Analysis of Runs of Homozygosity of cattle living in different climate zones

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Lay Summary

Domestication and evolution of cattle originated different modern breeds in different places worldwide. The interaction between natural and artificial selection and the adaptation to environment shaped the genome, and the three different types of cattle here considered (taurus, indicus and composite) may harbor different selection signatures. To study the difference among types and region of origin (tropics, temperate, and continental zones), Regions of Homozygosity (ROH) were used. ROH are continuous homozygous chromosomal segments identical by descendent, which characteristics can give information about inbreeding occurrence and natural and artificial selection. Moreover, it had been investigated which genes were mapped in these regions, and if interesting differences pertaining to environmental adaptation or fitness in general, could be observed.

Teaser Text

Genotypes of 3,263 cattle belonging to 204 different breeds from all around the world were analyzed to investigate patterns of ROH. The results confirmed that ROH can be used to identify selection signatures and, in particular, in this study genes associated with environmental adaptation had been identified.

Abstract

Aim of this study was to analyze the distribution and characteristics of runs of homozygosity in *Bos taurus taurus* and *Bos taurus indicus* breeds, as well as their crosses, farmed all around the word. With this aim in view, we used SNP genotypes for 3,263 cattle belonging to 204 different breeds. After quality control, 23,311 SNPs were retained for the analysis. Animals were divided in seven different groups: 1) Continental taurus, 2) Temperate taurus, 3) Temperate indicus, 4) Temperate composite, 5) Tropical taurus, 6) Tropical indicus, and 7) Tropical composite. The climatic zones were created according to the latitude of their country of origin: i) Continental, latitude ≥ 45°; ii) Temperate, 45°< Latitude >23.26°; iii) Tropics, Latitude ≤ 23.26°. Runs of homozygosity were computed as 15 SNPs spanning in at least 2 Mb; number of ROH per animal (nROH), average ROH length (meanMb), and ROH-based inbreeding coefficients (F_{ROH}) were also computed. Temperate Indicus showed the largest nROH, whereas Temperate Taurus the lowest value. Moreover, the largest meanMb was observed for Temperate Taurus, whereas the lowest value for Tropics Indicus. Temperate Indicus breeds showed the largest F_{ROH} values. Genes mapped in the identified ROH were reported to be associated with the environmental adaptation, disease resistance, coat color determinism, and production traits. Results of the present study confirmed that runs of homozygosity could be used to identify genomic signatures due to both artificial and natural selection.

Keywords: Runs of Homozygosity, Taurus, Indicus, Hybrid, cattle breeds, environmental adaptation

List of Abbreviation

ROH: Runs of Homozygosity

IBD: Identical by Descendent

PCA: Principal Component Analysis

GRM: Genomic Relationship Matrix

GLM: Generalized Linear Model

ROH_{REP}: Repeated Runs of Homozygosity

F_{ROH}: ROH-based inbreeding coefficient

L_{ROH}: ROH lengths per animal

L_{GEN}: Total genome length

SNP: Single Nucleotide Polymorphisms

NCBI: National Center for Biotechnology Information

nROH: Number of ROH per animal

BTA: Bos taurus autosome

Introduction

Modern cattle breeds arise from the extinct wild auroch (*Bos Primigenius*), that has been domesticated about 8.500 years ago in the Fertile Crescent, during the early Neolithic development of pastoralism (Diamond, 2002; Magee & Bradley, 2006). There are two main hypotheses about the origins of *Bos taurus taurus* and *Bos taurus indicus*. The first is that *Bos taurus taurus* derived from *Bos primigenius*, and then *Bos taurus indicus* would have been derived from *Bos taurus taurus* because of artificial selection during pastoral movements to India, in 4000 BC approximately (Magee & Bradley, 2006). The second hypothesis, which is largely accepted, is that modern cattle arose from two different domestications of aurochs, and *B. taurus indicus* would derive from a southern Asian subspecies of aurochs, the *B. primigenius namadicus* (Bradley et al., 1998).

In any case, the modern breeds are the result of a complex interaction between natural and artificial selection, and adaptation to environment (Gautier et al., 2010; Taberlet et al., 2011). *Bos taurus indicus* is characterized by a shoulder hump and is diffused in Eurasia and eastern Africa, whereas *Bos taurus taurus* has no hump and it is diffused mainly in Europe, North and West Africa, and Middle East (Bruford et al., 2003). Indicine cattle usually present larger ears and excess skin across the entire ventral midline, especially around the neck and chest (Utsunomiya et al., 2019). The long exposure to harsh environments shaped their genome, with lower nutritional demands and more adapted to digest low-quality forages (Hennessy et al., 2000; Obeidat et al., 2002).

After indicine and taurine post-Neolithic diffusion across Eurasia and Africa, they have been crossed to obtain hybrids with intermediate characteristics. Because of different evolution histories, the genomes of animals belonging to the three different types (taurus, indicus, and composite) living under distinct environmental conditions, may harbor different selection signatures (Senczuk et al., 2021). Among the techniques used to investigate these signals, Runs of Homozygosity (ROH) are getting an increasing popularity. ROH are continuous homozygous chromosomal segments identical by descendent (IDB) (Gibson et al., 2006). The length of the ROH is a temporal indicator of the inbreeding occurrence: recent inbreeding results in longer ROH, whereas old inbreeding is associated with shorter ROH because recombination events tend to break the segments. ROHs can be also due to either artificial or natural selection because homozygous genotypes arise from the fixation of favorable alleles at selected loci. Different studies have reported relationships between ROH and local adaptation or production and reproduction traits (e.g., Mastrangelo et al., 2017; Doekes et al*.,* 2019; Cesarani et al., 2021; Antonios et al*.,* 2021).

As already mentioned, also the environmental adaptation left traces in the genome of the species. In the literature there are increasing examples of ROH associated to environmental adaptation in different species. Àlvarez et al. (2020) found significant regions in the Djallonkè sheep, a West African local breed, harboring some genes associated to immunity, resistance to infections and to parasites, and response to stress, which are important functions for the adaptation to the environment of the hot-humid and trypanosome challenged area in which this breed is farmed. Peripolli et al. (2020), analyzing the ROH hotspots in indicine and taurine Brazilian cattle breeds, found two genes involved in the temperament and body size traits, which are associated with stress responsiveness and climate condition tolerance, respectively. Other candidate genes were associated with parasite vector resistance, reproduction traits, coat color, and morphology traits. All these traits are related with the local environmental adaptation and could have helped these breeds to overcome the many stressing factors typical of several Brazil environments. Another example of environmental selection signatures in the genome of livestock is the study of Cesarani et al. (2022) about the Sarda dairy sheep breed. These authors analyzed the genome of ewes farmed at different altitude levels (plain, hill, and mountain) and they reported differences in ROH lengths and frequencies among the three groups, suggesting the role of the environment in the evolution of the analyzed breed and the possible existence of different subpopulations.

Given the multiplicity of environments where taurine and indicine breeds (and their crosses) are farmed, it could be of interest to test if relationships among ROH and adaptation reported by analyses carried out at local level can be confirmed worldwide. With this aim in view, we investigated the distribution of ROH in the genomes of several indicine and taurine cattle (and their hybrids) farmed all around the world to characterize the ROH patterns and to detect ROH islands that contain the candidate genes related to specific traits.

Material and Methods

Animal Care and Use Committee approval was not needed as data were obtained from preexisting databases.

Animals and genotypic data

In this study, SNP genotypes for a total of 3,263 cattle belonging to 204 different breeds were available. Genotypes were retrieved from previously published studies (Decker et al., 2014; François et al., 2017; Upadhyay et al., 2017; Ben Jemaa et al., 2018; Ramljak et al., 2018; Mastrangelo et al., 2018; Yurchenko et al., 2018) or online public repository and were merged in a previous study (Mastrangelo et al., 2020). All individuals were genotyped with the Bovine SNP50K BeadChip (v1 and v2). Several of these available datasets contained filtered SNPs; therefore, they did not report all the markers present in the original file (about 54K). In fact, the number of common overlapping markers among the datasets that remained after the merger was about 25K. Breeds with fewer than 3 samples were removed. To reduce the bias from over-represented breeds, data were restricted to a maximum of 30 animals per breed. After these edits and quality control (Mastrangelo et al., 2020), 23,311 SNPs mapping on the 29 autosomes were retained for the analysis (with no imputation). The positions of all retained markers were updated on ARS-UCD 1.3 assembly. Number of animals per breed ranged from 3 to 30, with an average value of 16±7. Breeds originated from all around the world: Asia, Africa, Americas, Australia, and Europe. For each breed, latitude and longitude were retrieved using the centroid of the origin area. Animals were divided in seven groups: 1) Continental taurus, 2) Temperate taurus, 3) Temperate indicus, 4) Temperate composite, 5) Tropical taurus, 6) Tropical indicus and 7) Tropical composite. The three geographic zones were created according to the latitude of the Countries of origin: i) Continental, latitude ≥ 45°; ii) Temperate, 45°< Latitude >23.26°; iii) Tropics, Latitude ≤ 23.26°. Details about the involved dataset are reported in Table S1.

Principal component analysis

The genetic structure of the cattle populations was analyzed using a principal component analysis (PCA), which is a multivariate technique aimed to reduce the total variance of a system is a smaller number of new variables (Morrison, 1976). Individual PCA scores (i.e., new values associated to the animals) are often used to highlight clusters or trends in the investigated dataset. A dispersion plot of the scores of the first two PCs extracted from the genomic relationship matrix (GRM), built according to VanRaden (2008), was used to display the genetic stratification among zones and types. Scores of the first two PCs were compared using an ANOVA test and means were declared significant for P < 0.05 (Tukey HSD test).

Runs of homozygosity

Consecutive ROH were computed using the "*detectruns*" R package (Biscarini et al., 2018). The following parameters were adopted to define a ROH: at least 15 homozygote SNPs in a row covering a minimum of 2 millions base pairs; no heterozygote or missing allowed. These strict parameters were adopted to avoid false ROH calling. Number of ROH per animal (nROH) and average (meanMb) ROH length were computed. A ROH that started and finished at the same positions within chromosome was defined as unique. These unique ROH could be identified in more than one animal; regions found in more than one sample were identified as repeated (ROH_{REP}; Cesarani et al., 2018; Macciotta et al., 2021).

According to McQuillan *et al*. (2008), the ROH-based inbreeding coefficient (F_{ROH}) was calculated for each animal as:

$$F_{ROH} = \frac{L_{ROH}}{L_{GEN}}$$

where L_{ROH} was the sum of all ROH lengths per animal and L_{GEN} was the total genome length covered by SNP (2.48 Gbp).

For each SNP, the ratio between number of animals with a given SNP inside a ROH and total number of animals was defined as SNP_{ROH}. These values were compared among the seven identified groups using an ANOVA test and means were declared significantly different for $P < 0.05$ (Tukey HSD test). SNP were flagged as significant if their SNP_{ROH} exceeded the 99th percentile of the chromosomal distributions (Macciotta et al., 2021). These values led to the use of different thresholds fo each chromosome within each group. According to the SNP_{ROH} values, ROH islands were defined as genomic region with adjacent significant SNPs ±250kb downstream and upstream (Manca et al., 2020).

Gene discovery was carried out in the significant regions highlighted with the ROH_{REP} and SNP_{ROH} analysis. Annotated genes were retrieved from the UCSC Genome Browser Gateway (http://genome.ucsc.edu/) and the National Center for Biotechnology Information (NCBI) (www.ncbi.nlm. nih.gov) databases.

Statistical analysis

The nROH parameter was analyzed using the following generalized linear model (GLM) with a lognormal distribution:

$$\text{nROH} = \mu + \text{GROUP} + \text{bPCs} + \text{e} \qquad [1]$$

where:

μ is the overall mean; GROUP is the fixed effect of the considered group (7 levels; i.e., Continental taurus, Temperate taurus, Temperate indicus, Temperate composite, Tropical taurus, Tropical indicus, and Tropical composite); bPCs are the covariates of the principal components extracted from the GRM associated to variance greater than 1%; e was the residual term.

Differences in the ROH mean length were investigated using the following mixed linear model with a lognormal distribution:

$$\text{meanMb} = \mu + \text{GROUP} + \text{CHROM} + \text{ANIM} + \text{bPCs} + \text{e} \quad [2]$$

where:

μ is the overall mean; GROUP is the fixed effect of the considered group (7 levels; i.e., Continental taurus, Temperate taurus, Temperate indicus, Temperate composite, Tropical taurus, Tropical indicus, and Tropical composite); CHROM is the fixed effect of chromosome (29 levels); ANIM is the random effect of animal (3,177 levels considering animals with at least 5 ROH); bPCs are the covariates of the principal component extracted from the GRM associated to variance greater than 1%; and e is the random residual term. The two random effects were assumed to be normally distributed with parameters $N(0, I\sigma_a^2)$ and $N(0, I\sigma_e^2)$, where **I** is an identity matrix and σ_a^2 and σ_e^2 the variances associated with the animal and the residual random effects, respectively. Mixed models were computed using SAS PROC GLMMIX (SAS Inc. 2012). The effect of PCs were included in all models to account for the population stratification.

Results and Discussion

Principal component analysis

Figure 1 shows the plot of the first two principal components extracted from the GRM matrix. The PC1, which explained 88.18% of the total variance, showed that all the taurus had negative or strictly positive values, whereas indicus were at positive values. As expected, composite showed intermediate values. The PC2 explained about 3.41% of the total variance and it showed all the animals living at Tropics with positive values, or only a little negative in the case of the tropics composite. On the contrary, animals living in the Continental or Temperate zones showed values around 0 or negative. Both PC1 and PC2 scores were significantly different ($P<0.0001$) among the seven considered groups. The plot could be seen as bidimensional triangle and it is similar to the ones reported in comparable studies (e.g., Decker et al., 2014; Mastrangelo et al., 2020; Magnier et al., 2022). In fact, PCA may decipher the geography of the subjects, as it can reflect migrations, isolation by distance, and exchanges among neighboring populations (Reich et al., 2008).

Analysis of Runs of Homozygosity

A total of 136,922 ROHs were found in 3,177 animals (considering the animals with at least 5 ROH). As far as the distribution among the groups is concerned, Continental taurus showed the largest number (47,445 ROH, 35% of the total), whereas Temperate composite the lowest number (2,036 ROH, 1% of the total). The same proportions were found also considering a minimum ROH length of 4Mb instead of 2Mb (data not shown).

Table 1 shows the results of the mixed model analysis for both nROH and meanMb. All the three fitted PCs were significant for both analyzed traits. GROUP was highly significant for both nROH and meanMb (P<0.0001). Temperate indicus showed the highest number of ROH per animal (124.62±17.70), whereas Temperate taurus showed the lowest nROH (27.52±18.44). As far as the mean ROH length is concerned, Temperate taurus showed the largest value (5.90±0.16), whereas Tropics indicus the lowest value (3.90±0.32). The Temperate and Tropics composite showed intermediate values both for the average number of ROH (41.55±11.96 and 48.73±21.16, respectively) and for the mean length (4.45±0.31 and 4.07±0.25, respectively). Nothangel et al. (2010) demonstrated that the number and the length of ROHs in human genomes are correlated with the latitude of their sample origin, although not with the longitude, maybe because the major migrations in Europe have followed a South to North gradient. In goat, Bertolini et al. (2018) reported significant differences for ROH patterns (ROH number and coverage) between the sub-geographical groups with a broad geographic distribution. A study on the pattern of ROH in world-wide sheep populations showed clear differences in the number of ROHs among breeds and regions, ranging from 50 in Southwest European breeds to 5,542 in North European breeds (Nosrati et al., 2021). In the present study, the nROH was moderately and negatively correlated with the latitude of origin (-0.42, P<0.0001); thus, nROH increased as the latitude decreased. In goat, the differences in climate between the Northern and Souther groups have resulted in different ROH lengths and numbers (Cortellari et al., 2021). The relationship between ROH features and environment was also recently observed in sheep (Cesarani et al., 2022) where animals living in hot environments exhibited a higher number of ROH compared to animals living in cold environments. The findings in humans, goat and sheep were confirmed in the present study where the Tropics, i.e., zone with the hotter climate and lower values of Latitude, showed the largest number of ROH per animal.

These results could have been influenced by the ascertainment bias, which effect is larger in indicus since the Bovine SNP50 BeadChip was originally derived from the sequencing of taurus breeds (e.g., O’Brien et al., 2014; Utsunomiya et al., 2014). The utility of a specific SNP genotyping platform is influenced by its development and the application of such platforms can adversely impact on population-specific SNP parameters estimated for breeds that were not represented in its design. Breeds with unclear, but presumably diverse ancestry, may therefore display variation in these parameters due to the origin of the investigated SNP. This might have resulted in ascertainment bias into autozygosity estimates for indicus populations. However, studies on sequence data revealed a larger genetic variability of the indicine breeds (Murray et al., 2010). Moreover, the traditional breed formation is largely a European phenomenon, and it is absent in the African cattle. Purfield et al. (2012) highlighted that African *Bos taurus taurus* breeds, humped *Bos taurus indicu*s breeds and indicine/taurine hybrids, tended toward low levels of ROH per genome, reflecting traditional management practices in Africa, characterized by less controlled mating. On the contrary, indicus breeds, mostly raised at the tropics, showed the higher number of ROH but with the lower average ROH length. This is probably because the natural selection due to environmental adaptation acted on these breeds long time ago, and these ROH have been broken by recombination events due to progression of the generations. Indeed, short ROH are older and probably derive from environmental adaptation, whereas long ROH are recent and probably due to artificial selection (Macciotta et al*.,* 2021), or inbreeding due to non-optimal management or small population size. Therefore, the lowest average ROH length (meanMb) in indicus breeds may be due to the involved SNP chip (ascertainment bias), but it may also be due to an ancient inbreeding. Saravanan et al. (2021), in a study on taurus and indicus breeds, showed the variations in the frequency of different ROH-length classes. In the smaller length category (< 5 Mb), the Ongole breed (indicus) showed the highest number of ROH, whereas in the longer length category (>40 Mb), the largest number of ROH was observed for the Jersey breed (taurus). Several indicus breeds showed zero number of ROH in the longer length category (>40 Mb). A study performed on whole-genome sequencing data from European and African taurines, in addition to four indicine populations, reported that genome ROHs did not vary greatly among the investigated breeds (Upadhyay et al 2019). Mastrangelo et al. (2020) confirmed these findings, as their results showed that African populations (both taurine and zebuine cattle) had ROH patterns comparable with those of most European taurine breeds. Moreover, the length of ROH represents an important source of information on demographic and genetic processes; therefore, the results in indicus breeds could be also due to admixed events or different selection pressure.

Individual ROH-based inbreeding coefficients (Table 2) were computed considering four different minimum ROH length (F_{ROH} > 2Mb, F_{ROH} > 4Mb, F_{ROH} > 8Mb and F_{ROH} > 16Mb). As expected, F_{ROH} values decreased as the minimum ROH length increased (Table 2). The largest $\mathrm{F}_{\mathrm{ROH}}$ values were computed always for Temperate indicus, whereas the lowest were observed for Tropics composite in the first two classes ($F_{\mathrm{ROH}} < 8$ Mb) and for Tropics indicus in the last two classes ($F_{\mathrm{ROH}} > 8$ Mb). Also in this case, the different $\mathrm{F}_{\mathrm{ROH}}$ values computed in the identified groups using various minimum ROH length could be ascribed to the above-mentioned reasons (ascertainment bias, admixture events, selection pressure). In sheep, the frequencies of ROH class lengths of 8–16Mb and >16Mb were lowest for European breeds and highest for Southwest Asian breeds followed by African and Asian populations (Nosrati et al., 2021). The largest average inbreeding coefficients for the first two classes (F_{ROH} > 2Mb and F_{ROH} > 4Mb) were observed for indicus, as also reported in Mastrangelo et al. (2020); moreover, indicus showed the same value (i.e., not significantly different) of taurus from 8 Mb.

Figure 2 shows the Manhattan plot of $\mathrm{SNP}_{\mathrm{ROH}}$ computed for all markers within each of the seven identified groups. Although the distribution of the ROH among group was relatively balanced and the signals were moderate in height, we found several outstanding peaks with a high percentage of SNPs in ROH, especially in Temperate and Tropics indicus. On average, Temperate indicus showed the largest $\mathrm{SNP}_{\mathrm{ROH}}$ (18.80%), whereas Tropics composite the lowest (6.94%) value (Table 1). A total of 887 SNP was flagged as significant; however, no SNP exceeded the threshold of 99% in all the seven groups (Table S2).

Analysis of the shared ROHs

Removing the duplicated regions, 94,925 unique ROH were found. As reported in Table 3, the top shared ROH were mainly found in the European breeds, which was expected because of their larger sample size. The first region on BTA12 was found in 94 animals, of which the 84% were from European taurine breeds; while the remaining were found in other 7 taurus breeds, 1 African composite breed, and 5 indicus breeds from India. Interestingly, Martikainen et al. (2020) found a ROH on BTA12 (65.13-66.37 Mb), which is included in the larger region highlighted in the present study, negatively associated with the interval from calving to the first insemination in Finnish Ayrshire cattle. The second region (BTA16) was found in European breeds the 77% of the times; the other animals were of taurine (11), composite (1) and indicine (8) breeds. The breeds which shared the third region (BTA27) were mostly worldwide (13%) and European (77%) Taurus; the same ROH was also found in 1 composite and 4 indicus breeds. Finally, the fourth region (located on BTA15) was shared by European breeds for 69%. It was shared also by other 7 taurus, 3 composite, and 5 indicus breeds.

The ROH shared by the largest number of animals (94), across TYPE and ZONE, was found on BTA12. Two genes that map in this region, *GPC5* and *GPC6,* were found to be associated with reproduction traits in cattle (Dubon et al., 2021; Purfield et al., 2019; Purfield et al*.,* 2020). Others two genes located in this region, *GPR180* and *SOX21*, are involved immune functions (Minozzi et al*.,* 2010) The *GPR180* gene was associated also with clinical ketosis (Soares et al., 2021). Finally, the *DCT* gene was associated to coat color (Jung et al., 2020), a trait related to environmental adaptation (e.g., Gaughan et al., 2019; Laible et al., 2021).

The second most frequent ROH, spanning about 3.7 Mb, was located on BTA16, and it was shared by 91 animals (Table 3). This region was particularly rich of annotated genes. A first group are those associated with feed efficiency: *FMOD, GOLT1A,* (Chen et al., 2011), *ATP2B4* (Yang et al., 2021), *SNRPE* (Connor et al., 2010), *MDM4* (Rathert et al., 2020). Another group of genes annotated in this region are involved in disease resistance and immune functions: *RBBP5* (Swanson et al., 2009), *KLHDC8A* (McConnel et al., 2020), *RAB7B* (Ibeagha-Awemu et al., 2021), *ZC3H11A* (Rossetti et al., 2011), *SLC26A9* (Rinaldi et al*.*, 2010). A cluster of 12 genes that map in this region was reported to be associated to clinical ketosis in Holstein cattle (Soares et al., 2021): *IKBKE*, *RASSF5*, *EIF2D*,

DYRK3, *MAPKAPK2*, *IL10*, *IL19*, *IL20*, *IL24*, *FCMR*, *PIGR* and *FCAMR*. Three of them (*IKBKE, RASSF5*, and *FCMR*) have been also associated to female reproduction in cattle (Guarini et al., 2019; May et al., 2022). Other genes involved in reproduction that map in this ROH island are: *EIF2D* (Singh et al., 2018), *PPP1R15B* (Melo et al., 2018), *KISS1* (Singh et al., 2020), *LRRN2* (Gaddis et al., 2016), *ETNK2* (Hummitzsch et al*.,* 2014), *PIK3C2B* (Mota et al., 2022), *SRGAP2* (Forde et al., 2012), and *PRELP* (Rodríguez-Alonso et al., 2019). We also identified several genes associated to disease resistance and immune response: *IL20* (Moré et al., 2019), *IL10* (Fonseca et al., 2009), and *IL19* (Saravanan et al*.,* 2021). Two genes in the cluster were of particular interest, being associated to thermotolerance: *DYRK3* (Dikmen et al., 2015), and *FCAMR* (Dado-Senn et al., 2018). Another gene related to environmental adaptation within this region is the *SOX13* (Wiener et al., 2021). This ROH located on BTA 16 harbors also genes related to production traits. A first group are those related to beef traits, such as: *BTG2* (Sasaki et al., 2006), *AVPR1B* (Srikanth et al., 2020), *ELK4* (de las Heras-Saldana et al*.,* 2020), and *CDK18* gene (Pan et al., 2021). Another gene, *REN*, was found to be associated with body traits (Cole et al., 2011). A second group of genes consisted of those related to dairy traits. The *NUCKS1* (Yuan et al., 2019) and the *LAX1* (Iso-Touru et al., 2016) genes were found to be associated with milk yield. A cluster of 5 genes was associated with lactose yield (Costa et al., 2019): *CNTN2*, *TMEM81*, *RBBP5*, *DSTYK* and *TMCC2*. The *PM20D1* was found associated with protein yield (Xu et al., 2019). Other genes were related to milk fatty acid composition (Iung et al., 2019): *MFSD4A*, *SLC45A3* and *SLC41A1*.

The third most frequent ROH mapped on the BTA27 and included 12 genes. Some of them (*ERICH1*, *DLGAP2, KBTBD11* and *ARHGEF10*) were not found previously highlighted. Two other genes, *CLN8* and *MYOM2,* were reported to be associated with environmental adaptation in buffaloes (Mokhber et al., 2018). *CSMD1* (Gonzalez et al*.,* 2020) and *ANGPT2* (Tetens et al., 2013) were found to be related to dairy traits. In this ROH island are located also genes involved in beef traits, as *MCPH1* (Lim et al., 2013), *AGPAT5*, and *XKR5* (Edea et al., 2020). Finally, the *TAP* gene was reported to be involved in resistance to bovine respiratory disease (Berghuis et al., 2014).

The fourth ROH, mapped on the BTA15, was shared by 77 animals and it included 23 genes. Among these, 5 were not reported previously in study on cattle: *IZUMO1R*, *ANKRD49*, *GPR83*, *KBTBD3* and *DDI1*. Some of them were found related with immune functions: *CASP4* (Kabara et al., 2010; Sharifi *et al.,* 2018), *CASP1* (Shen et al*.,* 2019), *PDGFD* (Welderufael et al., 2018), *MMP12* (Evans et al., 2014), and *MMP7* (Kosciuczuk et al., 2017). The *TMEM123* was reported to be downregulated in feed restriction-induced ketosis in Holstein (Loor et al., 2007). Some of the genes located in this region are related to environmental adaptation: *MSANTD4* and *GRIA4,* reported to be related to cold-stress resistance (Igoshin et al., 2019), and *MMP3*, associated to adaptation to hypoxic environment (Chen et al., 2018). Several genes were reported to be associated with reproduction: *DCUN1D5, MMP13, MMP20*, *MMP27, MRE11, MMP1, MMP3, MMP8* and *MMP13* (Guarini et al., 2019; Walker & Biase, 2020; Wathes et al., 2011). *MMP8* was identified also as candidate gene for the identification of *Mycobacterium avium* subsp. *Paratuberculosis* infection (Blanco Vázquez et al., 2020). Finally, we identified two genes associated to dairy traits: *AASDHPPT* (Saravanan et al., 2021), and *DYNC2H1* (Strillacci et al., 2014).

In the most shared ROH located on BTA12, we found genes mainly associated with reproductive and immune traits; the second region, on BTA16, included genes related to meat traits, body conformation, and feed efficiency, but also to milk traits; in the third shared ROH located on BTA27, some interesting genes associated with environmental adaptation in buffaloes and other associated with meat production were retrieved; finally, the fourth shared ROH (BTA15) included genes mainly associated with immune function and reproductive disorders.

In general, meat traits included fat deposition, growth, body size, backfat thickness and carcass quality traits, but also residual feed intake and feed intake. Milk traits, instead, included CLA milk content, milk yield, lactose yield, protein yield and somatic cell score. The immune functions regarded ketosis, antibody response to *Mycobacterium avium* subsp. *Paratubercolosis,* response and recoverability from mastitis, resistance to tick infestation, response to inflammation and susceptibility to brucellosis. The reproductive function covered quality of bull semen, pregnancy, conception rate, calving difficulty and oocyte developmental competence, but also reproductive disorders. Finally, the genes associated with environmental adaptation were found related both to cold-stress and heat-stress resistance. More details about the genes mapped in these four shared ROHs are reported in the Table S3.

Conclusion

Results of the present study confirmed that runs of homozygosity could be used to identify genomic signatures due to both artificial and natural selection. Temperate indicus showed larger numbers of ROH per individual which resulted in larger inbreeding coefficients. However, Temperate taurus had numerical higher mean ROH length and Composite, both Tropics and Temperate, showed always intermediate values. Despite the limitation of the ascertainment bias, limited number of genotyped animals for indicus and reduced genomic coverage of the SNP dataset used, differences in ROH and an interesting list of potential genes have been identified, which will be the foundation for future investigations.

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Disclosures

The authors declare no conflicts of interest.

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Figure Legend

Figure 1. Plot of the first two principal components extracted from the genomic relationship matrix (GRM).

Figure 2. Manhattan plot of SNP_{ROH} computed for all markers within Type and Zone. The green dots represent SNP exceeding the 99th percentile of the SNP_{ROH} distribution.

Table 1. Basic statistics and results of the statistical analyses.

	Animals		ROH		Model			
	N	%	N	%		nROH[1]	meanMb[1]	SNP$_{ROH}$
					PC1	(P<0.001)	(P<0.001)	–
					PC2	(P<0.001)	(P<0.05)	–
					PC3	(P<0.001)	(P<0.001)	–
					CHROM	–	(P<0.001)	–
GROUP[2]						(P<0.001)	(P<0.001)	(P<0.001)
Continental Taurus	1,314	41%	47,445	35%		36.11±21.64^{F}	4.9±0.18^{BC}	8.25±1.87^{D}
Temperate Composite	49	2%	2,036	1%		41.55±11.96^{E}	4.45±0.31^{BC}	7.82±5.24^{E}
Temperate Indicus	174	5%	21,684	16%		124.62±17.70^{A}	4.28±0.37^{BC}	18.80±13.66^{A}
Temperate Taurus	1,205	38%	33,159	24%		27.52±18.44^{G}	5.90±0.16^{A}	7.85±1.44^{E}
Tropics Composite	109	3%	5,312	4%		48.73±21.16^{D}	4.07±0.25^{B}	6.94±5.47^{F}
Tropics Indicus	156	5%	18,625	14%		119.39±39.66^{B}	3.90±0.32^{BC}	15.78±11.09^{B}
Tropics Taurus	170	5%	8,661	6%		50.95±24.81^{C}	5.26±0.25^{AC}	9.22±3.74^{C}

[1] nROH = number of ROH per animal; meanMb = mean of ROHs length per animal; SNPROH = ratio between number of animals with a given SNP inside a ROH and total number of animals

[2] Continental = Latitude ≥ 45°; Temperate = 45°< Latitude >23.26°; Tropics = Latitude ≤ 23.26°

Table 2. Inbreeding coefficients (mean±SD) estimated according to different minimum ROH length in the seven considered groups.

Group[1]	$F_{\mathrm{ROH}} > 2$ Mb		$F_{\mathrm{ROH}} > 4$ Mb		$F_{\mathrm{ROH}} > 8$ Mb		$F_{\mathrm{ROH}} > 16$ Mb	
	Mean	n	Mean	n	Mean	n	Mean	n
Continental Taurus	0.08 ± 0.06^{C}	1,314	0.06 ± 0.05^{B}	1,292	0.04 ± 0.04^{B}	1,182	0.03 ± 0.03^{B}	805
Temperate Composite	0.08 ± 0.03^{C}	49	0.05 ± 0.02^{BC}	48	0.03 ± 0.02^{B}	44	0.02 ± 0.01^{B}	24
Temperate Indicus	0.19 ± 0.08^{A}	174	0.08 ± 0.08^{A}	174	0.06 ± 0.08^{A}	130	0.06 ± 0.07^{A}	86
Temperate Taurus	0.08 ± 0.07^{C}	1,205	0.07 ± 0.07^{AB}	1,122	0.06 ± 0.06^{A}	944	0.05 ± 0.05^{A}	686
Tropics Composite	0.07 ± 0.05^{C}	109	0.03 ± 0.04^{C}	106	0.03 ± 0.04^{B}	49	0.03 ± 0.03^{B}	29
Tropics Indicus	0.16 ± 0.06^{B}	156	0.05 ± 0.04^{BC}	156	0.02 ± 0.03^{B}	112	0.02 ± 0.02^{B}	48
Tropics Taurus	0.09 ± 0.05^{C}	170	0.05 ± 0.05^{B}	170	0.04 ± 0.05^{AB}	133	0.04 ± 0.04^{AB}	77

[1] Continental = Latitude ≥ 45°; Temperate = 45°< Latitude >23.26°; Tropics = Latitude ≤ 23.26°

Table 3. TOP shared runs of homozygosity.

Region			Continental	Temperate	Temperate	Temperate	Tropics	Tropics	Tropics
BTA	Mb	Animals	Taurus	Composite	Indicus	Taurus	Composite	Indicus	Taurus
12	63.40-69.68	94	38	–	4	47	2	2	1
16	1.03-4.77	91	32	1	5	46	–	5	2
27	0.43-6.04	86	34	1	2	42	–	2	5
15	1.03-6.30	77	32	3	8	29	3	1	1

[1] Continental = Latitude ≥ 45°; Temperate = 45°< Latitude >23.26°; Tropics = Latitude ≤ 23.26°

Figure 1

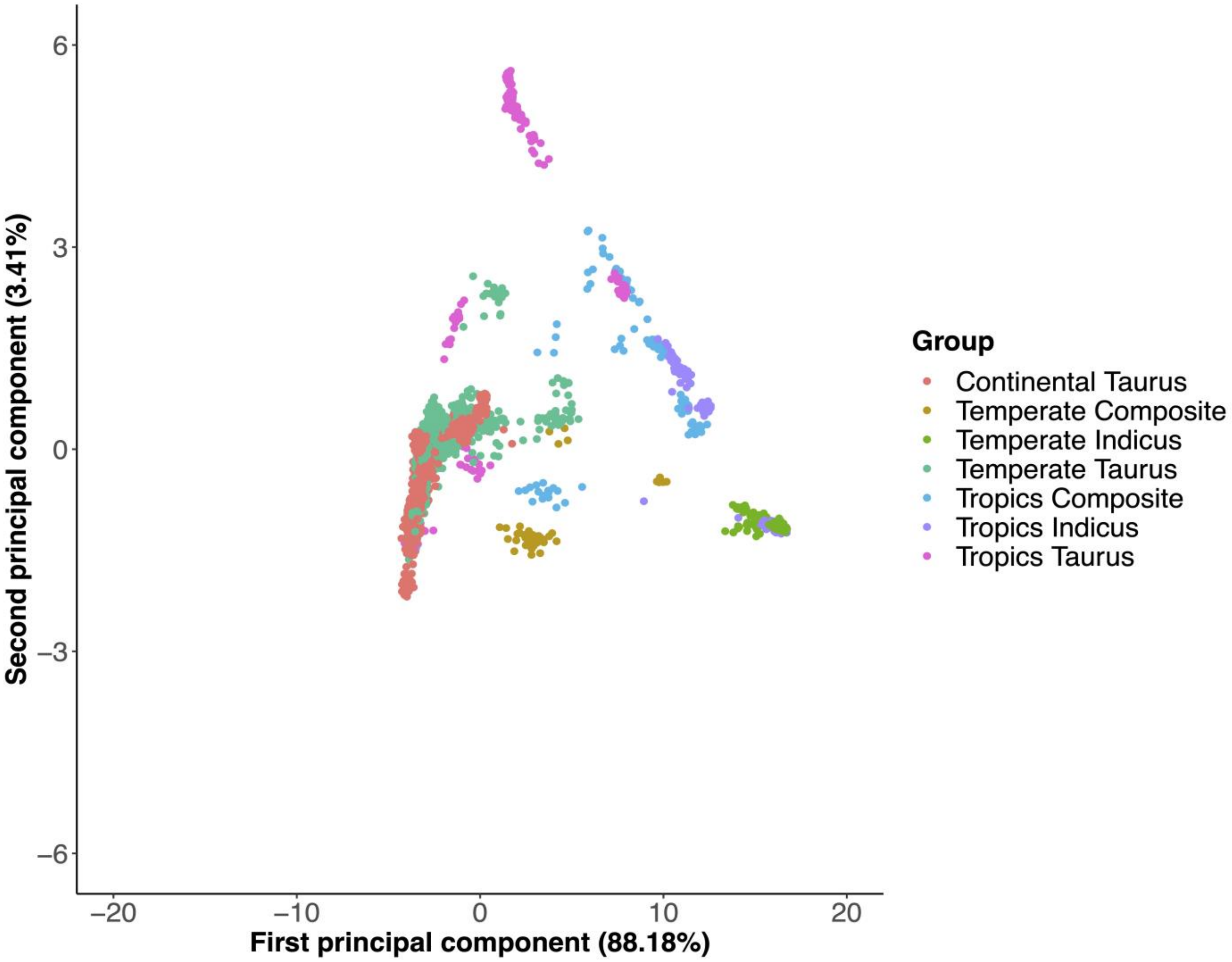
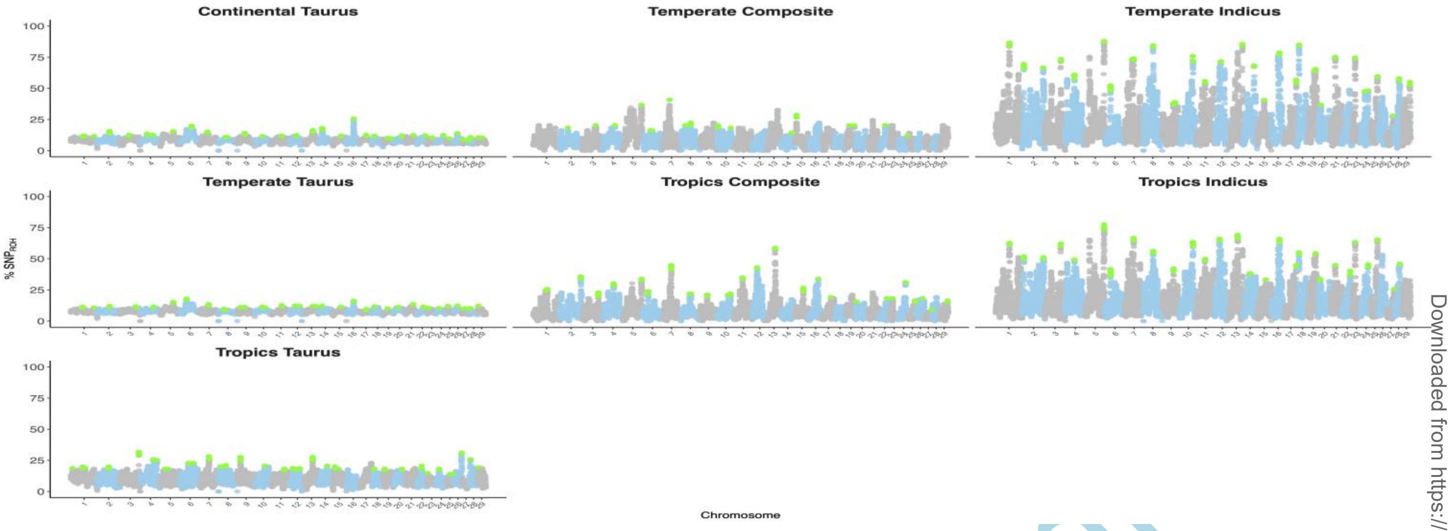

6
3
0
−3
−6
Second principal component (3.41%)
−20
−10
0
10
20
First principal component (88.18%)
Group
● Continental Taurus
● Temperate Composite
● Temperate Indicus
● Temperate Taurus
● Tropics Composite
● Tropics Indicus
● Tropics Taurus

Figure 2


Continental Taurus
Temperate Composite
Temperate Indicus
Temperate Taurus
Tropics Composite
Tropics Indicus
Tropics Taurus
100
75
50
25
0
% SNP$_{ROH}$
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29
Chromosome