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Unveiling the Genomic Signatures for Tropical Adaptation in Kangayam Cattle by De-correlated Composite of Multiple Selection Signals

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ABSTRACT

Background: This study aimed to identify genomic regions under selection in Kangayam cattle of Tamil Nadu using a de-correlated composite of multiple signals (DCMS) framework.

Methods: BovineHD SNP array data were retrieved from the WIDDE repository and the ICAR Krishi-Kosh portal. After quality control, autosomal SNPs were used for subsequent analyses. Fixation index, integrated haplotype score, modified haplotype homozygosity, Tajima's D and nucleotide diversity, were calculated and integrated using the DCMS approach. Genomic windows with false discovery rate (FDR) adjusted q<0.001 scores were considered for subsequent analysis. Functional annotation, QTL enrichment, protein-protein interaction (PPI) network analysis and hub gene identification were performed to interpret biological relevance.

Result: Genomic regions identified after DCMS analysis, harbored genes related to muscle development, metabolism, immunity, thermotolerance, reproduction and milk composition, including *MSTN*, *BMP7*, *PRKAG3*, *BoLA-DRB3*, *IL8R*, *ABCA1* and members of the *SLCO* gene family. PPI and hub gene analyses highlighted transport and metabolic pathways, with *SLC22A7* and *ABCC9* emerging as key nodes. This study presents the first DCMS-based selection signature map for Kangayam cattle, uncovering coordinated selection across interconnected biological pathways.

Key words: DCMS, Gene, Indigenous, Selection signatures, Thermotolerance.

INTRODUCTION

India has the world's largest livestock population, contributing about 31% to agricultural Gross Value Added (GVA) and 5.5% to the national GVA (BAHS, 2025). Besides its economic importance, livestock enhances resilience to climate variability and supports rural and tribal livelihoods (Khan *et al.,* 2025b; Sharma *et al.,* 2021a). Cattle constitute the largest livestock population with 193.46 million animals, placing India first globally. However, indigenous cattle populations have declined by 6%, highlighting the need for their conservation. Indigenous breeds are valued for their adaptation to local environments, cultural significance and economic importance (Vyas *et al.,* 2026; Sharma *et al.,* 2021b). Tamil Nadu, with ≈9.5 million cattle, is home to four indigenous breeds: Kangayam, Pullikulam, Umblacherry and Bargur. Among these, Kangayam, a Mysore-type breed native to the semi-arid region of western Tamil Nadu, is renowned for its draught ability and cultural significance (Fig 1). Developed by the Pattogar of Palayakottai, it is widely used for heavy transport and cultural events such as Jallikattu. The breed is characterized by a colour transition from red calves to grey adults, average body weights of 540 kg in bulls and 380 kg in cows and distinct morphological features (AGRI-IS). Despite its importance, the genetic basis of its adaptation remains poorly understood.

Advances in next-generation sequencing and high-density SNP arrays have enabled the identification of genomic regions under selection (Khan *et al.,* 2025a). Commonly used methods, including F_{ST}, iHS and XP-EHH, detect different aspects of selection (Voight *et al.,* 2006), whereas composite approaches such as the de-correlated composite of multiple selection signals (DCMS) integrate multiple statistics to improve detection power (Grossman *et al.,* 2010). By accounting for covariance among individual statistics, DCMS further enhances the accuracy of selection signature detection (Ma *et al.,* 2015). Although widely applied in taurine cattle, DCMS-based studies in Indian zebu breeds remain limited to Sahiwal and Belahi (Illa *et al.,* 2021; Muansangi *et al.,* 2025; Chavan *et al.,* 2025).

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In contrast, DCMS-based genomic studies in indigenous draught breeds from peninsular South India are scarce. Kangayam has historically been selected for strength, speed, trotting endurance and adaptation to hot semi-arid environments (Manomohan *et al.,* 2021). However, agricultural mechanization, increasing maintenance costs and extensive crossbreeding with exotic taurine breeds have reduced the population and economic importance of indigenous draught cattle (Vani *et al*., 2022). Although conservation and selective breeding programmes have been initiated, the genomic basis of tropical adaptation in this breed remains poorly understood. Therefore, the present study aimed to identify genomic signatures associated with tropical adaptation in Kangayam cattle using DCMS approach.

MATERIALS AND METHODS

Data retrieval and quality control (QC)

A total of 192 cattle genotyped with the BovineHD-BeadChip (777,962 SNPs) were analyzed. Kangayam (n=16), Gir (n=15), Sahiwal (n=13), Tharparkar (n=17) and Ongole (n=17) genotypes were obtained from ICAR-Krishi Kosh portal (Dixit *et al.,* 2020), whereas brown-swiss (n=22), holstein (n=54) and jersey (n=38) were retrieved from WIDDE repository (Sempéré *et al*., 2015). All analyses were performed at AGR Lab-II, ICAR-NBAGR, Karnal, from January to April 2026. The Kangayam cattle sample size was consistent with FAO guidelines (Lenstra, 2023), which state that approximately 15 animals per population are sufficient for detecting selection signatures when high-density SNP genotypes (*i.e*., >1 SNP per kb) are available. QC was performed using PLINK v1.9 (Purcell *et al*., 2007). Non-autosomal markers were excluded and SNPs with a call rate (CR≤95%), minor allele frequency (MAF≤0.05), Hardy-Weinberg equilibrium (HWE p≤0.001) and missing genotypes more than 10% were removed. The filtered genotypes were subsequently phased using SHAPEIT v2.17 for downstream analyses (Delaneau *et al.,* 2012).

Inter-and intra-population selection signature analysis

Population level selection signatures were investigated using inter-population and intra-population approaches. To enable a Kangayam-versus-all comparison for identifying breed-specific selection signatures in Kangayam cattle, genetic differentiation between Kangayam and the pooled reference population comprising Gir, Sahiwal, Tharparkar, Ongole, Holstein, Jersey and Brown-Swiss was estimated as fixation index (F_{ST}) per SNP using PLINK v1.9, followed by smoothing in R v4.6.1 (Weir and Cockerham, 1984). Within population selection signatures were evaluated using haplotype and allele frequency-based statistics. Integrated haplotype score (iHS) was calculated from SHAPEIT v2.17 phased genotypes generated using 35 Markov chain Monte Carlo iterations comprising 7 burn in, 8 pruning and 20 main iterations with a genetic recombination map (Delaneau *et al*., 2012). SELSCAN v2.0 integrated extended haplotype homozygosity to an EHH threshold of 0.05 after excluding rare variants (MAF<0.05) and iHS values were normalized across derived allele frequency bins (Voight *et al*., 2006; Szpiech and Hernandez, 2014). Modified haplotype homozygosity (H_{12}) and LASSI were estimated in LASSIP v1.1.1 from phased multilocus genotypes after excluding loci with more than 10% missing genotypes, using the likelihood ratio framework to detect hard and soft selective sweeps (Harris and DeGiorgio, 2020). Tajima's D and nucleotide diversity (π) were estimated in VCFTOOLS v0.1.16 (Danecek *et al*., 2011). Tajima's D was calculated for each breed and chromosome using nonoverlapping 300-kb windows, with missing values replaced by zero. Nucleotide diversity was estimated using the-site-pi option and both statistics were smoothed in R v4.6.1 using the runmed function with a 31 SNP window (k = 31, endrule = "constant") (Tajima, 1989; Nei and Li, 1979).

Integration of multi-statistic selection signals

Selection signatures were identified using the DCMS approach by integrating F_{ST}, iHS, H_{12}, π and Tajima's D

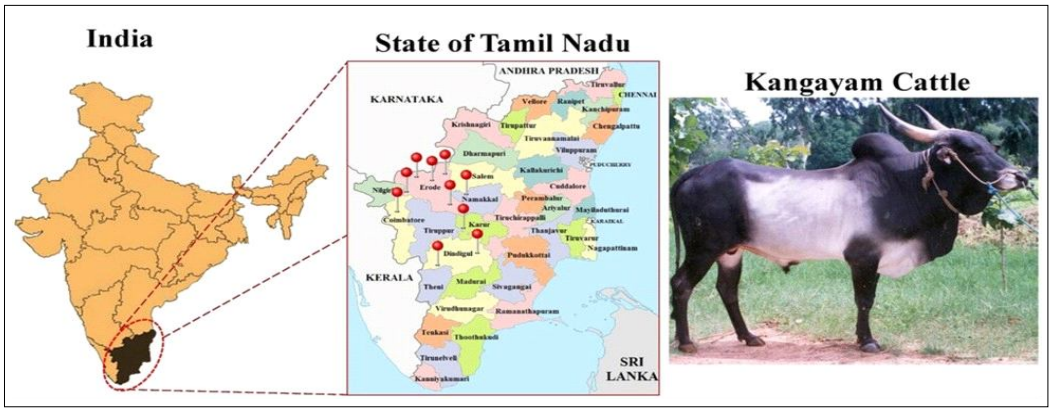

Fig 1: Breeding tract and geographical distribution of Kangayam cattle (Source: AGRI-IS).

(Ma *et al.,* 2015). Given the high marker density of the BovineHD-BeadChip (>777,000 SNPs), summary statistics were aggregated into non-overlapping 10-kb windows to minimize stochastic variation from individual SNPs while retaining sufficient resolution for candidate region detection and maintaining a balance between genomic resolution and statistical robustness (Yurchenko *et al.,* 2018). Within each window, weighted mean F_{ST} and maximum absolute iHS values were retained. A Spearman correlation matrix derived weights from absolute correlations to reduce redundancy among statistics following the decorrelation procedure implemented in the MINOTAUR framework (Verity *et al.,* 2017). DCMS scores were calculated as the weighted sum of $\log_{10}$ transformed p-values derived from fractional ranks, according to the formula:

$$DCMS_{Score} = \sum_{t=1}^{5} \frac{-Log_{10}(1 - r_t + 10^{-10})}{w_t}$$

Significant regions were defined by values exceeding three standard deviations above the mean and FDR adjusted q<0.001, with the top 1% prioritized. Data processing, statistical integration and visualization were performed in R v4.6.1 using dplyr, data.table, ggplot2 and openxlsx for downstream functional analyses.

Gene annotation, functional enrichment and network analysis

Genomic regions with q<0.001 were annotated for candidate genes and QTLs using GALLO v1.4 with the UMD3.1.1 assembly and Animal QTL Database (Fonseca *et al.,* 2020; Rosen *et al.,* 2018; Hu *et al.,* 2013). Chromosome based enrichment and pathway analysis were performed using PANTHER v19.0 (Thomas *et al.,* 2003). Protein coding genes within DCMS peaks were further analyzed using STRING v12.0 to construct protein interaction networks (Mering *et al.,* 2003), visualized in Cytoscape v3.10.4 and hub genes were identified using the MCC algorithm in CytoHubba (Chin *et al.,* 2014).

RESULTS AND DISCUSSION

De-correlated composite of multiple signals (DCMS)

After QC, 684,048 high quality autosomal SNPs were retained. The genome wide distribution of selection signals is presented in Fig 2. Pairwise correlation analysis showed strong positive correlation between nucleotide diversity (π) and H_{12}, indicating overlapping low diversity regions, whereas iHS showed negative correlations with H_{12} and π, reflecting different sweep dynamics. F_{ST} displayed weak correlations with iHS and π, consistent with its role in population differentiation (Table 1). These complementary patterns justified DCMS integration. More than 5000 significant windows were detected, of which the top 1% were prioritized, yielding 53 genomic windows containing 47 unique annotated genes, with q-values as low as 2.45×10^{-6} and a maximum DCMS score of 4.677 (Supplementary Table S1).

Gene annotation functional enrichment and network analysis

Analysis of significant DCMS regions using the bovine QTL database identified protein coding genes and QTLs

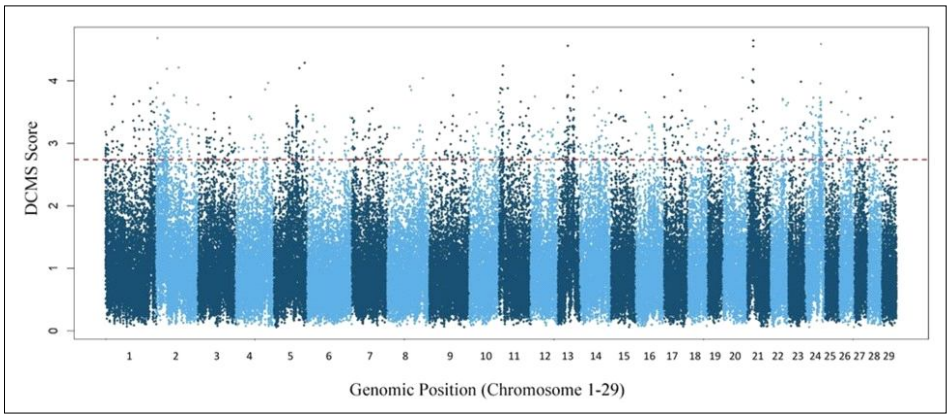

Fig 2: Manhattan plot showing the genomic regions identified by the DCMS in Kangayam cattle.

Table 1: Correlation between various statistical approach used to detect selection signature in Kangayam cattle.

	iHS	π	Tajima's D	H_{12}	F_{ST}
iHS	1	-0.282	-0.014	-0.31	0.045
π	-0.282	1	0.558	0.687	0.141
Tajima's D	-0.014	0.558	1	0.431	0.348
H_{12}	-0.31	0.687	0.431	1	0.127
F_{ST}	0.045	0.141	0.348	0.127	1

Supplementary Table S1: Candidate genes and their associated biological roles identified through gene annotation and QTL enrichment of significant DCMS genomic windows.

Chromosome	Region (Mb)	q-Value	Candidate Gene(s)	Trait/biological function
BTA 01	143.99-144.00	4.35E-04	*SLC37A1, PDE9A*	Milk alpha-casein %, weaning weight, milk fat yield
BTA 01	26.85-26.86	9.60E-04	*ROBO1*	Milk protein yield, milk yield, milk fat %
BTA 02	3.74-3.75	2.45E-06	*IL8R, MSTN*	PTA type, longissimus muscle area, milk fat yield
BTA 02	74.19-74.20	6.21E-05	*IL8R, PRNP*	Milk fat yield, udder depth, lung percentage
BTA 02	32.31-32.32	6.21E-05	*IL8R*	Milk fat yield, udder depth, lung percentage
BTA 02	4.34-4.35	2.57E-04	*MSTN, IL8R*	PTA type, longissimus muscle area, milk fat yield
BTA 02	58.79-58.80	8.96E-04	*PRKAG3, IL8R*	Milk fat yield, udder depth, lung percentage
BTA 02	101.65-101.66	9.84E-04	*IL8R*	Milk fat yield, udder depth, lung percentage
BTA 02	1.29-1.30	9.84E-04	*MSTN*	Muscle development (Myostatin), PTA type
BTA 02	101.66-101.67	9.84E-04	*IL8R*	Milk fat yield, udder depth, lung percentage
BTA 03	106.12-106.13	9.84E-04	*CTPS1, RLF*	Clinical mastitis, carcass weight, soundness
BTA 04	107.36-107.37	2.57E-04	*PRSS2*	Milk fat %, scrotal circumference, parasite load
BTA 04	97.09-97.10	4.81E-04	*PRSS2*	Milk fat %, fat thickness, scrotal circumference
BTA 05	108.26-108.27	3.78E-05	*SLC37A1, NINJ2*	Milk alpha-lactalbumin %, milk yield, rump length
BTA 05	89.12-89.13	6.21E-05	*SLCO1A2, SLCO1B3*	Milk fat %, milk yield, milk protein yield
BTA 08	96.28-96.29	1.79E-04	*ABCA1*	Foot angle, calving ease, stillbirth
BTA 08	57.52-57.53	3.87E-04	*PRNP*	Carcass weight, body weight, clinical mastitis
BTA 08	62.72-62.73	4.81E-04	*PRNP*	Clinical mastitis, somatic cell count, dystocia
BTA 09	59.98-59.99	8.96E-04	*PRNP*	Milk fat yield, milk alpha-casein %, udder cleft
BTA 11	11.39-11.40	5.62E-05	*ALMS1, EXOC6B*	Body weight, residual feed intake, somatic cell count
BTA 11	9.22-9.23	1.23E-04	*PHYH*	Scrotal circumference, body weight, RFI
BTA 11	4.59-4.60	4.35E-04	*FER1L5*	Scrotal circumference, body weight, stature
BTA 11	24.86-24.87	4.39E-04	*HAAO*	Residual feed intake, somatic cell count, sperm
BTA 11	8.59-8.60	4.74E-04	*Intergenic*	Scrotal circumference, body weight, RFI
BTA 11	2.80-2.81	6.84E-04	*FER1L5*	Scrotal circumference, TB susceptibility
BTA 12	10.86-10.87	9.84E-04	*OLFM4*	Multiple birth, weaning weight, LM area
BTA 13	29.65-29.66	2.60E-06	*DNMT3B*	Teat placement, weaning weight, fat thickness
BTA 13	64.51-64.52	1.23E-04	*GSS, ITCH*	Teat length, PCV decrease (Trypanotolerance)
BTA 13	62.95-62.96	3.76E-04	*DNMT3B*	Teat length, PCV decrease (Trypanotolerance)
BTA 13	30.27-30.28	8.96E-04	*BMP7*	Teat placement, weaning weight, fat thickness
BTA 13	27.96-27.97	9.84E-04	*PHYH*	Teat placement, weaning weight, fat thickness
BTA 13	65.41-65.42	9.84E-04	*PHF20, UQCC1*	Teat length, weaning weight, udder attachment
BTA 14	52.05-52.06	4.23E-04	*Intergenic*	Milk protein %, milk protein yield, tick resistance
BTA 14	39.58-39.59	5.93E-04	*Intergenic*	Milk protein %, milk protein yield, tick resistance
BTA 15	32.54-32.55	5.20E-04	*SORL1*	Semen volume, rump angle, heel depth
BTA 17	24.43-24.44	1.23E-04	*RIMBP2*	Milk alpha-casein %, average daily gain
BTA 17	48.05-48.06	5.20E-04	*RIMBP2*	Milk alpha-casein %, body weight, calving ease
BTA 17	1.70-1.71	9.84E-04	*TLL1*	Longissimus muscle area, rump angle
BTA 20	58.57-58.58	1.73E-04	*ANKH*	Milk protein yield, milk protein %, abnormal sperm
BTA 21	19.60-19.61	2.45E-06	*SLCO1A2*	Stillbirth, gestation length, clinical mastitis
BTA 21	19.55-19.56	2.60E-06	*SLCO1A2*	Stillbirth, gestation length, clinical mastitis
BTA 21	16.24-16.25	2.44E-04	*ADAMTSL3*	Stillbirth, body weight, average daily gain
BTA 21	19.61-19.62	2.50E-04	*SLCO1A2*	Stillbirth, gestation length, clinical mastitis
BTA 21	19.50-19.51	2.57E-04	*SLCO1A2*	Stillbirth, gestation length, clinical mastitis
BTA 23	35.65-35.66	2.50E-04	*BOLA-DRB3*	Immunoglobulin G level, milk protein yield
BTA 24	51.66-51.67	2.60E-06	*ABCA1*	Oleic acid content, feed conversion, nematode burden
BTA 24	50.90-50.91	2.61E-04	*ABCA1*	Oleic acid content, feed conversion, nematodes
BTA 24	50.31-50.32	2.61E-04	*ABCA1*	Oleic acid content, feed conversion, nematodes
BTA 24	48.63-48.64	9.84E-04	*ZBTB7C*	Oleic acid content, feed conversion, nematodes
BTA 24	23.05-23.06	9.84E-04	*DTNA, NOL4*	Body depth, body form composite index
BTA 26	27.20-27.21	5.93E-04	*PRNP*	Body form index, myristic acid content
BTA 27	19.30-19.31	9.89E-04	*CSN3*	Milk protein (Kappa-casein), non-return rate

reflecting combined natural and artificial selection in Kangayam cattle. Functional annotation showed enrichment for milk production, growth, feed efficiency, carcass traits, immunity, reproduction and morphology, indicating genomic regions previously associated with tropical adaptation and economically important traits. QTL enrichment revealed trait specific signals across multiple chromosomes, with milk related traits showing the greatest enrichment (Fig 3). Milk fat yield showed the highest enrichment followed by milk fat percentage and the milk C14 index, suggesting strong selection on milk composition. Moderate enrichment was observed for myristoleic, caprylic, capric, palmitoleic and lauric acids, milk phosphorus content, milk protein yield and protein percentage, whereas body weight, ketosis, marbling, tenderness and shear force showed comparatively lower enrichment. Overall, milk related QTLs were most abundant (1766), followed by meat and carcass (587), production (389), reproduction (303) and relatively fewer health and exterior QTLs (Fig 4). Milk fatty acid composition is an economically important trait influenced by genes regulating lipid synthesis and milk quality, including stearoyl CoA desaturase (Yadav *et al.,* 2026).

Significant DCMS windows were distributed across multiple autosomes and overlapped genes previously associated with production, tropical adaptation, immunity, reproduction and metabolism. Genes related to muscle development, growth and energy metabolism included *MSTN, BMP7, PRKAG3, PHF20* and *UQCC1*, which have been associated with skeletal muscle development, carcass traits, glycogen metabolism and production traits (Szabó *et al.,* 2025; Costilla *et al*., 2023; Sun *et al.,* 2023).

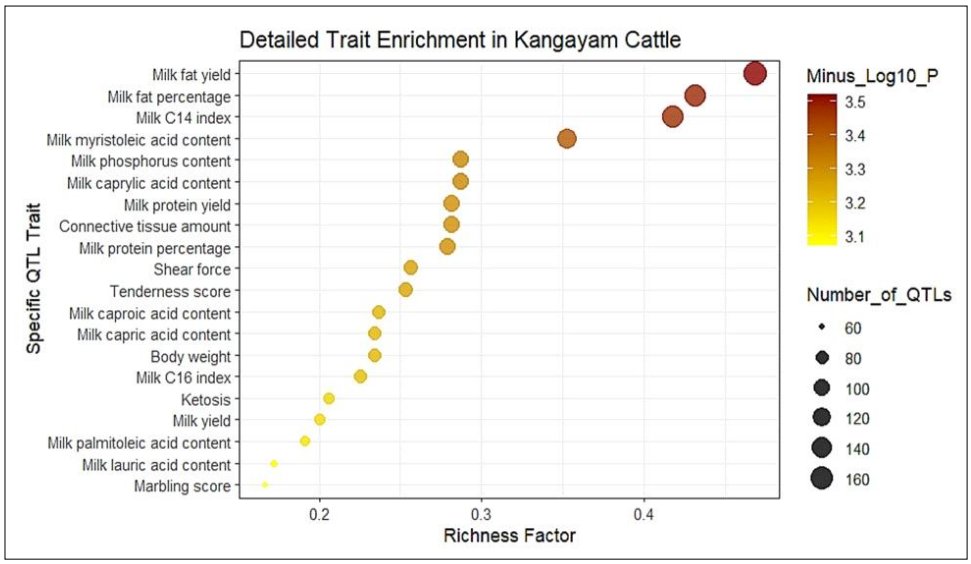

Fig 3: QTL enrichment across various traits in Kangayam cattle.

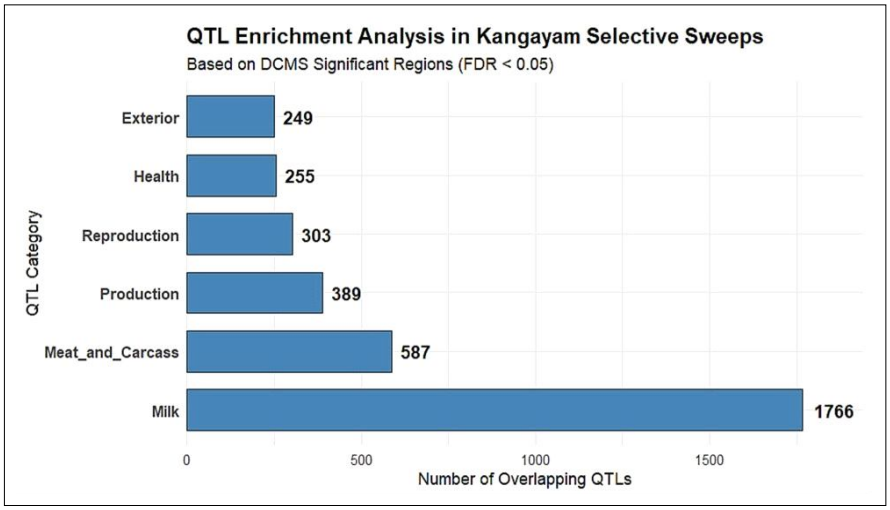

Fig 4: Distribution of annotated QTLs across major trait categories in Kangayam cattle.

Genes related to milk production and composition included *SLC37A1, CSN3, ABCA1, SLCO1A2, SLCO1B3* and *PDE9A*, which have previously been linked with milk yield, milk fat composition, mineral transport, lipid metabolism and milk protein traits (Sanchez *et al.,* 2021; Pedrosa *et al.,* 2021; Barwar *et al.,* 2023; Liu *et al.,* 2024), consistent with the predominance of milk related QTLs. Selection signals also overlapped immune related genes including *OLFM4, ITCH, BoLA DRB3, PRNP, NINJ2* and *CTPS1*, previously implicated in immune response, inflammation and disease resistance (McHugo *et al.,* 2025; Holloway *et al.,* 2024; Bykova *et al.,* 2023; Imran *et al.,* 2012; Roshan *et al.,* 2025; Rios *et al.,* 2023). Transporter and metabolic genes including *ABCC9, ABCA1, SLC22A7, SLC10A1, SLCO1A2, SLCO1C1, PHYH* and *GSS* have previously been associated with cellular transport, lipid metabolism, oxidative metabolism and homeostasis (Pedrosa *et al.,* 2021; Liu *et al*., 2024; Yang *et al*., 2025; Neto *et al.,* 2026), whereas reproductive genes *FER1L5, RLF, RIMBP2* and *ADAMTSL3* have been linked with fertility and developmental processes (Neupane *et al*., 2018; Rios *et al*., 2023; Fathoni *et al*., 2024).

Although DCMS studies in Indian cattle have been limited to Sahiwal and Belahi (Muansangi *et al.,* 2025; Chavan *et al.,* 2025), selection signature studies in Gir, Ongole, Hariana and Tharparkar have also identified candidate genes associated with production, immunity, reproduction and tropical adaptation (Dixit *et al.,* 2021; Sukhija *et al.,* 2024; Dash *et al.,* 2025). Similarly, the present analysis identified candidate genomic regions overlapping genes previously associated with these biological processes, while the genomic signatures observed in Kangayam likely reflect its distinct evolutionary history and long-term selection as a specialized Indian draught breed of southern peninsular.

Gene network analysis and hub genes identification

The PPI network revealed coordinated biological interactions among candidate genes (Fig 5), indicating that DCMS identified interconnected genomic regions rather than isolated loci. A major cluster comprised transporter genes *ABCC9, SLCO1A2, SLCO1C1* and *ABCA1,* previously associated with transport and cellular homeostasis (Pedrosa *et al*., 2021; Liu *et al.,* 2024). Another cluster containing *SLC37A1, ABCA1* and *ADAMTSL3* supported coordinated metabolic regulation (Sanchez *et al.,* 2021), whereas *MSTN, BMP7* and *PRKAG3* linked muscle development with metabolic processes (Szabó *et al.,* 2025). Cytoscape identified *SLC22A7* and *ABCC9* as major hub genes, with *SLC10A1* and *SLCO1A2* as secondary hubs (Fig 6). *SLC22A7* mediates transport of endogenous metabolites and xenobiotics and contributes to metabolic homeostasis (Momper and Nigam, 2018), whereas *ABCC9* encodes the sulfonylurea-receptor-2, a regulatory subunit of ATP sensitive potassium channels involved in cellular energy sensing, ion transport and protection against metabolic stress (Flagg *et al.,* 2010).

Although these candidate genes overlap genomic regions previously associated with tropical adaptation and economically important traits in cattle, the present findings are based on computational analyses. Furthermore, high density SNP array data may underrepresent rare or population specific variants because of ascertainment bias. Future integration of whole genome sequencing,

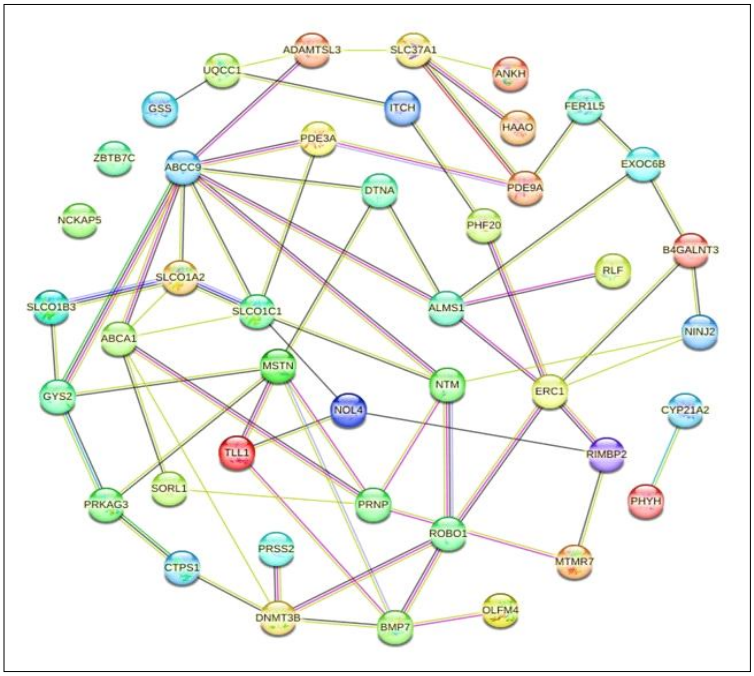

Fig 5: PPI network of candidate genes under selection in Kangayam cattle.

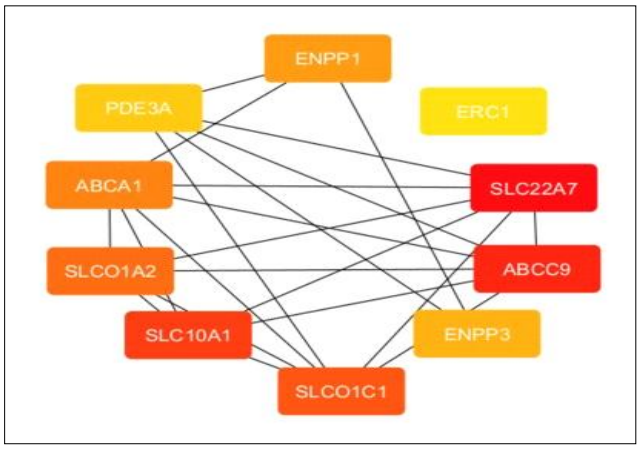

Fig 6: Hub gene network of candidate genes under selection in Kangayam cattle.

transcriptomics, functional genomics and larger populations will enable higher resolution characterization and functional validation of candidate genes underlying tropical adaptation in Kangayam cattle.

CONCLUSION

The DCMS framework identified genomic regions under selection in Kangayam cattle and provided insights into the genetic basis of tropical adaptation, endurance and production traits. A total of 53 significant regions enriched 47 genes related to muscle development, metabolism, immunity, thermotolerance, reproduction and milk traits, including *MSTN, BMP7, PRKAG3, BoLA DRB3, IL8R, ABCA1* and *SLCO* family genes. QTL enrichment demonstrated the predominance of milk, muscle and health related traits, whereas network analysis identified *SLC22A7* and *ABCC9* as major hub genes, highlighting coordinated metabolic and transport pathways. Although these findings provide valuable genomic resources, they are based on computational analyses and require functional validation. Future integration of whole genome sequencing, transcriptomics and functional genomics will improve understanding of the molecular mechanisms underlying tropical adaptation in Kangayam cattle and support the conservation, genomic characterization and future breeding of indigenous Indian cattle.

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Disclaimers

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Informed consent

Not applicable as this study did not involve any live animal experimentation.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. No funding or sponsorship influenced the design of the study, data collection, analysis, decision to publish, or preparation of the manuscript.

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