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Genomic scans for selection and runs of homozygosity in southern Italian turkey populations

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ABSTRACT

Basilicata and Apulian (BAS-APU) turkeys, a native population in the Basilicata and Puglia regions of southern Italy, are known for their high meat quality and tolerance to local conditions. Understanding the genomic patterns of BAS-APU turkeys is critical for effective breeding and preservation strategies. In this study, we characterized runs of homozygosity (ROH), and selection signatures using the integrated haplotype score (iHS) and ROH approaches. A total of 73 BAS-APU turkeys from five populations were sequenced (12X). The inbreeding coefficients based on ROH ranged from 0.177 to 0.405. A total of 120,956 ROH were detected in BAS-APU populations. We identified 27 genomic regions that harbor 61 candidate genes in ROH islands in which single nucleotide polymorphisms (SNPs) occur in more than 90 % of individuals. In addition, we detected 608 genomic regions under positive selection using the iHS method being 104, 98, 130, 102, and 174 for BAS, APU_C, APU_M, APU_PN, and APU_PS, respectively. For both methods, most of the genes within these regions are related to production performance, reproduction, immune responses, and adaptation. This study contributes significantly to our understanding of the genetic makeup of native turkey populations in southern Italy. The identified genes under selection can aid future breeding and conservations programs for southern Italian native turkeys. The results of inbreeding levels, especially in the absence of complete pedigrees or when only a few samples are available, which is often the case for local breeds, will help to avoid genetic relatedness in the mating plan in breeding and conservation plans for BAS-APU populations. Also, the detected genes in the selective sweep regions could be used as a marker-assisted selection to improve productive traits and adaptation of BAS-APU local populations.

Introduction

Domesticated turkeys are valuable agricultural animals and an important source of meat. Turkey is the second most popular poultry meat worldwide (Baéza et al., 2022). Its superior and cost-effective properties make it the preferred source of meat at various geographical latitudes of the world (Hristakieva, 2021). Europe contributed 37.2 % of the world's turkey meat over the last five years (FAO, 2023). All domesticated turkeys (*Meleagris gallopavo*) originated from wild turkeys in North and South America (Aslam et al., 2014). According to Zeder (2006), animal domestication is a long process of human-animal interaction that leads to a continuous series of states from wild to fully domesticated animals. Although morphological and genetic changes within a species may result from this relationship throughout time, these changes often take place at different points in the domestication process (Zeder, 2006). Turkeys were introduced in Europe, including Italy at the

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beginning of the 16th century from the Spanish colonies in Central America. They were brought to Italy in 1520 and their rapid spread, especially in the south, confirms their integration into the Italian agricultural and culinary heritage (De Grossi Mazzorin and Epifani, 2016; Maltin and Jakobsson, 2023). Bone remains, also indicate that they were used for food starting already in 1600, and they are described in cooking recipes of the time (Eiche, 2004; De Grossi Mazzorin and Epifani, 2016).

Indigenous Italian turkey breeds are a source of genetic variability that must be preserved and exploited. These native turkey breeds have unique production traits, are resistant to disease and adapted to local conditions (Bernini et al., 2021; Marelli et al., 2022). Selection within the Italian breeds carried out by farmers during the last five centuries has resulted in the prevalence of strong variation in feather colors, body dimensions and weights, leading to differentiation between breeds (Marelli et al., 2009; Colli et al., 2011; Marelli et al., 2022). These divergences may also have been facilitated by Italy's geopolitical structure in the Middle Ages, characterized by a division into a vast number of minor states with highly restricted exchange of products and populations, resulting in each turkey population being genetically isolated from the rest (Strillacci et al., 2019). Basilicata and Apulian turkeys (BAS-APU) are raised in the Basilicata and Puglia regions of southern Italy. They have different plumage colors: buff, and black with streaks of buff or white. The body weight of adult birds is up to 8 kg for males and 4 kg for females. They lay 50 to 60 eggs per year. BAS-APU populations are rustic and adapted to local climate conditions. These unique traits of local breeds will help them adapt to climate change conditions and increase production to ensure food security. Local breeds also represent a key element of diversity to achieve resilience (Restoux et a., 2022). Therefore, a more sustainable paradigm for genetic improvement of animals that can adapt to climatic change (like greater temperatures) and agricultural practices (like free range, local forages, etc.) must be developed (Hoffman, 2010). In this regard, conventional local poultry breeds can serve as an important source of genetic variety for upcoming breeding programs (Notter, 1999; Restoux et a., 2022).

Whole genome sequencing allows for monitoring genomic variability within and across populations, examining the distribution of both homozygosity and heterozygosity within genomes (Aslam et al., 2012; Bernini et al., 2021), and identifying genomic regions and genes that have undergone selection (Aslam et al., 2014; Strillacci et al., 2020; Bello et al., 2023). The challenges facing local breeds stem from small population sizes and the lack of appropriate breeding programs. Consequently, the mating of related individuals increases resulting in inbreeding and leading to decreased performance due to increased homozygosity, a phenomenon known as inbreeding depression (Hedrick and Garcia-Dorado, 2016). Thus, genome-wide analyses have been proposed to detect inbreeding levels in different turkey breeds, such as the estimating the genomic inbreeding coefficient based on runs of homozygosity (F_{roh}) (Marras et al., 2015; Bernini et al., 2021; Adams et al., 2021).

Domestication and selection are the major driving forces responsible for the determinative genetic variability in breeds. The strong selection for specific phenotypes of different productive traits (Almeida et al., 2019; Adams et al., 2021) has resulted in selection for specific genomic regions also known as selection signatures (Strillacci et al., 2018). Selection signals can be described as the reduction, removal, or adjustment in genetic variation in genomic areas proximal to causal variants in response to either natural or artificial selection pressures (Aslam et al., 2014). Such variations commonly influence numerous features and contribute to breed formation (Sallam et al., 2023). Nowadays, runs of homozygosity (ROH) and integrated haplotype score (iHS) methods are used to identify selection signatures in turkey and other livestock species (Mastrangelo et al., 2017; Bernini et al., 2021; Saravanan et al., 2021; Sallam et al., 2023). ROH consists of homozygous genomic segments that occur when two haplotypes are derived from a common ancestor (Rostamzadeh Mahdabi et al., 2021; Tian et al., 2023). ROH is a useful tool for both detecting selective sweeps and estimating the inbreeding coefficient (Marras et al., 2015; Strillacci et al., 2020; Adams et al., 2021). Strillacci et al. (2020) identified short ROH involving genes associated with abdominal fat and egg traits in commercial and Mexican turkey breeds. Bernini et al. (2021) detected some genes in a ROH island that could be subjected in selection on chromosome 10 including *PTGS2* and *PLA2G4A* genes related to reproduction efficiency traits in seven Italian breeds.

Statistical analysis based on proportion extended haplotype homozygosity (EHH) is considered more accurate than single allele frequency methods in identifying regions with high homozygosity (Sabeti et al., 2007). Among these EHH-derived statistics, iHS, a within-population test, is the most prevalent (Bello et al., 2023). This method has been successfully applied to identify selection signatures in various species, including chickens (Fleming et al., 2016; Fleming et al., 2017; Mastrangelo et al., 2017), sheep (Gouveia et al., 2017; Saravanan et al., 2021; Karabas and Yilmaz, 2024), goats (Sun et al., 2023), and cattle (Gautier et al., 2017; Wang et al., 2019; Ben-Jemaa et al., 2020). These studies have contributed to critical predictions for genetic resource conservation and breeding programs (Abied et al., 2020). Further studies are needed to identify selection signatures in Italian turkey breeds and in the current study we present ROH, estimates for F_{ROH}, and selection signatures using ROH and iHS methods in BAS-APU turkey populations.

Materials and methods

Animals and sampling

The Basilicata population (BAS) is reared on a farm in the mountains in Potenza, Basilicata, Italy. The Apulian M (APU_M) and Apulian PS (APU_PS) populations were raised in two small farms in Potenza, Basilicata, Italy. The Apulian PN (APU_PN) and Apulian C (APU-C) were raised in two small farms located in Brindisi and Lecce, Puglia, Italy, respectively, as presented in Fig. 1. A total of 73 blood samples (approximately 2 mL each) were collected from the wing veins of Basilicata (46), Apulian M (7) and Apulian PS (8) populations Apulian PN (7) and Apulian C (5). The samples were stored in Vacutainers® tubes containing EDTA as an anticoagulant. More details about populations and sampling were mentioned in our pervious manuscript (Saleh et al., 2025).

Sequencing, mapping and variant calling

DNA extraction and whole genome sequencing (coverage = 12X) were assessed at Neogen (Ayr, Scotland, UK) using a commercial kit. The Burrows-Wheeler Aligner BWA-MEM v0.7.17 (Li and Durbin, 2009) was used to align raw reads to a new turkey reference genome assembly [Meleagris gallopavo (Turkey) – GCA_905368555.1 (MGAL_-WU_HG_1.0)] (Barros et al., 2023), resulting in a BAM file for each animal. Subsequently, these BAM files were sorted and indexed using SAMtools v.1.9 (Li et al., 2009) and processed to remove duplicate reads using the Samtools dedup function (Li et al., 2009). Mapping statistics outputs were generated using Qualimap (Okonechnikov et al., 2016).

Variant calling was conducted using Freebayes software (Garrison and Marth, 2012). Thresholds set for the variant calling were a minimum base quality of 10, minimum fraction of the alternate allele of 20 %, and minimum alternate count of 2. The variant call format (VCF) files of the BAS populations were converted to plink files using PLINK v1.9 software (Chang et al., 2015). Additional filtration was conducted using Bcftools (Danecek and McCarthy, 2017). Samples with a missing call rate of more than 90 % were filtered. After filtration, a total of 5,104,710 single nucleotide polymorphisms SNPs and 73 birds were left for the analysis.

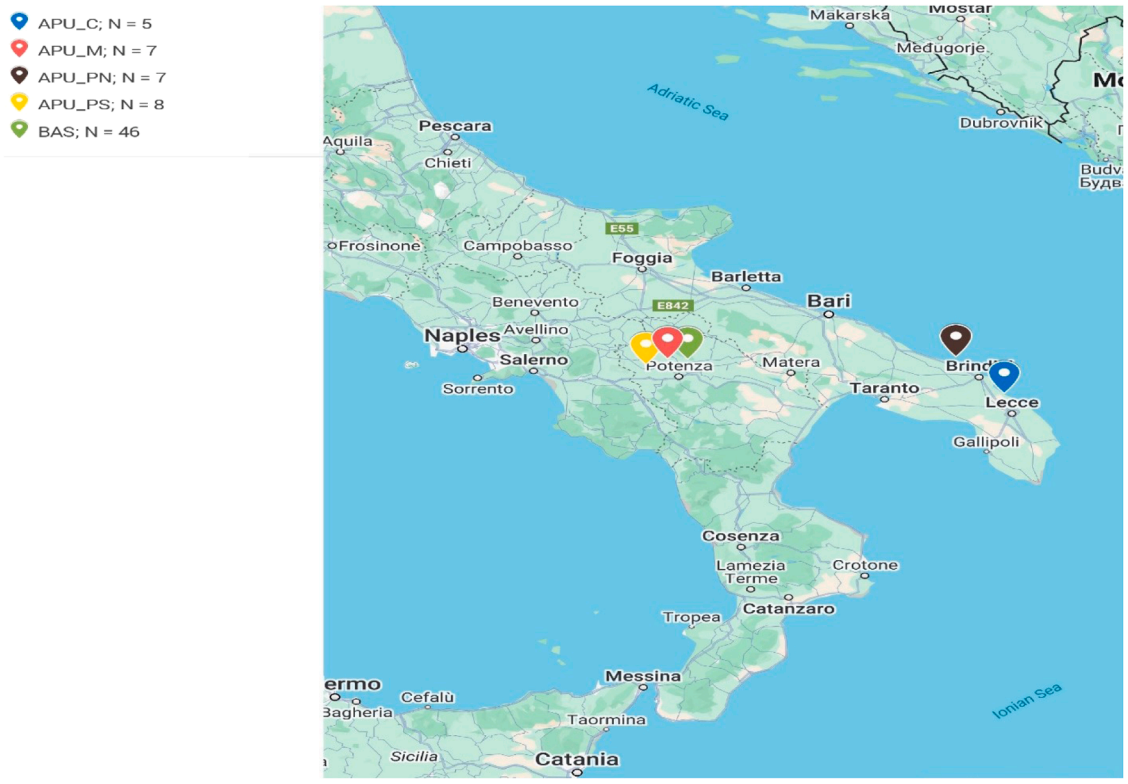

Fig. 1. Map showing the location of sampling for Italian turkey populations. APU_C = Apulian C population; APU_M = Apulian M population; APU_PN = Apulian PN population; APU_PS = Apulian PS population; BAS = Basilicata population; N = Number of birds.

Population structure and genetic diversity indices

The principal component analysis (PCA) was investigated using PLINK v.1.9 software (Chang et al., 2015), and visualized using the R package ggplot2 (Wickham et al., 2016). The observed and expected heterozygosity (H_o and H_e), and minor allele frequency (MAF) were calculated using PLINK v.1.9 software (Chang et al., 2015). The average and standard deviation for each population were estimated using R (R Development Core Team, 2017).

Genome wide detection of ROH

The PLINK v1.9 software command –homozygous (Chang et al., 2015) was used for the detection of ROH, using the following settings for ROH identification as recommended by (Ceballos et al., 2018): –homozyg-kb 100 –homozyg-window-missing 5 –homozyg-window-threshold 0.05 –homozyg-window-het 1 –homozyg-window-snp 50 –homozyg-snp 50 –homozyg-density 50 –homozyg-gap 100. The detectRUNS R package was used to visualize the results (Biscarini et al., 2018). The detected ROHs were divided into 4 categories: 0.1 to 0.25 Mb, 0.25 to 0.5 Mb, 0.5 to 1 Mb, 1 to 2 Mb and >2 Mb (Sun et al., 2024; Wang et al., 2024). These size classes correspond to approximately 250-500 generations, 100-250 generations, 50-100 generations, and 50 generations ago, respectively (Ferenčaković et al., 2013; Signer-Hasler et al., 2022). The total number and mean number of ROH for each animal, the number and mean length of ROH per population per chromosome, and the number of ROH per length category were calculated.

Inbreeding coefficients estimation

Two methodologies were used to estimate inbreeding coefficients based on ROH (F_{roh}) and based on the assessment of observed and expected homozygosity (F_{hom}). F_{roh} was calculated using the detectRUNS R package (Biscarini et al., 2018). F_{roh} is defined based on the proportion of the total length of genome that is within ROH in a bird genome (1,000,000,000 bp in the MGAL_WU_HG_1.0) (McQuillan et al., 2008). F_{hom} for all individuals was estimated based on the assessment of observed and expected homozygosity using PLINK v1.9 software (Chang et al., 2015).

Genome wide detection of selective sweeps

First, we used the ROH method to detect selection signals within the BAS-APU populations. The proportion of SNPs present in the ROH was computed by calculating the number of occurrences of each SNP in the ROH and dividing this by the total number of birds. This result was visualized using the R package qqman (Turner, 2018). The threshold for positive selection signals was defined as SNPs that appeared in more than 90 % of the individuals within a ROH island across all populations.

Second, we used iHS to identify selection signatures for each population separately. We used PLINK v.1.9 software (Chang et al., 2015) with the command –indep-pairwise 10 10 0.3 to conduct linkage equilibrium pruning (r2>0.3) to reduce computing time, resulting in 1,717,694 million variants covering the entire genome. The genotype phasing program Beagle v5.0 was used with default criteria to phase and impute missing genotypes (Browning et al., 2018). This test is based on the decay of extended haplotype homozygosity, computed for ancestral (0) and derived alleles (1) at each core SNP (Voight et al., 2006). The standardized iHS was performed as:

$$iHS = \frac{In\left(\frac{iHH_A}{iHH_D}\right) - E_p\left[In\left(\frac{iHH_A}{iHH_D}\right)\right]}{SD_p\left[In\left(\frac{iHH_A}{iHH_D}\right)\right]}$$

Where iHH_A and iHH_D denote the EHH score for ancestral and derived core alleles, respectively. $E_p\left[In\left(\frac{iHH_A}{iHH_D}\right)\right]$ and $SD_p\left[In\left(\frac{iHH_A}{iHH_D}\right)\right]$ represent

the expectation and standard deviation within the frequency bin *p*.

The iHS scores were calculated for each SNP using the R package rehh (Gautier et al., 2017). The iHs scores were transformed into two-sided p-value using the formula: piHS = $-\log_{10}[1-2|\Phi(iHS)-0.5|]$, where Φ(iHS) is the cumulative Gaussian distribution function of iHS (Gautier et al., 2017). piHS values can be defined as −log 10(− P value), considering that iHS values are normally distributed under neutrality. Since the iHS values are very high for the BAS population compared to the APU_C, APU_M, APU_PN, and APU_PS populations, we set two different thresholds. Significant SNPs were those with piHS ≥5 for APU_C, APU_M, APU_PN and APU_PS populations, and piHS ≥7 for BAS population (P value − = 0.0001).

The complete list of annotated genes for the new reference genome of Meleagris gallopavo was downloaded from Ensembl online database (GCA_905368555.1). The official gene symbol or Ensemble IDs were classified within the identified ROH islands and iHS scores using the intersectBed command of BEDTools software (Quinlan and Hall, 2010).

Results

Population structure and genetic diversity

A total of 6,755,783 variants were detected across all sequenced individuals, of which 5,787,540 were SNPs and 864,174 were InDels. A PCA was conducted to assess the population genetic structure (Fig. 2). PCA1 accounted for 32.7 % of the total genetic variation among the BAS-APU populations, illustrating that the BAS population was separated from the APU_C, APU_M, APU_PN and APU_PS populations. PCA2 explained 15.4 % of the total genetic variance across all the birds in the studied populations. PCA2 showed the APU_C population was distinct from the APU_M, APU_PN and APU_PS populations. Additionally, the APU_M, APU_PN and APU_PS populations were close to each other, with overlap between APU_PN and APU_PS populations.

We estimated parameters of genetic diversity (He, Ho and MAF) (Table 1). APU_C population had the highest measures of Ho (0.339), He (0.243) and MAF (0.188), while BAS population had the lowest means of Ho (0.177), He (0.16), and MAF (0.118). The genetic diversity of the APU_M population was comparable to that of APU_PN population.

Genomic distribution of ROH

The number of ROH identified in APU_C, APU_M, APU_PN, APU_PS and BAS populations were 4,346, 11,059, 11,256 and 10,519 and 83,738, respectively with means of 870 ± 117, 1581 ± 101, 1608 ± 143, 1315 ± 232 and 1821 ± 229 per individual, respectively (Table 2, see Additional file 1: Table S1). The average length of ROH ranged from 187 to 212 kb per population. The minimum length of ROH 187 kb was observed in APU_C population, while the maximum length of ROH 234 kb was detected in BAS population. The largest number of ROH segments was in the category from 0.1-0.25 Mb, while the smallest number of ROH was recorded in class from 1-2 Mb. Only one ROH segment larger than 2 Mb was recorded in APU_C population (see Additional file 1: Table S1). These findings highlight variation among BAS-APU turkey populations in terms of the distribution of ROH, providing insight into genetic variations. The mean length of ROH in Mb per chromosome was plotted for BAS-APU populations (see Additional file 2: Figure S1). Additionally, the percentages of ROH coverage by chromosome were calculated (see Additional file 2: Figure S2). Chromosome 1 had the

Table 1
Population diversity parameters for Basilicata and Apulian turkey populations

Population	N.	Ho ± SD	He ± SD	MAF ± SD
APU_C	5	0.339 ± 0.329	0.243 ± 0.203	0.188 ± 0.177
APU_M	7	0.215 ± 0.27	0.177 ± 0.204	0.136 ± 0.169
APU_PN	7	0.221 ± 0.288	0.172 ± 0.203	0.131 ± 0.167
APU_PS	8	0.264 ± 0.303	0.195 ± 0.209	0.148 ± 0.169
BAS	46	0.177 ± 0.235	0.16 ± 0.191	0.118 ± 0.156

N, number of individuals per population; Ho, observed heterozygosity; He, expected heterozygosity; MAF, average minor allele frequency; The abbreviations of each population were mentioned in Fig. 1.

Table 2
Summary statistics of ROH in Basilicata and Apulian turkey populations.

Population	Min. ROH	Max. ROH	Average ROH N. ± SD	Min. ROH Length (kb)	Max. ROH Length (kb)	Mean ROH Length (kb)
APU_C	729	1014	870 ± 117	166	204	187
APU_M	1369	1672	1581 ± 101	201	224	212
APU_PN	1407	1741	1608 ± 143	200	223	212
APU_PS	987	1685	1315 ± 232	189	218	200
BAS	548	2061	1821 ± 229	164	234	204

Min. is minimum; Max. is maximum; N. is number; For population abbreviations, see Fig. 1.

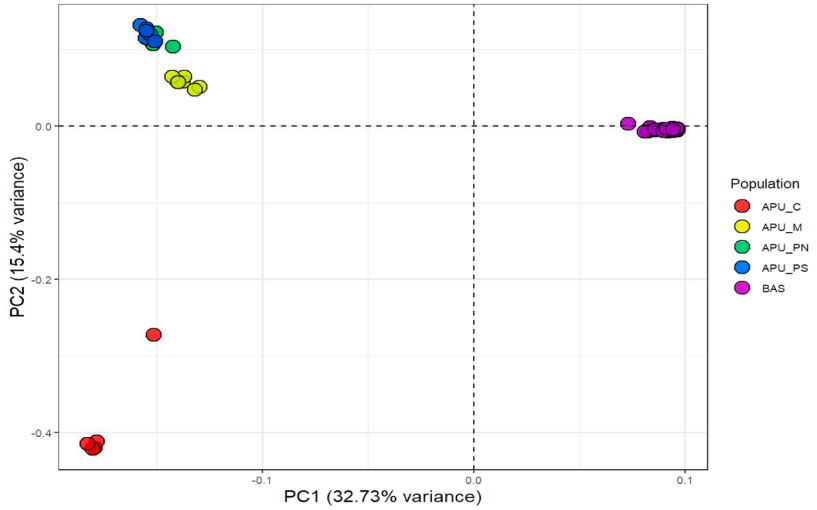

Fig. 2. Principal components analysis of five Italian turkey populations. For population abbreviations, see Fig. 1.

highest percentage of ROH coverage, while chromosomes 27 and 31 expressed the lowest percentage of ROH coverage.

The summary of the overall number of ROH and the overall length in Mb per animal is shown in Fig. 3. Most individuals in the BAS population had the highest number and longest length of ROH. In contrast, the lowest number of ROH and shortest length of ROH were observed in individuals of the APU_C population.

Inbreeding coefficients

The F_{roh} estimates were calculated based on ROH for each population separately (Fig. 4). The F_{roh} scores ranged from 0.177 to 0.405. The highest F_{roh} was recorded for the BAS population, while the lowest F_{roh} value was recorded for the APU_C population. The F_{roh} values per chromosome were estimated for the BAS-APU populations (see Additional file 2: Figure S3). Chromosomes 17 had the largest F_{roh} value in APU_M population and chromosome 22 in APU_PN population ($F_{roh} \sim 0.63$), followed by chromosome 6 ($F_{roh} \sim 0.6$) in BAS. The same trend of F_{hom} was observed for the studied population, and the F_{hom} values ranged from -0.397 in APU_C population to 0.282 in BAS population.

Genome wide selective signatures

The frequency of SNPs in a ROH was calculated for all populations to detect potential genomic regions with selection signatures. Significant ROH islands, defined as SNPs occurring in >90 % of individuals, were identified and visualized in the Manhattan plot (Fig. 5). In total, 27 genomic regions within ROH islands were identified (see Additional file 1: Table S2). These regions comprised 61 genes, with 22 regions containing candidate genes such as *DOCK10, NYAP2* and *COL22A1*. The highest peaks were observed on chromosomes 11 (7.96-8.21Mb), 3 (89.01-89.89Mb), 5 (39.88-40.14Mb) and (44.98-45.12Mb), 4 (12.38-12.45Mb) and 10 (19.24-19.33Mb). These genomic regions and their candidate genes are related to various economic characteristics such as immune response, adaptation, growth performance, nutrition, and productive traits.

The iHS analysis was conducted to detect significant selective sweeps in each population (Fig. 6). Selection signatures were identified using a threshold of the top 1 % [-log10(p-value) > 5] in APU_C, APU_M, APU_PN, and APU_PS populations and [-log10(p-value) > 7] in BAS population (see Additional file 1: Table S3, S4, S5, S6 and S7). In APU_C population, 98 genomic regions displaying selective signals were identified, encompassing 173 genes (see Additional file 1: Table S3). The top selective signals were detected on chromosomes 1 (0.1 to 0.89Mb), 6 (2.26 to 2.64Mb), 7 (2.19 to 2.30Mb), 23 (6.16 to 6.75Mb), 24 (1.54 to 1.55Mb), 27 (2.52 to 2.84Mb), and 29 (1.07 to 1.53Mb) (Fig. 6a). In APU_M population, we identified 208 candidate genes in 130 genomic regions under selection signatures (see Additional file 1: Table S4). These regions included high SNP counts on chromosomes 1 (0.1-0.75, 73.12-738, 152.03-152.88 and 154.0-154.44), 2 (99.43-99.44Mb), 3 (2.13-2.64Mb), 5 (27.47-27.70 and 29.43-29.56Mb), 22 (1.6Mb) and 29 (0.23-95Mb) (Fig. 6b). For the APU_PN turkey population, 102 genomic regions were identified as selective sweeps, encompassing 174 annotated genes (see Additional file 1: Table S5). Noteworthy regions on chromosomes 1 (0.19-0.88Mb), 7 (3.16-3.84Mb), 22 (1.6-1.62Mb) and 29 (2053-2.97Mb) could potentially be significant sweeps (Fig. 6c). We identified 174 regions as selection sweeps, encompassing 122 genes within regions under positive selection in the APU_PS turkey population (see Additional file 1: Table S6). The top peaks of SNPs in the identified regions were predominantly located on chromosomes 1 (0.1-0.82, 3,04-3.16, 73.31-73.81, 154.01-154.41, 157.09-157.98Mb), 3 (20.04-2.82Mb and 42.85Mb), 4 (0.18-0.96Mb), 6 (51.25-51.34Mb), 31 (0.5-0.96Mb) and 33 (0.14-54Mb) (Fig. 6d). These regions included candidate genes associated with production traits. Similarly, in the BAS population, a total of 104 genomic regions and 157 genes were identified (see Additional file 1: Table S7), with top selective sweeps highlighted on chromosomes 1 (0.1 to 0.38Mb, 73.12 to 73.98Mb and 154.01 to 154.41Mb), 3 (1.29 to 1.94Mb and 2.04 to 2.35Mb), 4 (0.13 to 0.92Mb), 5 (29.43Mb and 58.99Mb), 6 (51.28 to 51.30), 8 (0.19Mb), 9 (75.26 to 75.27Mb), 29 (0.91 to 0.95Mb) and 31 (0.5 to 0.96Mb) (Fig. 6e).

Discussion

Genetic diversity and population structure

In this study, whole-genome sequence data from BAS-APU populations in the south of Italy were analyzed to assess genomic diversity and population structure. Principal component analysis (PCA) revealed

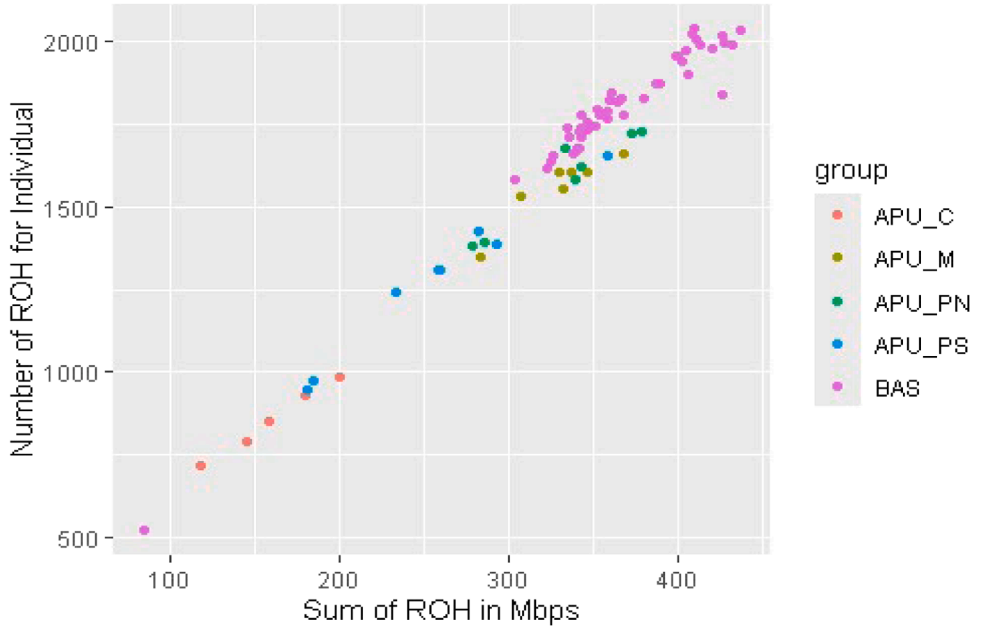

Fig. 3. Sum number of runs of homozygosity (ROH) and total length of ROH in Mb per bird of five Italian turkey populations. For population abbreviations, see Fig. 1.

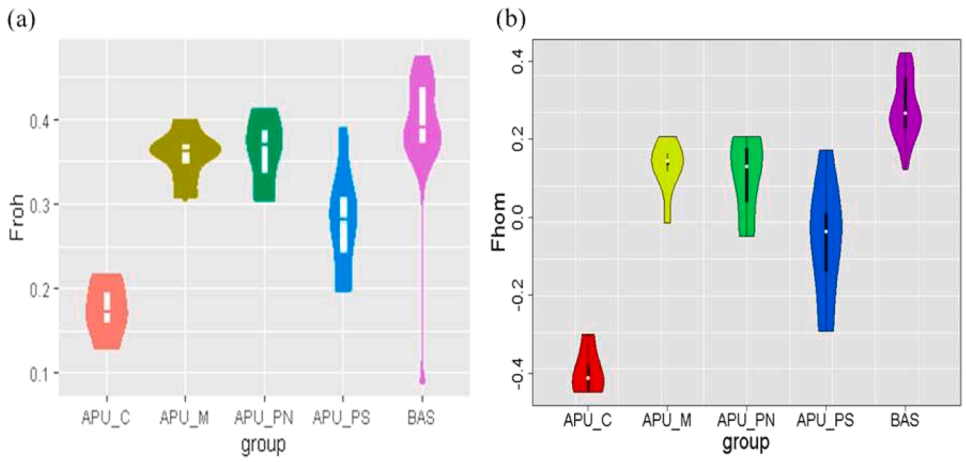

Fig. 4. Inbreeding coefficient in all studied populations. (a) Inbreeding coefficient based on ROH. (b) Inbreeding coefficient based on the observed and expected homozygosity. For population abbreviations see Fig. 1.

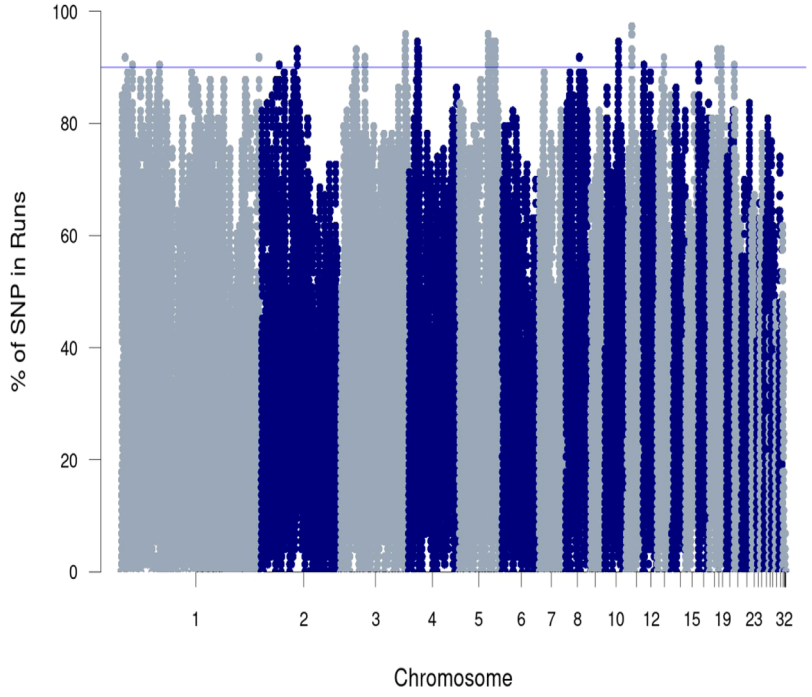

Fig. 5. Manhattan plot of the percentage of SNP in the run of homozygosity across Basilicata and Apulian turkey populations in Italy.

a clear separation of the BAS population from the others along the first principal component, with further differentiation of the APU_C population from APU_M, APU_PN, and APU_PS populations along the second principal component. The isolation of BAS from other populations may be due to the fact that BAS population is raised on a farm in the mountains and also as we have reported the farm has not included new blood for the past 50 years. Additionally, the PCA results suggest a shared genetic makeup among birds within each population. Genomic diversity parameters were used to study genetic differences both between and within populations or breeds (Cendron et al., 2021). The findings indicated that the APU_C population had a higher level of genetic diversity, whereas the BAS population exhibited the lowest level. This disparity in genetic diversity could be attributed to the breeding strategies employed, such as natural and random mating in APU_C population, or potential crossbreeding with other populations (Mpenda et al., 2019). The lower genetic diversity in the BAS population may result from factors such as high inbreeding, genetic drift, and small population size. These observations align with previous studies by Bernini et al. (2021) who identified similar levels of genetic diversity in some Italian turkey breeds. The understanding of the level of genomic diversity and population genetic structure in livestock is important for selection and preservation programs (Baes et al., 2019; Bernini et al., 2021; Cendron et al., 2021). In practical perspective, our findings support the idea that one of the most important factors in preserving genetic diversity is the size of the founder population. However, even in populations that began with a limited number of founders, genetic diversity can be maintained with careful management. We have shown that the inbreeding rate is more affected by the number of families and population size than by picking a large number of male and female founders. Performing such population control requires meticulous pedigree recording and combining breeders into a single, sizable breeding nucleus or a number of smaller, closely related ones. This implies that a significant portion of the original genetic diversity will be preserved.

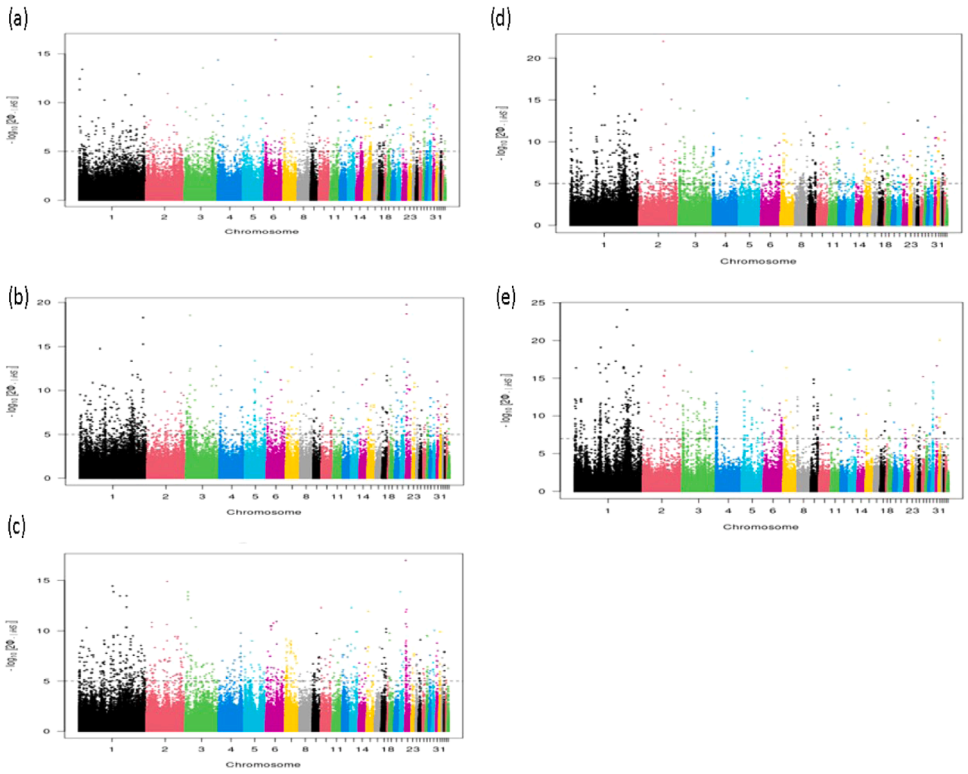

Fig. 6. Manhattan plots of genome wide distribution of standardized (iHS) in Apulian C (a), Apulian M (b), Apulian PN (c), Apulian PS (d) and Basilicata (e) Italian turkey populations.

Runs of homozygosity

In recent years, runs of homozygosity have emerged as an informative approach for providing valuable insights into various aspects of genetic research, including inbreeding coefficient estimation, identification of regions under selection pressure, and demographic history. In this study, ROH patterns in the Italian BAS-APU populations differed considerably (Table 2, see Additional file 1: Table S1). The BAS population had the highest total number of ROH in all categories and the highest mean number of ROH per individual, while the lowest values were observed in the APU_C population. Most of the identified ROH were short (0-0.25Mb) in BAS-APU, enabling high resolution due to the SNP density provided by sequencing. Also, the highest frequency of ROH in individuals and the highest total length of ROH in Mb was detected in BAS population and the lowest frequency and total length were observed in APU_C population. Differences in ROH between populations may be due to breeding and management practices, for example in the BAS population they had a high level of inbreeding as a result of mating between related individuals and thus a large number of ROHs. The low number of ROH in APU_C may be due to the presence of heterozygous individuals. Other studies on ROH in turkeys are based on array data rather than sequence data. Marras et al. (2018) stated that the total mean of ROH is 126.21, and the average ROH length is ~ 1.7Mb in turkey commercial line. Strillacci et al. (2020) identified 1809, 1438 and 355 ROHs in commercial, Mexican_cl_1 and Mexican_cl_2 turkey populations, respectively. Also, they found that the largest number of ROH were recorded for 0-2Mb class in all populations and the highest number and length of ROH per animal was in Mexican_cl_1. Adams et al. (2021) reported that the mean number of ROH per sample was ranged from 81.68 to 87.14 in A, B and C commercial lines. Bernini et al. (2021) identified 20,858 ROH in seven Italian turkey breeds and the largest number of ROH was in the category 1-2Mb. The highest number of ROH in the BAS population could be attributed to factors, such as population bottlenecks, genetic drift, and inbreeding. ROH regions' length plays a crucial role in understanding inbreeding, since longer ROHs are indicative of artificial selection or more recent inbreeding, while shorter ROHs are indicative of earlier inbreeding (Hedrick and Garcia-Dorado, 2016; Adams et al., 2021). In our current investigation, the prevalence of a greater number of shorter ROH segments, particularly notable in the BAS population, could suggest a relatively high level of inbreeding. This observation aligns well with the concurrent findings of low genetic diversity within this population (Bortoluzzi et al., 2018; Cendron et al., 2021; Zhang et al., 2023). The number of ROH on chromosomes differed, with chromosome 1 having the greatest frequency of ROH (see Additional file 2: Table S2). This observation is consistent with previous research indicating a positive correlation between the physical length of chromosomes and the occurrence of ROH (Li et al., 2022; Wang et al., 2024).

Inbreeding coefficients

The evaluation of inbreeding coefficients, F_{roh} and F_{hom} across the BAS-APU populations revealed notable differences. The BAS population had the highest inbreeding value for F_{roh} (0.405), and F_{hom} (0.282), while the APU_C population had the lowest value for F_{roh} (0.177), and F_{hom} (-0.379). Interestingly, chromosomes 27, 30, and 31 consistently displayed the lowest F_{roh} values across the BAS-APU populations (see Additional file 2: Figure S3). The higher level of inbreeding in the BAS group may be due to the smaller number of families and lack of breeding management. The F_{hom} negative inbreeding values in the APU_C and APU_PS groups result from individuals being more heterozygous than expected. These findings align with previous studies (Marras et al., 2018; Strillacci et al., 2020; Bernini et al., 2021; Adams et al., 2021), corroborating the relative high level of inbreeding observed in the BAS turkey population. It underscores the importance of implementing measures to mitigate inbreeding and prevent potential loss of genetic diversity.

Genomic wide signatures of selection

To detect selective sweeps in BAS-APU populations, we used ROH and iHS methods. Notably, there are a number of statistical methods for identifying selection signatures both within and between populations; however, as Liu et al. (2022) point out, each approach has limitations. Consequently, two complimentary statistical techniques (ROH and iHS) were taken into consideration in this work in order to remove false positive results brought on by these restrictions.

Long-term domestication and adaptation have resulted in breed-specific characteristics. The high frequency of ROH segments within the genome provides insight into the genetic foundation of these breed-specific characteristics (Liu et al., 2021). The threshold was set to more than 90 % of the frequency of SNPs in a ROH in all individuals of the five-turkey population. Twenty-seven ROH hotspots were identified as candidate selection signals across the five populations (see Additional file 1: Table S2). Three ROH islands with the highest frequency were located on chromosomes 11 (7.96-8.21Mb), 3 (89.01-89.89Mb) and 5 (39.88-40.14Mb). On chromosome 11, this region harbors the *DOCK10* gene which is associated with the immune response in turkeys (Monson et al., 2015) and broilers (Li et al., 2019). *DOCK10* operates as a GEF for Rac1 and Cdc42 (Ruiz-Lafuente et al., 2015). Consequently, *DOCK10* causes HeLa cells to exhibit elevated ruffling and filopodial activity (Ruiz-Lafuente et al., 2015). *DOCK10* has been linked to amoeboid-like mobility in melanoma cells, which is consistent with its role in cell remodeling (Gadea et al., 2008). The highest levels of *DOCK10* expression occur in circulating leukocytes, mostly T and B cells, and interleukin-4 (*IL-4*) upregulates B cells (Alcaraz-García et al., 2011). NYAP is a family of phosphoproteins that includes *Myosin16/NYAP3, NYAP1,* and *NYAP2*. Developing neurons and the regulated remodeling of the actin cytoskeleton are the primary sites of expression for NYAPs. The *NYAP2* gene (Bernini et al., 2021), which was associated with growth traits in a Yorkshire purebred pig population (Meng et al., 2017). The region on chromosome 5 harbors several potential genes under selection like *TRAPPC9*. The *TRAPPC9* gene is a key member of the nuclear factor kappa B (NF-κB) family, which plays a crucial role in innate immunity and inflammation (Khan et al., 2020). *TRAPPC9* gene is related to daily gains in camels (Bitaraf Sani et al., 2021) and related to milk fat and immunity in cattle (Khan et al., 2022). The *COL22A1* gene has shown significant expression related to heat stress in turkey (Reed et al., 2021). The *KCNK9* gene is involved in the transport of potassium ions (K); The *LRRC38* gene regulates large K (BK) channels, and the *KCNK9* gene facilitates the diffusion of potassium ions through a narrow pore channel (Zhang and Yan, 2014). The *KCNK9* gene is linked to post-partum blood Ca concentration and regulate physiological process in cattle (Hur et al., 2009; Cavani et al., 2022). Another gene on chromosome 5, is *NRXN3*, a gene associated with temperament (Paredes-Sanchez et al., 2019; Ruiz-De-La-Cruz et al., 2023), fertility traits and heat stress in cattle (Reverter et al., 2017; Freitas et al., 2021). These findings suggest that these regions have likely been subjected to strong selective pressures, potentially due to their role in crucial traits such as immunity and adaptation.

The detection of selective sweeps using different approaches could be seen as compelling proof of selection activity in a certain genomic region. However, the absence of evidence from one method does not preclude the possibility of selection occurring in a gene or genomic region (Gouveia et al., 2017). In this study, 834 candidate genes were detected within 608 genomic regions putative under selection in the APU_C (98), APU_M (130), APU_PN (102), APU_PS (174) and BAS (104) populations. We identified a genomic region on chromosome 1 (0.09-0.90Mb) containing 49 candidate genes in BAS-APU populations (see Additional file 1: Table S3, S4, S5, S6 and S7). Among these genes, the *PPP6R2* is related to residual feed intake in Cobb broilers (Liu et al., 2018). Another region on chromosome 1 (73.12-73.98Mb) with 7 candidate genes was detected in APU_M, APU_PN and BAS populations. Within this region, the *ANO2* gene is associated with adaptation in chickens (Verlinden et al., 2022). *ANO2* is also known to act as calcium-activated chloride channel, influencing processes such as transepithelial ion transport, muscle contraction, and phototransduction (Pedemonte and Galietta, 2014; Picollo et al., 2015). Additionally, *ANO2* has been identified as candidate gene associated with metabolic body weight (Hardie et al., 2017), and milk yield during the peak stage of lactation in dairy cows (Connor et al., 2008; Jiang et al., 2019; Zare et al., 2022). We further identified a region on chromosome 1 (154.01-154.41Mb) with 9 genes potentially under selection in APU_M, APU_PS and BAS populations. Among these genes, *MZT1* was found to be significantly associated with breast muscle weight in chickens (Kang et al., 2021). A genomic region comprising 8 genes were identified on chromosome 3 (2.01-2.92Mb) has potentially been under selection in APU_M and APU_PS and BAS populations. The *TPK1* gene plays an important role in metabolism in chickens (Seol et al., 2019), heat tolerance in Nigerian native chickens (Gheyas et al., 2022), as well as organ weight and thiamine metabolic in pigs (Banerjee et al., 2020; Li et al., 2023). On chromosome 29, we discovered a region (0.23-0.97Mb) harboring 12 genes in APU_M and BAS populations. The *ACYP2* gene located at this location has been implicated in heat stress responses (Srikanth et al., 2019), eggshell strength (Liu et al., 2013), and metabolic pathways in chickens (Liu et al., 2020). *ACYP2* has also been associated with body size and growth traits in goats (Zhao et al., 2024). Finally, a region on chromosome 31 (0.5-0.96Mb) containing 35 candidate genes, including *VDR*, which has been shown to be linked to metabolic processes in the ovary and oviduct (Hrabia et al., 2023), as well as Marek's disease resistance in chickens, was detected in APU_PS and BAS populations.

Conclusion

The findings of this study provide valuable insights into the inbreeding levels and genetic architecture of southern Italian turkey populations. By employing run of homozygosity and integrated haplotype score methods, we identified several selective sweeps, highlighting regions of the genome under positive selection. The candidate genes within these genomic regions are associated with key traits, including production, reproductive capabilities, immunity, heat stress response, and feather formation. Notably, some of these genes are involved in heat stress adaptation, a particularly relevant trait in the southern Italian environment. Overall, our results enhance understanding of the genetic makeup of these turkey populations. These results provide critical information to guide selection and conservation programs, focusing on preserving genetic diversity and enhancing desirable traits.

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Authors' contributions

Conceptualization: M.S.S and V.L.; Data curation: AC, M.S.S., G.C and P.D.; Formal analysis: M.S.S and M.F.L.D.; Funding acquisition: V.L and A.C.; Investigation: M.S.S., M.F.L.D., M.A.M.G. and V.L.; Methodology: M.S.S., M.F.L.D and V.L.; Project administration: A.C. and V.L.; Resources: P.D and A.C.; Software: M.S.S and M.F.L.D.; Supervision: A.C., V.L. M.F.L.D and M.A.M.G.; Validation: E.C., N.P and E.C.; Visualization: M.S.S and A.C.; Roles/Writing - original draft: M.S.S.; Writing—review and editing: M.F.L.D, M.A.M.G., V.L., P.D., E.C., N.P., E.C., G.C. and A.C.

Ethics approval and consent to participate

All experimental procedures involving the handling of animals were

approved by the Ethical Committee for Animal Experimentation of the Department of Veterinary Medicine, University of Bari Aldo Moro, Italy Prot. N. 2999 – III / 13 (Approval Number: 19/24).

Consent for publication

Not applicable.

Declaration of competing interests

The authors declare no competing interests.

Availability of data and material

The datasets used and/or analyzed during the current study are available at https://www.ncbi.nlm.nih.gov/sra/PRJNA1197539

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Supplementary materials

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