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Genetic diversity and selection signatures in related Mediterranean breeds: Sarda, Pag, and Istrian sheep

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ABSTRACT

Local sheep breeds in southern Europe are highly adapted to their environments, often characterized by hot climate and poor pasture availability, where other types of agriculture would not be possible. In order to better exploit these livestock resources, genomic regions associated with adaptation could be identified. The objective of this work was to use population genetic and genomic approaches to identify shared and private signatures of selection between an Italian breed, Sarda (SAR); and two Croatian breeds, Pag (PAG) and Istrian (IST) sheep. Common genomic regions will give insights into Mediterranean climate adaptations and past crossbreeding, while differences will provide information on specific environmental adaptations and selection pressures. A total of 4791 (825 SAR, 2683 PAG, 1283 IST) sheep were SNP genotyped (40,995 SNP after quality control). Population structure was studied through linkage disequilibrium and admixture. To identify signatures of selection, we used four approaches, runs of homozygosity (ROH), Wright's fixation index (F_{ST}), cross population extended haplotype homozygosity (XP-EEH), and ratio of extended haplotype homozygosity between populations (Rsb). According to F_{ST} results, SAR and IST were the most divergent breeds. The latter breed showed the largest ROH-based inbreeding. A large selection signature on chromosome 6 (33.26–46,31 Mb) was found by all involved approaches as associated with IST. The results of the present study enabled the identification of common and private regions among three Mediterranean sheep breeds raised under similar environmental conditions.

1. Introduction

The genetic diversity of sheep is being eroded, primarily due to the replacement of local breeds with specialized and higly selected cosmopolitan ones. Local breeds are adapted to specific environments, are hardy and resilient, and could serve as an important reservoir of genetic diversity. For all these reasons, local breeds could play a crucial role in addressing future challenges represented by climate change and emerging diseases. According to Carabaño et al. (2021), Mediterranean countries represent an hotspot remarkably susceptible to the impacts of climate change. Three examples of local sheep breeds in the Mediterranean region are the Sarda (SAR), Pag (PAG), and Istrian (IST) breeds. SAR, widely farmed throughout Italy, is native to the island of Sardinia (Cesarani et al., 2019) and it represents the largest dairy sheep in Italy (Pulina et al., 2018). PAG is a Croatian sheep breed native to the Pag island that comes from crossing the island local breed with Negretti, Bergamo, and Gentile di Puglia breeds in 1870 (Drzaic et al., 2022). Additionally, in order to improve the milk yield of this breed, PAG has been crossed with SAR animals (Drzaic et al., 2022). Finally, IST is a local Pramenka type sheep breed of the Northern Adriatic area which, because of historical border changes, has been fragmented into separate populations in Slovenia, Croatia, and to a lesser extent Italy (Salamon et al., 2015). The formation of this breed began around 1770 by crossing the local population with foreign rams of several more productive breeds (Ramljak et al., 2024), such as the Italian Bergamasca, Gentile di Puglia, Southdown, Merinolandschaf, Merino, Awassi, and East-Friesian (Dzidic

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et al., 2004; Putinja, 2005; Drzaic et al., 2022; Pocrnic and Dzidic, 2021).

The genomes of these three breeds have been shaped by their distinct evolutionary histories. The three breeds are raised in similar Mediterranean environments, mainly under semi-extensive farming systems. Thus, the breeds could have developed common adaptation to the low-input and semi-arid Mediterranean conditions. As far as their productive aptitude, the SAR is classified as a dairy breed (Carta et al., 2009), whereas PAG and IST are considered dairy oriented dual-purpose breeds (Ramljak et al., 2024), thus reflecting the influence of artificial selection applied by the breeding programs. For example, the breeding program for milk production in SAR started around 1960 (Carta et al., 2009). The combined effects of these artificial and natural selection pressures could have left traces known as selection signatures (Cesarani et al., 2019; Lukic et al., 2023). Furthermore, there are various indications that two Croatian breeds, and particularly Pag sheep, have been historically bred by rams from various Italian breeds (e.g., Špehar et al., 2019). Investigating these genomic regions could help in elucidating the biological mechanisms of selection and highlighting candidate genes responsible for variation in traits of interest (Zhao et al., 2016). Among the different approaches that have been proposed to detect selection signatures, runs of homozygosity (ROH) and Wright's fixation index (F_{ST}) are well established, whereas there is an increasing interest of extended haplotype homozygosity (EHH) derived statistics. ROH, continuous stretches of homozygous genotypes (Gibson et al., 2006) without heterozygosity in the diploid state, can arise from the mating of related individuals and, thus, they are more frequent after demographic events that decrease the effective population size, such as bottlenecks and genetic drift (Purfield et al., 2012). For the same reason, they can be used as a temporal indicator of inbreeding: long ROH are due to recent inbreeding (VanRaden et al., 2011), whereas shorter ROH arise from the originally long segments eventually broken down in size due to recombination over a number of generations (Forutan et al., 2018). The F_{ST} statistic (Wright, 1949) measures the degree of genetic differentiation between populations on the basis of differences in locus-specific allele frequencies and, thus, it identifies the loci that are differentially fixed in different populations. The cross-population extended haplotype homozygosity (XP-EHH; Sabeti et al., 2007) test is a haplotype-based differentiation method that compares two populations on the basis of corresponding haplotypes and SNP, with the aim to identify signals of divergent selection, i.e, present in one population and not in the other. The ratio of EHHs between populations (Rsb; Tang et al., 2007) is a complementary test to the XP-EHH that compares EHH for the same SNP in two different populations, highlighting alleles with high frequency (near fixation) in a population that are polymorphic in the other population. When integrated, different statistical methods can ensure more confidence in selection signature identification (Grossman et al., 2010; Mastrangelo et al., 2023), allowing the implementation of knowledge about the history and the differentiation processes of the breeds to be taken into consideration (Eydivandi et al., 2021). Since the four above mentioned techniques (ROH, F_{ST}, Rsb, and XP-EHH) have different sensitivity and specific limitations in identifying selection signatures, their combined use could lead to the same or different results. In the first case, the identification of the same selection signature could increase its reliability and strength. Thus, the aim of this study was to use these different population genetic approaches to identify common and differing genomic regions between SAR, PAG, and IST sheep. Common regions will give insights into adaptations to the Mediterranean climate and past crossbreeding, whereas differences will provide information on specific environmental adaptations and selection pressures. Additionally, the use of four different but complementary techniques to identify selection signatures could help to identify the same genomic regions, giving strength to the selection pressure hypothesis, or not overlapping results that can be associated to different sensitivity among methods.

2. Materials and methods

2.1. Data

A total of 4791 genotyped animals were included in this study: SAR (825), PAG (2683), and IST (1283). All animals were genotyped with the Ovine SNP50 v1 BeadChip (Illumina Inc., San Diego, CA, USA). Quality control was carried out using PLINK v. 1.9 (Purcell et al., 2007; Chang et al., 2015): SNP were retained if they did not deviate from the Hardy-Weinberg Equilibrium ($P > 0.01$), if they had a minor allele frequency greater than 1 %, and if their call rate was larger than 95 %. Moreover, SNP were remapped to update genomic position of all markers to the ARS-UI_Ramb_v2 release of the *Ovis aries* assembly, and those mapped on allosomes or unmapped were discarded. The three datasets were then merged retaining 40,995 SNP in common among all three breeds.

2.2. Linkage disequilibrium and population structure analysis

Linkage Disequilibrium (LD) was computed using the *Haploview* software (Barrett et al., 2005), as the squared correlation coefficient of allele frequencies at pairs of loci (r^2) between SNP within a 10 kb distance of each other. Population structure was analyzed using Admixture software (Alexander et al., 2009) testing one to five groups both at genome-wide and chromosome levels.

2.3. Runs of homozygosity (ROH) detection

ROH were detected using the consecutive method (Marras et al., 2015) implemented in the *detectRUNS* package of R (Biscarini et al., 2019). The following parameters were used to define ROH: a minimum of 20 consecutive homozygous SNP covering at least 1 Mb, with no heterozygous or missing markers allowed inside the run. Only animals with at least five ROH were considered for computing the number of ROH per animal (nROH) and their average length (meanMb). ROH were grouped based on their length in five classes: 1–2, 2–4, 4–8, 8–16, and > 16 Mb. The ROH-based inbreeding coefficient (F_{ROH}) was computed as the ratio between the total sum of ROH length per animal divided by the genome length covered by SNP (McQuillan et al., 2008). The nROH, meanMb, and F_{ROH} were compared across breeds using ANOVA (significance threshold $P < 0.05$). ROH shared by at least 10 animals in each breed were defined as common selective signatures, whereas ROH within each breed, and not identified in any animals of the other two breeds, were defined as breed-specific selection signatures or privateROH (Cesarani et al., 2021).

2.4. Wright's fixation index (F_{ST})

Pairwise F_{ST} estimates for the three breeds were computed using PLINK v. 1.9 (Purcell et al., 2007). F_{ST} raw values were smoothed with a local weighted regression technique (LOWESS) to facilitate the interpretation of the results and to remove background noise (Pintus et al., 2014). According to the F_{ST} smoothed values, outlier markers were identified when their values simultaneously exceeded: i) three standard deviations from the chromosomic mean, ii) the 99th percentile of the overall genome-wide distribution.

2.5. Extended haplotype homozygosity across populations

Haplotypes were reconstructed from SNP genotypes using the *fastPHASE* 1.4 software (Scheet and Stephens, 2006). Within each breed, the chromosomes were separately tested using 10 random starts of the expectation–maximization (EM) algorithm (-T), 40 iterations (-C), with 50 haplotypes sampled (-H) from a particular random start, considering 20 clusters (-K), and with a rate of missingness of 0.05. The phased haplotypes were analyzed using the *rehh* package of R (Gautier and

Vitalis, 2012; Gautier et al., 2017): the files were converted by the function *data2haplohh* to a suitable format for Rsb and XP-EHH analyses. Each chromosome was analyzed by the function *scan_hh*. The resulting objects were analyzed performing pairwise comparisons among the three breeds (i.e., SAR vs IST, SAR vs PAG, and IST vs PAG). The *ines2rsb* function was used to for Rsb analysis and *ies2xpehh* was used for the XP-EHH analysis. For both tests, SNP were flagged as significant by the *calc_candidate_regions* function, including a minimum of 1 SNP per window, when their Bonferroni adjusted p-value was lower than 0.01. The Rsb test identifies alleles that are close to fixation in one population and not in the other (Tang et al., 2007), whereas XP-EHH indicates the extent of haplotype fixation. Thus, we decided to consider the SNP highlighted by both tests (i.e., Rsb and XP-EEH) in each comparison as they may identify different selection signatures.

2.6. Gene and quantitative trait loci enrichment

Genes mapped within or close (±250 kb; Manca et al., 2020) to common ROH, privateROH, and significant regions from both XP-EEH and Rsb analyses, were identified using information from the NCBI database (National Center for Biotechnology Information, www.ncbi.nlm.nih.gov) and described according to available literature. For the same regions, quantitative trait loci (QTL) from the literature and significant enrichment (cutoff of corrected Bonferroni p-value of 0.05) in these findings were identified using the *GALLO* package in R (Fonseca et al., 2020a).

3. Results and discussion

In this study, we employed population genetic approaches to identify shared and private signatures of selection among three Mediterranean sheep breeds: Sarda (SAR), Pag (PAG), and Istrian (IST). Our results showcase two major points for discussion: (i) population structure analyses characterised genetic diversity within populations and described how these breeds are related to each other, and (ii) identified signatures of selection have given us insights into regions important for milk and meat production and adaptation. Thus, we have presented signatures of selection results in a trait-centric organisation.

3.1. Population structure

The trends of r^2 according to the distance among markers were similar in the three breeds (Fig. 1). As observed in several species and breeds (McRae et al., 2002; Du et al., 2007; Khatkar et al., 2008), the LD decreased as the distance among SNP increased. The overall average r^2 values were 0.05 ± 0.03, 0.04 ± 0.03, and 0.02 ± 0.03, in SAR, IST, and PAG, respectively. LD levels vary according to the different parameters, such as levels of artificial selection and effective population sizes (Qanbari et al., 2010; Zhao et al., 2014). As expected, because of the more intense artificial selection, LD values were higher in SAR. On the contrary, lower r^2 values are usually associated with lower selection pressures.

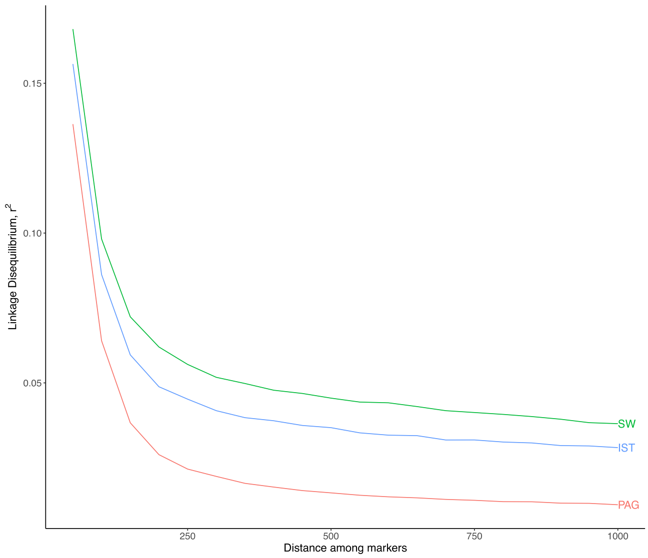

Fig. 1. Linkage Disequilibrium estimated through the squared correlation coefficient of allele frequencies at pairs of loci (r^2) over distance among markers.

An ADMIXTURE analysis was used to investigate the extent of admixture among SAR, PAG and IST breeds. As reported in Fig. 2 and Table 1, the ADMIXTURE analysis showed that the red cluster, attributed to IST, exhibited the highest level of admixture. Indeed, it was the cluster with the lowest average coancestry coefficient (0.801) with itself, showing a contribution of the green cluster (attributed to PAG) of 0.172 and the blue (attributed to SAR) of 0.027. On the contrary, the green cluster (PAG) had the highest coefficient (0.857) with itself, with a small contribution of the other two clusters (0.074 red and 0.068 blue). The blue cluster (i.e., SAR) showed an intermediate situation. The SAR was previously reported in another ADMIXTURE analysis to be strongly admixed with the other Sardinian sheep breed, the Sardinian Black (Mastrangelo et al., 2014; Chessari et al., 2023); in the latter study, as well as in a study by Ciani et al. (2014) on 19 sheep breeds, the IST breed and the SAR showed no admixture. The distinctiveness of the SAR breed could reflect genetic isolation due to the geographic insularity (Ciani et al., 2014). In contrast, PAG and IST have been shown to have similarities in population structure (Drzaic et al., 2022).

With regards to ROH features (Table 2), the SAR showed the highest number of ROH per animal (54.55 ± 26.10), probably because, among the three breeds, it is under the strongest selection pressure. Moreover, this difference could be due to the different effective population size. At the same time, SAR showed the lowest ROH average length (3.17 ± 3.24), whereas the IST showed the highest (3.88 ± 4.52). Similar values were reported for SAR by Cesarani et al. (2022), who reported a nROH and meanMb of 56.9 ± 13.4 and 3.88 ± 4.71, respectively. However, Mastrangelo et al. (2018a) reported a lower nROH (20.83) but a greater meanMb (4.56) for SAR, and this difference could be due to the more permissive ROH search parameters adopted by the latter authors, who allowed for 1 heterozygote and 1 missing genotype inside the run. Similarly, in the same study (Mastrangelo et al., 2018a), nROH (16.29) and meanMb (4.58) were also lower for IST.

When considering ROH classes (defined by length), the three breeds showed the same trend: almost half of total runs were between 1 and 2 Mb long, and the percentage of runs in each class decreased as the length increased in all three breeds. About 80 % of runs were less than 4 Mb, and this result matched with what was already reported by previous studies on sheep (Mastrangelo et al., 2018a; Abied et al., 2020; Selli et al., 2021; Cesarani et al., 2022). The IST breed had the highest ROH average length and the highest F_{ROH} (0.08 ± 0.07). In contrast, the lowest F_{ROH} (0.04 ± 0.05) was observed for PAG, which had the lowest number of ROH per animal. Previous estimates of F_{ROH} have been similar to those seen in this study; Mastrangelo et al. (2018a) reported a F_{ROH} of 0.041 ± 0.035 for SAR and 0.031 ± 0.023 for IST, and Drzaic et al. (2022) found a F_{ROH} of 0.035 ± 0.008 for PAG and 0.053 ± 0.010 for IST.

The weighted F_{ST} value between SAR and PAG was 0.06 and between SAR and IST was 0.08, whereas the value between the two Croatian breeds (i.e., PAG and IST) was 0.04. The latter was expected, given the geographic closeness, and the same value had already been reported in the literature for this comparison (0.041; Drzaic et al., 2022). The lower distance between SAR and PAG compared to SAR-IST was also expected due to possible historic crossbreeding. The value found for the SAR-IST comparison is very close to that (0.077) reported by Chessari et al. (2023). The F_{ST} smoothed values per SNP in each comparison are graphically represented in Fig. 3, and the number of SNP per

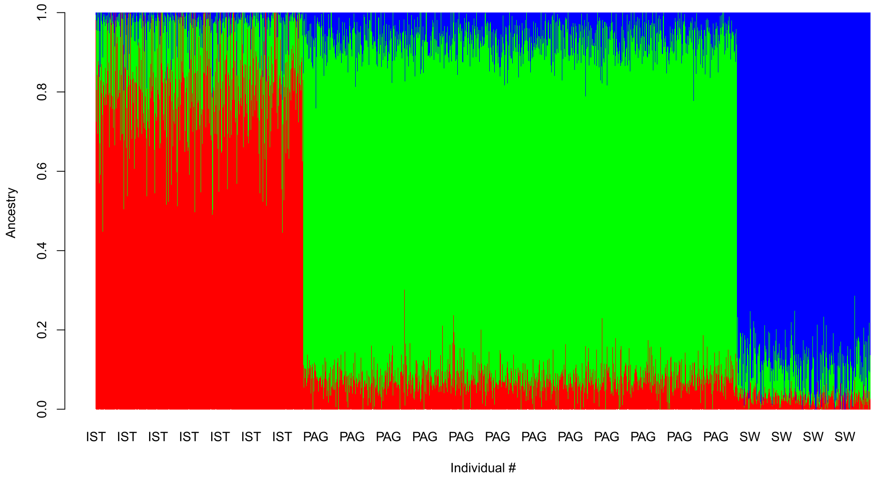

Fig. 2. Maximum likelihood estimation of individual ancestries (ADMIXTURE analysis) with Istrian (IST), Pag (PAG) and Sarda (SW) sheep populations.

Table 1
Average coancestry coefficients computed using the ADMIXTURE software.

	IST	PAG	SAR
IST	0.801	0.172	0.027
PAG	0.0741	0.857	0.068
SAR	0.0295	0.081	0.830

Table 2
Runs of homozygosity (ROH) features for each breed.

	Pag	Sarda	Istrian
Total number of ROH	73,634	44,789	66,935
Animals with ROH	2588	821	1264
ROH per animal	28.45 ± 22.30^b	54.55 ± 26.10^a	52.95 ± 33.38^a
ROH average length	3.56 ± 4.13^b	3.17 ± 3.24^c	3.88 ± 4.52^a
Distribution			
1–2 Mb	48.90 %	46.61 %	42.78 %
2–4 Mb	27.14 %	32.58 %	30.42 %
4–8 Mb	14.66 %	14.88 %	16.49 %
8–16 Mb	6.95 %	4.67 %	7.51 %
> 16 Mb	2.35 %	1.25 %	2.80 %
Average inbreeding (F_{ROH})	0.04 ± 0.05^c	0.07 ± 0.04^b	0.08 ± 0.07^a

^{a,b,c} Significant differences between means ($P < 0.05$).
Values are reported as mean ± standard deviations.

chromosome of which the fitted value exceeded both 3 standard deviations from the chromosomic mean and the top 99th percentile is reported in Table S1. A total of 367, 316, and 248 SNP were identified for SAR-PAG, SAR-IST, and PAG-IST comparisons, respectively.

3.2. Signatures of selection

Shared ROH among different populations can highlight genomic regions associated with important traits (Purfield et al., 2012; Mastrangelo et al., 2018b). A total of 914 ROH were shared among the three breeds (with at least one animal for each breed with these shared ROH), but only two ROH were shared by at least 10 animals per breed: one on OAR12 (from 767,946 to 4656,965 Mb, shared by 18 IST, 27 PAG, and 10 SAR) and one on OAR17 (from 386,815 to 1,597,667 Mb, shared by 30 IST, 13 PAG, and 30 SAR). The genes mapped on these two ROH are presented in Table S2.

The two most common privateROH in each breed were investigated (Table 3). These privateROH can highlight genomic regions that harbor genes associated with economically important traits for which a population has been artificially selected for, or fitness traits particularly important for environmental adaptation to the geographic region where the population is farmed.

The genes located in the most shared privateROH for each breed are presented in Table S3.

Candidate regions highlighted by both XP-EHH and Rsb approaches for each comparison are reported in Table 4 and presented as Manhattan plots in Figures S1 and S2. The genes located in these selection signatures are described in Table S4.

Finally, we compared selection signature findings by breed, identifying those regions where multiple methods identified a result (Table S5 for PAG and SAR, and Table S6 for IST).

3.3. Milk production

All three breeds in this study produce milk, which is used to make cheese, so we especially anticipated finding ROH with candidate genes and QTL associated with milk production traits. One of the shared ROH amongst the three breeds (OAR12, from 767,946 to 4656,965 Mb) contained two genes associated with milk production (Dhorne-Pollet et al., 2012; Alipoor et al., 2023). There was also a privateROH on OAR19 (37,135,230–41,206,522 bp) identified in 41 SAR animals that overlapped with four significantly enriched ($P < 0.05$) QTL associated with milk fat yield (Li et al., 2020). Also with the XP-EHH and Rsb methods, in the SAR-IST comparison, the IST breed overlapped with two significant QTL described as milk fat yield, whereas, in the IST-PAG comparison, the same breed overlapped with the two milk fat yield QTL, with one associated to milk yield persistency.

3.4. Meat production

Lambing is needed for a new lactation to begin in sheep, so although the focus for these populations is the production of milk, lambs are born in the process. Selection pressure could likely have favoured animals with better meat production qualities, thus we expected to find selection signatures also related to these traits. Amongst the identified shared ROH, one mapped on OAR12 and overlapped with five QTL that were significantly enriched for meat color, muscle pH, and shear force terms, whereas the second, on OAR17, overlapped with one QTL associated with body circumference. In the shared ROH on OAR12 we identified ten genes that have been associated with meat traits in sheep, such as muscle and adipose tissue development, feed intake, post-weaning average daily gain, and fat deposition (Jiao et al., 2022; Kizilaslan et al., 2022; Lin et al., 2023; Fonseca et al., 2023; Gao et al., 2024; Zhang et al., 2024), whereas in the second (on OAR17), three genes were associated with fat deposition (Fonseca et al., 2023a) and post-weaning average daily gain (Kizilaslan et al., 2022).

PrivateROH in PAG revealed an ROH on OAR2, shared by 24

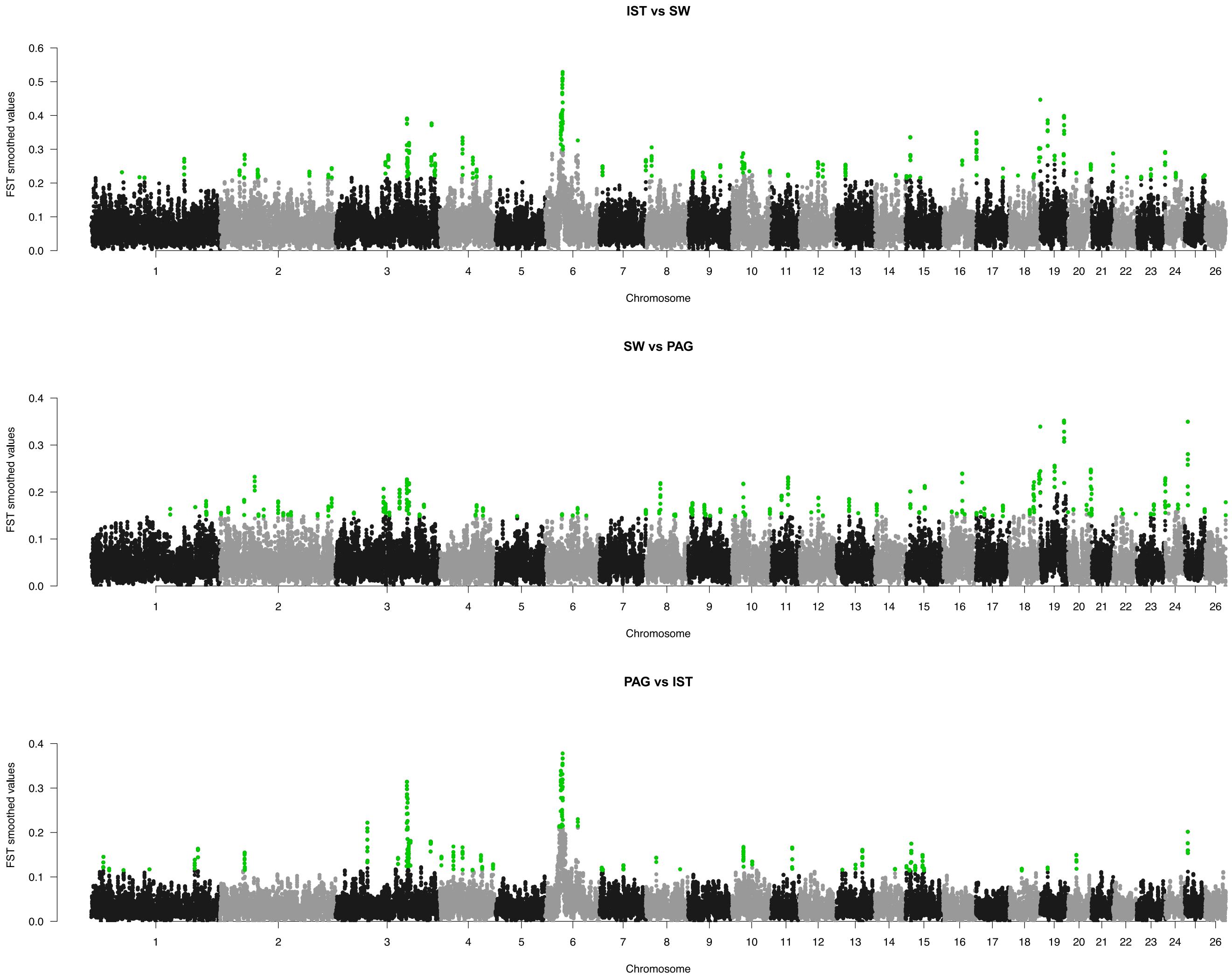

Fig. 3. Manhattan plot of the Wright's fixation index (FST) smoothed values with comparisons from Istrian (IST) versus Sarda (SW) sheep, SW versus Pag (PAG) sheep, and PAG versus IST.

Table 3
Most shared runs of homozygosity (ROH) within each breed (privateROH).

Breed	Chromosome	Region (bp)	Animals	QTL[1]	Genes[1]
Istrian	6	33,262,143–39,505,603	42 (%)	126	24
	9	10,672,443–12,215,743	42 (%)	2	–
Pag	2	52,629,166–54,056,372	24 (%)	2	30
	3	183,633,309–184,848,268	23 (%)	1	7
Sarda	19	32,904,704–34,135,331	68 (%)	–	4
	19	37,135,230–41,206,522	41 (%)	4	11

[1] Number of genes and QTL mapped ±250 kb upstream and downstream from identified regions.

animals, that overlapped with two significant QTL associated with body weight (Cinar et al., 2020). Within this ROH, three genes have been associated with meat production traits in sheep: ewe mature weight (Cinar et al., 2020) and meat quality (Revelo et al., 2023). On OAR3, another privateROH in PAG contained two genes which have been previously associated with weaning weight (Abousoliman et al., 2021).

In the SAR privateROH we identified genes associated with productivity for meat (Krivoruchko et al., 2021), feed restriction response (Reed et al., 2022), and growth traits (Kizilaslan et al., 2022; Liu et al., 2024). Using XP-EHH and Rsb techniques, in the selection signatures identified in the SAR-PAG comparison, there were genomic regions in SAR which overlapped with four significant QTL: one on OAR9 and two on OAR19 were associated with water holding capacity (a meat and carcass trait), whereas the other one on OAR19 was associated with the Kleiber ratio (growth efficiency). Genes in these signatures of selection have been associated with body weight of young rams (Wang et al., 2023), meat production (Krivoruchko et al., 2023), average daily gain (Pasandideh et al., 2018), feed restriction response (Reed et al., 2022), and growth traits (Kizilaslan et al., 2022; Liu et al., 2024).

Several ROH and signatures of selection in IST were associated with meat production. In the F_{ST} analysis where SAR and IST were compared, 122 significant QTL were identified related to meat and carcass traits, and body conformation, whereas in the PAG-IST comparison, there were 121 significant QTL which also included those associated with meat and carcass traits, and body conformation.

The XP-EHH and Rsb analyses identified selection signatures in IST

Table 4
Candidate regions identified by both cross-population extended haplotype homozygosity (XP-EHH) and ratio of extended haplotype homozygosity between populations (Rsb).

Confrontation	Breed	Chr	Region (bp)	QTL[1]	Genes[1]
SAR vs PAG	SAR	9	33,559,587–33,620,900	–	1
			35,414,967–35,640,409	1	2
		19	32,782,456–32,904,704	–	6
			33,487,599	–	1
			34,198,929–34,481,909	–	2
			35,395,602–35,553,063	–	3
			36,091,168–36,564,593	2	1
			37,168,538–37,180,886	–	2
			38,128,930–38,146,216	1	2
			39,033,451–39,397,750	–	3
SAR vs IST	IST	6	31597,111–31878,668	2	2
			33,894,508–35671,914	4	3
			36,903,742	8	9
			37,533,595	15	3
			37,883,086–40,597,982	91	8
IST vs PAG	IST	3	155,245,905–155446,364	–	6
			155,892,944–156326,520	1	4
			158,040,270–158396,272	–	1
		6	29,689,846–30,128,325	3	2
			30,848,277–33,282,642	3	5
			33,873,847–35,715,656	4	3
			36,721,300–36,946,226	8	9
			37,344,980–37,630,085	15	8
			37,883,086–40,742,705	91	9
			41,661,723–42,185,254	1	1
			42,910,315	–	1
			43,168,704–43,538,458	–	–

[1] Number of genes and significantly enriched QTL mapped ±20 kb upstream and downstream of identified regions.

(from the SAR-IST comparison) which overlapped with 120 significant QTL, of which 35 were associated with body weight, 21 with height, 21 with body length, 20 with shin circumference, three with total bone, eight with bone area, five with fat weight in carcass, and five with total fat area. The selection signatures identified for the IST breed in the IST-PAG comparison were very similar to those already identified by the SAR-IST comparison and overlapped with 126 significant QTL divided into 12 terms which included: body height (21), body length (21), body weight (36), shin circumference (20), total bone (4), meat omega-3 fatty acid content (1), bone area (8), fat weight in carcass (5), total fat area (4), and total lambs born (3).

In IST we identified one region on OAR6 (33.26–46,31 Mb) that was found to be a selection signature with all the techniques we employed in this study (i.e., privateROH, F_{ST}, Rsb and XP-EEH). This region overlapped with 130 significant QTL, divided into eight terms related to production and meat and carcass: body height (21 QTL), body length (21), body weight (40), bone area (11), fat weight in carcass (6), shin circumference (20), total bone (7), and total fat area (4). This region on OAR6 contained 39 genes (Table S6). With regards to meat production traits, genes were previously found to be associated to monthly weight and feed efficiency (Li et al., 2024), adipogenesis and fat metabolism (Zhou et al., 2017), fat deposition (Mastrangelo et al., 2019), adult weight (James et al., 2022), and meat (Suhendra et al., 2024) traits. Finally, three genes were related to live weight (Ramos et al., 2023), three to birth weight (Mohammadi et al., 2020), 13 to body weight (Al-Mamun et al., 2015; Khazaei-Koohpar et al., 2024), and eight genes have been associated with growth traits (Matika et al., 2016; La et al., 2019; Feng et al., 2020; Li et al., 2023). Among the genes already associated in literature with growth traits in sheep, the *NCAPG* and *LCORL* must be mentioned since they are usually reported together in selection signatures found by a large number of studies on sheep (Kijas, 2014; Rochus et al., 2018; Yurchenko et al., 2019; Posbergh and Huson, 2021; Ceccobelli et al., 2023).

3.5. Adaptation

While the three breeds have a primary focus on dairy production and secondary focus on lamb production, we did expect to find other historic and adaptive signatures of selection. At one time, fibre production was important, and all three breeds are believed to have been crossed with Merino sheep, known for their wool production (Porter et al., 2016; Putinja, 2005; Drzaic et al., 2022).

Three genes associated to wool production (Liu et al., 2018; Li et al., 2020; Zhang et al., 2023) were found in the ROH shared between the three breeds mapped on OAR12. A gene associated with dermal fibroblasts functions important for wool fiber determination mapped in the other shared ROH (OAR17; Li, S. et al., 2020). A privateROH (on OAR2) with two genes associated with wool production (Anaya et al., 2024) and hair follicle morphogenesis (Yang et al., 2019) was identified in IST breed, and for the same breed a signal from XP-EHH and Rsb analyses with a gene associated with wool fiber properties (He et al., 2021) was found on OAR3. Of particular interest, in the region on OAR6 (33.26–46, 31 Mb) that was found in IST using all the different methods (i.e., privateROH, F_{ST}, Rsb and XP-EEH) mapped nine genes associated with wool quality (Ramos et al., 2023).

A privateROH on OAR19 with a gene associated with productivity for wool (Krivoruchko et al., 2021) was found in SAR. For the same breed, also a signal from XP-EHH and Rsb analyses identified two genes: the one associated with productivity for wool (Krivoruchko et al., 2021) already identified by the private ROH on OAR19, and another one mapped on OAR9, associated with wool and hair follicle morphogenesis (Li, S. et al., 2020).

Functional traits like those related to reproduction and resistance to diseases are important for the sustainability of a breed. Among the ROH shared between the three breeds, the one on OAR12 contained six genes associated with fertility traits in sheep (Caraty et al., 2007; Zhang et al., 2017; Song et al., 2022; Safhi and Ateya, 2023; Ren et al., 2024; Song et al., 2024), and 10 genes associated with reproductive traits in other species of interest (Gaddis et al., 2016; Card et al., 2017; Melo et al., 2018; Fonseca et al., 2020b; Pan et al., 2021; Tahir et al., 2021; Mota et al., 2022; Qin et al., 2024). Additionally, in PAG sheep a privateROH (on OAR2) containing one gene associated with oocyte maturation (Rouhollahi Varnosfaderani et al., 2020) was found.

Several candidate genes and overlapping QTL associated with disease resistance were highlighted in the present study. In the shared ROH among breeds on OAR12, 14 genes associated with immunity traits in sheep, such as response to *Fasciola hepatica*, paratuberculosis, bluetongue, and other environmental pathogens and parasites (Rincheval-Arnold et al., 2002; Ingham et al., 2008; Gossner et al., 2017; Pisanu et al., 2018; Chitneedi et al., 2021; Niedziela et al., 2021; Soares et al., 2021; Lu et al., 2022), were located. Additionally, there were 15 other genes in this ROH that were previously associated with immunity traits in other livestock species such as cattle and goats (Bhuiyan et al., 2017; Moré et al., 2019; McConnel et al., 2020; Olech et al., 2021; Soares et al., 2021; Chai et al., 2022; Mantilla Valdivieso et al., 2022; Urbańska et al., 2022). For PAG, a privateROH on OAR2 contained a gene associated to antigen defense (Berton et al., 2017) and another associated to infection response (Zhang et al., 2024). A privateROH identified in 42 IST animals on OAR 9 overlapped with two QTL related to maedi-visna virus susceptibility (White et al., 2012), although this ROH does not overlap with any genes. Additionally, the region on OAR6 (33.26–46, 31 Mb) that was found in IST using different analyses, contains a cluster of 11 genes that have been associated with gastrointestinal parasite resistance (Vera et al., 2024).

The Mediterranean basin is characterised by hot summers, and breeds like PAG can live in harsh environments (e.g., strong wind) with poor pasture quality. Selection signatures associated with environment and adaptation were therefore expected. Five genes associated with adaptation (Fam et al., 2018; Wang et al., 2022; Zhang et al., 2022; Luna-Ramirez et al., 2023; Wang et al., 2023; Yudin and Larkin, 2023) mapped in the ROH on OAR12 was shared among the three breeds. Additionally, for each of the three breeds there were unique findings: a privateROH on OAR2 for PAG containing a gene associated with heat tolerance (Wang et al., 2019); a privateROH on OAR19 for SAR containing genes associated to adaptation in the tropics (Yaro et al., 2019) and to cold season nutrient stress (Liu et al., 2023); and a selection signature in IST on OAR3 containing a gene associated with heat stress response during spermatogenesis (Song et al., 2022).

4. Conclusions

Different techniques, such as ROH, F_{ST}, Rsb and XP-EHH, were used to identify selection signatures. The across breed analysis highlighted shared genomic regions that harbour genes associated with milk and meat production, adaptation and functional traits, thus reflecting the common evolution of the Sarda (SAR), Pag (PAG), and Istrian (IST) sheep breeds due to natural and artificial selection. For example, two ROH shared by at least 10 animals of each breed were found on OAR12 and OAR17, respectively. The genes mapped in these two shared runs were mainly associated with immune traits, fertility, and meat production. Moreover, each breed showed some private signatures of selection for different traits that reflected specific genetic adaptation. Interestingly, all the employed techniques (i.e., privateROH, F_{ST}, Rsb, and XP-EHH) identified the same genomic region, on chromosome 6, only for the Istrian breed. Thus, it could be hypothesized that the selection pressure on this signature has been particularly strong. In this specific genomic region, genes previously associated with meat production, wool quality, and resistance to parasites were mapped. Besides this common result for the Istrian breed, the four techniques used in this study led to different results, and this highlights how they have different sensibilities to selection signatures and that there is not one method to identify all selection signatures. Moreover, the selection signatures found could be a starting point for further analysis regarding important traits, both among and within populations, such as fitness, adaptability and immunity, particularly focusing on their value in an ever-changing environment.

CRediT authorship contribution statement

Jelena Ramljak: Writing – review & editing, Project administration, Data curation. **Ante Kasap:** Writing – review & editing, Project administration, Data curation. **Marija Špehar:** Writing – review & editing, Project administration, Data curation. **Alberto Cesarani:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Formal analysis, Data curation, Conceptualization. **Nicolò Pietro Paolo Macciotta:** Writing – review & editing, Supervision, Project administration, Data curation. **Ivan Pocrnic:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Data curation, Conceptualization. **Laura Falchi:** Writing – review & editing, Writing – original draft, Formal analysis. **Christina Marie Rochus:** Writing – review & editing, Writing – original draft.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.smallrumres.2025.107654.

Data availability

The genotypes of PAG and IST breeds used in this study belong to the Croatian Agency for Agriculture and Food. Restrictions apply to the availability of these genotypes, which were used under license for this study.

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