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Research Article

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Landscape Genomics Reveals Environmental Adaptation in Burkina Faso Taurine Cattle Populations

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Abstract

Background: The unique environment of Burkina Faso, characterized by diverse agroecological zones and variable climatic conditions, presents a challenging yet informative context to understand the genetic adaptations of native taurine cattle populations. Local livestock populations provide important means of livelihoods and have significant economic and cultural values. This study aimed to investigate the genomic signatures of adaptation to different environments in local Lobi and Gourounsi cattle populations.

Methods: We employed a landscape genomics approach on a dataset of 342 animals sampled from different environmental zones in Burkina Faso. Climate data including temperature, precipitation, solar radiation, wind speed and water vapor pressure were retrieved for the sampling locations. We assessed genotype-environment associations using a latent factor mixed model and identified significant associations after correcting for multiple testing.

Results: The analysis revealed 41 SNPs significantly associated with at least one climatic variable. These SNPs overlapped 141 protein-coding genes involved in reproduction, environmental adaptation and energy trade-offs. These genes are involved in processes such as glucose/lipid metabolism, resource allocation, taste and olfactory perception and response to infectious diseases. The results also highlighted potential adaptations to hot and cold temperatures and suggest a possible adjustment to long-distance walking.

Conclusions: These findings provide insights into the genomic adaptations of taurine cattle populations in Burkina Faso to their local environment. The identified genes and biological processes contribute to understanding the mechanisms behind adaptation to climate, energy balance and disease resistance. Our results have implications for livestock management and breeding strategies, as they shed light on the genetic basis of traits related to productivity, resilience and adaptation. Further research and validation might help to fully comprehend the

functional significance of these genetic associations and their potential applications in breeding programs and conservation efforts. Overall, this study contributes to the broader field of landscape genomics and enhances our understanding of the genetic adaptations of taurine cattle in the face of environmental challenges.

Keywords: Taurine cattle, Burkina Faso, Landscape genomics, adaptation, genotype-environment association

Background

West Africa possesses a substantial diversity of cattle breeds belonging to both cattle species, *Bos taurus* and *Bos indicus*. This diversity is the result of a complex evolutionary history. *Bos taurus* is believed to be the first ever domesticated cattle to tread African soil through the Northern part of the continent via Egypt tracing back to 6th millennium BC [1]. It is hypothesised that this taurine population migrated westward via the Northern African coast to flee Sahara increasing desiccation [2–4] and eventually penetrated the tsetse fly challenged West African forests where it acquired its trypanotolerance fitness [5, 6]. More recent studies proposed that the distinctive genomic background also resulted from substantial post domestication introgression with now-extinct North African aurochs populations (*Bos primigenius africanus*) [7, 8]. A further cattle introduction involving zebus (*Bos indicus*) occurred around 3,000-2,500 years BC following the Arab settlement on the East coast [9]. The zebu subsequently penetrated the Sahel regions in different waves via pastoralists movements [9]. The 19th century great rinderpest catalysed the zebu expansion on the continent, deeply modifying the African cattle genetic make-up [9]. Benefiting from increased fitness to dry environment, long walks and their capacity to valorise poor pasture, the zebu cattle has strongly introgressed the original African taurine cattle, replacing the taurine phenotype in the northern

73 part of West Africa. Currently, only few pure African taurine populations exist, reared by tribes
74 in the rainy forest area.

75 Two main populations of short-horn, taurine cattle are found in Burkina Faso, the Lobi and
76 Gourounsi cattle breeds [10]. The Lobi cattle, reared by the homonymous tribe, are found in
77 the southwestern region of the country in the Sudanian agro-ecological zone. The Gourounsi
78 cattle, reared by the Gourounsi tribe, are found in the Central West and Central South regions,
79 with the Central South region in the Sudanian agro-ecological zone and the Central West region
80 in the Sudano-Sahelian agro-ecological zone (North Sudanian). These populations are primarily
81 raised under traditional free grazing and transhumant management systems and are well adapted
82 to the diverse agro-ecological zones in which they live [11]. In these areas, taurine cattle are
83 seen as an important source of wealth and stability for those who own them. They serve as a
84 form of savings and investment, as they can be sold or traded when necessary. Additionally,
85 taurine cattle play a significant role in social events such as weddings, dowry ceremonies,
86 funerals, serve as a symbol of wealth and status and are often used in rituals and celebrations
87 [12].

88 Despite their adaptative and cultural significance, the genetic integrity of Burkina Faso taurine
89 cattle is increasingly threatened by continuous introgression with indicine zebu populations,
90 largely driven by the higher productive performances (meat and milk) of crossbred animals.
91 Moreover, anthropogenic activities and global warming have contributed to the reduction of the
92 rainforest habitat where the indigenous taurine cattle reside [13–15]. Importantly, the
93 implementation of effective and efficient conservation measures demands knowledge on the
94 genetic background of the focal taurine populations [16–18]. In the context of climate change,
95 untangling the relationship between adaptive genomic signals and environmental heterogeneity
96 in Burkina Faso taurine indigenous populations is crucial to guide their conservation and
97 selection for productivity under challenging conditions [19].

Over the past decade, landscape genomic methods have been successfully applied to investigate adaptative evolution of various cattle breeds evolving in heterogeneous environments worldwide [20–22]. Such approaches allow the identification of genomic regions potentially involved in local adaptation and provide valuable insights into evolutionary responses to environmental constraints. To the best of our knowledge, despite the ecological importance of native taurine cattle of Burkina Faso, no landscape genomic study has been undertaken on these populations. In the present study, we therefore aimed to (i) describe the diversity and genetic structure of local Burkina Faso taurine cattle and (ii) investigate signatures of local adaptation in Burkina Faso taurine cattle populations by means of landscape genomic approaches. The results of this study will be instrumental to support effective conservation measures and preserve the genetic integrity of the indigenous taurine cattle in Burkina Faso.

Methods

Sampling and genotyping

The sampling scheme was designed to explore the environmental adaptation of local taurine cattle across two distinct agro-ecological zones. Burkina Faso territory can be divided in four main agroecological zones based on the rain fall and the vegetation (North Sahelian, South Sahelian, North Sudanian, South Sudanian; Figure 1). The North Sudanian zone encompasses nearly one fourth of Burkina Faso total area. The landscape appears as a mosaic of plains and low mountains that can reach 500 m altitude. The soil is poor and made of laterite and the vegetation is represented by a mix of thorny scrub and savanna grassland. The mean annual rainfall ranges between 500 mm and 900 mm. This region is the distribution area of Gourounsi cattle from Tenado, while Lobi and Gourounsi cattle from Nahouri are mostly spread in the South Sudanian agroecological zone (Fig. 1). The South Sudanian zone is the wettest area of Burkina Faso, with >1,000 mm annual rain. The soil is rich and the vegetation is a mosaic of

bushy savannas and forests standing along watercourses. These types of riverside vegetation are the preferred biotopes of tsetse flies [23]. The landscape is rugged and dotted with hills. In all these agroecological zones, rain falls during a single rainy season stretching from May-June to September-October and is characterized by a high degree of temporal and spatial variability. The dry season extends from the end of October to May. A total of 837 georeferenced individuals including 483 samples of the two main local taurine populations (Lobi and Gourounsi) and 354 Lobi x Zebu crossbred (Supplementary Table S1) were selected in three provinces (Poni, Nahouri and Sanguie; Figure 1).

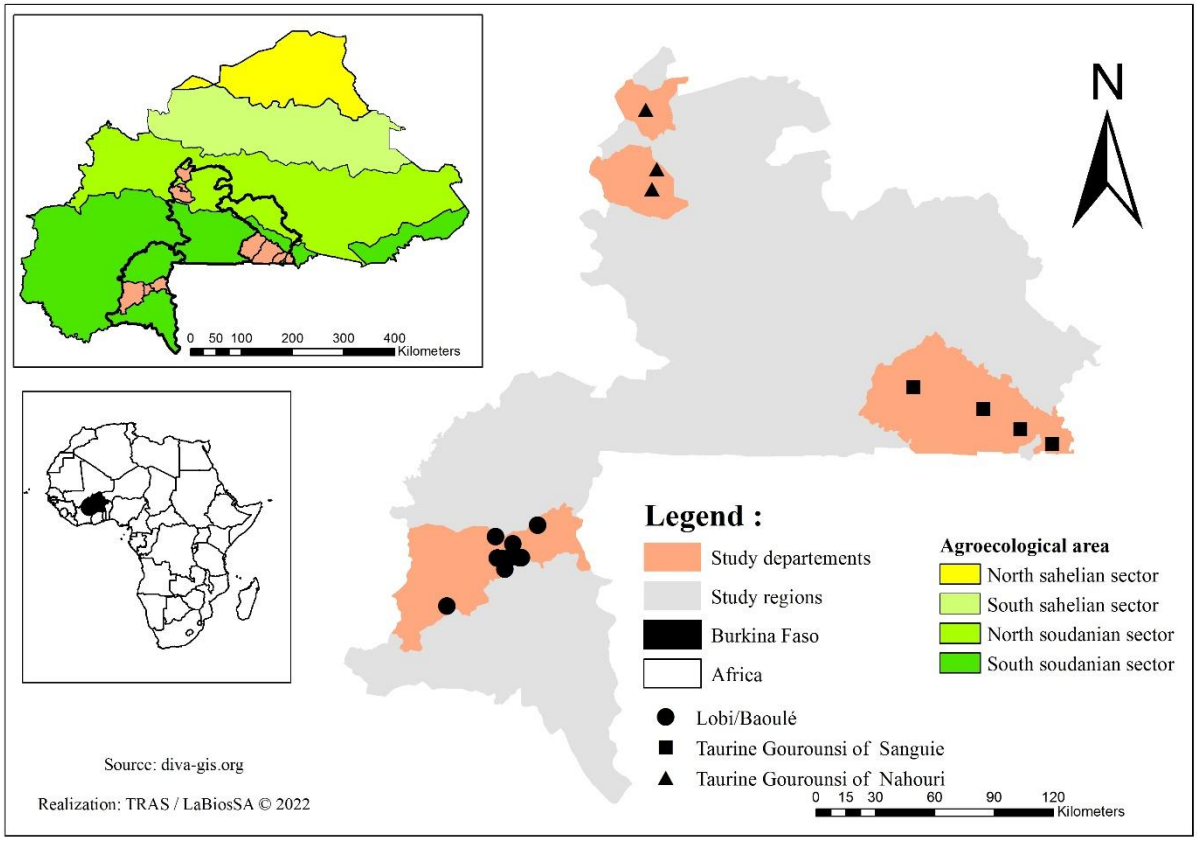


Figure 1. Sampling area in Burkina Faso: location of Burkina Faso within Africa (bottom-left inset) and national agroecological zones with study departments in orange (top-left inset). In the main map, study regions are grey and study departments orange; sampling sites are shown as circles (Lobi, BB), triangles (Gourounsi of Sanguié, FGT) and squares (Gourounsi of Nahouri, FGN).

The genome-wide single nucleotide polymorphisms (SNPs) used in this study were created in framework of a community-based breeding programme (CBBP) ; [15, 24] in Burkina Faso, with the ethical approval number CE-UJKZ/2023-09. In brief, the farmers in the focal areas were interviewed in detail to avoid relatedness of sampled cattle. ETDA-blood samples were collected in the framework and DNA was extracted using MasterPure DNA Purification Kit (Biozym, Illumina Inc, USA). DNA samples were then quantified using a Nanodrop spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA) and stored at 4 °C until shipment for genotyping, which was conducted at Neogen (Lincoln, United States) using the Illumina Bovine SNP 50K BeadChip, featuring 53,714 SNPs. SNPs positions were updated according to the ARS-UCD1.2 reference genome. Additional European taurine, Central African taurine, pure West African taurine and Asian zebu genomic data retrieved from public repositories [25] were added to the dataset for comparisons (Supplementary Table S1).

Genetic Diversity analysis

SNP pruning of genotype data was carried out using PLINK v2.0 [26]. Loci having >1% missing genotypes, samples with more than 1% missing genotypes, minor allele frequency <0.01, located on sex chromosome or with missing geolocation information were removed. Individuals with more than second degree relatedness as estimated using the KING robust pair-wise kinship coefficient [27] as implemented in PLINK v2.0, were removed.

Observed heterozygosity (H_o) values and inbreeding levels for each population (F_{ROH}) were computed using KING v2.3.0[27]. Effective population size (N_e) was estimated using SNeP v1.11 [28] applying Sved and Feldman's recombination adjustment [29] .

Population structure analysis

Prior to population structure analyses, data was pruned for linkage disequilibrium (LD) >0.2 using the '--indep-pairwise' flag in PLINK v2.0 with sliding windows of 50 SNPs and step size

of 5 SNPs. Burkina Faso taurine cattle population structure was inferred using ADMIXTURE v.1.3.0 [30] and visualized using AIDmixture v0.1 (https://dx.plos.org/10.1371/journal.pone.0231162). To this aim, a supervised clustering was performed using i) Angus, Brown Swiss and Holstein, ii) Lohani and Tharparkar and iii) N'Dama as reference populations for the European taurine, indicine and African taurine gene pools, respectively. A principal component analysis (PCA) was performed as implemented in PLINK v2.0 and visualised via R custom script. A Neighbour-Net graph using Reynolds' distances, computed with a custom script, was constructed using SplitsTree v4.14.6 [31]. F_{ST} values were calculated in PLINK v2.0, applying Weir and Cockerham (1984) method to assess the degree of population differentiation. Pairwise F_{ST} estimates were subsequently visualised as a heatmap in RStudio [32] using the *pheatmap* v1.0.13 package [33].

Landscape Genomics Analysis

Landscape Genomics analyses were performed using the set of 342 animal sampled in the Lobi, Gourounsi Nahouri and Gourounsi Tenado cattle distribution areas (Figure 1). Climate data at a spatial resolution of 30 arc seconds for the time span between 1970 and 2000 were retrieved from the WorldClim database [34]. Monthly climate data for: minimum, mean and maximum temperature, precipitation, solar radiation, wind speed, water vapor pressure and total precipitation values have been retrieved at the sampling locations using the *extract* function from the *raster* v3.6.3 R package [35]. To lower the dependency between models and spare computation time, we used the R function '*caret::findCorrelation'* to control for multicollinearity [36]. We iteratively reduced collinearity between variables by randomly removing the most correlated variables of the climatic data until the maximum correlation across all variables was lower than $|r^2| < 0.7$. We performed latent factor mixed model (LFMM) analyses using '*lfmm2'* function implemented in the R package LEA v3.23.0 [37] to assess genotype-environment associations. A genotype *x* environment association was considered

significant if the relevant P-value was lower than the nominal significance threshold of 0.01 after Benjamini & Hochberg correction for multiple testing.

The significantly associated SNPs were annotated by intersecting the candidate genes with the *Bos taurus* genome assembly using the R package *GALLO* v1.1 [38]. We then conducted Gene Ontology (GO) analysis to investigate the associations and biological functions of the genes in relation to the studied environmental variables. For the analysis, we utilized the PANTHER database (http://pantherdb.org/) assuming significance for a false discovery rate (FDR) <0.05. As reference, we employed a customized background set of 19,363 genes, which included all genes retrieved after the annotation process using *Bos taurus* as reference. Two types of analyses were performed. First, we scanned the gene lists associated with each environmental variable separately against the background set to identify significantly overrepresented GO terms. This allowed us to determine which biological functions were significantly enriched in relation to each specific environmental variable. Second, we conducted an overrepresentation analysis using the complete list of identified genes. This analysis aimed to retrieve broader biological processes based on GO terms, providing a comprehensive understanding of the potential biological functions associated with the genes, regardless of the specific environmental variables.

Local ancestry and adaptive introgression

To investigate the ancestry composition of the genomic regions identified by genotype environment association analysis, local ancestry inference was performed for all SNPs significantly associated with environmental variables in the LFMM analysis. The objective was to determine whether LFMM candidate loci were preferentially associated with indicine, African taurine, or European taurine ancestry components. Local ancestry inference was conducted using ELAI v1.01 [39] under a three-way admixture model. Nine combinations of seven reference populations were used as ancestry sources: three indicine breeds (Tharparkar,

Gir and Lohani), three European taurine breeds (Holstein, Brown Swiss and Angus) and one African taurine breed (N'Dama). For each focal population and each autosome, ancestry was inferred independently across all nine combinations of one indicine and one European taurine reference population, while maintaining N'Dama as the African taurine reference population. For each SNP and each population, ELAI computes posterior ancestry dosage values as the expected number of ancestral allele copies on a diploid scale (0-2). Consequently, we divided them by two to obtain ancestry proportions that ranged from 0 to 1 and summed to 1 across the three components (indicine, European taurine and African taurine) at each SNP. The resulting proportions were then averaged across the nine reference-source combinations. This approach is conceptually based on the consensus-ancestry rationale of the Consistently Introgressed Windows of Interest (CIWI) framework [25, 40], which reduces the dependence of local-ancestry inference on any single reference panel by combining results from multiple reference-population combinations. Mean local ancestry proportions were then obtained for the three ancestry components (indicine, European taurine and African taurine) at the exact position of each LFMM candidate SNP.

We then used the resulting indicine ancestry proportions (*iap*) to prioritize candidate loci according to the strength and the consistency of local introgression signals. A SNP with $iap \geq 0.5$ in at least two populations was classified as showing high introgression. A SNP with *iap* between 0.35 and 0.5 in at least two populations was classified as showing moderate introgression. The lowest threshold for *iap* was set at 0.35 that under a three-source model ancestry represents the minimum value at which a given ancestry becomes a dominant component at a given locus. Requiring the threshold to be met in at least two populations reduces the influence of population-specific stochastic variation and increases confidence that the detected signals reflects shared patterns of introgression.

To assess whether elevated indicine signals were not driven by isolated genotyping or phasing artefacts, we explored the surrounding haplotype of each candidate SNP identified as having either moderate or high *iap*. For each SNP meeting such criteria we defined a ±50 kb flanking window and computed a window-average *iap* as the mean indicine ancestry over all SNPs within it, applying the same category thresholds. Only candidate SNPs showing concordance between the exact-position and window-average were treated as the most robust candidates and retained for further analyses.

We characterized the genomic context of these retained loci by retrieving protein-coding and non-coding genes overlapping each window from the ARS-UCD1.2 bovine reference genome using the GALLO v1.1 package [38] and by extracting overlapping quantitative trait loci (QTL) from the Cattle QTL database [41].

Results

Populations diversity

After filtering, 800 individuals belonging to 14 cattle populations were analysed at 28,089 SNPs positions (Supplementary Table S1). Observed heterozygosity ranged from 0.176 (Tharparkar) to 0.414 (Holstein) and F_{ROH} varied from 0.005 (Ankole-Watussi) to 0.18 (Tharparkar) (Table 2). Among the west African taurine cattle, the highest H_o values were found in the Gourounsi cattle (0.338 and 0.333 in Tenado and Nahouri, respectively) and the lowest value was recorded in the N'Dama taurine cattle population (0.279). Overall, the European taurine cattle populations showed the highest H_o values (0.376-0.414) followed by African crossbreed cattle populations (0.319-0.335), whereas the Asian indicine cattle presented the lowest values (0.176-0.205). Asian indicine recorded the highest F_{ROH} values (0.03-0.180) and the lowest values were found in African taurine and crossbreed cattle (0.01-0.02). European taurine cattle recorded higher F_{ROH} (0.05-0.08) values than their West African counterparts (0.01-0.03).

Central African crossbreed and West African taurine cattle recorded the highest N_e estimates (952 and 929, respectively) and European taurine and the Asian zebu cattle the lowest (95 and 54, respectively).

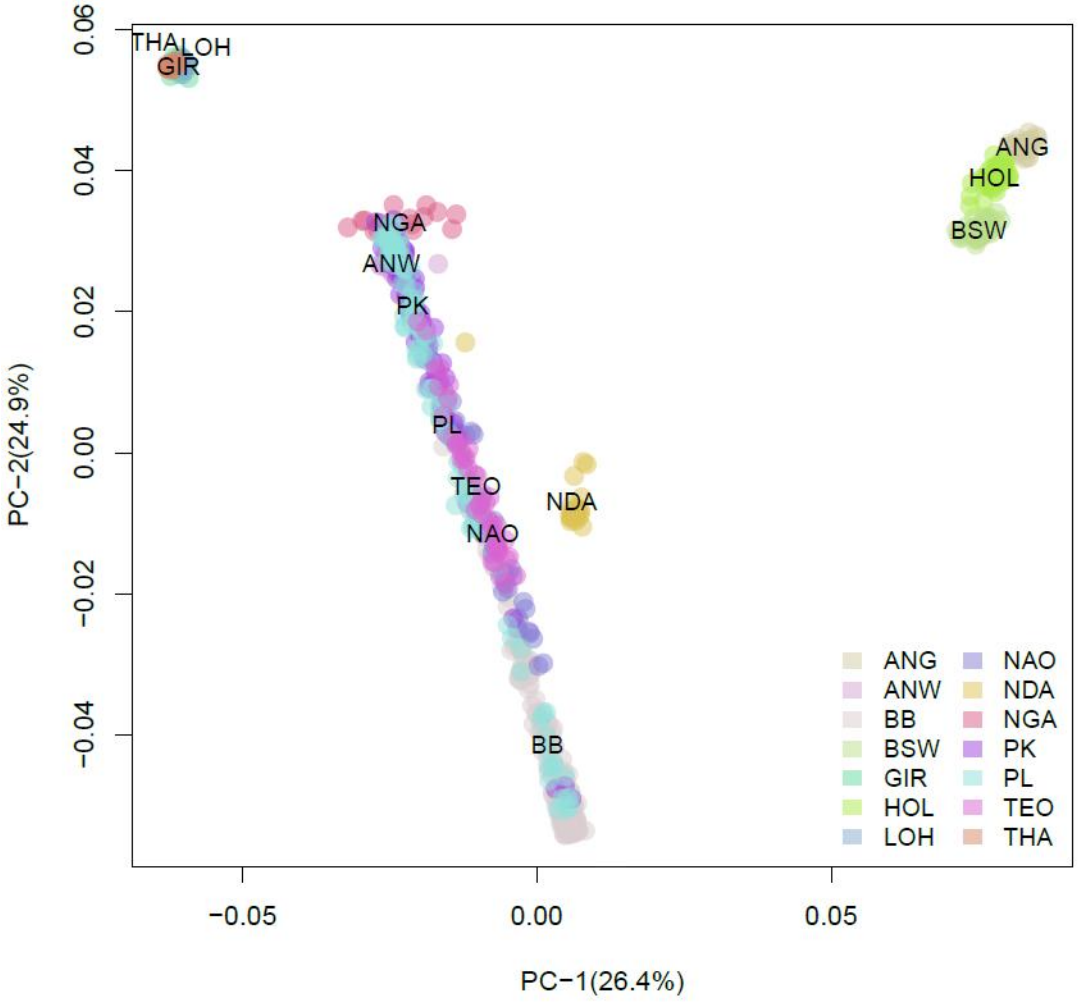
Table 1. Observed heterozygosity (H_o), Run of homozygosity (F_{ROH}) and effective population size (N_e) of West African taurine, European taurine, Asian zebu and African crossbreed cattle.

Breed	**Acronym**	*N*	**Origin**	***Ho* (SD)**	***FROH* (SD)**	***Ne***
B. taurus from Africa						
Lobi/Baoulé	BB	250	Bouroum-Bouroum/Burkina Faso	0.289 (0.03)	0.026 (0.05)	579
N'Dama	NDA	25	West Africa	0.278 (0.03)	0.022 (0.05)	719
Gourounsi of Nahouri	FGN	34	Nahouri/Burkina Faso	0.333 (0.03)	0.019 (0.05)	929
Gourounsi of Sanguié	FGT	45	Sanguié/Burkina Faso	0.338 (0.01)	0.009 (0.02)	912
B. taurus from Europe						
Angus	ANG	30	Europe	0.401 (0.02)	0.053 (0.04)	196
Brown Swiss	BSW	42	Europe	0.374 (0.02)	0.08 (0.03)	95
Holstein	HOL	40	Europe	0.413 (0.02)	0.053 (0.03)	132
B. indicus						
Gir	GIR	25	India	0.204 (0.01)	0.031 (0.03)	307
Lohani	LOH	12	India/Pakistan	0.195 (0.02)	0.091 (0.09)	76
Tharparkar	THA	10	Pakistan	0.176 (0.02)	0.181 (0.08)	54
Crossbreeds *(B. taurus x B. indicus)*						
Ankole-Watussi	ANW	24	Central Africa	0.317 (0.01)	0.005 (0.01)	952
Nganda	NGA	18	Central Africa	0.335 (0.01)	0.023 (0.05)	174

-	PL	111	Lorepeni/Burkina Faso	0.321 (0.03)	0.024 (0.05)	348
-	PK	134	Kampti/Burkina Faso	0.321 (0.02)	0.015 (0.04)	948

Population structure

In total, 800 individuals and 19,068 SNPs passed LD pruning and were used to investigate the population genetic structure. The first two principal components (PC) combined accounted for 51.3% of the total variance, clustering the individuals in four distinct groups pertaining to Asian, European, Central and West African cattle. The first PC (26.4% total variance) discriminated European taurine from African cattle and Asian zebus, whereas the second PC (24.9% total variance) discriminated among the African cattle populations (Figure 2). In this respect, the second PC enables to depict African cattle populations based on their admixture level with zebuine ancestry. To explore potential sub clustering within the West African breeds we performed an additional PCA with these breeds only (Supplementary Figure 2). The first PC separated the West African breeds according to their proportion of indicine ancestry, ranging from the least admixed breed (Lobi) to the most highly admixed breeds (PL, PK). The second PC clustered the highly admixed individuals. However, some Lobi individuals clustered with breeds showing different levels of admixture. To investigate this pattern and ensure that it was not driven by the larger number of Lobi samples, we randomly subsampled the dataset to 34 individuals per breed and reconstructed the PCA plot for the West African breeds (Supplementary Figure 1a-d). The results were consistent across all iterations and similar to those obtained from the PCA performed on the complete West African cattle dataset.



283

284 Figure 2. Principal Component Analysis plot of West African and reference breeds. For
285 population abbreviations see Table 1.

286 To provide additional insight into West African cattle relationships and divergence patterns, we
287 constructed a Neighbour-Net graph based on Reynold's distances (Figure 3). Complying with
288 the PCA plot findings, the Neighbour-Net shows four geographically consistent clusters: a first
289 one grouping European taurines (Angus, Brown Swiss and Holstein), a second one including
290 West African taurines and crossbreeds (N'Dama, Lobi, Gourounsi and Lobi crossbreeds) and a
291 third cluster including Central African crossbreeds (Ankole-Watussi and Nganda) adjacent to a
292 fourth cluster grouping indicine cattle breeds. Within the West African cattle populations
293 cluster, different branch length is observed between less admixed (N'Dama and Lobi) and

strongly admixed populations (Gourounsi and Lobi crossbreeds). Within this West African cluster, a well-developed net connects all Burkina Faso taurine and crossbreed populations.

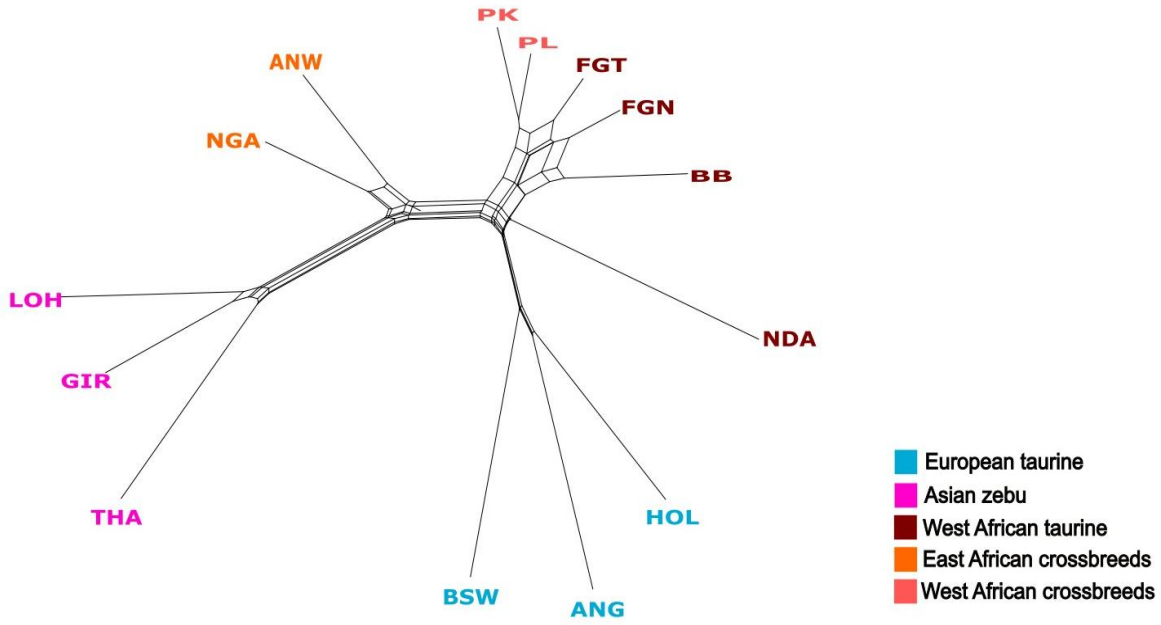


Figure 3. Neighbour-Net of pairwise Reynold's distances among the investigated cattle breeds. For population abbreviations see Table 1.

Admixture results mirrored PCA and Neighbour-Net results. All the African taurine cattle populations presented levels of admixture that can be classified under three levels of indicine ancestry. A first level includes Lobi and N'Dama showing <20% of indicine ancestry. The second level includes Gourounsi (Nahouri and Tenado) with ~20-45 % of indicine ancestry. Finally, all Central African Sanga cattle (Ankole-Watussi & Nganda) and Lobi crossbreds (from Kampti & Loropeni) populations of Burkina Faso have ~45-75% of indicine ancestry (Figure 4). However, some individuals from Lorepeni appeared to be pure taurine.

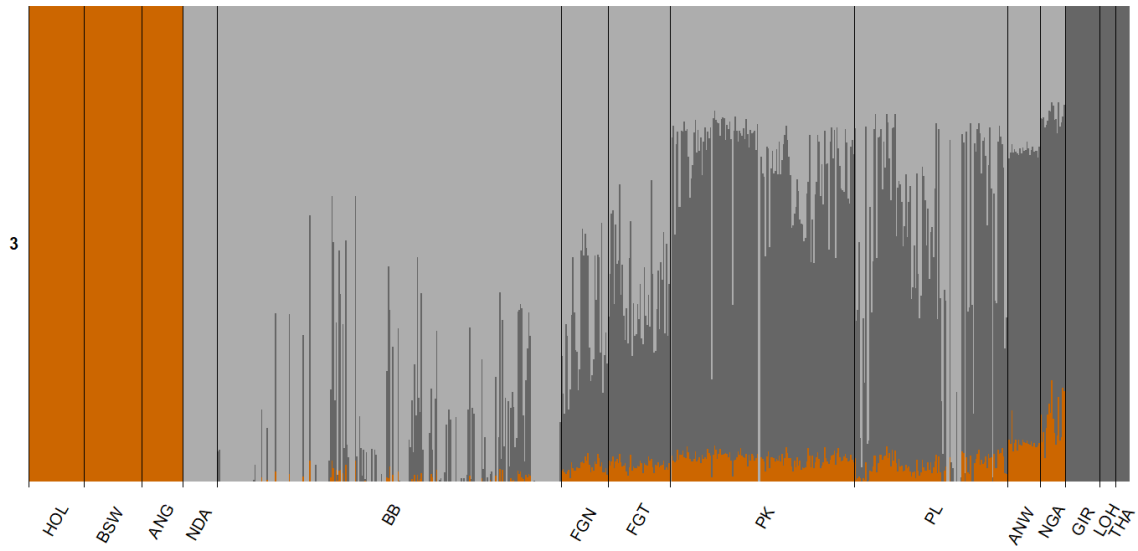


Figure 4. Supervised admixture analysis, the orange and light grey components are representative of European and African taurine, respectively and the dark grey colour reflects indicine ancestry. For population abbreviations see Table 1.

Pairwise FST

Genetic differentiation among populations was quantified using pairwise F_{ST} and the resulting matrix, together with its hierarchical clustering, is shown as a heatmap (Figure 5). The populations separated into two groups: the West African taurine and crossbred populations on one side and the indicine and European breeds on the other. Differentiation within the West African group was consistently low, with the smallest values between Gourounsi cattle breeds (F_{ST} = 0.004) and between PK and PL (F_{ST} = 0.011). Between the indicine breeds, the European breeds and the West African taurine populations, differentiation exceeded 0.3, whereas the European breeds were only moderately differentiated from the local taurine populations (F_{ST} = 0.157 for Holstein-Gourounsi Nahouri to 0.205 for Angus-Lobi).

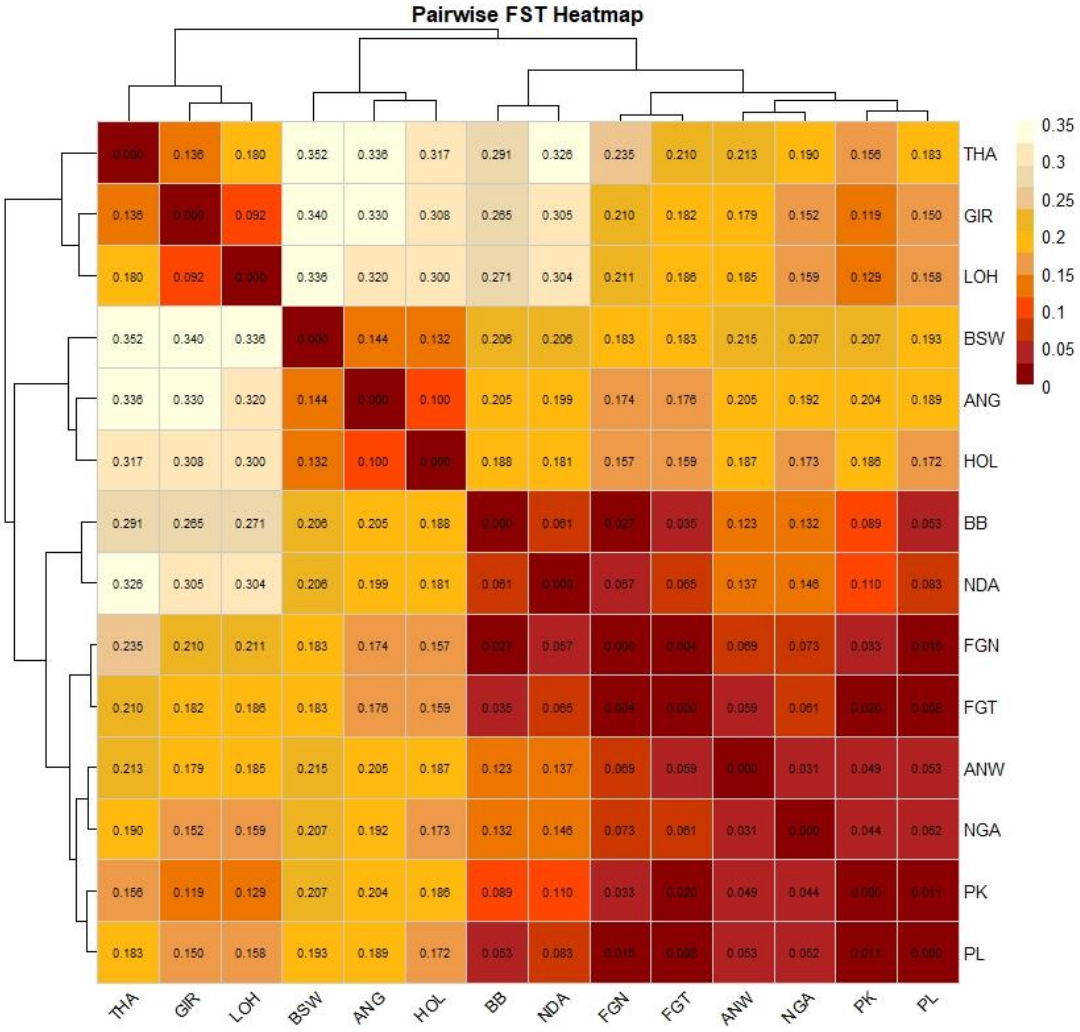


Figure 5. Heatmap showing pairwise F_{ST} values among fourteen cattle populations. The color gradient ranges from dark red to pale yellow for low and high differentiation, respectively.

Landscape genomic

To identify genomic signatures of adaptation to climate in Burkina Faso native taurine cattle populations, we performed a genotype environment association study using 27,816 SNPs and 342 individuals. After reducing the collinearity of the environmental variables, we retrieved six environmental variables: Precipitation of wettest quarter (bio16), precipitation in July (prec07) and wind speed in March, April, May and November (wind03, wind04, wind05 and wind11, respectively; Figure 6) and used them as predictors for the LFMM analysis.

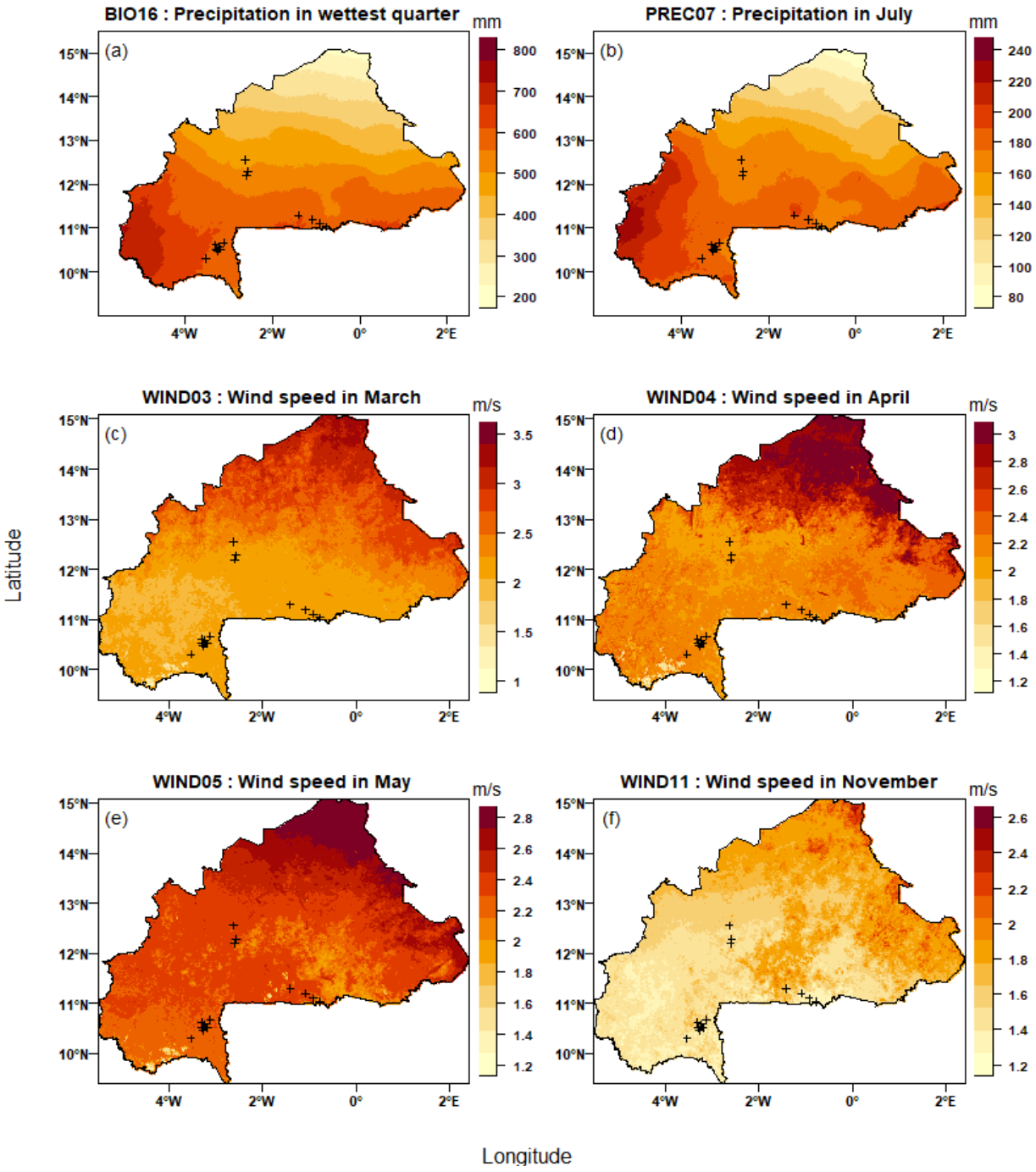
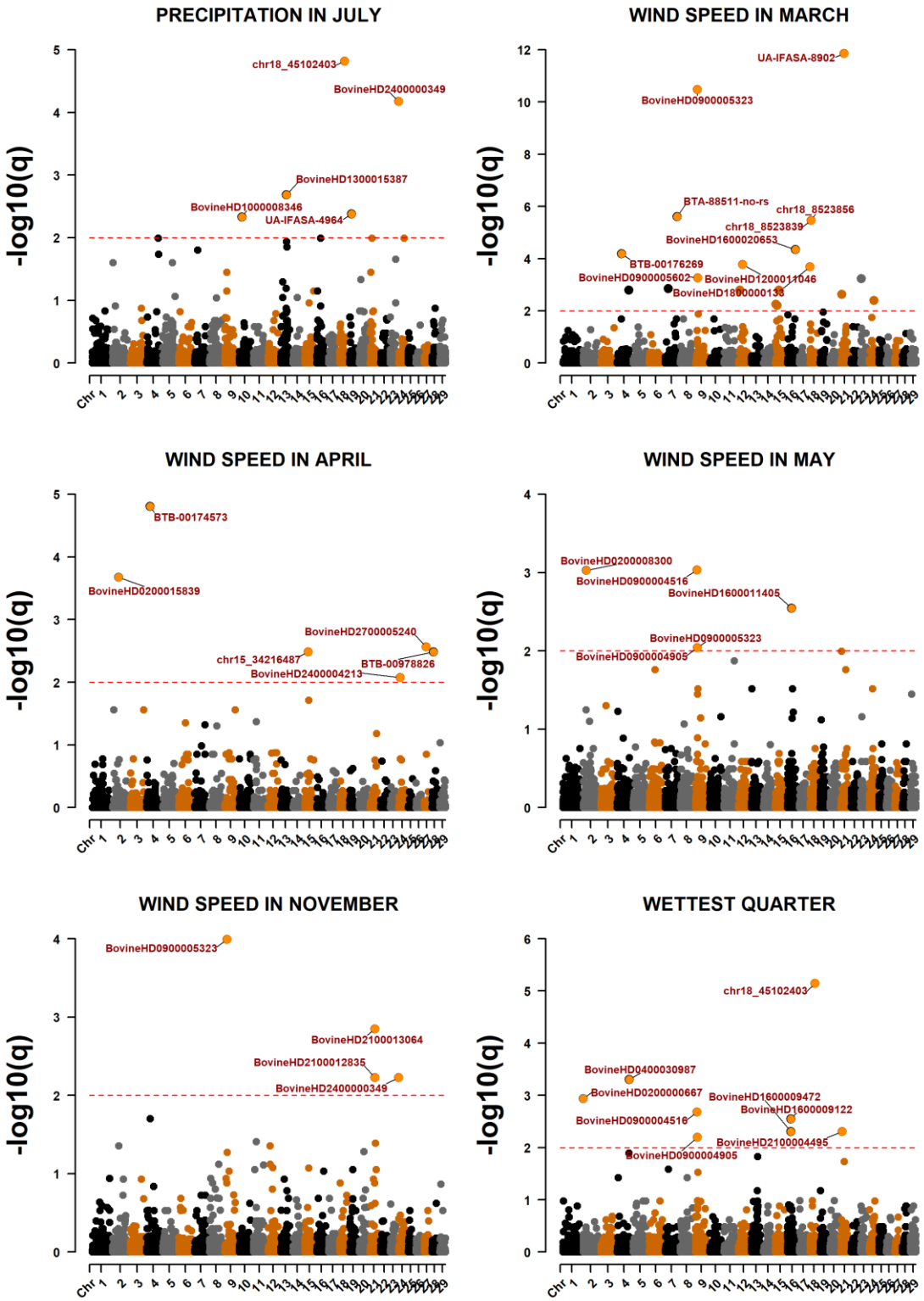


Figure 6. Climatic data used in this study. Maps display the geographical distribution of annual mean values for the six climate variables. a) precipitation in wettest quarter (bio16); b) Precipitation in July (prec07); c) wind speed in March (wind03); d) wind speed in April (wind04); e) wind speed in May (wind05); f) wind speed in November (wind11).

LFMM identified 41 SNPs, in 16 distinct chromosomes, significantly associated (FDR <0.01) with at least one climatic variable (Figure 7). The associated SNPs overlapped 141 protein-coding genes annotated in the cattle genome (Supplementary Table S5-S10).



339

340 Figure 7. Manhattan plot of LFMM analysis identifying chromosome-specific SNPs

341 significantly associated with geographical variables ($p < 0.01$, red line).

342

343 Table 2. Most relevant genes associated with the environmental data.

SNP ID	Chr	Position	Annotated gene	Biological function
bio16				
BovineHD0200000667	2	2350226	*U6*	Participate into spliceosome formation [42], Associated with carcass traits in cattle [43]
BovineHD1600009122	16	32132473	*KIF26B*	involved in foetal kidney development, cell proliferation, differentiation and migration [44]
BovineHD1600009122	16	32132473	*ZBTB18*	zinc finger transcriptional repressor involved in neuronal differentiation and cortical development [45, 46]
BovineHD1600009472	16	33222120	*AKT3*	plays a crucial role in synthesis of milk fats and cholesterol and involved in the TLR pathways as proinflammatory cytokines [46]
BovineHD2100004495	21	16393485	*KLHL25*	encodes a negative regulator of lipid synthesis [47]
prec07				
ENSBTAG00000015148	10	25638425	*METTL3*	regulates the UV-induced DNA damage response [48], involved in the adaptation of Mediterranean cattle breads [49]
ENSBTAG00000016664	13	54210696	*SLC2A4*	related to adipogenic processes linked to glucose uptake and cell differentiation[50]
ENSBTAG00000007498	13	54210696	*ZGPAT*	Involved in milk production [51]
ENSBTAG00000014769	13	54210696	*GMEB2*	Heat stress signal transduction from pituitary to hepar [52]
ENSBTAG00000021685	13	54210696	*EEF1A2*	related to fatty acid[52]
ENSBTAG00000010383	13	54210696	*YTHDF1*	Plays a major role in hypoxia adaptation [53]
ENSBTAG00000009354	19	18700829	*EVI2A*	associated with tail morphology and fat deposition in sheep [54]
ENSBTAG00000009353	19	18700829	*EVI2B*	associated with tail morphology and fat deposition in sheep [55]
ENSBTAG00000025213	19	18700829	*OMG*	associated with tail morphology, fat deposition [56] and to gastrointestinal nematode infection resistance in sheep [54].
wind11				
BovineHD0900005323	9	19511519	*U6*	Participate into spliceosome formation [42], Associated with carcass traits in cattle [43]

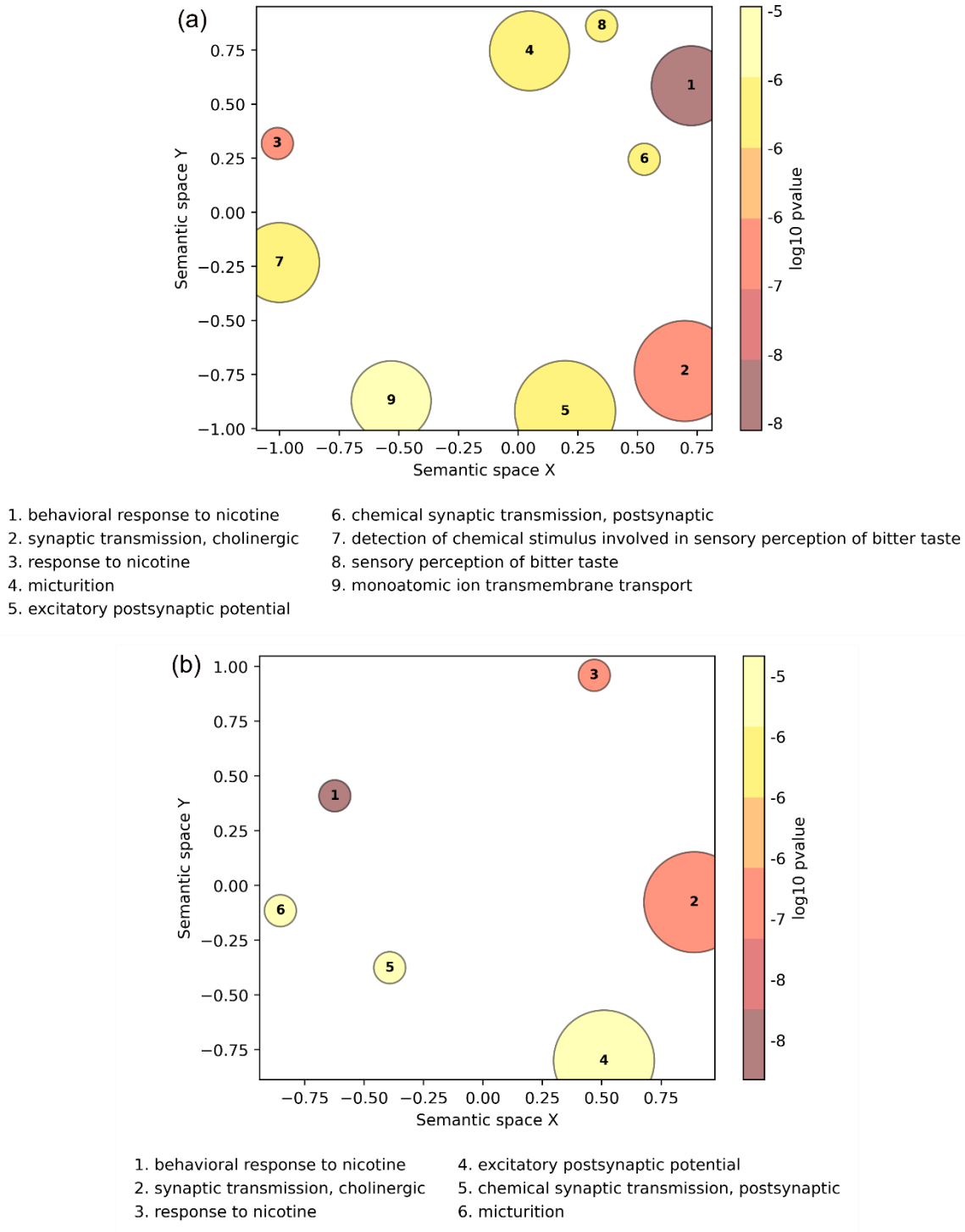
BovineHD2100013064	21	45289020	*CFL2*	Associated with muscle development and maintenance of normal muscle morphology [57]
BovineHD2100013064	21	45289020	*PPP2R3C*	associated with the white forehead stripe [58]
wind05				
BovineHD0900005323	9	19511519	*U6*	Participate into spliceosome formation [42], Associated with carcass traits in cattle [43]
BovineHD1600011405	16	40136604	*SUCO*	associated with bone development [59]
BovineHD1600011405	16	40136604	*FASLG*	modulates the immune response against *T. cruzi* in mice [60, 61]
wind04				
BTB-00174573	4	33445992	*GRM3*	linked to the sheep [62] and fox behavior [63]
chr15_34216487	15	34216487	*GRAMD1B*	related to feed efficiency and fertility index [64]
chr15_34216487	15	34216487	*SAAL1*	associated with abnormal proliferation of synovial fibroblasts [65]
BTB-00978826	28	15436077	*SLC16A9*	associated with uric acid and carnitine levels [66, 67]
BTB-00978826	28	15436077	*MRLN*	regulator of skeletal muscle physiology [68]
BTB-00978826	28	15436077	*CCDC6*	associated with growth traits [69]
wind03				
BTA-88511-no-rs	7	108992486	*MAN2A1*	Strong link with Fasciola hepathica [70]
ARS-BFGL-NGS-102963	15	6914643	*ANGPTL5*	co-ordinate the partitioning of triglyceride-derived fatty acids among different tissue beds [71]
BovineHD1500004009	15	15944293	*PIWIL4*	related to the development of the animal reproductive system and male fertility [72]
BovineHD1500009218	15	34021926	*GRAMD1B*	related to feed efficiency and fertility index [64]
BovineHD1600020653	16	72682722	*HHAT*	associated with weaning weight in Zebú cattle [73]
chr18_8523839	18	8523839	*SNORA70*	associated to reproductives traits, Feed intake, Conformation, Milk [74] and scrotum circumference [75]
chr18_8523856	18	8523856	*HSD17B2*	associated with earlier puberty in cattle [76]
UA-IFASA-8902	21	31138070	*UBE2Q2*	associated with cattle muscle stem cell and skeletal muscle development regulation [77]
ENSBTAG00000012870	23	4713759	*BMP5*	Development of bovine embryos [78, 79], associated with chest circumeference [80]
BovineHD2300001086	23	4713759	*HMGCLL1*	associated to ketosis [81]
BovineHD2400012328	24	44931413	*7SK*	close to genes playing a major role in bull sperm quality and fertility traits[75, 82]

344

Among the genes associated with the hot and dry period (March, April, May), *5S_rRNA*, *ELOVL4*, *GRAMD1B*, *SH3BGRL2*, *TTK*, *U6* were shared by at least two variables (Supplementary Figure 3), *GRAMD1B* and U6 have been described as strongly correlated with dry fed matter intake and feed efficiency index [64], whereas *ELOVL4* is related to elongation of very long chain fatty acids 4 [83] .

We investigated the role in biological pathways of each set of genes associated with each environment variable via GO analysis. Significant enrichment was detected in several biological processes, most notably synaptic transmission involved in micturition (GO:0060084; FDR = 1.04×10^{-3}), micturition (GO:0060073; FDR = 1.66×10^{-3}), excretion (GO:0007588; FDR = 7.78×10^{-3}), as well as processes related to chemical synaptic transmission and sensory perception of bitter taste (Figure 8a) (Supplementary Table S12).

Finally, the global gene-set enrichment analysis, performed using all genes identified as significantly associated with the different environmental variables revealed nine overrepresented biological processes related respectively to synaptic transmission involved in micturition (GO:0060084), behavioural response to nicotine (GO:0035095, micturition (GO:0060073), synaptic transmission, cholinergic (GO:0007271), response to nicotine (GO:0035094), excitatory postsynaptic potential (GO:0060079), chemical synaptic transmission, postsynaptic (GO:0099565), regulation of postsynaptic membrane potential (GO:0060078) (Figure 8b).



364

365 Figure 8. Semantic similarity scatterplot summarizing enriched Gene Ontology (GO)

366 biological processes for a) environmental variable wind03 and for all variables b).

Local ancestry patterns

Of the 41 SNPs significantly associated with at least one climatic variable, 29 were represented on the reference panel used for local-ancestry inference and could therefore be assigned reliable ancestry estimates by ELAI; these were screened for indicine ancestry as candidates for putative adaptive introgression. Indicine ancestry at these candidate SNPs increased consistently along the population gradient, from very low values in Lobi (0.03–0.08) to the highest values in PK (0.26-0.66). Across all 29 SNPs, PK invariably showed the highest indicine proportion and Lobi the lowest (Table 3).

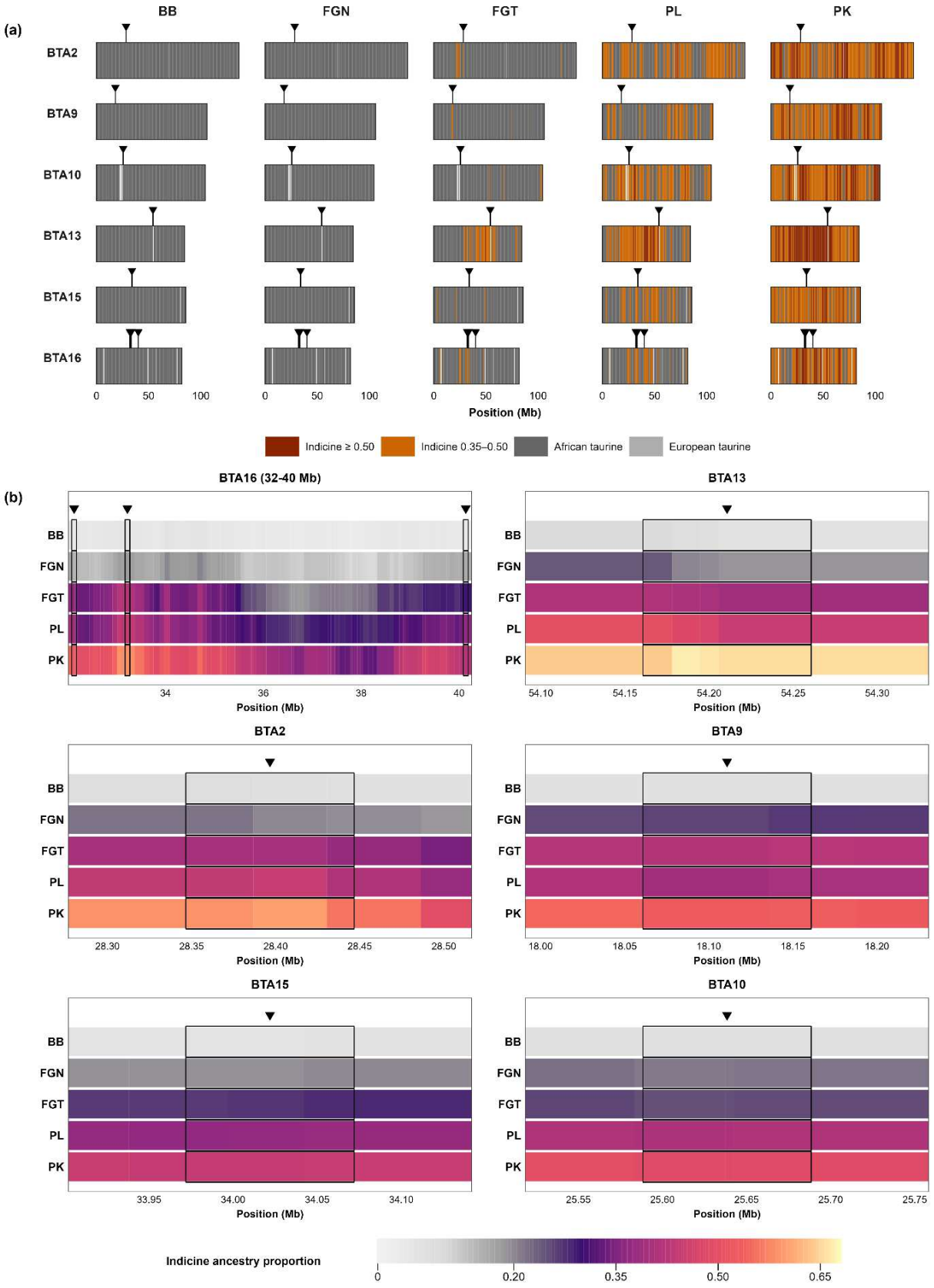
No candidate SNP reached an indicine proportion ≥0.50 in two or more populations. Eight SNPs reached indicine ancestry ≥0.50 in PK alone, which is the most introgressed population, while remaining below 0.50 in the four other populations (Table 3). Nine of the 29 candidate SNPs met the moderate-introgression criterion and were carried forward to haplotype-level confirmation (Table 3).

Table 3. Summary of the eight candidate loci exhibiting consistent indicine introgression across populations, including window-average indicine ancestry and associated cattle QTL. Window-average indicine proportions are the mean over a ±50 kb interval centred on each SNP. Genes and QTL were retrieved within 50 kb of each SNP (ARS-UCD1.2; Cattle QTLdb). BTA, *Bos taurus* autosome; Env., associated environmental variable. Population abbreviations are defined in (Table 1).

SNP	Chr.	Env.	Window-avg indicine (±50 kb)			Gene(s)	QTL
			FGT	PL	PK		
BovineHD1300015387	13	Prec07	0.40	*0.47*	**0.66**	*KCNQ2, CHRNA4*	-
BovineHD0200008300	2	Wind05	0.39	*0.44*	**0.60**	*lncRNA*	residual feed intake; milk kappa-casein
BovineHD0900004905	9	Bio16	0.41	0.39	0.53	intergenic	age at puberty; body weight; muscle iron
BovineHD1500009218	15	Wind03	0.27	0.37	0.44	*GRAMD1B*	lactation length; subcutaneous fat
BovineHD1600011405	16	Wind05	0.30	0.36	0.42	*SUCO, FASLG*	shear force; tick resistance
BovineHD1000008346	10	Prec07	0.25	0.41	0.49	*OR10G3, SALL2, METTL3, TOX4*	average daily gain; gestation length; pregnancy rate
BovineHD1600009122	16	Bio16	0.36	0.37	0.52	intergenic	-
BovineHD1600009472	16	Bio16	0.42	0.44	0.59	intergenic	inseminations per conception

To confirm that these signals reflected locally consistent haplotypes rather than single-marker inference noise, each candidate was re-evaluated over ±50 kb windows and the same thresholds were applied to the window-average indicine proportion. Eight of the nine loci retained their classification and were carried forward as the most robust candidates (Figure 9): BovineHD0200008300 (BTA2), BovineHD0900004905 (BTA9), BovineHD1000008346 (BTA10), BovineHD1300015387 (BTA13), BovineHD1500009218 (BTA15), BovineHD1600011405, BovineHD1600009122 and BovineHD1600009472 (BTA16; Table 3). Only BovineHD1800000133 (BTA18) met the criterion at its exact physical position but not under the window-average definition and was therefore not retained. Five of the eight retained loci (BovineHD1300015387, BovineHD0200008300, BovineHD0900004905, BovineHD1600009122 and BovineHD1600009472) recorded moderate indicine ancestry in

Gourounsi Ténado and PL and additionally reached high introgression (≥ 0.50) in PK, so that each of these five loci represents a single graded signal spanning three populations rather than two. At the remaining three loci (BovineHD1500009218, BovineHD1000008346 and BovineHD1600011405), the two qualifying populations were PL and PK.



406

407 Figure 9. Chromosome painting of the six target chromosomes (BTA2, 9, 10, 13, 15 and 16)

408 carrying candidate SNPs, shown for the five West African taurine and crossbred populations

(BB, FGN, FGT, PL and PK), ordered from the least (BB) to the most (PK) introgressed. a) Genome-wide painting of each target chromosome: for each population, indicine local ancestry is averaged in 0.4-Mb bins and each bin is coloured by its mean indicine proportion as ≥ 0.50 (dark red) or 0.35–0.50 (orange), or, where indicine ancestry is lower, by the predominant taurine component (African taurine, dark grey; European taurine, light grey). Inverted triangles mark the positions of the eight retained candidate SNPs. b) Fine-scale painting of the six candidate regions, showing per-SNP indicine local ancestry on a continuous lava scale; black rectangles delimit the ±50-kb windows centred on each candidate SNP and inverted triangles indicate the target SNPs.

Genomic annotation of the retained candidate loci

The eight loci confirmed at the haplotype level were annotated for overlapping genes and QTL within ±50 kb (Table 3). Four windows harboured a protein-coding gene, one contained a long non-coding RNA (lncRNA) and three were intergenic. Seven of the eight loci additionally overlapped previously reported QTLs.

BovineHD1300015387, harboured *KCNQ2* and *CHRNA4* but did not overlap any catalogued QTL. BovineHD1500009218 overlapped *GRAMD1B* and QTLs for lactation length and subcutaneous fat thickness. BovineHD1600011405 flanked *FASLG* and *SUCO* and overlapped two QTLs for tick resistance and meat shear force, respectively. BovineHD0200008300 contained the lncRNA ENSBTAG00000052783 and overlapped three QTLs related to residual feed intake and milk kappa-casein percentage. BovineHD0900004905 was intergenic and overlapped QTLs for body weight and age at puberty. BovineHD1000008346 harboured *SALL2*, *METTL3* and *TOX4* and overlapped reproduction- and growth-related QTL, while the two BTA16 loci were intergenic; and loci BovineHD1600009122 lay within a QTL for inseminations per conception.

Discussion

Diversity in the taurine cattle populations of Burkina Faso

In this study, we investigated the presence of genetic adaptation associated with the heterogenous environment occupied by Burkina Faso taurine cattle populations. African cattle populations, particularly West African, are described to have low selection pressure and unmanaged mating [84, 85] The combination of these factors fosters a diverse gene pool, potentially enhancing genetic diversity [11, 85, 86]. In our data, we recorded lower H_o in African taurine and crossbred populations than European taurine cattle. Such findings are likely due to the ascertainment bias in the SNP array that has been designed on European breeds, as also reported by other [15, 25, 87–90]. We also observed lower inbreeding than European taurine and indicine cattle populations, in line with previous findings [15]. The low levels of inbreeding observed in the studied populations may reflect the extensive, low-input management systems widely practiced across Burkina Faso. Under these systems, cattle are typically managed in large communal herds, with mating occurring predominantly through uncontrolled natural breeding and limited artificial selection or systematic use of a restricted number of breeding sires. Such management practices are likely to maintain relatively large effective population sizes and, consequently, reduce the accumulation of genome-wide homozygosity and inbreeding over generations [15].

Population Structure and admixture in Lobi and Gourounsi cattle

Consistent with earlier studies, the first PC gathered the majority of the variance and enabled to differentiate populations involved in this study according to their ancestry and thus to rank them according to their admixture level[88, 91, 92]. The PCA distributed populations according to their admixture levels, with the less admixed populations (N'Dama and Lobi) clustering close to European taurin breeds and the strongly admixed populations (Nganda, Ankole-

Watussi and Lobi crossbreed from Kampti) tightly clustering adjacent to the indicine breeds. Moderatly admixed populations (Gourounsi Nahouri and Gourounsi Tenado) were found in between the taurine and indicine clusters, which is reflected also in the Neighbor-Net and admixture results. Comparable levels of admixture have been reported from other West African countries investigating the same breeds breeds [15, 91] In this regard, all west African cattle included in this study showed ancestry components of indicine origin. Consistent with these findings, Kim *et al.* (2020) reported that indicine ancestry ranges from 10% to over 90% across African cattle, peaking in the Sahelian belt. More recently, [93] analyzed cattle from 10 West African populations including Burkina Faso and confirmed that most N'Dama individuals retained high taurine ancestry, whereas crossbreeds and Sanga type breeds clustered closer to zebu, reflecting a north-south gradient of indicine introgression. In Burkina Faso, traditionally, the practice of crossbreeding has been deeply intertwined with specific ethnic groups, most notably the Fulani community. However, recent findings suggest a dynamic shift in breeding practices, indicating a departure from the previous reliance on ethnic-based premises and the emergence of new driving factors[84]. Indeed, an increasing proportion of sedentary Lobi people that used to keep the Lobi cattle breed pure have started crossing them with zebu to benefit of their enhanced traction fitness and higher market price conferred by a heterosis effect. However, pure nucleus herds are maintained for cultural needs (e.g., dowry) and may explain the relatively lower admixture level of Lobi cattle compared to the Gourounsi cattle populations. Nevertheless, Lobi cattle herded by the Lorepeni and Kampi people showed higher levels of indicine ancestry than those kept by the Bouroum-Bouroum people. This disparity in admixture levels is likely due to the predominant presence of semi-transhumant farmers among Kampti and Lorepeni breeders, who are cognizant of the enhanced resistance to diseases conferred by crossbred cattle when contrasted with their pure zebu counterparts [84, 85]. Regarding the history of Gourounsi cattle breeding, the first mentioning of these taurine cattle

in literature described them as ‘Mere’ [94] which is a Fulani term to describe crossbreeds. Hence, this taurine population has been likely facing generations of zebu introgression [9].

Landscape genomics reveals genes related to animal production and environmental adaptation

Production and reproduction related genes

In this study, we used landscape genomics to detect potential genomic signature of adaptation to local environmental conditions in native taurine populations from Burkina Faso. Successful adaptation in an iteroparous species requires the accumulation of favourable traits that enhance resilience to environment constraints and ultimately support reproductive success. Thus, populations carrying favourable adaptive variants may be better able to withstand environmental constraints and maintain reproductive performance, reflecting a shift from simple stress tolerance toward long-term resilience.

In domestic animals, adaptive variants have accumulated through trade-offs between natural selection and human-mediated selection. We intercepted *IFG1R, CCDC6* and *CFL2* previously described to play a role in growth traits in the highly selected Qinchuan cattle [69, 95–97] whereas *U6*, was previously associated with carcass yield in European commercial taurine breeds [43]. However, these genes were also found to be under positive selection in N’Dama, a much less managed west African indigenous cattle breed [98]. Differences in the management system and the demographic history of the different breeds, as well as the association of these genes to different environment variables (bio16, wind04, wind11) might suggest they are less likely to be solely attributed to human selection and likely the result of fitness. Therefore, genes associated with reproductive traits may also be interpreted as part oof the adaptative response shaped by environmental stressors and the biological processes underlying resilience.

Environmental adaptative genes and resource allocation

Mapping the most appropriate biological processes/genes that are likely to explain the adaptation of Burkina Faso taurine cattle populations to their environment should be done in the light of a clear description of the environmental stressors. As theorized by Boggs, (2009), physiological trade-offs are more acute with increasing environment stress. Taurine cattle from Burkina Faso can be find in the Sudanian and the Sudano-sahelian agro-ecological zones. Burkina Faso livestock farming is essentially based on free grazing and the exploitation of naturally occurring herbaceous and ligneous plant species during the wet season. However, during the dry season, due to qualitative and quantitative forage shortage, farmers must exploit crop residues such as rice straw, millet, sorghum and corn stalks, fodder trees and shrubs for animal nutrition. These cereal residues constitute low-input feed resources of poor nutritive value, with a low crude protein content (2–9%) that generally falls short of the herd's maintenance requirements during the dry season [99]. Cattle in Burkina Faso are exposed to various external and internal parasites and stock diseases [100]. To survive in this environment, they require a range of genes that enable efficient processes related to mobilization of body reserves, effective mechanisms for poor forage utilization, efficient storage mechanisms and the ability to adapt to changes in plant species consumed based on the season.

There is a complex association between resource acquisition and resource availability [101]. In this respect, biological processes that may sustain resource acquisition are under the direct influence of environmental stressors as they are among the drivers of adaptative fitness. Taste receptors have been described by [102] to be among the best features that may help an animal survive in its environment. We have identified three taste receptors genes (*TAS2R39*, *TAS2R40* and *TAS2R60*) that were significantly associated with wind speed in March (wind03). In Burkina Faso, March corresponds to the middle of the dry season, a period characterized by forage shortage in both quality and quantity. At this time of the year, animals must survive by

feeding on the available herbaceous and ligneous plants in their environment. The high variability observed in taste receptors genes in this study may therefore reflect the adaptation of Burkina Faso taurine cattle populations to diverse dietary repertoires, depending on the resource availability [102], while preventing the consumption of plant toxins [103]. In the same line, olfactory receptors provide information allowing animals to locate and choose food, recognize predators and choose partners [104]. This study identified seven olfactory receptors genes: two associated with wind03 (*OR2R3*, *OR10AC1*) and five with prec07 (*OR4E1*, *OR4E2*, *OR10G1*, *OR10G1C*, *OR10G3*). The presence of unique olfactory receptors genes associated with these two environmental variables may reflect the diversification of their usage (feed choice) in relation to the forage availability and quality. The rainy season begins in July, marking the beginning of abundant and rich forage, whereas March is associated with forage shortage in both quantity and quality. Both months are characterized by blowing winds: the dry and hot Harmattan in March and the humid and fresh Monsoon in July. Importantly, olfactory receptor genes were found to be associated with dry matter intake in Nellore cattle [105] and feed efficiency in Holstein cattle [106]. Likewise, among the intercepted genes *GRAMD1B* [64, 107] has been associated with feed efficiency.

Adaptative genes and energy trade-off

When resources are limited, trade-offs occur if individual variation in resource allocation exceeds variation in resource acquisition [108]. Consistent with this framework, we identified several genes involved in metabolic processes directly or indirectly related to energy balance. The intercepted genes can be divided in two groups, those correlated with the hot season (wind03 and wind04) are involved in glucose/lipid degradation while those correlate with rainy or cold season (prec07 and wind11) are correlated with lipid/glucose synthesis. In the first group, *TNFRSF6B* (prec07) has been reported to play a role in response to lipopolysaccharide [109], whereas *SLC2A4RG* (prec07) is involved in adaptogenic processes and glucose uptake

555 [50], *OMG* (prec07) plays a role in metabolism during food deprivation and *TAS2R39* (prec07)
556 has been linked to pigs back fat thickness and bitter taste perception in humans [110, 111]. In
557 the second group, *GSTK1* (wind03) is involved in lipid metabolism and energy production, with
558 expression negatively correlated with fat deposition in mammals [112], *ZNF202* (wind04) is
559 involved in lipid metabolism in humans [113] and *SPTSSA* (wind11) catalyzes sphingolipid
560 biosynthesis [114].
561 All these genes are involved in alternative metabolic processes of glucose, energy management
562 and fat metabolism, which are relevant adaptive strategies allowing animals to balance their
563 resources in response to changes in their environment, such as harsh conditions during the dry
564 season and resource abundance during the rainy season [115, 116]. Among the genes identified,
565 *SPTSSA* provides an illustrative example of a gene potentially involved in energy-allocation
566 trade-offs. Sphingolipids have been reported to be elevated in female plasma during gestation
567 [117]. The association between *SPTSSA* and wind speed in November (wind11) may therefore
568 reflect an adaptive response to the limited and fluctuating resources available to taurine cattle
569 populations in Burkina Faso under low-input management systems. In Burkina Faso, calving
570 generally occurs between July and October, when feed resources are relatively abundant.
571 However, given the approximately nine-month gestation period in cattle, many females are
572 likely to be pregnant in November, which marks the beginning of the cold dry season. This
573 pattern suggests that these populations may rely on energy reserves accumulated during the
574 rainy season to sustain reproductive investment during the dry season.

575 **Taurine cattle adaptation to heat and long walk**

576 Several genes identified in this study may play a role in adaptation to heat stress, including
577 *PPP2R3C*, *METTL3*, *SRP54*, *MRLN* and *SNORA70*. *PPP2R3C* is associated with coat
578 pigmentation and melanin production, traits that may influence the ability of cattle to cope with
579 hot and sunny environments. *METTL3* regulates the UV-induced DNA damage response [48]

and has also been linked to heat adaptation in Mediterranean cattle breeds [118]. Intriguingly, we also identified genes that may be related to musculoskeletal function and locomotor performance. For instance, *SAAL1* has been associated with abnormal proliferation of synovial fibroblasts, a process linked to synovitis progression in mice and humans [119]. This association may indicate a potential genetic component of susceptibility to joint inflammation, which could contribute to the ability of taurine cattle to tolerate long-distance walking under extensive management conditions.

Interestingly, we found that the myoregulin gene (*MRLN*) was associated with wind speed in April (wind04). April is the hottest month of the year in Burkina Faso. Wind04 also showed strong correlations with mean and maximum temperatures in December, as well as with maximal temperature and solar radiation in January, both of which correspond to the coldest months in the country. This finding may therefore be relevant to seasonal climatic variability and suggests a possible role of *MRLN* in adaptation to thermal stress. *MRLN* impedes Ca^{2+} uptake into the sarcoplasmic reticulum. In mice, [68] reported that genetic deletion of myoregulin enhances Ca^{2+} handling in skeletal muscle and improves exercise performance, supporting the role of *MRLN* as an important regulator of skeletal muscle physiology. This is of particular interest because taurine cattle have been suggested to be less adapted to long-distance walking than indicine cattle [11]. Compared with the Sahelian zone, where animals often need to follow long migration routes to access pasture, taurine cattle in Burkina Faso generally undertake short-distance movements, likely because vegetation is more abundant in the Sudanian zone than in the Sahelian zone. Thus, variation in or near *MRLN* may reflect local adaptation related to skeletal muscle function, locomotor demands and thermal stress. However, comparative analyses of *MRLN* expression or function in taurine and indicine cattle would be needed to test whether this gene differs between these groups. Similarly to *MRLN*, *SNORA70*

has been associated with metabolic adaptation in populations adapted either to cold or hot environmental conditions [120].

Adaptation to diseases

Some of the genes found associated with climatic variables in this study have been previously implicated in infectious disease resistance. One of the most striking examples is *MAN2A1*, which has been strongly linked with *Fasciola hepatica* infection and is involved in an immune response pathway [70]. In our study, this gene was associated with wind speed in March (wind03). In Burkina Faso, March is characterized by drought and grass scarcity, conditions that may force cattle to congregate around limited water points, thereby increasing repeated exposure to parasites and pathogens. Moreover, the Southwest and Central-South regions, corresponding respectively to Lobi and Gourounsi Nahouri cattle sampling areas, are among the areas with the most important water courses, which may further influence exposure to water-associated parasites. In addition to *MAN2A1*, the candidate region on BTA19 that spanned four genes (*NF1*, *EVI2A*, *EVI2B*, *OMG*), was associated with precipitation in July and has previously been linked to resistance to gastrointestinal nematode infection in traditionally managed Tunisian sheep [56]. July corresponds to the onset of the rainy season; a period generally associated with increased gastrointestinal nematode infection pressure. Finally, *FASLG* has been associated with reduced trypanosomiasis susceptibility in mice [60, 61]. In our study, this gene was associated with wind speed in May, which was strongly correlated with precipitation of the wettest quarter of the year (bio16). Surprisingly, we also identified *HMGCLL1*, a gene associated with ketosis [81], despite the fact that taurine cattle in Burkina Faso are generally not milked and produce only small quantities of milk. Similarly, we detected *ZGPAT*, a gene involved in milk production through the regulation of protein synthesis, processing and secretion in mammary tissue [51]. These findings may suggest that genes classically associated

with dairy-related metabolic traits could also have broader roles in energy metabolism, physiological adaptation, or reproductive performance in low-input production systems.

Finally, we identified *SRP54*, a gene linked to in vitro granulocytic differentiation and essential for co-translational protein targeting to the endoplasmic reticulum [121]. *SRP54* has also been implicated in the expression of heat shock proteins [122]. Granulocytes contribute to immune responses against blood-borne parasites and an increased proportion of circulating granulocytes has been shown to mediate antiplasmodial immune memory [123], making *SRP54* an interesting candidate gene at the interface between immune response and heat-stress adaptation. However, further functional studies are required to determine whether variation in this gene contributes to disease resistance, thermal tolerance, or both in Burkina Faso taurine cattle populations.

Genes related to behaviour

Our study identified a gene related to behaviour, *GRM3*, as being one of the most significant genes associated with stress response modulation. This gene has previously been linked with variations in aggressiveness and tameness in fox populations [124]. Our findings suggest that compared to zebu cattle, Burkinabe taurine cattle exhibit more aggressive behaviour. It is possible that the milking routine of zebu cattle promoted selection for less aggressive traits, features not as necessary in the Lobi and Gourounsi taurine cattle.

GO enrichment biological processes

The GO enrichment analysis revealed a significant overrepresentation of genes associated with wind speed in March (wind03) in biological processes related to micturition, excretion and synaptic transmission involved in urinary regulation. Wind may act as an important selective pressure influencing water balance in taurine cattle. These findings are physiologically

coherent, as wind speed enhances evaporative water loss, particularly under hot and arid Sahelien conditions, therefore requiring adaptative adjustment in fluid balance.

Similar adaptative patterns have been reported in Xinjiang Mongolian cattle adapted to desert environments, where genes involved in water reabsorption and osmoregulation were identified as targets of selection [125]. In addition, the enriched pathways related to chemical synaptic transmission and bitter taste perception may reflect co-selection for toxin detection in grazing environments as hypothesis supported by [126] who reviewed selection signatures in indigenous African cattle and highlighted the pleiotropic roles of sensory genes in environmental adaptation. Together, these findings suggest that adaptation in Burkina Faso taurine cattle likely involves an integrated network of physiological, neural, metabolic and sensory mechanisms contributing to water conservation and environmental resilience.

Indicine introgressed loci/haplotypes in taurine cattle

Local ancestry analysis of environmentally associated SNPs reveals a gradient of indicine introgression across Burkinabe cattle populations, consistent with the continental admixture patterns previously described in African cattle [127, 128]. This continuity suggests that the local ancestry signals reported here should not be read as independent, locus-specific events, but as points along a shared demographic and evolutionary background, likely shaped by long-term admixture. Across the identified loci, we only recorded one occurrence of high indicine ancestry at a given SNP/haplotype, restricted to the most admixed population (PK), suggesting that strong introgression signals are not stably maintained across the taurine genomic background. In contrast, loci showing moderate introgression were the most common across populations and independent genetic backgrounds. However, these two patterns were not mutually exclusive. We found moderate indicine ancestry at five of the eight retained loci (located at chromosomes BTA13, BTA2, BTA9 and BTA16) in Gourounsi Ténado and PL, peaking to high introgression in PK, so that each represents a single introgression signal graded across three populations,

rather than two unrelated categories. Among the graded loci, long non-coding RNA ENSBTAG00000052783 overlapped QTLs for residual feed intake, a measure of metabolic efficiency known to differ between indicine and taurine cattle and of plausible relevance under the seasonal nutritional stress typical of West African agro-ecological systems [25, 30]. Long non-coding RNAs have been directly implicated in feed efficiency regulation in indicine cattle [129], lending independent plausibility to a regulatory role for ENSBTAG00000052783 at this locus, although the specific transcript has not itself been functionally characterized [129]. At the three loci where moderate introgression was confined to PL and PK, the *FASLG*-flanking locus (BovineHD1600011405) was the most informative. *FASLG*, is an immune-effector gene and overlaps two QTLs spanning tick resistance and meat shear force [41]. Tick resistance is one of the most clearly differentiated adaptive traits between indicine and taurine cattle [20, 130]. Its co-occurrence with an immune-related gene and a population-ordered introgression signal is a biologically coherent configuration, even though the association remains indirect and causality cannot be inferred from co-localisation alone. Taken together, these results are consistent with indicine introgression being retained, at a subset of loci, in genomic regions associated with traits of plausible relevance to environmental adaptation, rather than being randomly distributed with respect to genome function. QTL annotation provides the interpretive link between the ancestry signal and a candidate phenotypic consequence at six of the eight loci. Thus, the eight retained loci can be regarded as candidate adaptive haplotypes warranting fine-mapping and functional follow-up, not as demonstrated targets of selection.

Conclusions

Here, we explored the adaptation of Burkina Faso taurine cattle populations using a landscape genomics approach. By investigating the genetic basis of traits related to behaviour, stress response, metabolism and environmental resilience, we provide insights into how environmental factors may have shaped the genetic composition of these populations over time.

We identified candidate genes and associated biological functions suggesting a remarkable capacity of these breeds to respond to environmental challenges through energy-allocation trade-offs, disease resistance, including resistance to trypanosomiasis and mechanisms involved in physiological resilience.

Nevertheless, the identification of candidate genes potentially related to adaptation to long-distance walking raises questions about the historical and ecological factors governing the introgression from zebu cattle. Further investigation is required to gather additional evidence and better understand the functional implications of these genes. These findings open avenues for research and discussion on the adaptive strategies of taurine cattle, while also inviting critical examination of the historical, ecological and management factors that have shaped the genetic composition of these populations.

Moving forward, it will be crucial to expand this research by integrating multidisciplinary approaches and larger datasets to strengthen our understanding of the complex interplay among genetics, environment and cattle adaptation. Such efforts may inform targeted conservation and breeding strategies that prioritize the preservation of valuable adaptive traits within Burkina Faso taurine cattle populations.

List of abbreviations

ANG: Angus; **ANW**: Ankole-Watussi; **ARS-UCD1.2**: *Bos taurus* reference genome assembly; **BB**: Baoulé (Lobi); **bio16**: Precipitation of the wettest quarter; **BSW**: Brown Swiss; **BTA**: *Bos taurus* autosome; **CIWI**: Consistently Introgressed Windows of Interest; **DNA**: Deoxyribonucleic acid; **EDTA**: Ethylenediaminetetraacetic acid; **ELAI**: Efficient Local Ancestry Inference; **F**: Inbreeding coefficient; **FDR**: False Discovery Rate; **FGN**: Gourounsi of Nahouri; **FGT**: Gourounsi of Sanguié (Ténado); **FROH**: Inbreeding coefficient based on runs of homozygosity; **F_{ST}**: Fixation index; **GALLO**: Genomic Annotation in Livestock for positional candidate LOci; **GIR**: Gir; **GO**: Gene Ontology; **HOL**: Holstein; **Ho**: Observed

heterozygosity; **KING**: Kinship-based INference for Genome-wide association studies; **LD**: Linkage Disequilibrium; **LEA**: Landscape and Ecological Association (R package); **LFMM**: Latent Factor Mixed Model; **LOH**: Lohani; **NDA**: N'Dama; **Ne**: Effective population size; **NGA**: Nganda; **PANTHER**: Protein ANalysis THrough Evolutionary Relationships; **PC**: Principal Component; **PCA**: Principal Component Analysis; **PK**: Crossbred of Kampti; **PL**: Crossbred of Lorepeni; **PLINK**: Whole-genome association analysis toolset; **Prec07**: Precipitation in July; **QTL**: Quantitative Trait Locus/Loci; **RNA**: Ribonucleic acid; **ROH**: Runs Of Homozygosity; **SNP**: Single Nucleotide Polymorphism; **THA**: Tharparkar; **UV**: Ultraviolet; **wind03**: wind speed in March; **wind04**: wind speed in April; **wind05**: wind speed in May; **wind11**: wind speed in November.

Declarations

- **Ethics approval and consent to participate**

This study was submitted to and approved by the "Commission d'Éthique de l'Université Joseph KI-ZERBO" (Ethics Committee of Université Joseph KI-ZERBO), Ouagadougou, Burkina Faso, under reference number CE-UJKZ/2023-09. All blood sampling was performed by trained veterinarians in accordance with the approved protocol and with relevant national and institutional guidelines and regulations. Informed consent to collect samples was obtained from all animal owners prior to sampling.

- **Consent for publication**

Not applicable

- **Availability of data and materials**

The datasets supporting the conclusions of this article are included within the article and its additional files. The genotype data are provided as PLINK binary files (.bed, .bim, .fam) in

Additional file 3. All supplementary tables and figures are provided in Additional files 1 and 2.

- **Competing interests**

The authors declare that they have no competing interests.

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- **Authors' contributions**

PAB, MB and ASRT designed the study. ASRT and MB performed the data analysis. ASRT drafted the manuscript. MB and PAB critically revised the manuscript. YB, DO, AT, SKO, GM, JS and AS read and approved the final manuscript.

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Additional files

Additional file 1: Supplementary tables. (XLSX)

Table S1. Sampling details, from raw data to pruning steps. **Table S2.** Climate data variables description. **Table S3.** Climate data table sheet. **Table S4.** Climate data correlation table. **Table S5**. Most significant SNPs associated with precipitation in July (prec07) identified by the LFMM method. **Table S6.** Most significant SNPs associated with wind speed in March (wind03) identified by the LFMM method. **Table S7.** Most significant SNPs associated with wind speed in April (wind04) identified by the LFMM method. **Table S8.** Most significant SNPs associated with wind speed in May (wind05) identified by the LFMM method. **Table S9.** Most significant SNPs associated with wind speed in November (wind11) identified by the LFMM method. **Table S10.** Most significant SNPs associated with precipitation of the wettest quarter (bio16) identified by the LFMM method. **Table S11.** Overrepresentation analysis of

GO biological processes using PANTHER for all genes associated with the significant environmental variables. **Table S12.** Overrepresentation analysis of GO biological processes using PANTHER for genes associated with wind03.

Additional file 2. Supplementary figures. (.PDF)

Figure S1. Principal component analysis (PCA) plots for West African cattle breeds based on four sample subset iterations used to infer the effect of sample size on PCA configuration. (a) Iteration 1, (b) Iteration 2, (c) Iteration 3, (d) Iteration 4. Each subset iteration includes 34 samples per breed.

Figure S2. PCA plot for West African taurine cattle using the full dataset.

Figure S3. Gene Ontology overrepresentation analysis. (a) Overrepresented biological processes; (b) Venn diagram of genes identified for wind03, wind04 and wind05.

Additional file 3. Genotype dataset. (ZIP)

PLINK binary files (.bed, .bim, .fam)

Supplementary Files

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