Scientific Reports

https://doi.org/10.1038/s41598-026-59903-y

Article in Press

Genome-wide detection of selection signatures in native anatolian goat breeds

Received: 30 March 2026

Accepted: 24 June 2026

Published online: 03 July 2026

Cite this article as: Bayraktar M., Aytekin İ. & Şahin Ö. Genome-wide detection of selection signatures in native anatolian goat breeds. *Sci Rep* (2026). https://doi.org/10.1038/s41598-026-59903-y

Mervan Bayraktar, İbrahim Aytekin & Özcan Şahin

We are providing an unedited version of this manuscript to give early access to its findings. Before final publication, the manuscript will undergo further editing. Please note there may be errors present which affect the content, and all legal disclaimers apply.

If this paper is publishing under a Transparent Peer Review model then Peer Review reports will publish with the final article.

ARTICLE IN PRESS

© The Author(s) 2026. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

ARTICLE IN PRESS

Genome-Wide Detection of Selection Signatures in Native Anatolian Goat Breeds

Mervan Bayraktar[1*], İbrahim Aytekin[2], Özcan Şahin[2]
[1]Department of Animal Science, Faculty of Agriculture, Çukurova University, Adana, Turkey
[2]Department of Animal Science, Faculty of Agriculture, Selçuk University, Konya, Turkey
[*]Correspondence: mervan.bayraktar@gmail.com or mbayraktar@cu.edu.tr

Abstract
Background: Native Anatolian goat breeds are genetic resources shaped by traditional management, selection, and adaptation to diverse environments. Objectives: This study aimed to identify selection signatures in five goat breeds raised in Türkiye: Ankara, Damascus, Honamli, Kil, and Kilis. Methods: A total of 192 goats were genotyped using the Axiom Goat Genotyping Array containing 59,795 SNP markers. Genome-wide selection signatures were investigated using three complementary haplotype-based statistics: the integrated haplotype score (iHS), the integrated haplotype homozygosity pooled score (iHH12), and the number of segregating sites by length (nSL). Results: Across all analyses, 2,960 non-redundant gene–method–breed records were identified, corresponding to 2,385 unique candidate genes. The three methods revealed overlapping but complementary signals. iHS highlighted regions associated with production, pigmentation, growth, reproduction, and immunity; iHH12 identified a smaller set related to pigmentation, epithelial biology, immunity, metabolism, and reproduction; whereas nSL detected the broadest set, including regions linked to growth, lactation, lipid metabolism, pigmentation, immunity, reproduction, and vascular development. Repeatability analysis prioritized 276 core genes, 83 strong core genes, and 23 robust core genes recurrent across methods and breeds. Functional enrichment analysis highlighted melanogenesis, endocytosis, phosphatidylinositol signaling, Hippo signaling, calcium signaling, synaptic processes, and cytoskeletal regulation. Conclusions: These findings provide genomic resources for validation, conservation, and sustainable management.

Keywords: Turkish native goats; SNP; selection signatures; haplotype analysis; functional enrichment

Introduction

Goats (*Capra hircus*) were among the earliest domesticated livestock, and their domestication is closely associated with the Fertile Crescent and surrounding regions, including Anatolia and neighboring landscapes. Naderi et al. (2008) reported that the domestication of goats involved complex maternal lineages shared between wild and domestic populations, while Daly et al. (2018) showed, through ancient genome analyses, that early goat domestication was geographically structured and involved mosaic genomic processes. Because Anatolia is located close to one of the major centers of early goat domestication, native Turkish goat populations represent important genetic resources for understanding the genomic consequences of domestication, local adaptation, and human-mediated selection. This historical background makes Turkish goat breeds particularly relevant to studies of genetic diversity and selection signatures (Naderi *et al.* 2008; Daly et al. 2018).

Native Turkish goats are important from agricultural, ecological, and cultural perspectives. Türkiye possesses a diverse range of local goat genetic resources, including Ankara, Kilis, Honamli, Kil, and Damascus-type populations, each associated with different production systems and regional environments. Yilmaz et al. (2012) emphasized that Turkish goat breeds differ in production orientation, adaptation, and conservation status. For example, Ankara goats are historically associated with mohair production; Honamli goats are recognized for their relatively

ARTICLE IN PRESS

large body size and meat-type characteristics, whereas Kilis- and Damascus-type goats are more closely associated with milk or dual-purpose production under local management systems. These breed-specific characteristics suggest that both human-mediated selection and environmental adaptation may have contributed to the genomic differentiation of Anatolian goat populations.

Previous studies have shown that Turkish goat breeds harbor substantial genetic diversity and detectable population structure. Ağaoğlu and Ertuğrul (2012) reported high within-breed diversity using microsatellite markers, while Bulut et al. (2016) demonstrated genetic differentiation among several goat populations raised in Türkiye. Karsli et al. (2020) also reported high genetic variability and low inbreeding levels in indigenous Turkish goats. However, most available studies on Turkish goats have focused on microsatellite markers, mtDNA variation, or overall population diversity, and comparatively few have investigated genome-wide signatures of recent or ongoing selection in native Anatolian breeds using SNP-based haplotype methods. This represents an important knowledge gap because diversity studies can describe population relationships and overall variability. Still, they do not directly identify genomic regions that may have been shaped by recent selection.

Genome-wide selection signature analyses provide a useful framework for identifying genomic regions associated with adaptation, production traits, coat color, reproduction, immune response, and other complex biological processes in livestock. Voight et al. (2006) introduced iHS as a widely used haplotype-based statistic for detecting recent positive selection from extended haplotype homozygosity patterns, while Sabeti et al. (2007) demonstrated the broader utility of genome-wide approaches for detecting positive selection in populations. Garud et al. (2015) developed H12-based approaches to detect hard and soft selective sweeps, and Ferrer-Admetlla et al. (2014) introduced nSL. This haplotype-based method identifies selection signals without requiring recombination maps. Therefore, the combined use of iHS, iHH12, and nSL can provide complementary information on recent or ongoing positive selection and help distinguish method-specific signals from recurrent genomic patterns.

Genome-wide studies in goats have also demonstrated the utility of SNP-based approaches for detecting selection signatures associated with production and adaptive traits. Brito et al. (2017) reported that SNP-based genomic analyses across goat breeds can identify candidate regions associated with production, conformation, and adaptation. Other studies in goat populations have similarly reported selection signals related to growth, immunity, reproduction, environmental adaptation, and coat-color variation (Onzima et al. 2018; Chen et al. 2022; Gebreselase et al. 2024). Despite the recognized importance of Turkish goat breeds, a systematic genome-wide evaluation of within-breed selection signatures across multiple native Anatolian goat populations remains limited. In particular, it remains unclear which candidate genes and biological pathways are consistently detected across breeds and methods, and which signals are more likely to be breed-specific.

Against this background, the present study aimed to characterize genome-wide population structure and detect signatures of selection in five native Anatolian goat breeds using SNP data and three complementary haplotype-based statistics, namely iHS, iHH12, and nSL.

Animal material and ethical approval

A total of 192 native Turkish goats were included in this study, representing five breeds: Ankara, Damascus, Honamli, Kil, and Kilis goats. The animals were sampled from their native production environments to reflect the genomic diversity present within each breed. All sampled animals were between 1 and 2 years of age and were maintained under the routine feeding and management conditions of the respective farms.

ARTICLE IN PRESS

Ankara goats were sampled from Ankara province, a region characterized by a cold continental climate, and comprised 12 females and 12 males. Honamli goats were sampled from Antalya province, which has a relatively mild, humid climate, and comprised 9 females and 15 males. Kil goats were sampled from Konya province, another region with cold continental conditions, and included 19 females and 35 males. Kilis goats were sampled from Kilis province, characterized by hot climatic conditions, and included 15 females and 30 males. Damascus goats were sampled from Gaziantep province, which also has a hot climatic profile, and included 35 females and 10 males.

All animal handling and sampling procedures were carried out in accordance with national and institutional guidelines for the care and use of animals in research. The study protocol was approved by the relevant Institutional Animal Care and Use Committee (Approval No. 2025/12-9).

DNA extraction and genotyping

Genomic DNA was extracted using the QuickGene DNA whole blood kit S (DB-S) according to the manufacturer's instructions. Following DNA isolation, all samples were genotyped using the Axiom Goat Genotyping v2 Array, which contains 59,795 SNP markers and was developed for genome-wide analyses in goats. According to Thermo Fisher Scientific, this array was designed to provide broad genome coverage in goats and includes structural-variant content, making it suitable for population genomic studies, association mapping, and genomic selection applications. The genotype data obtained from this platform were used in all downstream analyses, including population structure, detection of selection signatures, candidate gene annotation, and functional enrichment.

Genotype quality control

Genotype quality control was conducted using PLINK v1.9. Markers were excluded if more than 10% of genotype calls were missing, if the minor allele frequency was below 0.05, or if they deviated significantly from Hardy–Weinberg equilibrium at $P < 0.0001$. These thresholds corresponded to SNP missingness > 0.10, MAF < 0.05, and HWE $P < 0.0001$.

These filtering criteria were applied to minimize the impact of poorly genotyped loci, rare variants with limited statistical power, and markers showing abnormal genotype distributions. After quality control, 46,321 high-quality SNPs were retained for downstream analyses. Only SNPs that met all filtering thresholds were used for population structure analysis, selection signature detection, candidate gene annotation, and functional enrichment analysis.

Principal component analysis (PCA)

PCA was performed to summarize genome-wide genetic variation among the five native Turkish goat breeds. Before PCA, linkage disequilibrium pruning was performed using PLINK v1.9 to obtain a set of approximately independent SNPs and minimize the potential influence of highly correlated markers on population structure inference. LD pruning was performed using a 50-SNP sliding window, a step size of 5 SNPs, and an LD threshold of $r^2 = 0.2$. Only SNPs retained after LD pruning were used for PCA.

To investigate the genetic relationships among breeds, PCA was performed in R (v4.5.2) using the prcomp function from the stats package. This approach enabled the reduction of the high-dimensional genotype matrix into orthogonal components representing the main axes of genomic differentiation. The first two principal components were used to visualize clustering patterns among individuals and breeds and to evaluate the extent of genomic structure, overlap, and divergence across the sampled goat populations.

Detection of selection signatures

ARTICLE IN PRESS

Signatures of recent or ongoing positive selection were investigated within each breed using three complementary haplotype-based statistics: integrated haplotype score (iHS), integrated haplotype homozygosity pooled (iHH12), and number of segregating sites by length (nSL). These analyses were performed using Selscan v2.1.1 (Szpiech & Hernandez 2014).
, which is designed for extended haplotype homozygosity-based scans of positive selection.
Before running Selscan, genotype data were phased using BEAGLE v5.5. Phasing was performed separately for each chromosome, and the phased genotype files were then used as input for iHS, iHH12, and nSL analyses. The selection signature analyses were carried out separately for each breed and chromosome using phased genotype data and chromosome-specific marker positions.
For each breed, iHS, iHH12, and nSL scores were calculated across the autosomal genome. The resulting scores were normalized before candidate signal detection. Normalization was performed separately for each statistic within each breed to make the score distributions comparable across genomic regions and to reduce the influence of method-specific scale differences. Candidate selection signals were defined using a unified empirical threshold based on the upper 1% tail of the genome-wide distribution of each statistic within each breed.

Candidate gene identification and annotation

Candidate genes were identified by extending each top 1% selection signal by ±50 kb upstream and downstream. This interval was used as a conservative positional annotation window rather than as a breed-specific LD decay-derived threshold. The use of a ±50 kb window is consistent with previous genome-wide selection signature studies in domestic goats, in which 50 kb upstream and downstream regions around top SNPs were used to define candidate genomic regions. For example, Wang et al. (2025) used 50 kb intervals upstream and downstream of top SNP sites to define genomic regions associated with environmental adaptability in goat populations, while Cai et al. (2024) identified 50 kb genomic intervals upstream and downstream of top SNP sites as candidate regions in Lvliang Black goats. Genes located within these intervals were extracted and used for downstream biological interpretation. Gene annotation was carried out using the domestic goat reference genome, Capra hircus ARS1, a chromosome-level assembly that provides comprehensive structural and functional annotations of caprine genes. In addition, the Axiom Goat Genotyping v2 Array was designed using marker coordinates anchored to the ARS1 assembly, thereby ensuring compatibility between the genotyping data and the reference genome annotation.

GO and KEGG functional enrichment analysis.

Genes located within candidate selection regions were subjected to Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway enrichment analyses using the GO/pathway enrichment analysis module of the SRplot online platform described by Tang et al. (2023), accessed in May 2026 (Kanehisa & Goto 2000; Kanehisa et al. 2016). Although SRplot is commonly used for scientific visualization, its GO/pathway enrichment module integrates enrichment-analysis functions based on the clusterProfiler framework and pathview for pathway-related visualization.
The input gene list consisted of genes located within candidate selection regions identified by iHS, iHH12, and nSL analyses. The background gene set was defined as all annotated protein-coding genes in the domestic goat reference genome, Capra hircus ARS1, which was also used for candidate gene identification and annotation. GO enrichment was evaluated across the three standard categories: Biological Process, Molecular Function, and Cellular Component. KEGG

ARTICLE IN PRESS

pathway enrichment analysis was performed to identify significantly overrepresented biological pathways among the candidate genes.

Multiple-testing correction was performed using the Benjamini–Hochberg false discovery rate method. GO terms and KEGG pathways with FDR-adjusted P values < 0.05 were considered significantly enriched. Enriched categories were interpreted in relation to biological processes relevant to milk production, growth, pigmentation, reproduction, immunity, cellular signaling, and environmental adaptation in goats.

Candidate gene overlap and Venn analysis

To evaluate the repeatability and overlap among candidate genes identified by the three haplotype-based selection statistics, Venn analysis was performed with InteractiVenn. Heberle et al. (2015) described InteractiVenn as a web-based tool for analyzing sets using interactive Venn diagrams, allowing comparison of up to six sets and exploration of shared and unique elements among lists. For each breed, candidate gene lists obtained from iHS, iHH12, and nSL analyses were used as separate input sets. The overlap among the three methods was evaluated to identify genes detected by more than one selection statistic. In addition, breed-wise candidate gene lists were compared to determine genes repeatedly detected across multiple breeds. Venn diagrams were generated to visualize method-specific, breed-specific, and shared candidate genes. The resulting intersections were used to classify candidate genes as unique, recurrent, or core selection candidates.

Results

Population structure revealed by PCA

PCA was performed to summarize genome-wide variation among the five native Turkish goat breeds and was visualized using the first two principal components (Figure 2). The first principal component (PC1) accounted for 12.56% of the total genomic variation, while the second principal component (PC2) explained 2.72%, indicating that the first two axes together captured 15.28% of the genome-wide variation.

The PC1–PC2 projection revealed breed-associated genomic structuring. Ankara goats showed a relatively distinct distribution, primarily separated along PC2, suggesting detectable genomic differentiation of this breed from the other populations. In contrast, Damascus, Honamli, Kil, and Kilis goats showed broader clustering patterns with partial overlap, indicating shared components of genomic variation among these breeds. In addition, a clearly separated group was observed toward the positive extreme of PC1, suggesting an additional axis of differentiation captured by the first principal component.

Genome-wide selection signature profiles and candidate gene screening

Genome-wide selection signatures were investigated separately across five goat breeds using three complementary haplotype-based statistics: iHS, iHH12, and nSL. Candidate genomic regions were defined for each breed and method as the upper 1% tail of the corresponding selection statistic distribution. Genes located within these top 1% candidate regions were compiled separately for each method–breed combination. This approach generated candidate gene sets for each of the 15 method–breed combinations and enabled the assessment of both breed-specific and recurrent candidate loci. After removing duplicated gene–method–breed combinations, a total of 2,960 non-redundant gene–method–breed records were obtained. These records corresponded to 2,385 unique candidate genes across the three methods and five goat breeds. Among the three methods, nSL identified the most unique candidate genes (1,329), followed by iHS (1,054) and iHH12 (577). At the breed level, Ankara goats had the highest number of unique candidate genes (684), followed by Damascus (646), Honamli (541), Kil

ARTICLE IN PRESS

(441), and Kilis (372). Candidate genes were detected by all three methods in each of the five breeds.

Method- and breed-specific distribution of candidate genes

The number of candidate genes differed among the method–breed combinations. In Ankara goats, iHH12 detected 277 genes, iHS 224, and nSL 288. In Damascus goats, iHH12 detected 124 genes, iHS detected 280 genes, and nSL detected 297 genes. In Honamli goats, iHH12 detected 81 genes, iHS 240, and nSL 283. In Kil goats, iHH12 detected 52 genes, iHS 206, and nSL 226. In Kilis goats, iHH12 detected 43 genes, iHS 104, and nSL 235.

Across the five breeds, nSL produced the largest candidate gene set in four breeds, whereas iHH12 produced the smallest candidate gene set in all breeds. The complete method–breed gene lists are provided in the Supplementary Table S1.

iHS-based selection signatures

The iHS analysis identified 1,054 unique candidate genes across the five native Anatolian goat breeds (Figure 3). The number of iHS candidate genes varied among breeds, with the highest in Damascus goats, followed by Honamli, Ankara, Kil, and Kilis. Rather than being restricted to a single functional class, iHS signals were distributed across genomic regions containing genes involved in several biologically relevant processes, including milk production, lipid metabolism, pigmentation, growth and body size, reproductive function, and immune response.

In Ankara goats, iHS signals were primarily represented by candidate regions containing genes involved in milk protein synthesis, pigmentation, cellular growth, and neural or prion-associated functions. In Damascus goats, the iHS candidate regions exhibited a broader functional profile, encompassing genes involved in cholesterol and lipid transport, fatty acid metabolism, coat color determination, reproductive regulation, and innate immune response. In Honamli, Kil, and Kilis goats, several iHS signals were located near genes previously associated with body size, skeletal growth, pigmentation, seasonal reproduction, glucose metabolism, and immune regulation. Representative candidate genes included loci such as LALBA and PAEP for lactation-related functions; LCORL and NCAPG for growth and body size; *KIT, MC1R, ASIP, TYR, TYRP1, DCT,* and *MITF* for pigmentation; and *MYD88, OAS1, STING1, CXCR1*, and *ICAM1* for immune-related processes.

The iHS results indicated that recent or ongoing incomplete sweep-like signals in these breeds were not limited to a single production or adaptation trait. Instead, they highlighted multiple functional categories that may reflect the combined effects of breed history, traditional management, coat-color differentiation, production-related selection, and local environmental adaptation. The complete breed-specific iHS candidate gene lists are provided in Supplementary Tables ST2–ST6 in the S2 file.

iHH12-based selection signatures

The iHH12 analysis identified 577 unique candidate genes across the five breeds (Figure 4). Compared with iHS and nSL, iHH12 yielded the smallest candidate gene set across all breeds, indicating a more restricted set of genomic regions with strong haplotype-homozygosity signals. The largest number of iHH12 candidate genes was detected in Ankara goats, whereas Kilis and Kil goats showed the fewest.

Functionally, iHH12 signals were mainly concentrated in genomic regions containing genes associated with pigmentation, epithelial and skin-related biology, immune and inflammatory response, metabolic regulation, reproduction, and muscle-related traits. Several candidate regions contained pigmentation-associated genes, including *KIT, MC1R, MITF, and MLANA*. Other iHH12 signals involved lipid oxidation and skin-related genes, including *ALOX12B, ALOXE3,*

ARTICLE IN PRESS

ALOX15, and *ALOX15B*. Immune-related signals were also observed, including genes involved in interferon response, innate immunity, and inflammatory signaling, such as *STING1, IL17C, IL17D, IL34, MX1, MX2, NCR1, CLEC7A,* and *NLRC4*. In addition, candidate regions included genes related to endocrine and reproductive function, such as *NR5A1, NR6A1, DMRT1, SHBG,* and *TAF4B,* as well as genes involved in glucose and lipid metabolism, including *SLC2A4, PPARG, UCP2, MTTP,* and *ACADVL*.

These results suggest that iHH12 highlighted a narrower but functionally coherent subset of candidate regions, particularly those related to coat-color variation, skin and epithelial functions, immune defense, metabolic regulation, and reproductive biology. The complete breed-specific iHH12 candidate gene lists are provided in Supplementary Tables ST7–ST11 in the S3 file.

nSL-based selection signatures

The nSL analysis identified 1,329 unique candidate genes across the five breeds, representing the largest candidate gene set among the three haplotype-based statistics (Figure 5). The number of nSL candidate genes was relatively high in all breeds, with Damascus, Ankara, Honamli, Kilis, and Kil goats all showing substantial numbers of candidate regions. This pattern indicates that nSL captured a broader set of haplotype-length-based selection signals than iHS and iHH12.

The nSL candidate regions included genes associated with growth and body size, milk production, lipid and energy metabolism, pigmentation, immune response, reproduction, and vascular development. Growth- and body-size-related signals included candidate regions containing *LCORL, NCAPG, PLAG1*, and *PDGFRA*. Milk- and lactation-related regions included LALBA and PAEP, whereas lipid- and energy-metabolism-related signals involved genes such as *ELOVL6, CIDEA, SCD, ACSL1, ANGPTL2, TBC1D1*, and *IDE*. Pigmentation-related candidate regions included *MC1R, MITF, KIT,* and *TYRP1*. Several nSL signals also involved genes related to immune and antiviral response, including *MYD88, OAS1, MAVS, STING1, IL12B, CD163, IL17C,* and *IL17D*. In addition, genes associated with reproductive and endocrine functions, such as *CYP11A1, BMPR1A, AMHR2, BRDT, SOHLH1, SPATA16,* and *MTNR1A*, were detected in different breeds. Candidate regions related to angiogenesis and vascular development, including *KDR, VEGFC, ANGPT2, FGF2, RSPO1,* and *RSPO2*, were also observed.

Overall, nSL detected the broadest spectrum of candidate regions and provided additional support for selection signals related to economically and adaptively important traits, including growth, lactation, pigmentation, reproduction, immunity, and environmental adaptation. The complete breed-specific nSL candidate gene lists are provided in Supplementary Tables ST12–ST16 in the S4 file.

Repeatability of candidate genes across methods and breeds

To evaluate the repeatability of candidate genes across analytical methods and breeds, each candidate gene was summarized by the number of methods in which it was detected, the number of breeds in which it was detected, and the number of method–breed combinations that supported the gene. Based on this framework, 1,911 genes were detected in only one method and one breed and were classified as method- and breed-specific signals. A further 198 genes were detected by at least two methods within a single breed. In addition, 193 genes were detected by at least two methods and at least two breeds. Finally, 83 genes were detected by all three methods and in at least two breeds. Accordingly, 276 genes were defined as core candidate genes because they were detected in at least two methods and at least two breeds. Within this core set, 83 genes were detected by all three methods and at least two breeds and were classified as strong core candidate genes. Among these 83 strong core genes, 23 were detected by all three methods and were

ARTICLE IN PRESS

repeated across the three breeds. These 23 genes were defined as robust core candidate genes. The 23 robust core candidate genes were *ACAP1, CBFA2T3, CLDN7, CTDNEP1, DVL2, ELP5, FANCA, GABARAP, LATS2, LRRTM2, PABPN1L, PER1, PHF23, RNF17, SATB1, SIL1, SNORA70, TMEM95, TTC28, VAMP2, XPO4, ZMYM2,* and *ZMYM5* (Figure 6). No candidate gene was detected across all three methods and all five breeds.

Breed-wise distribution of the 23 robust core candidate genes

The 23 robust core candidate genes were distributed across three of the five goat breeds. Ankara contained 21 of the 23 robust core candidate genes; Honamli contained 18; Kil contained 14; Damascus contained 9; and Kilis contained 8. The most frequent three-breed combination was Ankara–Honamli–Kil, which included 11 genes: *CLDN7, CTDNEP1, ELP5, GABARAP, LATS2, LRRTM2, PHF23, RNF17, SIL1, ZMYM2,* and *ZMYM5.* The Ankara–Honamli–Kilis combination included three genes: *ACAP1, DVL2,* and *XPO4*. The Ankara–Damascus–Honamli combination included two genes: *PER1* and *VAMP2*. The Ankara–Damascus–Kil combination included two genes: *CBFA2T3* and *PABPN1L*. The Ankara–Damascus–Kilis combination included two genes: *FANCA* and *SNORA70*. The Damascus–Honamli–Kilis combination included *SATB1*, the Damascus–Honamli–Kil combination included *TTC28*, and the Ankara–Kil–Kilis combination included *TMEM95*. The complete lists of core, strong core, and robust core candidate genes, along with their supporting methods, breeds, and method–breed combinations, are provided in Supplementary Table ST1 of the S1 file.

Enrichment analysis

Functional enrichment analysis was performed using candidate genes identified from the selection-signature analyses. To maintain consistency with the within-breed selection signature design, candidate genes were first summarized separately for each breed and each method. Non-redundant breed-specific candidate gene sets were then generated by merging the genes detected by iHS, iHH12, and nSL within each breed. These breed-specific gene sets were used for breed-specific enrichment analyses, while the overall non-redundant candidate gene set was used to summarize shared functional patterns across breeds (Figure 7).

For each enriched GO term and KEGG pathway, the term ID, description, gene ratio, background ratio, raw p-value, FDR-adjusted p-value, q-value, overlapping genes, gene count, Enrichment Score, and Fold Enrichment were reported in the Supplementary Tables. The Enrichment Score was consistently defined as −log10(raw p-value) and was used as a ranking and visualization metric. FDR-adjusted p-values were used to evaluate multiple-testing-corrected enrichment significance. Pathway enrichment analysis highlighted several functional categories among the candidate genes, including Endocytosis, Melanogenesis, Motor proteins, Phosphatidylinositol signaling system, Hippo signaling pathway, Glutamatergic synapse, GABAergic synapse, Calcium signaling pathway, Cholinergic synapse, and Regulation of actin cytoskeleton. The corresponding gene counts, raw p-values, FDR-adjusted p-values, q-values, Enrichment Scores, and Fold Enrichment values are provided in Supplementary Table ST17 in S5.

GO enrichment analysis across Biological Process, Cellular Component, and Molecular Function categories identified enriched terms related to pigment biosynthetic and metabolic processes, glycerolipid and glycerophospholipid biosynthetic processes, synaptic signaling, phospholipid binding, lipid transporter activity, membrane-associated cellular components, dendritic structures, and cell projection-related components.

A gene–pathway association network was constructed to visualize the relationships between candidate genes and enriched functional categories. Melanogenesis-related enrichment included

ARTICLE IN PRESS

pigmentation-associated genes such as *MC1R, MITF, KIT, TYR, TYRP1, ASIP,* and *DVL2*. Endocytosis and cytoskeletal regulation terms included genes related to vesicular trafficking and membrane remodeling, such as *DNM3, EPS15, EPN1, EPN3, VPS35, CHMP1A, CHMP5, ARPC2, ARPC5L, ARRB1, ARRB2,* and *CXCR1*. Synaptic pathway terms included genes such as *GRM1, HOMER1, GRIN3A, GABBR2,* and *GABARAP*. Phosphatidylinositol-related signaling terms included *PIK3CD, PIK3R6, INPP1, INPP4A, DGKA, DGKB, DGKD,* and *DGKE*. Hippo signaling included genes such as *STK3, LATS2, MOB1A,* and members of the *DLG* gene family. In contrast, motor protein enrichment included kinesin- and dynein-related genes, including *KIF* family genes, *DYNC2H1, DYNLL1, DYNLRB1*, and *DNAH* family genes.

Venn analysis of candidate genes across breeds

Venn analysis was performed to evaluate the distribution and overlap of candidate genes identified across the five native Turkish goat breeds. The total number of candidate genes detected in each breed was 684 for Ankara, 768 for Damascus, 712 for Honamli, 712 for Kil, and 701 for Kilis. The Venn diagram showed both breed-specific and shared candidate gene sets among the five breeds (Figure 8).

The highest breed-specific proportion was observed in Damascus goats, where 18% of candidate genes were unique to this breed. Ankara goats showed 17% breed-specific candidate genes, followed by Honamli at 15%, Kilis at 13%, and Kil at 13%. In addition to these breed-specific gene sets, several overlapping regions were detected among two or more breeds. The largest shared intersection among the five breeds represented 4% of the candidate genes, indicating a subset of common candidate genes detected across all breeds.

Pairwise and multi-breed overlaps were also observed among Ankara, Damascus, Honamli, Kil, and Kilis goats, with most shared intersections ranging between 1% and 2%. Several smaller intersections were close to 0%, indicating limited overlap for some breed combinations. Overall, the Venn analysis demonstrated that the candidate gene sets contained both breed-specific genes and recurrent genes shared among multiple breeds.

Discussion

PCA-based overview of genetic variation

PCA was used in this study as an exploratory approach to summarize the major axes of genome-wide genetic variation among the five native Turkish goat breeds. Patterson et al. (2006) described PCA/eigen analysis as a useful framework for visualizing genetic differentiation and major patterns of population structure in genome-wide marker data. In the present study, the PCA results provided a general overview of breed-associated genomic differentiation, with Ankara goats tending to form a separate cluster, particularly along PC2. In contrast, Damascus, Honamli, Kil, and Kilis goats showed broader overlap.

This PCA-based differentiation pattern is consistent with previous studies on Turkish goat genetic diversity. Ağaoğlu and Ertuğrul (2012) reported moderate genetic differentiation between Angora goats and other Turkish goat breeds based on microsatellite markers, supporting the distinct genetic position of the Angora/Ankara goat population. Similarly, Bulut *et al.* (2016) investigated eight domestic goat populations raised in Turkey, including Hair, Angora, Kilis, Honamli, and Shami goats. They reported measurable intra- and inter-population genetic diversity among Turkish goat breeds.

Breed-related interpretation of the main selection signals

The breed-related selection signals observed in the present study should be interpreted in relation to the known production background, ecological context, and management history of each goat population. Although selection signature analyses cannot, by themselves, demonstrate direct

ARTICLE IN PRESS

causal relationships between candidate genes and specific phenotypic traits, they may provide useful indications of genomic regions influenced by long-term breeding practices, local adaptation, demographic history, or a combination of these factors.

For Ankara goats, the detected signals can be considered in the context of the historical identity of the Angora lineage as a fiber-oriented breed originating from central Anatolia. Visser et al. (2016) emphasized both the Turkish origin of Angora goats and the genetic distinctiveness of Angora populations maintained under different regional breeding histories. In the present study, candidate genes such as *KIT, MC1R*, and *LIPH*, along with enrichment of melanogenesis-related pathways, are consistent with biological processes associated with pigmentation, follicular development, and skin-associated traits. Fontanesi et al. (2009) and Henkel et al. (2019) reported that variation in pigmentation-related genes, including *KIT, MC1R,* and *ASIP*, contributes to coat-color differentiation in goats, while *LIPH* has been associated with hair follicle development and hair shaft phenotypes in mammals. Therefore, the Ankara-related signals may reflect genomic components associated with fleece color, follicular biology, and integumentary function, which are relevant to the historical selection of this breed for mohair production.

The Ankara results also included metabolic and developmental candidate genes, including *ELOVL6, CIDEA, ENPP1, FOXC2, FGF2,* and *KDR*. These genes should not be interpreted as direct fiber-determining genes; rather, they may indicate broader physiological processes related to lipid metabolism, tissue maintenance, vascular development, and cellular regulation. Matsuzaka and Shimano (2009) described *ELOVL6* as an important regulator of long-chain fatty-acid metabolism, and studies in caprine tissues have suggested its involvement in lipid synthesis. Such biological functions may be relevant in animals maintained under both productive and environmental pressures, particularly in a breed characterized by continuous coat growth. Thus, the Ankara profile may reflect a combination of fiber-associated biology, metabolic regulation, and breed-specific historical differentiation rather than a single major selective event.

Damascus goats showed a distinct candidate-gene pattern, which can be interpreted in light of this breed's dairy-oriented background in the Near East. Raoof et al. (2017) reported favorable milk production and litter-size performance in Shami goats, while Yakan et al. (2021) documented transcriptional regulation of fatty-acid synthesis, oxidative stress, and inflammatory pathways during the transition from colostrum to milk in Damascus goats. In this context, signals involving *LALBA, PAEP, ABCG1, ABCG5, APOB, SREBF2,* and *ELOVL3* are consistent with biological processes associated with mammary secretion, lipid handling, and milk composition. Wu et al. (2008) also reported that goat *ABCG2* is associated with lactation-stage expression and secretion-related mammary biology. These findings suggest that part of the Damascus genomic profile may be related to dairy function. However, further phenotypic and functional validation would be required to confirm direct effects on milk traits.

The Damascus profile also included genes associated with reproductive biology and innate immune responses, including *NR5A1, NR6A1, LHCGR, AMHR2, BRDT, SOHLH1, SPATA16, MYD88, OAS1, MAVS, MX1,* and *MX2*. This pattern may indicate that reproductive capacity and immune-related mechanisms have contributed to the genomic differentiation of this breed. Deguine and Barton (2014) described *MYD88* as a central adaptor in innate inflammatory signaling, while Motwani et al. (2019) summarized the cGAS–STING pathway as an important component of nucleic-acid sensing and antiviral defense. In goats, Jain et al. (2023) reported the expression dynamics of OAS1 in the endometrium, suggesting that some immune-related genes may also be relevant to reproductive tissues. Therefore, the Damascus signals may reflect a

ARTICLE IN PRESS

combination of productivity, reproductive physiology, and host-defense mechanisms, rather than a set of unrelated single-gene findings.

For Honamli goats, the observed signals can be discussed in relation to the relatively large body size and meat-type characteristics reported for this breed. Turkish field studies have described Honamli goats as large-framed animals with favorable growth and carcass-related performance compared with several other indigenous breeds. Within this framework, the detection of candidate regions involving LCO

Recurrent core candidates and shared biological modules

In the present study, selection signatures were investigated using three complementary haplotype-based statistics, namely iHS, iHH12, and nSL, across five goat breeds. By integrating the results across methods and breed comparisons, we identified a robust panel of 23 recurrent core candidate genes: *ACAP1, CBFA2T3, CLDN7, CTDNEP1, DVL2, ELP5, FANCA, GABARAP, LATS2, LRRTM2, PABPN1L, PER1, PHF23, RNF17, SATB1, SIL1, SNORA70, TMEM95, TTC28, VAMP2, XPO4, ZMYM2,* and *ZMYM5*. These genes were classified as recurrent core candidates because their signals were repeatedly detected across the comparative framework, rather than being restricted to isolated method-specific findings. Thus, this gene set represents a more conservative and reproducible subset of candidate loci, providing a basis for distinguishing robust selection signals from sporadic or potentially method-dependent signals.

This recurrent core set warrants particular attention because it directly addresses the reliability of selection signatures detected across multiple analytical contexts. Notably, several of the 23 robust genes are not conventional headline livestock candidate genes, yet their recurrence across methods and/or breed combinations suggests that they may be involved in fundamental biological mechanisms underlying population differentiation and adaptive variation. For instance, Nielsen et al. (2019) described *DVL2* as an important component of WNT pathway specification, whereas Park et al. (2016) and Luo and Li (2022) emphasized the role of *LATS2* as a key regulator of Hippo signaling and growth control. Similarly, Li et al. (2007) reported that *ACAP1* contributes to endocytic recycling through a clathrin-associated complex, while Pausch et al. (2014) demonstrated the essential role of *TMEM95* in normal male fertility in cattle. Collectively, these recurrent loci suggest that the most repeatable selection signals in the present study are associated with a shared biological framework involving membrane trafficking, developmental signaling, cell proliferation, and reproductive competence.

Importantly, these findings indicate that the recurrent signals are not limited to genes directly associated with visible production or morphological traits. Instead, many of the core candidates appear to regulate upstream cellular and developmental processes from which breed-specific phenotypic differences may ultimately emerge. This interpretation also provides a plausible explanation for why the robust core genes were concentrated in particular three-breed combinations rather than being universally shared across all five breeds. Recurrent signals may reflect partially convergent selection on common physiological pathways; however, the specific demographic histories, breeding objectives, environmental pressures, and ecological conditions of each population likely determined whether these pathways generated sufficiently strong sweep-like patterns to be detected.

The inclusion of *PER1* among the recurrent core candidates further supports this interpretation. Pan et al. (2020) highlighted the importance of PER-family circadian genes in reproductive physiology, and previous goat studies involving *MTNR1A* have similarly emphasized the relevance of photoperiodic and seasonal regulation in caprine reproduction. Therefore, the recurrent detection of *PER1* across multiple breeds is biologically plausible, particularly in

ARTICLE IN PRESS

native goat populations maintained under extensive or semi-extensive management systems, where reproductive seasonality, forage availability, and climatic rhythms are closely interconnected, rather than indicating a single universal seasonality gene shared by all breeds, the present results suggest parallel or partially shared tuning of circadian and seasonal regulatory mechanisms in multiple, but not all, Anatolian goat populations.

Functional enrichment and the broader meaning of the pathway-level results

Functional enrichment analysis provides a broader biological context for interpreting the candidate genes identified in the selection signature analyses. Rather than pointing to a single narrow production trait, the main KEGG-enriched pathways, including Melanogenesis, Endocytosis, Motor proteins, Hippo signaling, Phosphatidylinositol signaling, Calcium signaling, and cytoskeletal regulation, suggest the involvement of several interconnected biological processes. These pathways are related to pigmentation control, intracellular trafficking, tissue development, receptor-mediated signaling, membrane dynamics, and cellular organization. Therefore, the enrichment results appear to reflect a complex biological background in which multiple physiological systems may have contributed to breed differentiation and local adaptation.

The enrichment of the melanogenesis pathway is particularly consistent with the repeated identification of pigmentation-related candidate genes across several breeds. In goats and other mammals, coat-color variation is often influenced by genes that function within broader developmental and regulatory networks rather than by isolated pigmentation loci alone.

Coat-color variation in goats has been associated with regulatory mechanisms involving *MC1R, KIT,* and *ASIP*, suggesting that pigmentation-related loci may operate within broader developmental and regulatory networks rather than as isolated genes (Fontanesi *et al.* 2009; Henkel *et al.* 2019; Guo et al. 2022). In this context, the enrichment of the melanogenesis pathway provides pathway-level support for the pigmentation-related signals observed in the present study. However, this result should be interpreted as evidence of biological consistency among candidate genes, rather than as definitive proof of direct selection on coat color across all breeds.

The enrichment of endocytosis and actin-cytoskeleton-related pathways is also biologically plausible, although these results require a cautious interpretation. Kozlov and Taraska (2023) emphasized that membrane curvature, vesicle formation, receptor recycling, and intracellular trafficking are fundamental processes in cellular function. Similarly, Li *et al.* (2007) showed that ACAP1-dependent endocytic recycling contributes to integrin transport and glucose homeostasis. In the present dataset, genes such as *ACAP1, ARRB1, ARRB2, EPS15, EPN1, EPN3,* and *VPS35* may reflect biological processes related to cellular transport, epithelial maintenance, immune signaling, pigmentation, growth, and metabolic regulation. These pathways are not specific to one phenotype, but they may contribute to several higher-order traits through their roles in cell communication, membrane remodeling, and tissue-level homeostasis.

In livestock populations maintained under long-term natural and artificial selection, pathway-level signals may sometimes provide a more informative perspective than individual candidate genes alone. This is because selection may act not only on single large-effect loci, but also on groups of genes involved in shared biological functions. From this perspective, the enrichment of endocytic, cytoskeletal, and membrane-associated pathways may suggest coordinated changes in cellular systems that support adaptation, productivity, and physiological resilience. Nevertheless, such interpretations remain inferential and should be supported by additional functional, transcriptomic, or phenotypic evidence.

ARTICLE IN PRESS

The enrichment of Hippo signaling and phosphatidylinositol-related pathways also fits the overall candidate-gene profile. Luo and Li (2022) and Nita and Moroishi (2024) described Hippo signaling as an important regulator of growth, regeneration, and tissue homeostasis. Therefore, the identification of genes such as *LATS2, STK3*, and DVL-related components is consistent with the presence of pathways involved in cellular growth control and developmental regulation. Similarly, phosphatidylinositol signaling is closely associated with membrane dynamics, metabolism, intracellular signaling, and responses to growth factors. Its enrichment is therefore consistent with a gene set that includes loci associated with growth, lactation, immune response, and adaptation.

The enrichment of calcium signaling, motor proteins, and synaptic-related categories should also be interpreted within a broad biological framework. Although these pathways are often associated with nervous-system functions, many of their genes have pleiotropic roles in neuroendocrine regulation, intracellular transport, secretion, membrane trafficking, and cell-to-cell communication. Therefore, their presence in the enrichment results does not necessarily indicate selection on neurological traits. More cautiously, these pathways may reflect general cellular and physiological mechanisms that contribute to reproduction, metabolism, immune regulation, and tissue maintenance.

The pathway-level findings suggest that the selection signals identified in this study are distributed across several biological modules rather than being concentrated in a single trait-specific pathway. The enriched pathways collectively point to processes associated with pigmentation, membrane trafficking, cytoskeletal organization, growth regulation, intracellular signaling, metabolism, reproduction, immunity, and tissue homeostasis. These results are consistent with the view that selection signatures in local goat breeds may reflect a polyfunctional adaptive background shaped by both production-related and environmental pressures. However, the functional enrichment results should be considered hypothesis-generating, and further validation using expression data, functional assays, and detailed phenotypic records would be necessary to clarify the biological contribution of these pathways in Ankara, Damascus, Honamli, Kil, and Kilis goats.

Study limitations and future perspectives

The findings of the present study should be interpreted in light of several limitations. Although the GoatSNP50 array provides useful genome-wide coverage for haplotype-based selection scans, medium-density SNP arrays have limited power to detect rare variants, narrow selection signals, causal mutations, and structural variants. Therefore, the genomic regions identified here should be considered candidate selection intervals rather than definitive causal loci. In addition, haplotype-based methods such as iHS, iHH12, and nSL detect genomic patterns consistent with recent or ongoing selection. Still, they do not directly reveal the biological mechanisms underlying phenotypic variation. For this reason, candidate genes detected by only one method or in a single breed should be interpreted cautiously and regarded as hypothesis-generating.

Despite these limitations, this study provides a useful genome-wide framework for understanding selection signatures in five native Anatolian goat breeds. The integration of breed-specific scans, multi-method, repeatability-based prioritization, and functional enrichment analysis enabled the organization of candidate signals into a biologically meaningful hierarchy. The results suggest that these breeds have been shaped by both breed-specific and shared selection pressures related to pigmentation, growth, reproduction, dairy function, immunity, cellular signaling, and environmental adaptation.

ARTICLE IN PRESS

Future studies should validate these candidate regions using higher-resolution genomic approaches, particularly whole-genome sequencing, together with detailed phenotypic records, transcriptomic data, environmental information, and functional analyses. Such integrated approaches will help clarify whether the detected signals are directly associated with production traits, local adaptation, or broader demographic and evolutionary processes. Overall, the present findings provide a foundation for future research on conservation genetics, local adaptation, and sustainable breeding strategies in native Anatolian goat populations.

Conclusion

This study contributes to the genomic characterization of native Anatolian goat breeds and provides a prioritized set of candidate genes and biological pathways for future investigation. The findings may serve as a useful resource for studies on local adaptation, conservation genetics, and the sustainable genetic management of indigenous goat populations. However, the candidate genes and enriched pathways identified here should be interpreted as putative signals of selection, and further validation using independent populations, detailed phenotypic records, transcriptomic data, and functional analyses will be necessary to clarify their biological roles.

Author contributions

M. Bayraktar: Conceptualization, methodology, formal analysis, validation, visualization, writing—original draft, and writing—review and editing. Ö. Şahin and İ. Aytekin: Data curation and investigation. All authors read and approved the final manuscript.

Funding Declaration

No organization or institution supported this study, and the authors received no financial grants or funding to conduct this research.

Competing interests

The authors declare no competing interests.

Data availability

All relevant data have been stated in the manuscript. SNP genotype data generated in the study is available in the Supplementary Information file.

References

1. Ağaoğlu Ö.K. & Ertuğrul O. (2012) Assessment of genetic diversity, genetic relationship and bottleneck using microsatellites in some native Turkish goat breeds. Small Ruminant Research 105, 53-60.
2. Brito L.F., Kijas J.W., Ventura R.V., Sargolzaei M., Porto-Neto L.R., Cánovas A., Feng Z., Jafarikia M. & Schenkel F.S. (2017) Genetic diversity and signatures of selection in various goat breeds revealed by genome-wide SNP markers. BMC genomics 18, 229.
3. Bulut Z., Kurar E., Ozsensoy Y., Altunok V. & Nizamlioglu M. (2016) Genetic diversity of eight domestic goat populations raised in Turkey. BioMed Research International 2016, 2830394.
4. Chen Y., Li R., Sun J., Li C., Xiao H. & Chen S. (2022) Genome-wide population structure and selection signatures of yunling goat based on RAD-seq. Animals 12, 2401.
5. Daly K.G., Maisano Delser P., Mullin V.E., Scheu A., Mattiangeli V., Teasdale M.D., Hare A.J., Burger J., Verdugo M.P. & Collins M.J. (2018) Ancient goat genomes reveal mosaic domestication in the Fertile Crescent. Science 361, 85-8.
6. Deguine J. & Barton G.M. (2014) MyD88: a central player in innate immune signaling. F1000prime reports 6, 97.
7. Fontanesi L., Beretti F., Riggio V., Dall'Olio S., González E.G., Finocchiaro R., Davoli R., Russo V. & Portolano B. (2009) Missense and nonsense mutations in melanocortin 1 receptor (MC1R) gene of different goat breeds: association with red and black coat colour phenotypes but with unexpected evidences. BMC genetics 10, 47.

ARTICLE IN PRESS

8. Garud N.R., Messer P.W., Buzbas E.O. & Petrov D.A. (2015) Recent selective sweeps in North American Drosophila melanogaster show signatures of soft sweeps. PLoS genetics 11, e1005004.
9. Gebreselase H.B., Nigussie H., Wang C. & Luo C. (2024) Genetic diversity, population structure and selection signature in begait goats revealed by whole-genome sequencing. Animals 14, 307.
10. Guo J., Sun X., Mao A., Liu H., Zhan S., Li L., Zhong T., Wang L., Cao J. & Liu G.E. (2022) A 13.42-kb tandem duplication at the ASIP locus is strongly associated with the depigmentation phenotype of non-classic Swiss markings in goats. BMC genomics 23, 437.
11. Henkel J., Saif R., Jagannathan V., Schmocker C., Zeindler F., Bangerter E., Herren U., Posantzis D., Bulut Z. & Ammann P. (2019) Selection signatures in goats reveal copy number variants underlying breed-defining coat color phenotypes. PLoS genetics 15, e1008536.
12. Jain A., Jain T., Mishra G.K., Chandrakar K., Mukherjee K. & Tiwari S.P. (2023) Molecular characterization, putative structure and function, and expression profile of OAS1 gene in the endometrium of goats (Capra hircus). Reproductive Biology 23, 100760.
13. Kanehisa M. & Goto S. (2000) KEGG: kyoto encyclopedia of genes and genomes. Nucleic acids research 28, 27-30.
14. Kanehisa M., Sato Y., Kawashima M., Furumichi M. & Tanabe M. (2016) KEGG as a reference resource for gene and protein annotation. Nucleic acids research 44, D457-D62.
15. Karsli T., Demir E., Fidan H.G., Aslan M., Karsli B.A., Arik I.Z., Semerci E.S., Karabag K. & Balcioglu M.S. (2020) Determination of genetic variability, population structure and genetic differentiation of indigenous Turkish goat breeds based on SSR loci. Small Ruminant Research 190, 106147.
16. Kozlov M.M. & Taraska J.W. (2023) Generation of nanoscopic membrane curvature for membrane trafficking. Nature reviews Molecular cell biology 24, 63-78.
17. Li J., Peters P.J., Bai M., Dai J., Bos E., Kirchhausen T., Kandror K.V. & Hsu V.W. (2007) An ACAP1-containing clathrin coat complex for endocytic recycling. The Journal of cell biology 178, 453-64.
18. Luo J. & Li P. (2022) Context-dependent transcriptional regulations of YAP/TAZ in stem cell and differentiation. Stem Cell Research & Therapy 13, 10.
19. Matsuzaka T. & Shimano H. (2009) Elovl6: a new player in fatty acid metabolism and insulin sensitivity. Journal of molecular medicine 87, 379-84.
20. Motwani M., Pesiridis S. & Fitzgerald K.A. (2019) DNA sensing by the cGAS–STING pathway in health and disease. Nature Reviews Genetics 20, 657-74.
21. Naderi S., Rezaei H.-R., Pompanon F., Blum M.G., Negrini R., Naghash H.-R., Balkız Ö., Mashkour M., Gaggiotti O.E. & Ajmone-Marsan P. (2008) The goat domestication process inferred from large-scale mitochondrial DNA analysis of wild and domestic individuals. Proceedings of the National Academy of Sciences 105, 17659-64.
22. Nielsen C.P., Jernigan K.K., Diggins N.L., Webb D.J. & MacGurn J.A. (2019) USP9X deubiquitylates DVL2 to regulate WNT pathway specification. Cell reports 28, 1074-89. e5.
23. Nita A. & Moroishi T. (2024) Hippo pathway in cell–cell communication: emerging roles in development and regeneration. Inflammation and Regeneration 44, 18.
24. Onzima R.B., Upadhyay M.R., Doekes H.P., Brito L.F., Bosse M., Kanis E., Groenen M.A. & Crooijmans R.P. (2018) Genome-wide characterization of selection signatures and runs of homozygosity in Ugandan goat breeds. Frontiers in genetics 9, 318.
25. Pan X., Taylor M.J., Cohen E., Hanna N. & Mota S. (2020) Circadian clock, time-restricted feeding and reproduction. International Journal of Molecular Sciences 21, 831.
26. Park G.-S., Oh H., Kim M., Kim T., Johnson R.L., Irvine K.D. & Lim D.-S. (2016) An evolutionarily conserved negative feedback mechanism in the Hippo pathway reflects functional difference between LATS1 and LATS2. Oncotarget 7, 24063.
27. Patterson N., Price A.L. & Reich D. (2006) Population structure and eigenanalysis. PLoS genetics 2, e190.

ARTICLE IN PRESS

28. Pausch H., Kölle S., Wurmser C., Schwarzenbacher H., Emmerling R., Jansen S., Trottmann M., Fuerst C., Götz K.-U. & Fries R. (2014) A nonsense mutation in TMEM95 encoding a nondescript transmembrane protein causes idiopathic male subfertility in cattle. PLoS genetics 10, e1004044.
29. Raoof S.O., Mahmud K.I. & Mohamad Y.A.S. (2017) Effect of frequent kidding on reproductive and productive traits in Shami goats: Salim Omar Raoof1; Kanyaw Ismail Mahmud1 and Younis Ahmad Sheakh Mohamad2. The Iraqi Journal of Veterinary Medicine 41, 157-62.
30. Sabeti P.C., Varilly P., Fry B., Lohmueller J., Hostetter E., Cotsapas C., Xie X., Byrne E.H., McCarroll S.A. & Gaudet R. (2007) Genome-wide detection and characterization of positive selection in human populations. Nature 449, 913-8.
31. Szpiech Z.A. & Hernandez R.D. (2014) selscan: an efficient multithreaded program to perform EHH-based scans for positive selection. Molecular biology and evolution 31, 2824-7.
32. Visser C., Lashmar S.F., Van Marle-Köster E., Poli M.A. & Allain D. (2016) Genetic diversity and population structure in South African, French and Argentinian Angora goats from genome-wide SNP data. Plos one 11, e0154353.
33. Voight B.F., Kudaravalli S., Wen X. & Pritchard J.K. (2006) A map of recent positive selection in the human genome. PLoS biology 4, e72.
34. Wu H.J., Luo J., Wu N., Matand K., Zhang L.J., Han X.F. & Yang B.J. (2008) Cloning, sequence and functional analysis of goat ATP-binding cassette transporter G2 (ABCG2). Molecular biotechnology 39, 21-7.
35. Yakan A., Özkan H., Çamdeviren B., Kaya U., Karaaslan I. & Dalkiran S. (2021) Expression patterns of major genes in fatty acid synthesis, inflammation, oxidative stress pathways from colostrum to milk in Damascus goats. Scientific Reports 11, 9448.
36. Yilmaz O., Kor A., Ertugrul M. & Wilson R.T. (2012) The domestic livestock resources of Turkey: goat breeds and types and their conservation status. Animal Genetic Resources/Resources génétiques animales/Recursos genéticos animales 51, 105-16.

ARTICLE IN PRESS

ARTICLE IN PRESS



Figure 1. Sampling regions of the native Turkish goat breeds used in this study. This figure was prepared by the authors using Microsoft PowerPoint for Microsoft 365

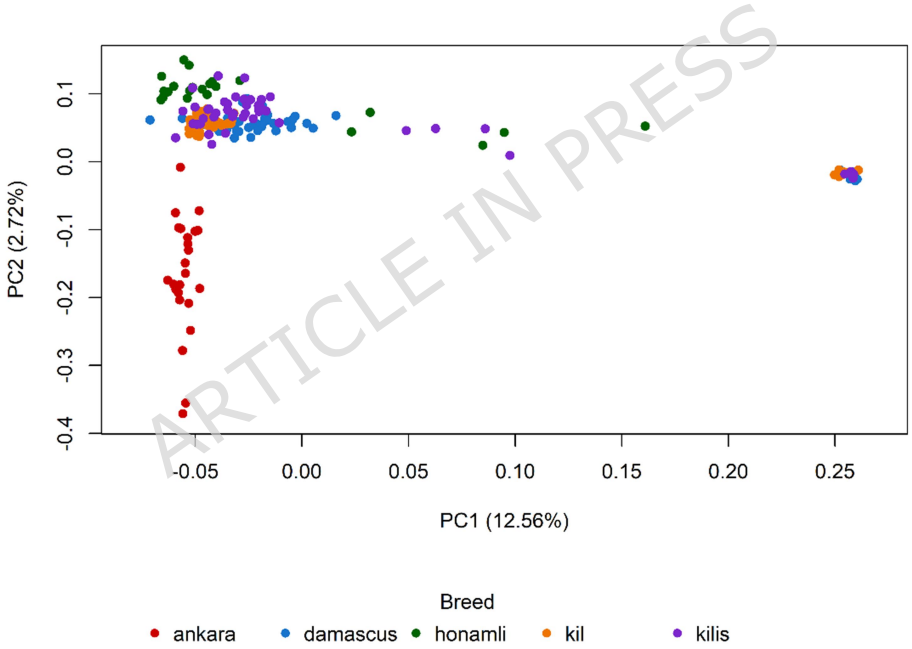


Figure 2. PCA plot showing the distribution of individuals from the native Turkish goat breeds

ARTICLE IN PRESS

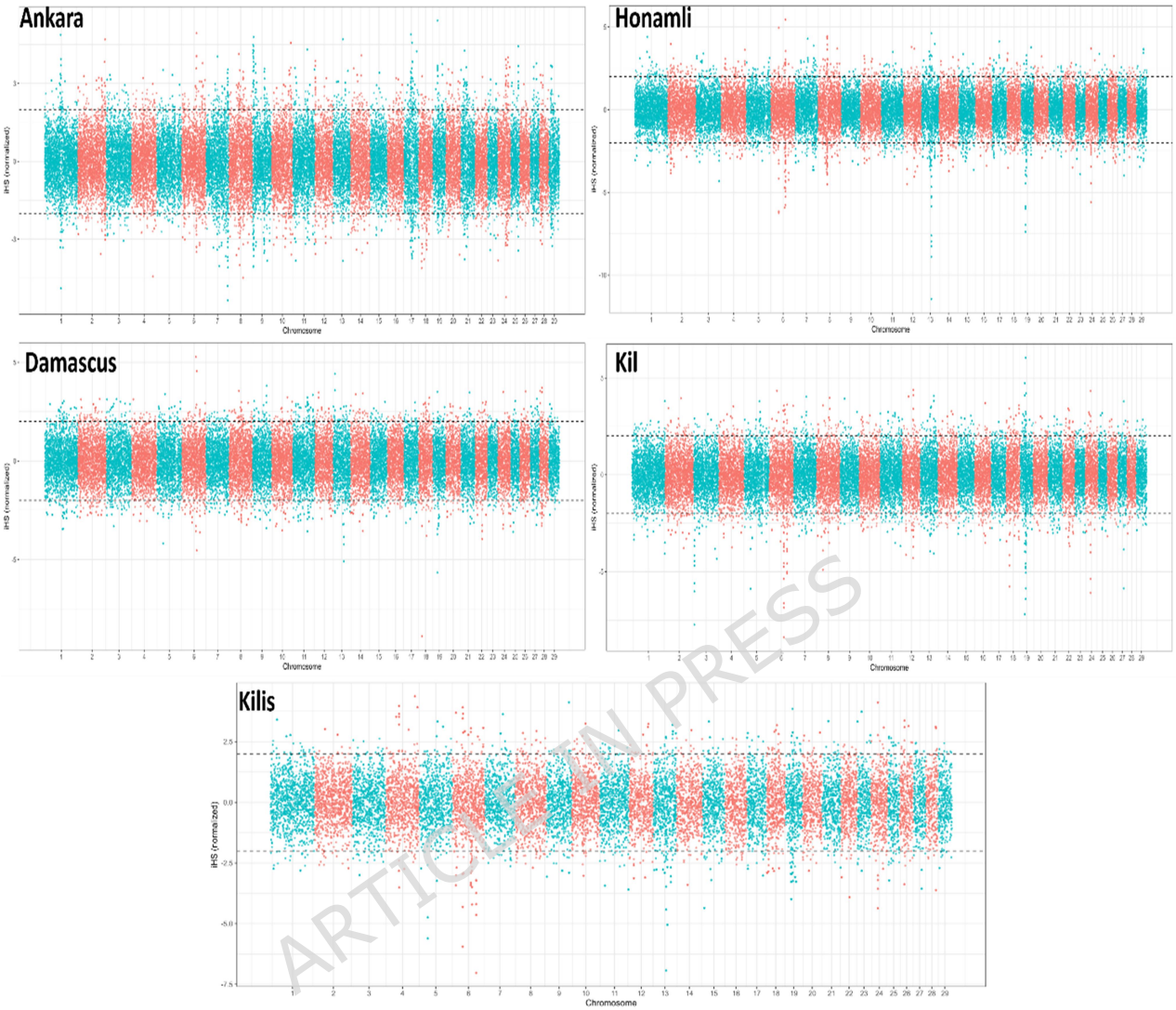


Figure 3. Genome-wide iHS-based selection signatures in five native Turkish goat breeds

ARTICLE IN PRESS

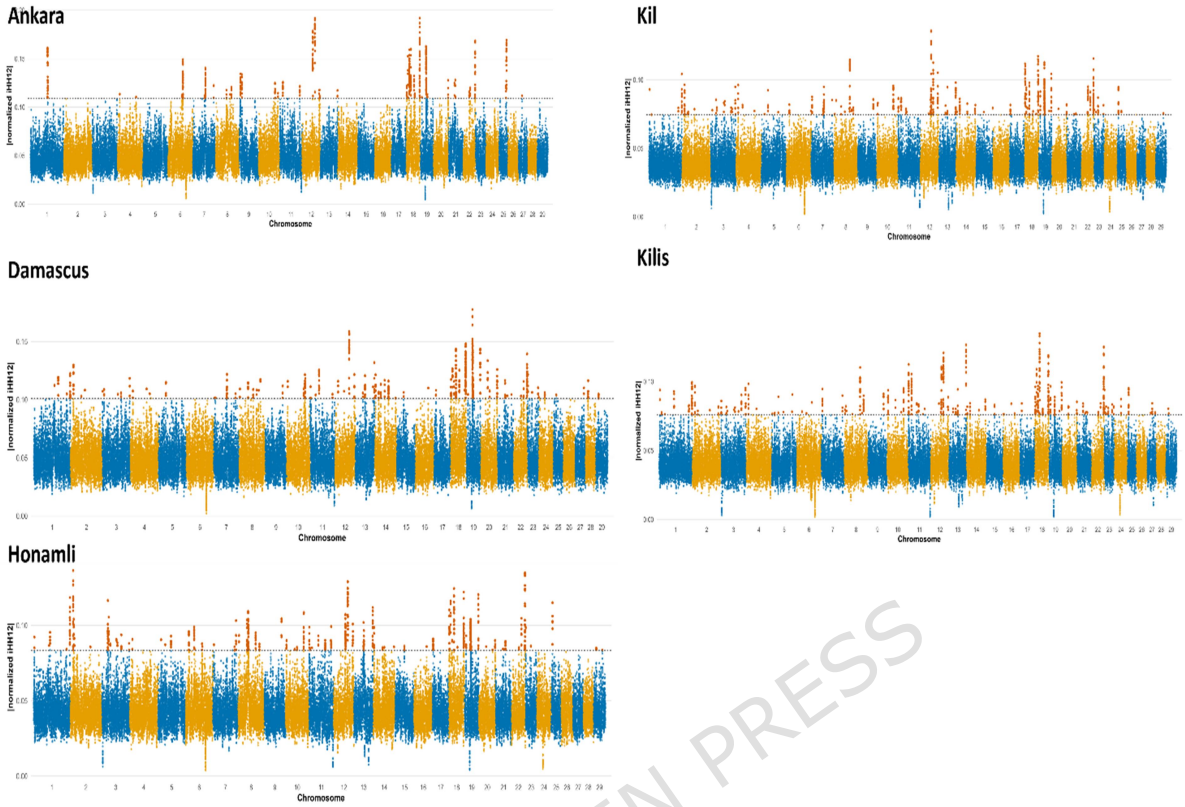


Figure 4. Genome-wide distribution of iHH12-based selection signatures across five native Turkish goat breeds

ARTICLE IN PRESS

ARTICLE IN PRESS

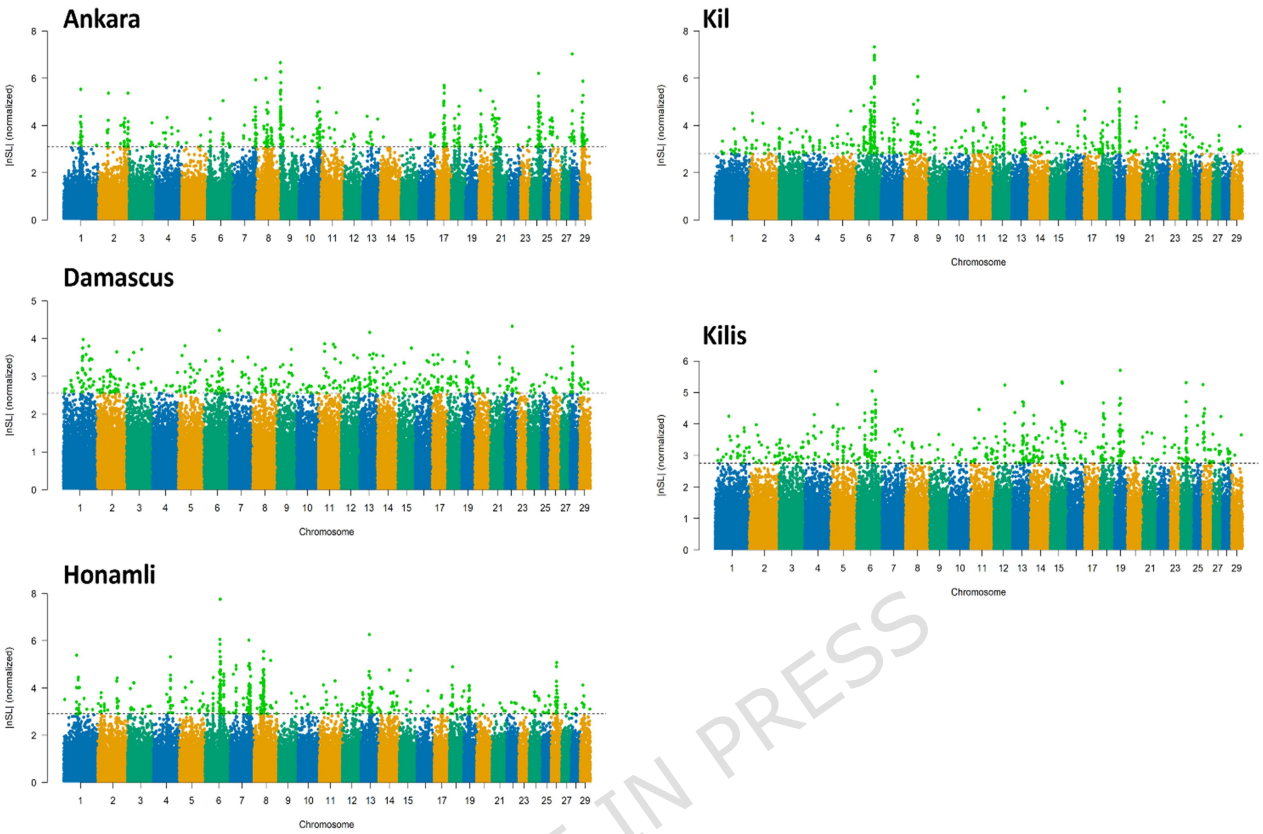


Figure 5. Genome-wide distribution of nSL-based selection signatures across five native Turkish goat breeds

ARTICLE IN PRESS

ARTICLE IN PRESS

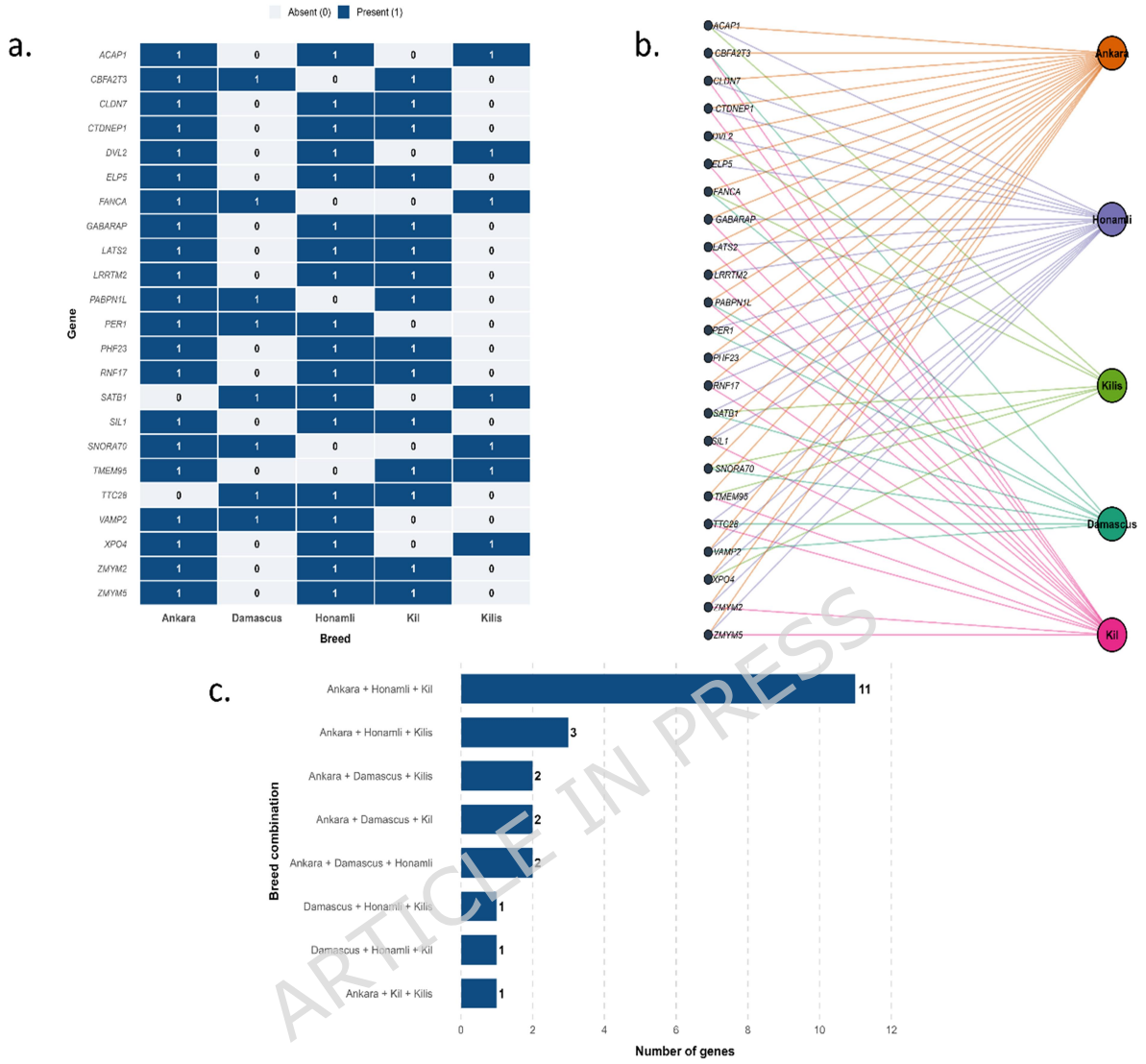


Figure 6. a. Breed-wise distribution of 23 robust core candidate genes, b. Network of robust core candidate genes and goat breeds, c. Distribution of three-breed combinations among robust core genes

ARTICLE IN PRESS

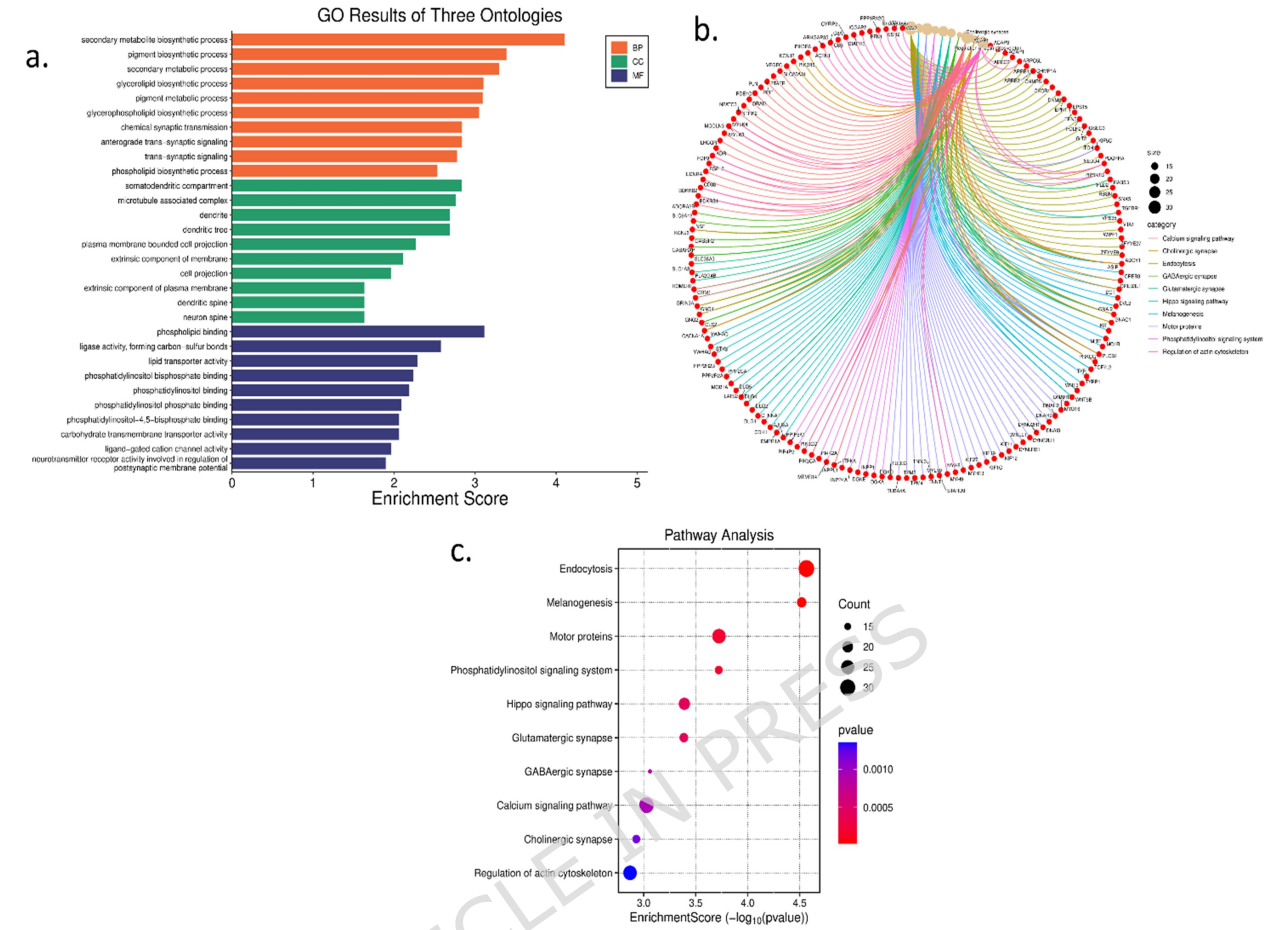


Figure 7. Functional enrichment analysis of candidate genes identified from selection signature analyses, a. Gene Ontology (GO) categories, b. a gene–pathway interaction network, and c. pathway enrichment results

ARTICLE IN PRESS

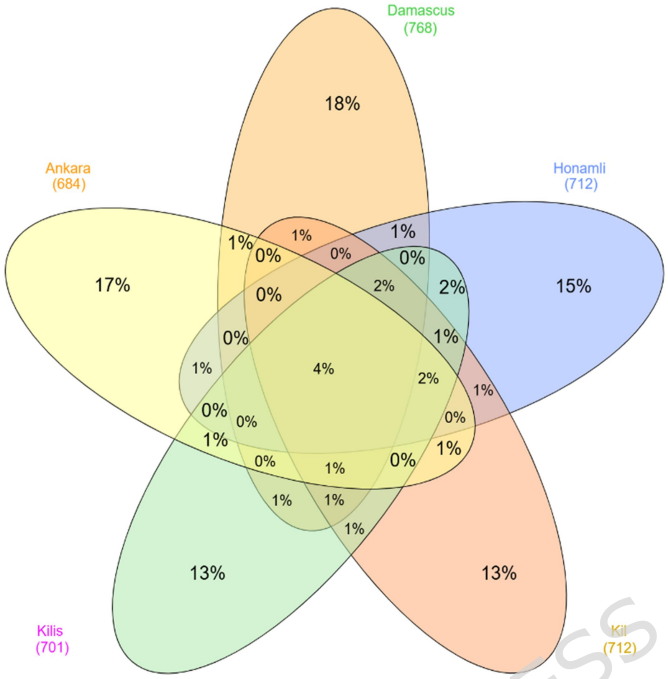


Figure 8. Venn diagram showing the overlap of candidate genes among the five native Turkish goat breeds

ARTICLE IN PRESS