moderate scenario—such as the northern Italian border and eastern Po Valley—again stood out, but with broader spatial

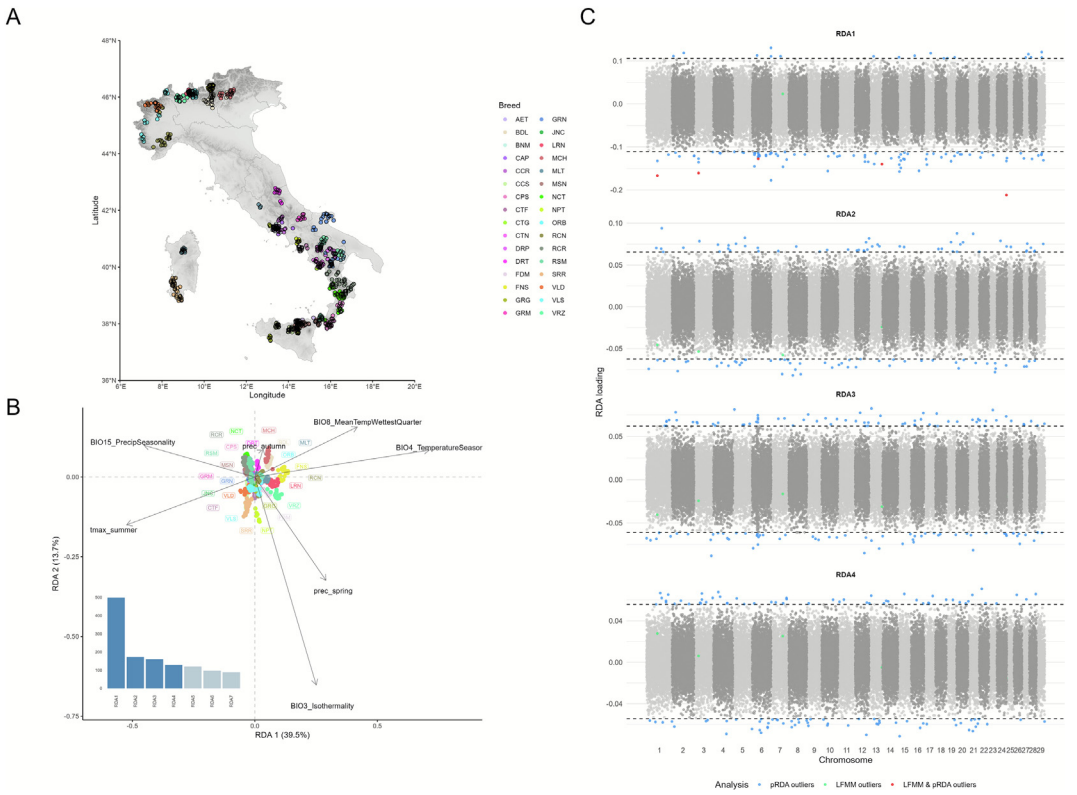

Fig. 6. Genotype–environment association (GEA) analyses in Italian goats. (A) Geographic distribution of samples used for GEAs. A small jitter was applied to the points to display individuals sampled from the same location. (B) Partial redundancy analysis (pRDA): biplot of individuals and environmental variables' loadings on the first two axes, and scree plot of axis inertia, with significant axes shown in dark blue. (C) Manhattan plot of single-nucleotide polymorphism (SNP) scores on the significant RDA axes. Blue points indicate SNP outliers for the given pRDA axis; red points mark putatively adaptive SNPs identified by both the latent factor mixed model (LFMM) and the corresponding pRDA axis; green points mark those identified only by LFMM. Breed codes are defined in Table 6.

extent. Additional vulnerable areas were also identified along the western ridge of the Ligurian and Tosco-Emilian Apennines, as well as in the Murgia-Gargano area of Apulia. The northern territory appeared highly heterogeneous, with some areas, such as the plains of Piedmont and Lombardy, showing the lowest g.o. values (Fig. 8A). As in SSP 2–4.5, the main driver of g.o. was BIO8 (r = –0.58), followed by BIO15 (r = 0.32) (Supplementary Figure S12). The complex geographical pattern of g.o. was reflected in average breed-level g.o., as the most vulnerable populations were spread across very different regions: BDL in the north, GRN in the south, and SRR in Sardinia (Table 6). As in the moderate scenario, Group 2 showed significantly higher values (0.41 ± 0.14) than Group 1 (0.35 ± 0.14) (*P*-value = 1.61×10^{-9}), but in this case, variability was higher within both groups (Fig. 8B).

Across both climate scenarios, the six significant axes of the weighted RDA produced g.o. estimates that were highly correlated with the unweighted estimates (r = 0.974 and 0.967 for SSP2-4.5 and SSP5-8.5, respectively), maintaining the overall spatial pattern. Nonetheless, differences between the two approaches increased with offset magnitude, indicating that weighting accentuated regions with the highest g.o. values (see Supplementary Material S1 for more details).

Finally, we performed a local spatial autocorrelation analysis on individual g.o. values averaged across the two scenarios, testing different numbers of clusters. Individuals consistently assigned to a group across all tested models are shown in Fig. 8C. Several breeds included a substantial proportion of individuals consistently placed in the low–low group, both from northern Italy (FNS, LRN, MCH, VRZ) and central Italy (BNM, CAP, CCR). In contrast, about half of GRN and one third of SRR and MLT were always classified in the high–high group. For the remaining individuals, group assignment stabilized only at higher K values, revealing vulnerability hotspots mainly in breeds from Sardinia, Campania, the Gargano area (Apulia), some areas of Sicily, and among BDL goats. Conversely, some goats from northern, central, and Calabrian populations appeared as cold spots. Interestingly, some BNM, CCR, NCT, and ORB were included in the low–high group, suggesting lower vulnerability compared to neighbouring goats, whereas some AET, MSN, RSM, and SRR showed higher vulnerability than their neighbours (high–low group) (Supplementary Figure S13).

Discussion

Local livestock breeds are vital components of agricultural biodiversity, providing resilience to environmental changes, important ecosystem services, and contributing to food security. The creation and evolution of these breeds are influenced by a complex interplay of factors, including environmental conditions, sociocultural practices, historical breeding preferences, policies, and management strategies (Tisdell, 2003; Alderson, 2009; Leroy et al., 2016). Monitoring these populations is essential to understand how demographic changes, management practices, and environmental pressures impact their genetic resources over time. Integrating genomic tools with temporal comparisons offers a comprehensive approach to assess changes in diversity, population structure, and inbreeding (Ajmone-Marsan et al., 2023), while landscape genomics enables the identification of genomic regions underlying adaptation and potential vulnerability (Passamonti et al., 2021). Such information is critical for prioritising conservation actions, supporting sustainable breeding strategies, and safeguarding the long-term resilience of livestock biodiversity,

Table 3
Subset of environmental variables used for genotype-environment association analyses in Italian goats.

Variable code	Definition	|r|>0.75
BIO3 (%)	Isothermality Corresponds to 100*BIO2/BIO7, namely the ratio between mean diurnal range (mean of monthly difference between maximum and minimum temperature) and temperature annual range (difference between maximum temperature of warmest month and minimum temperature of coldest month)	BIO2 (0.83)
BIO4 (°C)	Temperature seasonality Corresponds to the SD of the monthly mean temperature multiplied by 100	BIO7 (0.91) BIO6 (−0.83) BIO9 (−0.76) BIO11 (−0.80) tmax_summer (−0.77) tmin_winter (−0.82) tmin_autumn (−0.78)
BIO8 (°C)	Mean temperature of wettest quarter Corresponds to the mean of monthly mean temperature during the three consecutive months with the highest precipitation	
BIO15 (%)	Precipitation seasonality Corresponds to the annual CV of the monthly precipitation	BIO14 (−0.82) BIO17 (−0.81)
prec_spring (mm)	Total precipitation during spring Calculated as the median value of the average total precipitation in March, April, and May	BIO12 (0.93) BIO13 (0.82) BIO16 (0.78) BIO17 (0.77)
prec_autumn (mm)	Total precipitation during autumn Calculated as the median value of the average total precipitation in September, October, and November	BIO12 (0.87) BIO13 (0.94) BIO16 (0.98)
tmax_summer (°C)	Maximum temperature during summer Calculated as the median value of the average maximum temperature in June, July, and August	BIO1 (0.94) BIO10 (0.96) BIO11 (0.89) BIO5 (1.00) BIO6 (0.84) BIO8 (0.77) tmax_winter (0.91) tmax_spring (0.93) tmax_autumn (0.95) tmin_winter (0.83) tmin_spring (0.90) timin_summer (0.91) tmin_autum (0.87) elev (−0.87)

aligning with FAO's strategic objectives to conserve and sustainably use animal genetic resources (FAO, 2015a; 2022).

Italian goat demography, biodiversity, and recent evolution

Census data from the last 15 years (2010–2024) reveal a concerning decline in registered goat farms, with an overall reduction of about one−third. In contrast, the number of registered goats has shown more variability, likely reflecting the fluctuations in regional and national financial incentives supporting local breeds. Demographic information also allows the estimation of extinction risk, according to FAO criteria (FAO, 2013). Alarmingly, only five breeds (11%)—including the cosmopolitan Camosciata delle Alpi—are currently not considered at risk of extinction, whereas 15 (32%) are classified as endangered and 12 (26%) as critical. Moreover, 10 breeds had no registered animals or farms in 2024,

Table 4
Significant single-nucleotide polymorphisms (SNPs) from latent factor mixed model (LFMM) and partial redundancy analysis (pRDA) in Italian goats.

SNP	Position	Associated variable (LFMM)	Canonical axis (pRDA)	Genes
snp2286-scaffold1069-2525871	1:66 591 843	BIO8	RDA1	*KPNA1, PARP9*
snp44030-scaffold595-5911614	3:27 914 663	BIO8	RDA1	*LRP8*
snp26756-scaffold281-914407	6:37 569 967	BIO8	RDA1	
snp27546-scaffold2948-75069	7:71 850 309	prec_spring	–	*MXD3, RAB24, NSD1*
snp22907-scaffold2282-191752	13:78 652 699	BIO8	RDA1	
snp58824-scaffold960-1184341	24:59 375 683	BIO4, BIO8, tmax_summer	RDA1	

Environmental variable codes are defined in Table 3.

Table 5
Summary of the explained variance and variables associated with adaptively enriched redundancy analysis (RDA) canonical axes in Italian goats.

Canonical axis	Explained variance	Associated variables (score)
1	55.5%	BIO4 (0.71) tmax_summer (−0.52) BIO15 (−0.45)
2	14.4%	BIO3 (−0.65)
3	12.3%	BIO15 (0.60) prec_spring (−0.49) BIO8 (0.47)
4	9.5%	prec_autumn (0.87) prec_spring (0.55)
5	4.3%	BIO3 (0.51)
6	2.3%	BIO (0.63) tmax_summer (0.63)
7	1.8%	BIO4 (0.41)

Environmental variable codes are defined in Table 3.

thereby meeting the criteria for formal extinction. For these populations, efforts should focus on identifying genomic material outside the official herdbooks and promoting their registration, following appropriate phenotypic and genomic evaluations (Oldenbroek, 2007).

Beyond the identification of these suitable individuals, genomic analyses are also essential for monitoring existing populations. Indeed, they improve the accuracy of effective population size (N_e) and inbreeding estimates, and provide valuable insights into the history and evolutionary trajectories of each population, particularly when comparisons with historical datasets are possible (Howard et al., 2017; Ajmone-Marsan et al., 2023).

Our results highlight the strong relationship between geography and genomic composition, as previously reported in several studies (Nicoloso et al., 2015; Bertolini et al., 2018; Cortellari et al., 2021b; Denoyelle et al., 2021b; Petretto et al., 2024), with a clear differentiation between northern breeds and central–southern and insular populations. We also confirm previous findings that genetic sharing occurs primarily among breeds within the same breeding areas (Cortellari et al., 2021b). This is particularly evident for central–southern populations, likely due to the long history of horizontal transhumance, which allowed flocks from different regions to meet and intermix (Cortellari et al., 2021a). This process likely explains the high levels of admixture observed among these populations—although some breeds remain clearly distinct—all of which share a predominant ancestry component that can be described as the 'Mediterranean component'. This genetic background has been consistently detected in independent studies using different datasets and analytical approaches (e.g., Colli et al., 2018; Cortellari et al., 2021b; Di Civita et al., 2024; Floridia et al., 2025), including analyses that revealed its presence in both Italian and other Mediterranean breeds such as those from Greece.

In contrast, northern breeds have historically practised vertical transhumance, moving seasonally from plains to mountains within relatively restricted areas, which limited gene flow and exchanges with flocks from other valleys (Cortellari et al., 2021a). However, extending the dataset beyond Italian borders would make it possible to investigate potential gene flow among breeds across the entire Alpine arc, whether raised in Italy or in neighbouring countries. In this study, northern breeds were distinguished into three main groups by several analyses: one including specialised (Camosciata delle Alpi and Saanen) and north-western breeds (Roccaverano and Valdostana); one with breeds from Lombardy (Frisa Valtellinese, Bionda dell'Adamello, Verzaschese, Vallesana, Lariana, and Orobica, the latter being particularly distinct); and the Pezzata Mochena. Camosciata delle Alpi and Saanen are two dairy breeds originally from Switzerland that have become widely distributed across continents due to their high milk production. In Italy, they are commonly raised in intensive or semi-intensive sys-

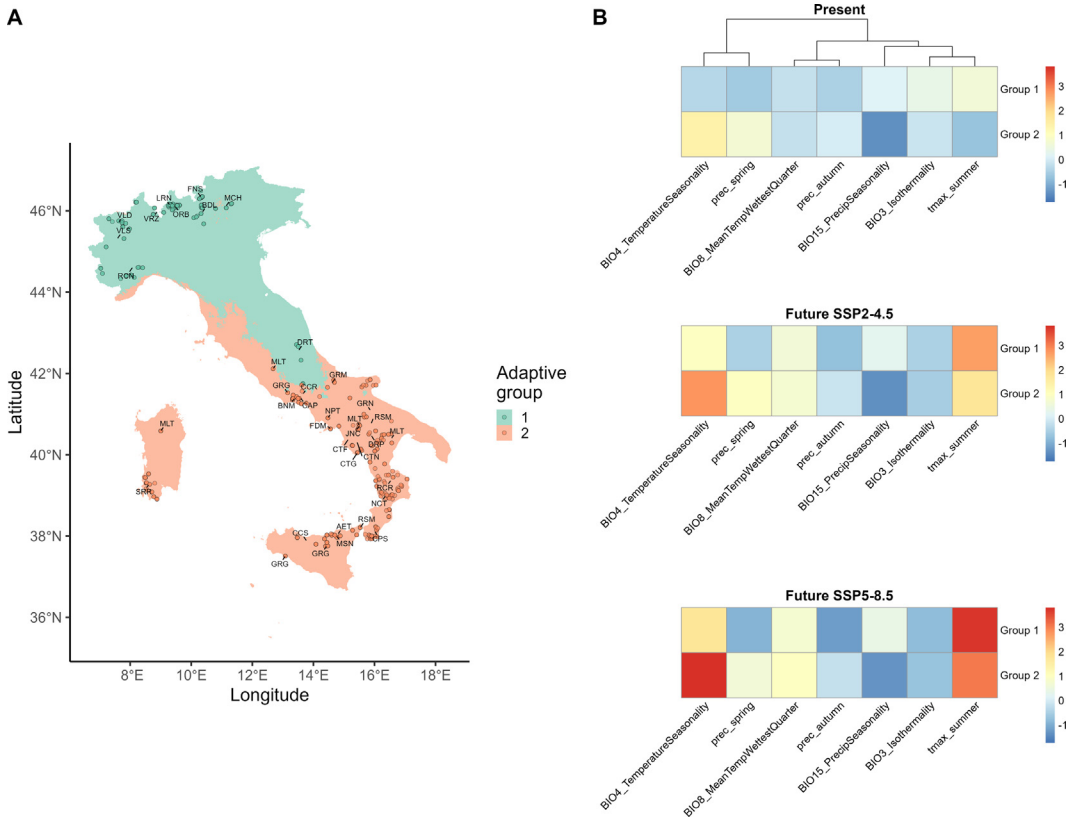

Fig. 7. Main adaptive groups in Italian goats, based on the current adaptive index across all axes (A) and heatmaps of the average scaled values of present and future (two scenarios) environmental variables (B). Breed codes are defined in Table 6, and environmental variable codes are defined in Table 3.

Table 6
Italian goat breed attribution to adaptive groups, based on the current adaptive index, and mean ± SD genomic offset (g.o.) under moderate (2–4.5) and severe (5–8.5) scenarios.

Breed	Breed Name	N	Centroid	Adaptive groups	g.o. 2–4.5	g.o. 5–8.5
AET	Argentata dell'Etna	27	(14.657, 38.038)	2	0.261 ± 0.067	0.394 ± 0.058
BDL	Bionda dell'Adamello	29	(10.386, 45.968)	1	0.222 ± 0.112	0.511 ± 0.192
BNM	Bianca Monticellana	27	(13.389, 41.388)	2	0.131 ± 0.006	0.344 ± 0.095
CAP	Capestrina	16	(13.53, 41.384)	2	0.141 ± 0.036	0.307 ± 0.096
CCR	Ciociara Grigia	12	(13.662, 41.497)	1 (25%), 2 (75%)	0.203 ± 0.076	0.391 ± 0.129
CCS	Comune di Sicilia/Mascaruna	35	(13.786, 37.878)	2	0.135 ± 0.005	0.464 ± 0.001
CPS	Capestrina	35	(16.053, 38.157)	2	0.191 ± 0.036	0.333 ± 0.017
CTF	Cilentana Fulva	5	(15.079, 40.443)	2	0.278 ± 0.073	0.487 ± 0.12
CTG	Cilentana Grigia	3	(15.444, 40.05)	2	0.197 ± 0.001	0.350 ± 0.009
CTN	Cilentana Nera	26	(15.431, 40.29)	2	0.208 ± 0.031	0.404 ± 0.069
DRP	Di Potenza	31	(15.949, 40.469)	2	0.179 ± 0.039	0.347 ± 0.076
DRT	Di Teramo	9	(13.499, 42.608)	1	0.238 ± 0.031	0.361 ± 0.066
FDM	Fulva dei Monti Picentini	14	(14.558, 40.637)	2	0.272 ± 0	0.505 ± 0
FNS	Frisa Valtellinese	26	(10.33, 46.338)	1	0.127 ± 0.006	0.311 ± 0.006
GRG	Girgentana	22	(13.886, 38.199)	2	0.218 ± 0.089	0.417 ± 0.047
GRM	Campobasso Grigia Molisana	8	(14.622, 41.772)	2	0.240 ± 0.015	0.401 ± 0.018
GRN	Garganica	35	(15.866, 40.994)	2	0.258 ± 0.114	0.598 ± 0.333
JNC	Jonica	2	(15.517, 40.718)	2	0.266 ± 0	0.419 ± 0
LRN	Lariana/Di Livo	21	(9.301, 46.147)	1	0.194 ± 0.05	0.161 ± 0.011
MCH	Pezzata Mochena	18	(11.143, 46.127)	1	0.117 ± 0.007	0.322 ± 0.029
MLT	Maltese	23	(11.408, 40.747)	2	0.237 ± 0.067	0.469 ± 0.11
MSN	Messinese	35	(14.659, 37.967)	2	0.267 ± 0.077	0.396 ± 0.061
NCT	Nicastrese	36	(16.324, 38.97)	2	0.226 ± 0.044	0.311 ± 0.036
NPT	Napoletana	8	(14.474, 40.906)	2	0.260 ± 0	0.494 ± 0
ORB	Orobica	24	(9.478, 46.095)	1	0.165 ± 0.034	0.337 ± 0.133
RCN	Roccaverano	19	(8.096, 44.654)	1	0.193 ± 0.016	0.456 ± 0.046
RCR	Rustica di Calabria	35	(16.534, 39.392)	2	0.215 ± 0.041	0.303 ± 0.029
RSM	Rossa Mediterranea/Derivata di Siria	31	(15.737, 39.601)	2	0.181 ± 0.039	0.397 ± 0.083
SRR	Sarda	35	(8.66, 39.229)	2	0.272 ± 0.064	0.533 ± 0.081
VLD	Valdostana	18	(7.627, 45.718)	1	0.253 ± 0.123	0.402 ± 0.164
VLS	Vallesana	17	(7.617, 45.368)	1	0.214 ± 0.061	0.32 ± 0.069
VRZ	Verzaschese	15	(8.838, 45.974)	1	0.186 ± 0.037	0.259 ± 0.078

tems, mainly in central and northern regions, and artificial insemination is used in about 10–15% of animals, often with French semen. Our analyses indicate moderate levels of inbreeding, with no evidence of excessive recent inbreeding. Despite their productive success, both breeds have shown a marked decline in registrations over the past 15 years, with losses of about one-third of Camosciata delle Alpi and two-thirds of Saanen.

The replacement of local breeds with specialised ones is a major driver of breed erosion (FAO, 2015b). However, crossbreeding with Camosciata delle Alpi and Saanen is reported to be limited in Italian local goats (Rubino, 1993), a finding that is confirmed by our results. Indeed, only one breed showed clear signs of introgression from Camosciata delle Alpi: the Roccaverano goat. This Piedmontese breed is reported to be of mixed origin, as suggested by its variable appearance, with some hypotheses linking it to goats introduced by Saracen soldiers during invasions in the region (Bigi and Zanon, 2020). Robiola di Roccaverano cheese is the first recognised Italian PDO product made with goat milk (blended with cow milk) and accepts milk only from Roccaverano, Camosciata delle Alpi, and their crosses. Interestingly, TreeMix also identified possible migration between Roccaverano and Sarda breeds, partially supported by the presence, although limited, of the Sarda cluster within the Roccaverano background.

Another distinctive north-western breed is the Valdostana, raised in Valle d'Aosta and made famous by traditional non-cruel fights, called "Batailles de Chèvres", events that since 1981 have attracted tourists and provided an economic opportunity for farmers. Morphologically similar to other Alpine populations, the Valdostana is distinguished by its large size and stocky conformation, concave profile, and especially its very developed sabre-shaped, ibex-like horns, present in both sexes and likely selected specifically for these competitions (Talenti et al., 2017; Bigi and Zanon, 2020). Genomic analyses confirm a distinct background for this breed, despite only average inbreeding values. However, registrations have declined dramatically: from about 1 500 heads across 200 farms in 2010 to only a single farm with 13 heads today.

Lombardy populations were all clearly distinguishable from one another. In particular, the Orobica exhibits a distinct genomic composition, as previously reported (Ajmone-Marsan et al., 2001; Crepaldi et al., 2001). This may be explained either by its origin, which some authors link to goats brought by charcoal workers from southern Italy that crossed with local Alpine populations, or by the strong isolation of the valleys where it is traditionally raised (Crepaldi et al., 2001; Bigi and Zanon, 2020). A southern origin may account for the Orobica's morphological traits—such as long hair and long diverging and slightly twisted horns, especially developed in males. On the other hand, isolation likely explains the very high inbreeding levels observed, which, however, show only limited signs of recent events, suggesting effective recent management. It is also worth noting that, despite exhibiting typical characteristics such as horns and long hair, Orobica official recognition was delayed due to the variability of its coat colour and was granted only after thorough studies on morphology and farming systems (Tartarini and Corti, 1989; Crepaldi et al., 2001; Corti and Brambilla, 2002).

Another case of polychrome goat is the Lariana (or Di Livo), a population raised in mountainous areas around Como. Its origins are uncertain, but it is believed to have descended from an original primary population ("Di Livo") that was later crossed with goats from other populations in the region, as farmers with limited resources often acquired surplus animals—frequently belonging to different breeds or crosses—from surrounding farms. This, combined with limited selection for morphological traits and uniformity, likely explains both its variable appearance and its complex genomic background, which includes contributions from many

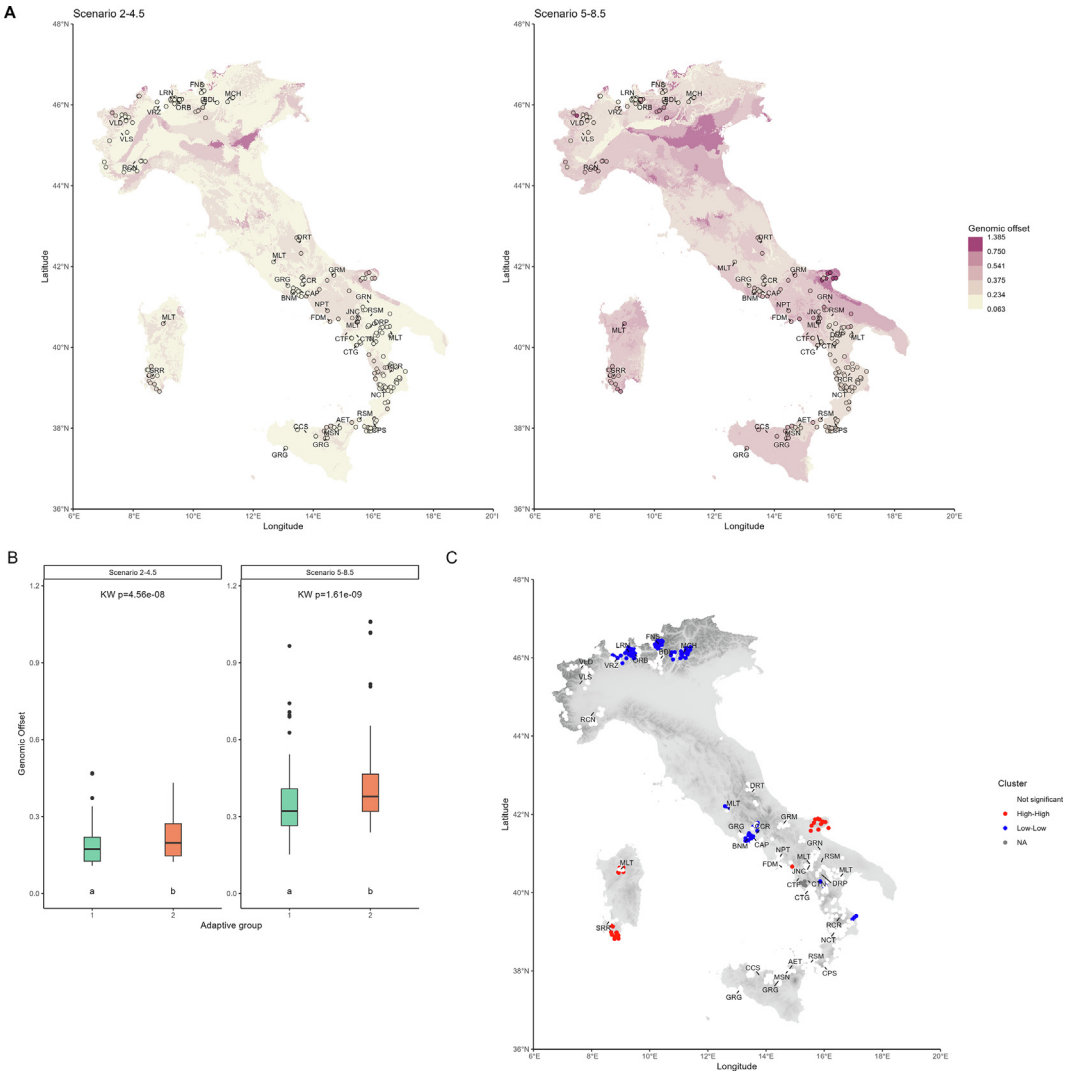

Fig. 8. Genomic offset estimation for Italian goats. (A) Genomic offset estimated under moderate (2–4.5) and severe (5–8.5) scenarios. (B) Differences in genomic offset values among individuals assigned to different adaptive groups, based on the Kruskal–Wallis test. (C) Statistically significant hot- and cold-spots of expected genomic vulnerability identified through local autocorrelation analysis. Only individuals consistently assigned to the same group across all tested K values are coloured. Results for each tested K are shown in Supplementary Figure S13. A small jitter was applied to display overlapping points. Breed codes are defined in Table 1.

northern breeds, particularly Verzaschese (reported to have largely replaced much of the local population), Bionda dell'Adamello, Orobica, and Frisa Valtellinese (whose contribution appears to have increased over the last 20 years, likely to improve Lariana meat production). In addition to the spread of more standardised breeds, particularly Verzaschese, and the difficulties in preserving highly variable breeds (Bigi and Zanon, 2020), the Lariana population has declined. This negative trend was further exacerbated by wolf predation and the expansion of luxury economic and touristic development of Lake Como, which are increasingly driving farmers to abandon pastoral activities in the region.

Interesting results were also obtained for the Pezzata Mochena, which takes its name both from the Bavarian population that settled in some valleys of Trentino-Alto Adige around the 14th century and from the typical black-and-white patched coat that characterises it. At the beginning of the 21st century, this population was on the verge of extinction, but regional projects and dedicated associations succeeded in obtaining official recognition and in promoting its recovery (Bigi and Zanon, 2020), although demographic data still classify it as critically endangered. Interestingly, this breed was consistently placed among northern populations, though slightly shifted towards those raised in central Italy. Moreover, when the Val Passiria (or Passeirer Gebirgsziege), another morphologically variable breed from the same eastern-Alpine region for which no registration data are currently available, was included in the dataset, the two appeared highly similar, confirming the hypothesis of historical crosses between them (Bigi and Zanon, 2020).

Among central Italian breeds, Bianca Monticellana and Capestrina stood out in our analysis for their early separation from other populations, while at the same time showing a clearly shared genomic background with each other and, to a lesser extent, with Ciociara Grigia. Despite being distinguishable by coat colour—white in the Bianca Monticellana, black (sometimes with Swiss markings) in the Capestrina, and grey in the Ciociara Grigia—all three breeds originated in Lazio and are commonly raised together in the same flocks or share grazing areas. This could explain their genomic similarities, already reported elsewhere (Di Civita et al., 2024). These findings suggest that Bianca Monticellana and Capestrina may represent two varieties of the same population, potentially warranting consideration as a single breed, which could also facilitate coordinated management and conservation actions

aimed at reducing inbreeding and maintaining genetic diversity. However, it is important to underline that any decision in this regard should be carefully evaluated by the breeder association together with the breeders, taking into account not only genomic evidence but also phenotypic characteristics, historical background, and practical management aspects. Interestingly, our results also indicate that recently sampled Capestrina and Bianca Monticellana show a much more uniform background than individuals from the IGC2 dataset, together with a marked and concerning increase of 4.5–6% in average inbreeding. This pattern may explain their early separation from other breeds, a feature not observed in previous studies, and underscores the need for targeted breeding programmes.

Ciociara Grigia, together with the Di Teramo breed, also displayed some of the greatest changes in genomic background over the past 20 years. In the IGC2 dataset, these populations included some individuals with a very distinct and uniform background, forming a breed-specific cluster, while other individuals showed a more admixed composition, mainly related to central populations, Pezzata Mochena, and the Mediterranean component. In contrast, all recent samples appeared admixed, with only minimal traces of their specific cluster. In light of these findings, further investigation of these breeds through broader sampling and ongoing genomic monitoring is warranted to validate the pattern and clarify whether the observed shift involves the entire population or if some individuals still retain components of the original genetic background, which could be instrumental in supporting recovery efforts. This pattern could also explain the marked reduction in F_{ROH} between historical and recent samples, particularly evident in the Di Teramo. Preservation efforts for these populations are urgently needed, especially considering their current census of about 130 registered animals, placing them at critical risk of extinction, compounded by losses resulting from earthquakes that affected their breeding range in 2009.

In Campania, two small populations are recognized: the Napoletana and the Fulva dei Monti Picentini, the latter officially recognized in 2022 but with no registered animals to date. In addition, three breeds of Cilentana are distinguished according to coat colour: Nera (black), Rossa (red), and Grigia (grey). Only the Cilentana Nera was included in our dataset. This breed was considered nearly extinct in the 1980s, but subsequently increased in numbers, likely through crosses with other breeds, including Garganica (Bigi and Zanon, 2020). Accordingly, we found that it had the lowest inbreeding values among all analysed populations and an admixed background mainly composed of the Mediterranean component, the Fulva dei Monti Picentini, and the Garganica cluster. By contrast, both Napoletana and Fulva dei Monti Picentini showed very high inbreeding, which could further aggravate their already precarious situation and contribute to genetic erosion.

As mentioned, the majority of southern populations shared a background dominated by a common ‘Mediterranean component’, which was combined with additional ancestries shaped by geography and breed history. In particular, most Sicilian and Calabrian populations showed similar genomic profiles and comparable inbreeding values, generally low but with substantial portions of long ROH. Argentata dell’Etna and Messinese (Sicily), as well as Rustica di Calabria and Nicastrese (Calabria), exhibited admixed backgrounds with very similar patterns across time, dominated by the Mediterranean component but also including contributions from Girgentana, Comune di Sicilia, Maltese, and Sarda clusters.

Another numerous Calabrian population is the Aspromontana. It takes its name from the rugged Aspromonte massif, where it originated, later spreading to surrounding provinces, and currently counts over 13 000 registered animals. Interestingly, gene flow from Girgentana was detected in several analyses.

The Girgentana is one of the most easily recognizable Sicilian goats, both genomically—due to its distinct genetic background—and phenotypically, thanks to its typical corkscrew horns resembling those of *Capra falconeri*. Because of this trait, several authors suggest an Asian origin, possibly from Himalayan *Capra prisca* or as a direct descendant of the markhor; however, these hypotheses have never been confirmed by genomic studies (Denoyelle et al., 2021b; Frölich et al., 2021). The first introduction of this breed to Italy is attributed to Arab settlers in the 9th century AD. Traditionally, it was raised in urban centres for fresh drinking milk, primarily used for feeding infants and the elderly (Portolano et al., 2004; Bigi and Zanon, 2020; Criscione et al., 2025). However, the breed experienced a severe bottleneck, as also reflected by our results showing very high—and still increasing—genomic inbreeding. In 1983, about 30 000 animals were recorded, but within a decade, the population had declined to only a few hundred, prompting the launch of recovery projects (Portolano et al., 2004). Recent registration trends show marked fluctuations and, currently, only about 750 animals remain.

Despite sharing much of the same breeding range, the Comune di Sicilia (or Mascaruna) shows little or no introgression from the Girgentana. This population was officially recognized in 2025, following a comprehensive morphological and genomic study (Tolone et al., 2022; Bionda et al., 2023; Floridia et al., 2025), which demonstrated its distinction from other Sicilian breeds but also revealed high variability in individual genomic backgrounds. Indeed, some individuals showed contributions from the Mediterranean ancestral pool, together with clusters from the Sarda and Maltese breeds.

Maltese and Rossa Mediterranea are widely valued for their excellent dairy aptitude, which enabled them to spread from Sicily—where they were originally imported from the Middle-eastern Mediterranean basin—to the rest of southern Italy (Bigi and Zanon, 2020). However, both breeds have shown a consistently negative trend in registrations over the last 15 years. Temporal comparison of Rossa Mediterranea highlighted higher admixture in recent samples, particularly with the Mediterranean component, as well as Nicastrese and Maltese clusters. For the Maltese, instead, we observed a clear substructure not related to temporal change but to sampling location: one cluster prevailed in goats sampled in Sardinia and Rome; the other in those sampled in Sicily and Calabria; an intermediate background was present in goats sampled in Basilicata. This latter cluster was also more evident in recent Sarda samples compared to those from IGC2, although only in limited proportions. As the name suggests, the Sarda is native to Sardinia, where it represents the predominant goat breed, especially in harsh and marginal mountainous areas unsuitable for sheep grazing. Given the strong caprine vocation of the island, the Sarda is the most numerous Italian goat breed (about 15 000 animals) and was included among breeds under selection programmes. However, in recent years, only a very limited number of bucks have been registered (36 in 2024), which qualifies it as vulnerable according to the FAO classification. For this reason, since 2025, it has been reclassified among breeds under conservation programmes.

Overall, our genomic and demographic analyses reveal a highly variable picture of Italian goat biodiversity, with breed-specific differences shaped by recent management practices, policy support, and historical trajectories. Beyond providing high-quality products, local goat populations sustain micro-economies and maintain marginal landscapes that might otherwise be abandoned. They also constitute a form of intangible heritage, reflecting centuries of traditional breeding, cultural practices, and adaptation to diverse environments. Integrating genomic tools with morphological, phenotypic, and breeder knowledge enables more accurate breed characterization and recognition, while guiding population management that preserves genetic diversity, maintains breed typicality, and valorizes resilient, well-adapted animals. Supporting

these practices can prevent depopulation of internal areas and reinforce the vital role of goat farms in safeguarding both the territory and its cultural and biological legacy.

Landscape genomics

The genomes of populations are shaped by mutation, genetic drift, gene flow, and both natural and artificial selection. Among these forces, spatially heterogeneous environmental pressures can drive local adaptation, favouring genetic variants that increase fitness in specific habitats and generating distinctive allele frequency patterns across populations (Savolainen et al., 2013; Dauphin et al., 2023). Understanding the genomic basis of such adaptation has become increasingly important for sustaining agricultural systems under climate change (FAO, 2015a). Local breeds are particularly valuable in this context, as they are often well adapted to challenging environments and tend to be resilient, hardy, and tolerant to stressors, pathogens, and parasites (FAO, 2015b). Italy, despite its modest size, provides an ideal system for studying goats, thanks to its environmental heterogeneity and the richness of local breeds shaped over centuries by traditional husbandry, extensive farming, and diverse environmental pressures.

Recent methodological advances have made it possible to study genomic–environment associations more effectively. Both univariate approaches, which test each SNP against environmental variables individually, and multivariate approaches, which account for the polygenic nature of adaptation, are now commonly used. Because neutral genomic structure can produce signals that mimic adaptation, it is critical to account for it in genotype–environment association analyses. For these reasons, we applied two complementary approaches in this study: a univariate method (LFMM) and a multivariate method (pRDA), correcting both for neutral genetic structure to reduce false-positive signals (Rellstab et al., 2015).

While pRDA identified over 400 outlier SNPs, LFMM detected only six significantly associated with environmental variables, yet remarkably, five of these were also among the pRDA outliers. These findings are consistent with the highly polygenic nature of local adaptation, where numerous small-effect loci collectively contribute to adaptive responses. Similar patterns—few univariate signals but widespread multivariate associations—have been reported in several other species, including ruminants, and are expected under complex adaptive architectures shaped by multiple selective pressures in addition to environmental adaptation (Rellstab et al., 2015; Stucki et al., 2017; Capblancq et al., 2018; Forester et al., 2018; Cortellari et al., 2021b; Bazzicalupo et al., 2023).

Three genes were found by both pRDA and LFMM analyses, all associated with axis 1—which was mainly driven by BIO4, tmax_summer, and BIO15—and BIO8: *LRP8*, *KPNA1*, and *PARP9*. In addition, a SNP associated with three variables in LFMM (BIO8, BIO4, and tmax_summer) and RDA1 was located in an intergenic region, but very close to *MC4R* (melanocortin-4 receptor). This melanocortin is involved in the leptin pathway, well known for its role in appetite regulation, food intake, meat production and quality, obesity predisposition, energy balance, and thermogenesis (Fan et al., 2005; Switonski et al., 2013; Hainer et al., 2020).

KPNA1 (Karyopherin Subunit Alpha 1) is part of the importin alpha family, which mediates nuclear protein import. This gene is abundantly expressed in the mammalian brain, where it regulates neuronal differentiation and synaptic function. Variants in this gene have been associated with schizophrenia development in humans, while knockout mice showed behavioural alterations such as reduced anxiety and impaired learning, memory, and sensorimotor gating (Girard et al., 2011; Panayotis et al., 2018; Sakurai et al., 2021). One of the main interacting genes with *KPNA1* is *RAG1*, which is involved in the activation of immunoglobulin V(D)J recombination, a process that allows the somatic rearrangements of antigen receptor genes during lymphocyte development (Fugmann, 2001; Jones and Simkus, 2009). Another crucial role of *KPNA1* in the immune system is the nuclear translocation of *STAT1*, *STAT2*, and *STAT3*, transcription factors that regulate inflammation and immunity, especially during viral infections, including small ruminant lentiviruses (Gomez-Lucia et al., 2013; Du et al., 2014; Wang et al., 2019). In addition, *STAT1* and *STAT3* are well known to be involved in cattle mastitis, to influence milk production traits in domestic ruminants (Khan et al., 2020), and to be important in the response to heat stress through several pathways, including reproductive function and immunity (Morales Dalanezi et al., 2019; Catozzi et al., 2020; Astuti et al., 2022; Laporta et al., 2025).

PARP9 (Poly(ADP-Ribose) Polymerase Family Member 9) also interacts with *STAT1*, regulating macrophage activation (Iwata et al., 2016). In general, the *PARP* family targets proteins for ADP-ribosylation and plays a fundamental role in innate immune signalling pathways as well as in the regulation of interferon-I responses during viral infections and antiviral response (Zhang et al., 2015; Xing et al., 2021; Zhu and Zheng, 2021). Additionally, *PARP9* is involved in fat metabolism through the expression of low-density lipoprotein (**LDL**) receptors and apolipoproteins in macrophages (Szántó et al., 2021).

This is especially interesting when considering that the third identified gene is *LRP8* (LDL Receptor Related Protein 8), a LDL receptor crucial in lipid metabolism and cholesterol uptake (Waltmann et al., 2014). Several studies on cattle species pointed out that this gene is highly expressed in granulosa cells, being involved in cholesterol transportation and the response to reactive oxygen species (**ROS**), with differential expression during heat stress conditions (White et al., 2001; Argov et al., 2005; Fayad et al., 2007). In addition, the protein encoded by this gene plays a critical role in the migration of neurons during development by mediating Reelin signalling (Santana et al., 2015), controls osteoblast differentiation through the Wnt/β-catenin pathway (Zhang et al., 2012; Lara-Castillo and Johnson, 2015), and allows selenium uptake, through selenoprotein P transportation, into several organs, such as brain, testis, and placenta (Burk and Hill, 2015; Solovyev et al., 2021). Selenoproteins are especially important for antioxidant defence and ROS regulation, reproductive function, immune response, and thyroid function (Mehdi and Dufrasne, 2016; Gorini et al., 2021). Since selenium concentration and bioaccessibility are highly variable worldwide, and within Italy as well, depending on soil properties and pedoclimatic factors—in particular rainfall— (Spadoni et al., 2007; Fordyce, 2013), the regulation of its receptors could represent a genomic adaptation to maintain selenium homeostasis in the organism. Moreover, the antioxidant properties of selenium help mitigate the detrimental effects of heat stress in several species (Zheng et al., 2022).

When considering all the genes identified by either LFMM or pRDA analysis, we observed that many have already been associated with environmental adaptation in goats (*KSR2*, *PPM1K*, *MAPK14*, *SPATA16*, *SASH1*, *JAK2*) (Mdladla et al., 2018; Denoyelle et al., 2021a; Peng et al., 2024), sheep (*MCPH1*, *NBEA*, *PKP2*, *PKP4*, *ANO2*) (Cao et al., 2020; Serranito et al., 2021), or across multiple ruminant species (e.g. *ENOX1*, *CCSER1*) (Mdladla et al., 2018; Serranito et al., 2021; Niu et al., 2024; Peng et al., 2024). This overlap supports the robustness of our signals and may indicate that Italian goat populations share adaptive responses with other livestock. Notably, some genes (*DCLK1*, *HDAC*, *NBEA*, *RNF150*, and *NLN*) were already detected in our previous landscape genomic study on IGC2 Italian goats (Cortellari et al., 2021b), possibly reflecting stable adaptation mechanisms specific to these populations.

More specifically, we found that *DLG2* was associated with day length adaptation in sheep (Cao et al., 2020), an important factor influencing reproductive regulation in small ruminants (Wood et al., 2020). In addition, we identified GO terms linked to rhythmic behaviour and ultradian rhythms, as well as *NPAS2*, a well-known circadian clock regulator (Wang et al., 2015). Circadian (daily) and ultradian (shorter) biological rhythms play a crucial role in coordinating the timing of internal physiological processes, preparing individuals for predictable environmental fluctuations. These rhythms operate at endocrine, metabolic, and neural levels, synchronising functions such as feeding and rumination cycles, thermoregulation, behaviour, and reproduction with environmental cues like temperature, light, and food availability (Yerushalmi and Green, 2009; Prendergast and Zucker, 2016; Li et al., 2021; Casey and Plaut, 2022).

Genes linked to adaptation in high-altitude environments included *EXTL1*, *PARP2*, *ACCS2*, *PPP1R12A*, *DCLK1* (Edea et al., 2019; Wen et al., 2022; Benjelloun et al., 2024; Niu et al., 2024) and, in particular, *FGF5* (Niu et al., 2024; Liu et al., 2025b), which was consistently found across species. Animals living at high elevations must cope with hypoxia, which matches the enriched GO terms related to oxygen transport and erythrocyte differentiation that we observed.

High altitudes also expose animals to intense UV radiation. Among our candidates, *LEF1* was previously associated with UV tolerance in sheep (Zhu et al., 2025) and with coat colour in goats (Diao et al., 2025; Luo et al., 2025). Since pigmentation is one of the most visible adaptive traits, it being related to UV radiation absorption/reflection and thus thermoregulation (Sejian et al., 2018; Nair et al., 2021), it is not surprising that we also identified other pigmentation-related genes such as *OCA2* (Shi et al., 2021; Apar et al., 2024), *RALY* (Nazari-Ghadikolaei et al., 2018), *SLC2A1* (Selçuk et al., 2024), *WNT6* (Wang et al., 2025), and *GLI3* (García-Gámez et al., 2011; Zhang et al., 2024).

Cold adaptation was reflected in several candidates, including *MYH2* (Liu et al., 2025b), *IFNGR1* (Igoshin et al., 2021), and *PRDM16*, a well-known regulator of fat browning and thermogenesis (Yan et al., 2022a; Li et al., 2023). *FGF5* again emerged (Liu et al., 2025b), reinforcing the hypothesis of it playing a pleiotropic role in regulating hair length and goat fibre traits (Li et al., 2019; Dan et al., 2025; Gong et al., 2025). Supporting this, we found a significant GO term related to hair follicle morphogenesis and additional fibre-related genes such as *CCSER1* (Lu et al., 2024), *DUOX1* (Nazari-Ghadikolaei et al., 2018), *LEF1* (Gong et al., 2022; Yan et al., 2022b; Li et al., 2024), and four keratins (*KRT25*, *KRT26*, *KRT27*, and *KRT28*) (Yu et al., 2009; Fu et al., 2020; Nai et al., 2025; Wu et al., 2025). Together, these results suggest that hair length and texture, like coat colour, are important targets of both anthropic and natural selection.

Lastly, since climatic conditions are expected to lead to hotter and drier environments (Cortellari et al., 2021b; Bionda et al., 2025), goat adaptation to these conditions will be increasingly important. In this context, we found *CACNA2D1*, previously associated with adaptation to arid environments in sheep (Zhu et al., 2025). Water balance is a major challenge in such conditions, consistent with the significant GO terms we observed for kidney and urinary system development. In addition, heat-tolerance genes emerged, including *KSR2* and *SLC22A8* (Aboul-Naga et al., 2022; 2025). We also detected *INSR*, whose signalling is reported to be disrupted under heat stress (Coleman et al., 2022; Dou et al., 2022; Mendonca et al., 2025) and which appears to be linked to feed efficiency (Mota et al., 2022), highlighting its possible role in both stress response and productivity.

Beyond overlaps with earlier studies, our analyses highlighted other pathways which might be relevant for environmental adaptation. Oxidative stress is a common challenge, as both hypoxia and heat stress increase ROS (Chauhan et al., 2021). Several antioxidant-related ontologies were enriched, supporting their role in resilience under harsh environments. Autophagy also emerged as a significant process. This catabolic and cytoprotective pathway is activated under conditions such as hypoxia, nutrient shortage, and infection to provide nutrients for vital cell functions and remove damaged cytosolic material (Dikic and Elazar, 2018). Several of our candidate genes (*DAPK2*, *OPTN*, *AMBRA1*, *ATG10*) (Roy et al., 2021; Tesseraud et al., 2021) are directly involved in autophagy, consistent with its role in maintaining cell homeostasis. Moreover, autophagy contributes to pathogen defence, as also demonstrated in domestic ruminants (Tesseraud et al., 2021).

Immune response is a particularly relevant adaptive context, as climate change can impair immune systems while simultaneously altering the distribution of pathogens and vectors (Filipe et al., 2020; Ciliberti et al., 2022). Consistently, we identified several immune-related genes, including loci associated with mastitis (e.g. *CACNA2D1*, *KCNQ1*, *SIRT7*) (Prajapati et al., 2017; Chen et al., 2019; Narayana et al., 2023); *PARP14* and *TMEM232* linked to small ruminant lentiviruses (Materniak-Kornas et al., 2024; Riggio et al., 2024); *NEDD4L* related to *peste des petits ruminants* (Xu et al., 2024); and *IFNGR1*, a receptor mediating interferon-γ responses to multiple infections including brucellosis in goats (Hasenauer et al., 2020). Interestingly, four genes (*DLG2*, *EPYC*, *GPHN*, and *DLNOL4LL*) were associated with foot and claw health in cattle (Croué et al., 2019; Stambuk et al., 2020; Butty et al., 2021; Sölzer et al., 2024), a relevant trait for goats grazing in rugged terrains where mobility is essential.

Parasitic infestations also represent a major constraint for extensive systems. We found the previously mentioned *LRP8* as well as *DUOX1* and *GATA3* (Ingham et al., 2008; Lins et al., 2024), all related to resistance against gastrointestinal nematodes. Supporting this, we identified GO terms linked to digestive function, stomach development, and gastric acid secretion, which are commonly impaired during parasitic infections (Mekonnen, 2021). Efficient digestion and feed utilisation are especially critical under harsh conditions. In this context, it is interesting to note that *CTBP1* and *LRPAP1* are associated with tail fat deposition in sheep (Xu et al., 2017; Taghizadeh et al., 2022; Mansourizadeh et al., 2024), a strategy evolved to cope with food scarcity (Kalds et al., 2021). We also identified *ACSS2*, associated with methane emissions in cattle (Fresco et al., 2025), a trait relevant for the mitigation of livestock's contribution to climate change. Feed efficiency is equally important for productivity, particularly in meat production when goats are raised under extensive management. Accordingly, several genes were linked to muscle development or meat quality (e.g., *FGF5*, *TEAD1*) (Hu et al., 2023; Chen et al., 2024) and to growth and body size (e.g., *CCSER1*, *JAK2*, *GLI3*, *STC2*) (Jin et al., 2013; Xu et al., 2023; Wu et al., 2024). Genes related to milk production and quality were also found (e.g., *ABCG2*, *CCSER1*, *ELF5*, *JAK2*) (Liu et al., 2024; 2025a; Li et al., 2025; Ma et al., 2025; Zheng et al., 2025), including *ACSS2* and *DPYD*, which are associated with the development of typical organoleptic traits of goat milk (Jia et al., 2022; Zhang et al., 2022). These morphological and production-related loci highlight how natural selection shapes traits that are simultaneously adaptive and economically relevant; nevertheless, it remains crucial to validate these candidate regions and genes through complementary approaches, such as expression analyses, functional assays, ad hoc experiments, or association studies in independent populations (Rellstab et al., 2015).

Taken together, the genes and GO terms identified are suggestive of a multifaceted adaptive landscape, where metabolic, immune, developmental, and morphological traits likely interact to confer resilience. This complexity reflects how livestock must respond simultaneously to climatic pressures, pathogen load, and production demands in heterogeneous environments such as Italy.

Future studies could refine these analyses by narrowing the focus to specific areas or populations while enhancing the resolution of both environmental and genomic data. For instance, tracking seasonal movements such as goat transhumance would make it possible to capture the full range of climatic conditions experienced throughout the year—particularly in mountainous regions, where sharp environmental contrasts can occur over short distances. Beyond commonly used climatic variables, additional data on vegetation, landscape features, lithomorphology, and land management could be integrated to provide a richer context. Moreover, combining high-resolution environmental information from farm- and pasture-level sensors with more detailed genomic datasets would further strengthen landscape genomic approaches, offering deeper insights into the genetic basis of adaptation in goat populations.

Adaptive vulnerability

Local goat breeds in Italy are predominantly managed under extensive farming systems. Such conditions have historically promoted long-term adaptation to the specific ecological features of their native environments, allowing these populations to persist and remain productive even under challenging circumstances (FAO, 2015b; Bionda et al., 2025). At the same time, their strong dependence on local environmental conditions makes them particularly sensitive to ecological shifts (FAO, 2015a). Given that environmental changes are increasingly recognised as rapid and profound at the global scale in recent decades (IPCC, 2023; Bionda et al., 2024; 2025), it becomes essential to identify which breeds may face heightened risk of maladaptation in the future, and which breeds, conversely, could serve as valuable reservoirs of adaptive variation.

Within this framework, the concept of genomic offset provides a quantitative approach to estimate the degree of mismatch between the current genetic composition of a population and the genetic composition expected to be required under future environmental conditions, such as those projected under climate change scenarios (Capblancq et al., 2020; Rellstab et al., 2021; Ahrens et al., 2023). Nevertheless, genomic offset is not without limitations (Rellstab et al., 2021; Ahrens et al., 2023). First, it inherently relies on a spatial-to-temporal pattern substitution when used to infer future vulnerability. Second, it assumes that the present genetic composition of a population reflects a perfect adaptation and optimal fitness to the current environment—an assumption that is unlikely to be universally valid. Third, it does not explicitly consider other evolutionary processes, such as genetic drift, gene flow, or artificial selection, which can strongly influence genomic variation in domestic species alongside environmental adaptation. Ideally, genomic offset predictions should be validated through controlled experiments, such as common garden trials, in which forecasted responses can be directly compared with empirical outcomes (Lotterhos, 2024). However, such experiments are often impractical, particularly for long-lived species or traits controlled by complex environmental interactions. As an alternative, when temporal genomic data are available, validation can be approached retrospectively. For example, genotype–environment association models can be applied to historical cohorts to assess whether alleles predicted to provide adaptive advantages have increased in frequency over time (Rellstab et al., 2021). Despite these caveats, genomic offset remains a useful proxy to approximate the relative vulnerability of different populations to environmental change (Capblancq et al., 2020; Rellstab et al., 2021). By highlighting contrasts in adaptive potential, it can provide valuable guidance for prioritising conservation efforts and developing management strategies tailored to safeguard genetic resources under future climate scenarios.

Our results highlight a heterogeneous landscape of future vulnerability for Italian goat breeds, with clear differences between regions and adaptive groups. Although the present adaptive index divided Italy into two main clusters, with one group covering northern and central-eastern areas and the other the southern, central-western, and insular regions, the projected shifts in the genomic offset suggest that vulnerability is not evenly distributed within or between these groups. Under moderate scenarios, the highest genomic offset values were concentrated along Alpine fringes, the eastern Po Valley, and other northern areas, while under severe scenarios, vulnerability hotspots expanded further into the Ligurian and Tosco-Emilian Apennines, the Murgia-Gargano area, and parts of Sardinia and Sicily. Importantly, however, few goat populations were actually sampled in the northern areas with the highest genomic offset, such as the eastern Po Valley. This reflects the fact that farms raising local goat breeds are sparse in these areas, despite the region's strong agricultural potential, as livestock production is dominated by other species and more intensive farming systems. As a consequence, with the exception of Bionda dell'Adamello, northern goats in our dataset mostly fell into low–low clusters, giving the impression of resilience, while in fact the absence of populations in vulnerable areas may conceal substantial risks for livestock more broadly. The high genomic offset predicted for this region, therefore, does not indicate an immediate conservation concern for existing goat populations, but rather highlights areas where current genetic backgrounds would likely be poorly matched to future environmental conditions if northern breeds were to be reintroduced or expanded there. From a management perspective, these projections can provide useful guidance for future planning—such as identifying suitable locations for ex situ conservation herds, relocation, or breed diversification—while also indicating that maintaining viable populations in regions with high predicted offset may require greater management effort or assisted adaptation measures to ensure that genotypes remain well aligned with changing environments. By contrast, southern and insular breeds consistently emerged as most vulnerable, both in their average genomic offset values and through their frequent assignment to high–high clusters. Breeds such as Garganica, which inhabit regions projected to become hotter and drier, may have limited adaptive margins to these compounded climatic stresses.

These results align with previous analyses showing that northern Italy, especially the Po Valley and Alpine arc, is undergoing the fastest warming in summer temperature–related variables, while southern Italy already endures high baseline heat stress, marked precipitation variability, and more frequent droughts (Bionda et al., 2024). Climate projections further suggest that some of the coldest regions today—including parts of the Alpine arc and the Adriatic coast—are likely to shift towards hotter and drier climate classes in the coming decades (Beck et al., 2018; Bionda et al., 2025), reinforcing the hotspot patterns we observed.

An additional layer to these patterns is the different genetic background of the populations: central–southern breeds tend to be more admixed with one another, whereas northern populations generally show more clearly defined genomic backgrounds. While admixture may increase standing variation and thus adaptive potential, it may also dilute fine-tuned local adaptations (Verhoeven et al., 2011; Pan et al., 2022). Conversely, the more homogeneous northern breeds might preserve stronger signatures of past adaptation but could be less flexible when facing the rapid climatic changes projected for their regions (Reed and Frankham, 2003; Willi et al., 2006).

Overall, our results indicate that future vulnerability is not confined to a single region but is distributed in different forms across Italy. Southern and insular populations face greater exposure due to current climatic constraints, while northern populations may

encounter sharper challenges if rapid warming undermines their historically stable adaptive backgrounds. Conservation and management strategies should therefore consider both dimensions—e nvironmental exposure and genetic history—recognising that adaptive capacity is shaped by the interplay between baseline conditions, future climatic trajectories, and the genetic structure of each population.

Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101732) can be found at the foot of the online page, in the Appendix section.

Ethics approval

Datasets were obtained from pre-existing data based on routine animal recording procedures; moreover, DNA sampling for all individuals was conducted using nasal swabs, and no invasive procedures were applied. Thus, in accordance with the 2010/63/EU guide and the adoption of the Law D.L. 04/03/2014, n. 26 by the Italian Government, an ethical approval was not required for our study.

Data and model availability statement

The data that support the findings of this study are available from Asso.Na.Pa. but restrictions apply to the availability of these data, which were used under licence for the current study, and so are not publicly available. For further information, please write to S.G. at direzione@assonapa.it.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

Acknowledgements

The Authors are grateful to all the breeders and to *Associazioni Nazionali Allevatori*, breed experts, and technicians who collaborated on the sampling, and in particular to Annalisa Amato, Carmelo Cavallo, and Luigi Varano.

The authors acknowledge support from the University of Milan through the APC initiative.

Financial support statement

This research was funded by the Italian National Rural Development Plan (PSRN) – sub-measure 10.2, through the projects "Conservation, Health and Efficiency Empowerment of Small Ruminant (CHEESR – CUP: J89H18000210005)" and "Sustainability Health Environment Economy Profitability & Genomic Organisation Animal (pheno)Typing" (SHEEP&GOAT – CUP: J82C21000800005). Project website: www.assonapa.it.

In addition, this study was carried out within the Agritech National Research Center and received funding from the European Union Next-GenerationEU (PIANO NAZIONALE DI RIPRESA E RESILIENZA (PNRR) – MISSIONE 4 COMPONENTE 2, INVESTIMENTO 1.4 – D.D. 1032 17/06/2022, CN00000022). This manuscript reflects only the authors' views and opinions, neither the European Union nor the European Commission can be considered responsible for them.

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