









Population structure, inbreeding and admixture in local cattle populations managed by community-based breeding programs in Burkina Faso

Dominique Ouédraogo^{1,2}  | Salifou Ouédraogo-Koné¹  | Bernadette Yougbaré^{2,3}  |
Albert Soudré⁴  | Bienvenue Zoma-Traoré^{1,2} | Gábor Mészáros²  |
Negar Khayatzadeh² | Amadou Traoré³ | Moumouni Sanou³ | Okeyo Ally Mwai⁶ |
Maria Wurzinger²  | Pamela A. Burger⁵  | Johann Sölkner² 

¹Institut du Développement Rural (IDR), Université Nazi Boni (UNB), Bobo-Dioulasso, Burkina Faso

²Division of Livestock Sciences, Department of Sustainable Agricultural System, University of Natural Resources and Life Sciences, Vienna, Austria

³Institut de l'Environnement et de Recherches Agricoles (INERA), Ouagadougou, Burkina Faso

⁴Unité de Formation et de Recherche en Sciences et Technologies (UFR/ST), Université Norbert Zongo, Koudougou, Burkina Faso

⁵Research Institute of Wildlife Ecology, Department of Interdisciplinary Life Sciences, University of Veterinary Medicine Vienna, Vienna

⁶International Livestock Research Institute (ILRI), Nairobi, Kenya

Correspondence

Pamela A. Burger, Research Institute of Wildlife Ecology, Department of Interdisciplinary Life Sciences, University of Veterinary Medicine Vienna, Savoyenstrasse 1, 1160 Vienna.
Email: pamela.burger@vetmeduni.ac.at

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Abstract

High-throughput genomic markers provide an opportunity to assess important indicators of genetic diversity for populations managed in livestock breeding programs. While well-structured breeding programs are common in developed countries, in developing country situations, especially in West Africa, on-farm performance and pedigree recordings are rare, and thus, genomic markers provide insights to the levels of genetic diversity, inbreeding and introgression by other breeds. In this study, we analysed key population parameters such as population structure, admixture and levels of inbreeding in three neighbouring populations of African taurine and taurine × Zebu crosses managed by community-based breeding programs in the South-West of Burkina Faso. The three populations were pure Baoulé (called Lobi locally) in sedentary production systems, Baoulé × Zebu crossbreds in sedentary systems and Zebu × Baoulé crossbreds in transhumant production systems, respectively. The total sample analysed included 631 animals and 38,207 single nucleotide polymorphisms after quality control. Results of principal component and admixture analyses confirmed the genetic background of two distinct ancestral populations (taurine and zebuine) and levels of admixture in all three breeding populations, including the presumably pure Baoulé group of animals. Inbreeding levels were moderate, compared to European dairy and beef cattle populations and higher than those of Brazilian Nelore cattle. Very few animals with inbreeding levels indicating parent–offspring or full sib mating were observed, and inbreeding levels indicating half sib mating were also rare. For the management of breeding populations, farmers were advised to exchange best young bulls. The crossbreeding levels of presumably pure Baoulé animals are of concern to the breeding program due to the high level of endangerment of pure African taurine cattle populations across West Africa. Future rounds of bull selection in the community-based breeding program will make use of genomic information about admixture levels.

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KEYWORDS

admixture, breeding, Burkina Faso, cattle, inbreeding, SNP, structure

1 | INTRODUCTION

Zebu (*Bos indicus*) and taurine (*Bos taurus*) are the main indigenous cattle genetic resources across a wide range of agro-ecological zones in West Africa. Local taurine cattle types of African ancestry are genetically distinct from European taurine cattle (Decker et al., 2014; Kim et al., 2020) and are typically very small in body size (Traoré et al., 2015). The African taurine cattle are only kept in the tsetse-infested and trypanosomiasis endemic Sudano-Guinean area due to their tolerance to trypanosomiasis (Soudré et al., 2013). The desire of farmers to increase the body size of their cattle has led to an increase in crossbreeding of the taurine with heavier bodied Sahelian Zebu cattle in both the transitional Sudan-Sahel and the Southern Sudano-Guinean areas (Traoré et al., 2015). The crossbreeding is often practiced indiscriminately and thus threatens the genetic integrity of taurine cattle in the area (Alvarez et al., 2014).

In the South of Burkina Faso, the crossbreeding with Sahelian Zebu to “upgrade” the taurine Baoulé cattle, which are locally called “Lobi,” now threatens the existence of this local cattle breed. The Lobi cattle has an important cultural role for the Lobi ethnic people and is therefore a critical heritage, besides serving as a source of income and savings. The cattle are used for ploughing and constitute an important asset for socio-cultural ceremonies such as dowry and marriage related gift exchanges among families, for which Zebu type animals are not acceptable (Mopaté, 2015). There is an urgent need for conservation and within breed improvement of this locally adapted cattle to avert the ongoing genetic erosion that, if unchecked, will significantly limit its capacity to cope with changes in the production environment (Edea et al., 2013). Since 2016, three community-based cattle breeding programs, one for pure Baoulé and two for crossbreeds (i.e., Baoulé × Zebu crosses), have been implemented with the overall aim to increasing the animals’ body size and improving trypanotolerance (Ouédraogo, et al., 2020). The pure Baoulé program has been established in the sedentary pure Baoulé system (SPB), in which the farmers are natives of the local area and solely keep pure Baoulé cattle. The other two programs with crossbreeds have been set up, firstly in the sedentary mixed breed system (SMB) in which farmers are native, but keep pure taurine Baoulé as well as crossbreeds; and secondly in the transhumant Zebu and crossbred system (TZC), with predominantly migrants, who are mostly the Fulani people, who keep the Zebu and some crossbred animals (Ouédraogo, Soudré, Ouédraogo-Koné, Zoma, et al., 2020). However, the breeding management is

not well controlled, with replacement breeding bulls being mostly recruited from within these very herds, thus making the systems potentially highly susceptible to inbreeding.

Genetic diversity information is essential for the control of inbreeding and for effective utilization and exploitation of a breed's specific characteristics (Makina et al., 2014). Inbreeding refers to mating of parents who share one or more recent common ancestors (Curik et al., 2014). Understanding and control of inbreeding are key factors of genetic improvement strategies because increasing inbreeding reduces genetic variation and leads to inbreeding depression (Ferenčaković, Hamzić, et al., 2013).

Genetic characterization of livestock breeds is a strategic and critical first step in the development of a national/regional plan for the management of any Animal Genetic Resource (FAO, 2007). Characterization provides the key information needed to inform and guide breeding program design, decisions on genetic improvement options, and the sustainable management and utilization for such resources (FAO, 2007; Madilindi et al., 2020). To mitigate the global environmental changes such as climate change, use of locally adapted breeds and their improvement are reasonable options for coping with the extreme and unpredictable effects of climate change, especially biological stresses such as increased disease incidence, famine and drought (FAO, 2010; Madilindi et al., 2019).

Genetic markers have widely been used for the genetic characterization of West African cattle, including microsatellites (Alvarez et al., 2014; Kassa et al., 2019; Soudré, 2011) and single nucleotide polymorphisms (SNP) (Gautier et al., 2009; Tijjani et al., 2019). However, such markers have not yet been used to inform implementation of local cattle breeding programs. The aim of this study was to use high-throughput genomic markers to understand the current genetic make-up of local cattle populations involved in community-based breeding programs for pure Baoulé and their crosses with Fulani Zebu cattle breeds in South Western part of Burkina Faso.

2 | MATERIALS AND METHODS

2.1 | Study area, sample collection and DNA extraction

EDTA blood samples were collected from 658 animals in the South Western region of Burkina Faso. The animals were part of three breeding programs implemented in three

different production systems in the area: SPB in the district of Bouroum-Bouroum (BB), SMB in the commune of Loropéni (PL) and TZC systems in the commune of Kampti (PK) respectively (Figure 1). In this study, animals in SPB system were considered as pure African taurine (Baoulé), while animals in the other two production systems were considered as crossbred (Zebu × Baoulé). DNA was extracted from EDTA blood samples using the MasterPure™ DNA Purification Kit for Blood Version II (Biozym Scientific) following the manufacturer's protocols.

2.2 | Genotypes and data filtering

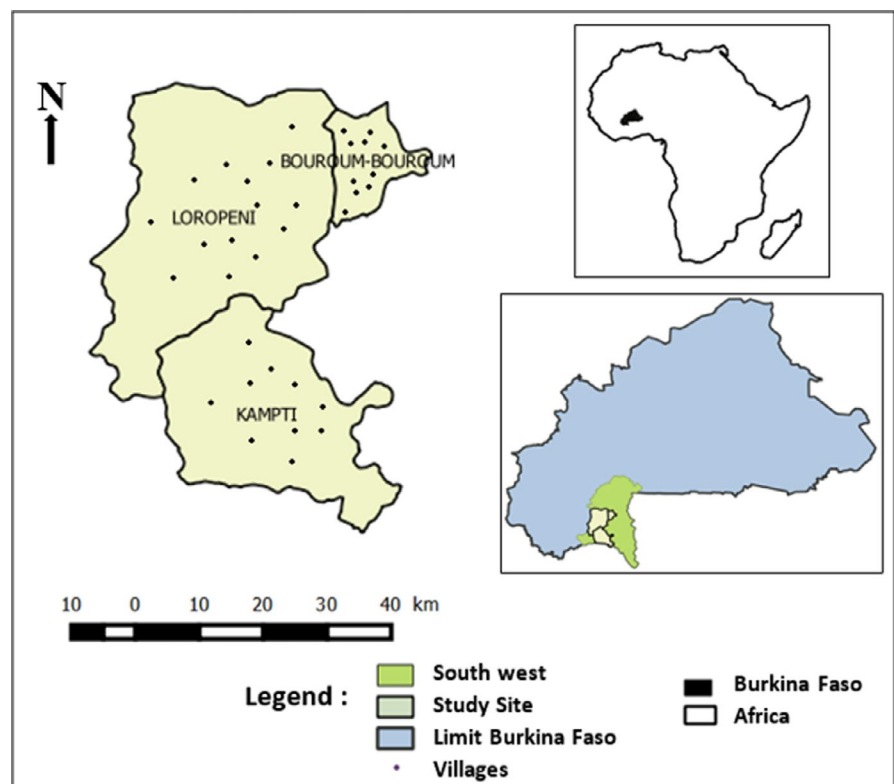
Genotyping was conducted using the Illumina Bovine SNP 50K Bovine BeadChip, featuring 53,714 SNPs. PLINK 2.0 (Chang et al., 2015; Purcell et al., 2007; Saravanan et al., 2019) was used to perform sample and SNP base quality control. SNPs were arranged according to the ARS-UCD1.2 reference genome. Samples with more than 10% missing genotypes (genotype call rate <90%), and SNPs with minor allele frequency <0.01 and deviation from Hardy–Weinberg equilibrium with Fisher's exact test (p -value < 10^{-6}) were filtered and not used in the downstream analysis. After filtering, 38,702 SNP and 631 animals (343 in SPB, 156 in SMB and 132 in TZC) were included in downstream analyses. For the estimation of genomic diversity (observed and expected heterozygosity), each population was filtered separately for individual and genotype call rates above 90%, respectively,

resulting in 46,618 SNPs in SPB, 46,523 SNPs in SMB and 46,475 SNPs in TZC. Finally, a symmetric identical by state matrix was created with PLINK to identify any potentially related individuals.

2.3 | Genetic diversity, population structure and admixture analysis

Principal component analysis (PCA) and admixture analysis were performed to infer the population structure and admixture among the three cattle populations based on the filtered SNPs. Individual-based PCA was performed for a *genlight* object through the function *glPca* in the R package Adegenet *v2.1.1*, and the *s.class* option was used to represent principal components of predefined groups (Jombart, 2008; Jombart & Collins, 2015) and to plot the first three eigenvectors. We used maximum likelihood estimation of individual ancestries implemented in the ADMIXTURE *v1.3.0* program (Alexander et al., 2009) to determine the proportion of admixture and potential gene flow among the three cattle populations (i.e., production systems). In order to infer the most preferable number of clusters (K) for the three populations, we ran ADMIXTURE from $K = 2$ to $K = 10$ and evaluated the smallest cross validation (CV) error. Expected (H_E) and observed (H_O) heterozygosities for each population were estimated in Adegenet using the *summary* function for a *genind* object. The R package dartR (Gruber et al., 2017) was used to convert a *genlight* into a *genind* object.

FIGURE 1 Map of Burkina Faso showing the three study areas. The administrative region of South-West is delimited in green. The yellow colour shows the three communes in which the breeding programs are being implemented. The black dots represent the villages where animals were sampled [Colour figure can be viewed at wileyonlinelibrary.com]



2.4 | Effective population size

Effective population size (N_e) is a genetic parameter that aids the understanding and modelling of the evolutionary history of the population and the genetic mechanism underlying complex traits (Hayes et al., 2003; Zhang et al., 2020). In this study, the relationship between variance in linkage disequilibrium (LD) and effective population size (N_e) was used to infer ancestral and recent effective population sizes. The N_e was estimated using SNeP software (Barbato et al., 2015) that allows the estimation of N_e trends across generations using SNP data and corrects for sample size, phasing and recombination rate based on the formula (Corbin et al., 2012).

$$N_{T(T)} = (4f(c_{(t)})^{-1} (E[r_{adj}^2 | C_t])^{-1} - \alpha$$

where N_T is the effective population size T generations ago calculated as $T = (4f(c_{(t)})^{-1}$ (Hayes et al., 2003), C_t is the recombination rate for specific physical distance between markers calculated by SNeP (Barbato et al., 2015) using default value (1 Mb ~ 1 cM), $r_{adj}^2 = r^2 - (\beta_n)^{-1}$ where r_{adj}^2 is

LD value adjusted for the sample size (n), $\beta = 1$ is the default value for unknown phase and α is as correction for the occurrence of mutation ($\alpha = 2.2$ as suggested by (Corbin et al., 2012).

2.5 | Identification of runs of homozygosity (ROH)

Runs of homozygosity are long homozygous stretches of DNA in the genome that are induced by transmission of identical haploid segments from a common ancestor of both parents of an individual. PLINK 2.0 code and the cgaTOH function (Zhang et al., 2013) were applied to compute ROH summary statistics and to calculate genomic inbreeding coefficients. The numbers of allowed missing and heterozygous genotype calls were dealt with according to ROH length, following Ferenčaković, Sölkner, et al. (2013). The genomic inbreeding coefficient of each individual was calculated as follows:

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

where L_{ROH} is the total length of all ROH in the genome of an individual, where the regions contain the minimum specified length of segments containing successive homozygous SNP, and $L_{AUTOSOME}$ refers to the specified length of the autosomal genome covered by SNP on the chip. In this study, we used ROH with minimum lengths of 1, 2, 4, 8 and 16 Mb, translating into 50, 25, 12.5, 6.25 and 3.125 generations of ancestry (Curik et al., 2014). Differences of inbreeding levels among populations were tested using Kruskal–Wallis tests. Pairwise comparisons were performed with Wilcoxon tests using R version 3.6.3.

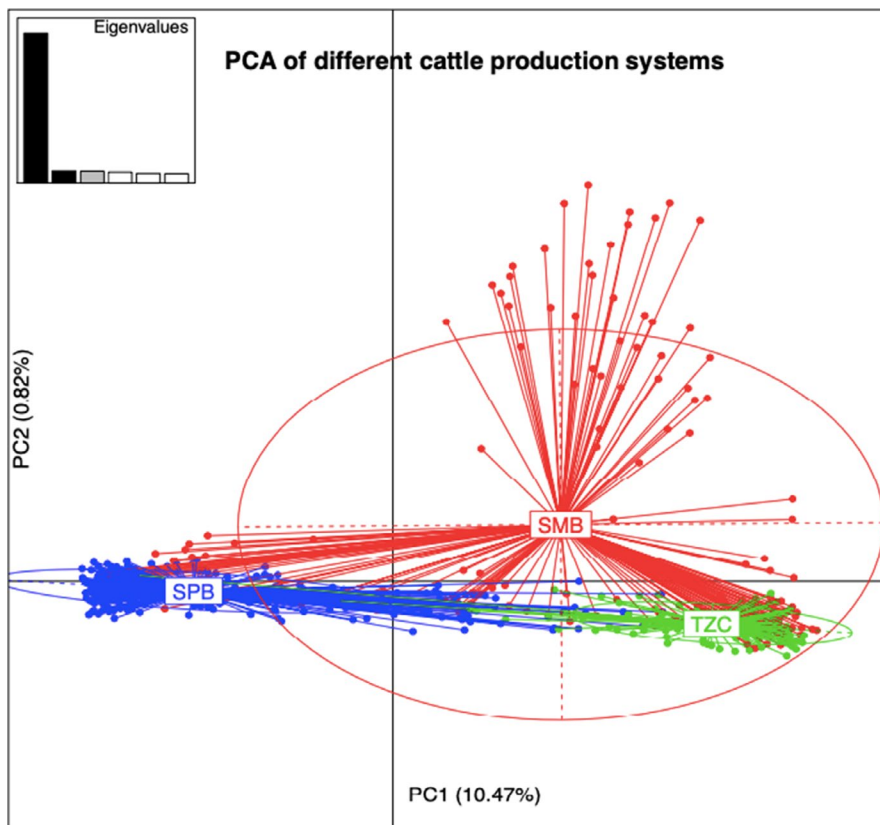


FIGURE 2 Principal component analysis obtained from 631 individuals and based on 38,207 SNPs to represent populations preclassified according to phylogenetic clustering. Individuals are plotted according to their coordinates on the first two components. The first two PCs (PC1–PC2) explained 10.47% and 0.82% of the total variation, respectively. Ellipses refer to the distribution of individuals within the groups. Population of Sedentary pure Baoulé system (SPB) is depicted in blue, while as populations of Sedentary mixed breed system (SMB), Transhumant Zebu and crossbred system (TZC) are in red and green, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Genetic diversity, population structure, admixture and effective population size

Principal component analysis was carried out to determine genetic relationships within and across the populations based on allele frequencies and levels of heterozygosity. We projected the genetic variation of each animal on the first three axes and incorporated production system information (SPB, SMB and TZC) for all samples (Figure 2). The three principal components (PC1, PC2 and PC3) explained 12.10% of the total variation. PC1 explained 10.47% of the total variation and showed that the main structuring is between the SMB population and the populations of the other two systems (SMB and TZC). PC2 described 0.82% of the total variation and reflected the genetic diversity among the populations of the SMB and TZC. Overall, there was gene flow visible between the three populations.

Admixture analysis was performed to investigate the extent of admixture of animals in the three production systems. Based on the lowest CV error, the best solution seemed to be nine clusters. However, regarding the history of the different populations and the practice of crossbreeding in the area, we chose to plot the admixture results for two and three assumed ancestries, $K = 2$ and $K = 3$ (Figure 3). For $K = 2$ the samples were split in two groups which are presumed pure

Baoulé animals in SPB and crossbreeds in the other two systems. Results revealed the presence of admixed individuals in each population/production system, confirming the PCA plots. For $K = 3$, a subgroup of animals became visible in the second cluster correlating with the individuals separated by PC2 (Figure 2). Almost all of these individuals were owned by a single breeder, and 34% of them (16 out of 47 animals) showed higher levels of relatedness (0.800–0.862) than all other investigated cattle (0.729–0.838). The estimated levels of genetic diversity (H_E/H_O) within each of the three populations ranged from 0.290/ 0.278 to 0.327/ 0.310 and were lowest in the sedentary Baoulé cattle population (Table 1).

Effective population sizes estimates (N_e), predicted from linkage disequilibria of adjacent SNPs for the current generation, were lowest (37) for the crossbred SMB population, somewhat higher for TZC (53) and highest for the pure Baoulé population, SPB (79) (Table 1). N_e values were predicted to have been much higher for past generations.

3.2 | Run of homozygosity characteristics and genomic inbreeding

Genomic inbreeding coefficients (F_{ROH}) at different length categories (>1, >2, >4, >8, >16 Mb) were analysed for the three populations. The detailed statistics of genomic inbreeding coefficient (F_{ROH}) are presented in Table 2. The

FIGURE 3 Results of admixture analysis on 631 individuals and 38,207 SNPs with an inferred number of cluster $K = 2$ and $K = 3$, respectively. Each individual is represented in a single bar. The black line divides the Baoulé cattle population of the Sedentary pure Baoulé system (SPB) from the crossbred populations in Sedentary mixed breed (SMB) and Transhumant Zebu and crossbred (TZC) systems [Colour figure can be viewed at wileyonlinelibrary.com]

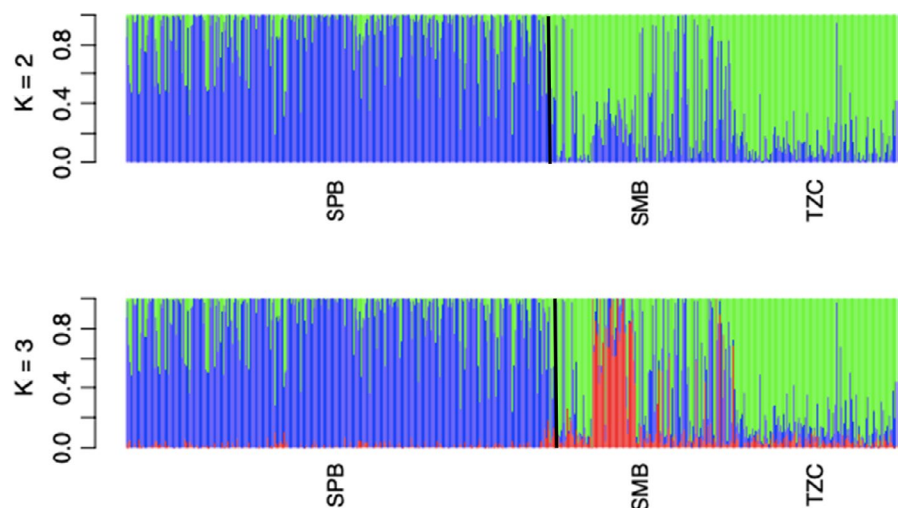


TABLE 1 Genetic diversity, expected (H_E) and observed (H_O) and effective population size (N_e) within the three cattle populations in the South-West of Burkina Faso

PS	N	H_E (SD)	H_O (SD)	N_{e_1}	N_{e_5}	N_{e_20}	N_{e_50}
SPB	343	0.290 (0.175)	0.278 (0.172)	79	216	556	1,009
SMB	156	0.327 (0.169)	0.309 (0.164)	37	114	308	709
TZC	132	0.319 (0.169)	0.310 (0.169)	53	217	584	887

Abbreviations: H_E/H_O , expected/ observed heterozygosity; N , Number of individuals; N_{e_1} ; N_{e_5} , N_{e_20} and N_{e_50} are the effective population sizes for the current generation, 5, 20 and 50 generations ago; PS, Production System; SD, Standard Deviation; SMB, Sedentary mixed breed; SPB, Sedentary pure Baoulé; TZC, Transhumant Zebu and crossbred.

TABLE 2 Descriptive statistics of the genomic inbreeding coefficients by ROH category of the three cattle populations in the South-West of Burkina Faso

	SPB		SMB		TZC	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
F_{ROH1}	0.106 (0.056) ^a	0.014–0.375	0.093 (0.056) ^b	0.009–0.361	0.098 (0.045) ^c	0.020–0.404
F_{ROH2}	0.042 (0.05)	0.000–0.332	0.039 (0.051)	0.000–0.301	0.037 (0.043)	0.001–0.364
F_{ROH4}	0.027 (0.048) ^a	0.000–0.311	0.024 (0.049) ^b	0.000–0.277	0.020 (0.043) ^{ab}	0.000–0.357
F_{ROH8}	0.021 (0.043) ^a	0.000–0.287	0.019 (0.045) ^b	0.000–0.255	0.014 (0.040) ^b	0.000–0.349
F_{ROH16}	0.016 (0.037)	0.000–0.252	0.015 (0.039)	0.000–0.252	0.011 (0.036)	0.000–0.341

Note: a, b, c: F_{ROH} not sharing superscripts within the same column indicate significant difference at $p < .05$. F_{ROH} were not significantly different in rows without superscripts.

Abbreviations PS, Production System; SD, Standard Deviation; SMB, Sedentary mixed breed; SPB, Sedentary pure Baoulé; TZC, Transhumant Zebu and crossbred.

genomic inbreeding coefficients of individual animals at different ROH lengths ranged from 0.000 to 0.404. Populations were significantly different ($p < .05$) for F_{ROH1} , F_{ROH4} and F_{ROH8} ; yet, differences were quite small. The distribution of the animals according to levels of inbreeding is shown in Figure 4. Only one animal each (i.e., <1%) in the three systems was likely a product of parent–offspring or full sib mating ($F_{ROH8} > 0.25$), and 3%–5% were likely products of half sib mating ($F_{ROH8} > 0.125$).

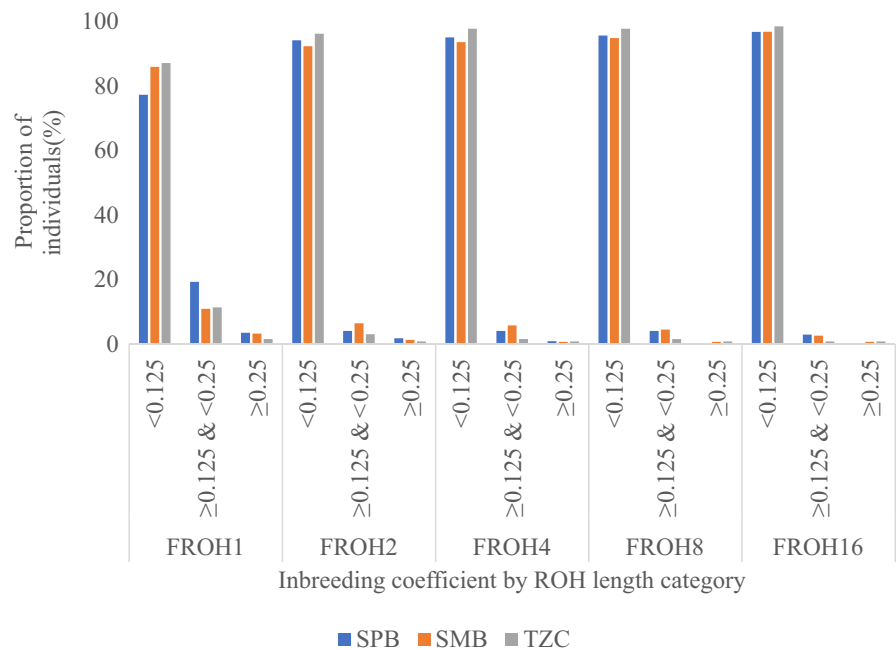
4 | DISCUSSION

4.1 | Population structure, admixture and effective population size

The PCA distinguished the pure taurine Baoulé animals in the SBP system and the crossbred animals in the SMB and TZC systems, respectively. The fact that the proportion of variance explained by the first principal component (10.47%) is much larger than that explained by the second (0.82%) is an indicator that two ancestries (taurine and zebuine) are driving the differentiation of the animals in the three locations. The clustering clearly reflects the prior status and knowledge about the three locations/systems, that is SBP farmers keeping mostly pure Baoulé, TZC keeping mostly Zebu, and SMB being in between. Lack of distinct separation of groups suggested that gene flow freely occurs among these three populations, as was observed in groups of cattle in semi-arid regions of Algeria and Morocco (Boushaba et al., 2018). The gene flow was confirmed by admixture analysis, which showed levels of admixture in these different populations. Previous investigations have already reported evidence of Zebu introgression in West African taurine cattle breeds. Indeed, Decker et al. (2014) reported that presumed taurine cattle in Western Africa feature 0%–19.9% indicine ancestry with an average of 3.3%. In Burkina Faso, the degree of introgression of White Fulani

zebuine cattle genes into Lobi taurine was estimated to be 24.3% and that of Gudali zebuine in N'Dama taurine was reported to be 11% by Alvarez et al. (2014). A similar study of taurine breeds in Benin showed on average 20% of introgression by Zebu (Kassa et al., 2019). This admixture of cattle in the South-West of Burkina Faso may be explained by historical and ongoing breeding practices in this area. The admixture of the population of SPB in which farmers are native and keep their traditional taurine Baoulé is likely due to uncontrolled mating of animals, given the communal use of pasture lands or grazing as well as watering points (Ouédraogo, Soudré, Ouédraogo-Koné, Zoma, et al., 2020). Admixture levels in this system support the assertion that, under the current production systems, maintaining a genetically distinct population of pure Baoulé animals in this area is difficult. SMB farmers, who are also native, originally kept their native taurine Baoulé. However, their desire to increase the body weights and presumably productivity in terms of meat production has continuously led them to introduce Zebu genes through crossbreeding, with the local herds increasingly being more crossbred. Kassa et al. (2019) explained the introgression of zebuine cattle in Benin by changes in farming practices, including the recruitment of Fulani people as herdsmen in non-Fulani areas. Fulani people have also been employed as herdsmen in the SMB system of the current study. Scheper et al. (2020) argued that transhumant Zebu keepers, mostly Fulani, contributed to Zebu admixture of local taurine breeds in Sahelian countries. Conversely, the admixture of the TZC population may be interpreted as introgression of taurine genes into Zebu. In this system, cattle owners are members of the Fulani ethnic group from the North of the country who settled in the area with their Zebu several years ago and over time have changed their lifestyle from nomadic to transhumant. They only seasonally move between the two locations, and put up and use semi-permanent housing structures in both locations. In a previous study, Ibeagha-Awemu et al. (2004) reported levels of introgression of African taurine genes

FIGURE 4 Distribution of the 631 individuals by level of genomic inbreeding coefficient by ROH category. The blue colour represents the individuals of SPB (Sedentary pure Baoulé system), and the orange and gray colours represent the individuals of SMB (Sedentary mixed breed system) and TZC (Transhumant Zebu and crossbred system), respectively [Colour figure can be viewed at wileyonlinelibrary.com]



of 7.5%, 15.5%, 8.1%, 8.5% and 38.2%, respectively, into White Fulani, Red Bororo, Sokoto Gudali, Wadara and Adamawa Gudali Zebu types.

Regarding effective population size, N_e , the lowest value for the admixed SMB population is according to population genetics theory. Nei and Li (1973) showed that when isolated populations begin to exchange genes through migration, LD tends to increase temporarily even for neutral loci. Similar patterns were observed in purebred and crossbred buffalo populations (Deng et al., 2019).

4.2 | Genetic diversity and inbreeding levels

Levels of genetic diversity and inbreeding are of great interest in managed livestock populations. We therefore estimated the genetic diversity in each population representing different production systems, and as expected, the lowest H_E/H_O values were identified in the sedentary Baoulé cattle population of Bouroum Bouroum (SPB; Figure 3), while the SMBs and transhumant crossbred populations showed higher levels of heterozygosity (Table 1). Taking into consideration the ascertainment bias (PérezO'Brien et al., 2014) of the Illumina Bovine SNP 50K Bovine BeadChip, which was designed based on eight European taurine and one African indicine breed, we compared the heterozygosity levels detected in the three populations with those observed in other taurine and indicine breeds over a global range (Orozco-terWengel et al., 2015). Among other Western African breeds, the H_O (0.278) estimated in native Baoulé from Bouroum Bouroum was slightly higher than results previously obtained in several N'Dama populations (0.209–0.237), Lagune populations (0.183) and previously

genotyped Baoulé populations (0.216). Compared to European taurine breeds, the H_O value, obtained in this study for Baoulé population, was within the range of values found in Jersey (0.263–0.277) or Brown Swiss (0.280) cattle in Europe. Due to the aforementioned ascertainment bias, the levels of heterozygosity in indicine breeds were expected to be lower than in the taurine breeds, as has been shown in Nelore cattle (0.161) or Zebu Bororo (0.241) and Zebu Fulani (0.240) (Orozco-terWengel et al., 2015). The observed higher levels of heterozygosity (0.310) in this study are most likely due to the human desired and induced admixture between taurine and indicine breeds within the different production systems (Figure 3).

High-throughput genotyping and ROH analysis provide a good tool for accurately estimating inbreeding levels, even in absence of pedigree information (Curik et al., 2014). So far, only few ROH studies have been performed for cattle in Africa. The few examples include those reported by Jemaa et al. (2018) and Purfield et al. (2012). Purfield et al. (2012) reported that African breeds had a tendency to have low F_{ROH} , compared to European cattle types, but the West African taurine breeds (Baoulé, Lagune, N'Dama and Somba) showed high variability in individual ROH levels within breed. The authors attributed these higher ROH levels within the African taurine breeds to the open village breeding systems, in which animals tend to mate more randomly and consanguineously than would be the case if the animals were kept in more confined and independent herds. Thus, some of the animals exhibit a pattern of ROH levels consistent with being highly inbred. Bororo and Fulani Zebu animals showed similar patterns, low levels of inbreeding in general, but a very small number of highly inbred animals found as well. Similar patterns of generally

low inbreeding levels with some outliers were also found for a group of North African cattle populations by Jemaa et al. (2018).

In the current study, we found F_{ROH} close to 0.10 at a minimum ROH length of 1 Mb, corresponding to 50 generations of ancestry, for all three populations. Mean inbreeding levels for a ROH length >4 Mb (i.e., 12.5 generations of ancestry) ranged from 0.020 to 0.027. While population differences were relatively small, the Baoulé population in Bouroum-Bouroum (SPB) displayed significantly higher F_{ROH} with minimum ROH lengths of 1, 4 and 8 Mb, compared to the two other populations. Population differences were not significant for F_{ROH2} and F_{ROH16} . This result was unexpected because during focus group discussions before and during implementation of community-based breeding programs, and the transhumant Fulani cattle keepers in Kampti (TZC) claimed to mostly use bulls born within their own herds; thus, we expected high levels of inbreeding caused by such practices, including possibilities of parent–offspring or half sib mating (Ouédraogo, Soudré, Ouédraogo-Koné, Zoma, et al., 2020). Indeed, only one animal each (i.e., <1%) in the three systems was likely resulted from parent–offspring or full sib mating ($F_{ROH8} > 0.25$), while 3%–5% were likely products of half sib matings (Figure 4).

Compared to well-managed European cattle breeds, F_{ROH} in this study were lower than observed in Brown Swiss, Holstein and Italian local dairy cattle breeds, close to what was reported for Fleckvieh, Norwegian Red and Tyrol Grey and higher than results reported in Polish Red, Limousin and Simmental (Ferenčaković, Hamzić, et al., 2013; Ferenčaković, Sölkner, et al., 2013; Mastrangelo et al., 2016; Szmatala et al., 2016). Zebuine Nellore cows of Brazil showed lower F_{ROH1} values (0.046) compared to those of the current populations (Zavarez et al., 2015). The moderate levels of inbreeding in the study area despite recruiting and using bulls born within the herds could be due to a relatively short time of bull use (i.e., bulls being used for only very short periods before being sold off for slaughter) thus limiting mating of related animals. In addition, the communal grazing and watering also provide opportunities for cross-herd mating, thus lowering inbreeding coefficients. It was also reported that exchange of best young bulls between herds is common, but should be strongly encouraged in the community-based breeding programs in the three study regions.

A similar study in African goats, kept under presumably similar village community systems, showed substantially lower inbreeding coefficients ($F_{ROH2} = 0.037$, average over a range of populations) contrary to what was expected in populations in which breeding is not controlled (Nandolo et al., 2019). The higher inbreeding coefficients obtained in this study could indicate that cattle herds in these systems may be managed more strictly than flocks of goats in many village systems across Africa.

5 | CONCLUSION

The results of this study support the existence of two main ancestries, that is taurine and zebuine in the cattle populations in the South-West of Burkina Faso according to the production systems, with various levels of admixture. The different populations show proportions of admixture due to ongoing traditional breeding and grazing practices. The cattle population in the sedentary “pure” Baoulé system includes a number of animals with Zebu proportions higher than expected. Although Lobi farmers emphasized the need for keeping their Baoulé pure and thus prioritizing conservation of this local cattle breed, crossbreeding continues to take place. Crossbred bulls with only little zebuine ancestry are unintentionally used because farmers are not able to morphologically determine the breed admixture levels. To mitigate this, development and deployment of affordable and quick genotyping methods are ongoing, to support selection of candidate breeding bulls using either SNP chip or a small set of ancestry informative markers, as part of the community breeding initiative. Our findings also show moderate inbreeding levels, which are comparable to some well-managed European dairy and beef cattle breeds. It must be noted that those levels of inbreeding are the result of traditional breeding, not the community-based breeding programs, implemented too recent to have an effect. Upon implementation of community-based breeding programs, farmers have been encouraged to exchange selected bulls to minimize the mating of related animals.

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CONFLICT OF INTEREST

All authors declare that there are no competing interests.

AUTHOR CONTRIBUTIONS

SJ, WM, MG, BPA, SA, TA, O-KS and MOA conceived the study. OD, YB and ZBL collected the samples, BY and SM extracted the DNA, OD, BY, KN, MG and BPA performed data analysis and OD wrote the manuscript. All authors provided valuable discussions, commented and approved the final manuscript.


ETHICAL APPROVAL

The blood samples were collected with the consent of animals' owners and using approved veterinary process in Burkina Faso to avoid animals suffering.

DATA AVAILABILITY STATEMENT

Quality controlled Bovine 50k SNP chip data, including 38,702 SNP of the 631 animals included in this study, were uploaded to DRYAD. The data set has been assigned a unique identifier, <https://doi.org/10.5061/dryad.2z34tmpj3> and is accessible via this temporary link: <https://datadryad.org/stash/share/170ziMEzuc9BT23KZJedDtgjXemGi0pnXaDn8AB3UW4>.

ORCID

Dominique Ouédraogo  <https://orcid.org/0000-0001-5752-1534>

Salifou Ouédraogo-Koné  <https://orcid.org/0000-0002-2907-4922>

Bernadette Yougaré  <https://orcid.org/0000-0002-7262-4635>

Albert Soudré  <https://orcid.org/0000-0002-3736-3695>

Gábor Mészáros  <https://orcid.org/0000-0002-5937-0060>

Maria Wurzinger  <https://orcid.org/0000-0001-9391-014X>

<https://orcid.org/0000-0001-9391-014X>

Pamela A. Burger  <https://orcid.org/0000-0002-6941-0257>

<https://orcid.org/0000-0002-6941-0257>

Johann Sölkner  <https://orcid.org/0000-0002-1517-5829>

REFERENCES

- Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, *15*, 1655–1664.
- Alvarez, I., Traoré, A., Fernandez, I., Cuervo, M. A., Lecomte, T., Soudré, A., Kaboré, A., Tamboura, H. H., & Goyache, F. (2014). Assessing introgression of Sahelian zebu into native *Bos taurus* breeds in Burkina Faso. *Molecular Biology Reports*, *41*, 3745–3754. <https://doi.org/10.1007/s11033-014-3239-x>
- Barbato, M., Orozco-terWengel, P., Tapio, M., & Bruford, M. W. (2015). SNeP: A tool to estimate trends in recent effective population size trajectories using genome-wide SNP data. *Frontiers in Genetics*, *6*, 109. <https://doi.org/10.3389/fgene.2015.00109>
- Boushaba, N., Boujenan, J., Moazami-Goudarzi, K., Flori, L., Saïdi-Mehtar, N., Tabet-Aoul, T., & Laloë, D. (2018). Genetic diversity and relationships among six local cattle populations in semi-arid areas assessed by a bovine medium-density single nucleotide polymorphism data. *Animal*, *13*, 8–14. <https://doi.org/10.1017/S1751731118001179>
- Chang, C. C., Chow, C. C., Tellier, L. C., Vattikuti, S., Purcell, S. M., & Lee, J. J. (2015). Second-generation PLINK: Rising to the challenge of larger and richer datasets. *GigaScience*, *4*, 7.
- Corbin, L. J., Liu, A. Y. H., Bishop, S. C., & Woolliams, J. A. (2012). Estimation of historical effective population size using linkage disequilibria with marker data. *Journal of Animal Breeding and Genetics*, *129*, 257–270. <https://doi.org/10.1111/j.1439-0388.2012.01003X>
- Curik, I., Ferenčaković, M., & Sölkner, J. (2014). Inbreeding and runs of homozygosity: A possible solution to an old problem. *Livestock Science*, *166*, 23–34.
- Decker, E. J., McKay, D. S., Rolf, M. M., Kim, J. W., Alcalá, M. M., Sonstegard, S. T., Hanotte, O., Götherström, A., Seabury, M. C., Praharani, L., Babar, E. M., de Almeida, C., Regitano, L., Yildiz, A. M., Heaton, P. M., Liu, W.-S., Lei, C.-Z., Reecy, M. J., Saif-Ur-Rehman, M., ... Taylor, F. J. (2014). Worldwide patterns of ancestry, divergence, and admixture in domesticated cattle. *PLoS Genetics*, *10*, e1004254.
- Deng, T., Liang, A., Liu, J., Hua, G., Ye, T., Liu, S., Campanile, G., Plastow, G., Zhang, C., Wang, Z., Salzano, A., Gasparini, B., Cassandro, M., Riaz, H., Liang, X., & Yang, L. (2019). Genom-wide SNP data revealed the extent of linkage disequilibrium, persistence of phase and effective population size in purebred and crossbred buffalo populations. *Frontiers in Genetics*, *9*, 688. <https://doi.org/10.3389/fgene.2018.00688>
- Edea, Z., Dadi, H., Kim, S.-W., Dessie, T., Lee, T., Kim, H., Kim, J.-J., & Kim, K.-S. (2013). Genetic diversity, population structure and relationships in indigenous cattle populations of Ethiopia and Korean Hanwoo breeds using SNP markers. *Frontiers in Genetics*, *4*, 35. <https://doi.org/10.3389/fgene.2013.00035>
- FAO (2007). *The state of the world's animal genetic resources for food and agriculture*. FAO.
- FAO (2010). *Progress report of the FAO on selected activities related to agricultural biodiversity*. Retrieved from www.fao.org/docrep/meeting/018/k5700e.pdf
- Ferenčaković, M., Hamzić, E., Gredler, B., Solberg, T. R., Klemetsdal, G., Curik, I., & Sölkner, J. (2013). Estimates of autozygosity derived from runs of homozygosity: Empirical evidence from selected cattle populations. *Journal of Animal Breeding and Genetics*, *130*, 286–293.
- Ferenčaković, M., Sölkner, J., & Curik, I. (2013). Estimating autozygosity from high-throughput information: Effects of SNP density and genotyping errors. *Genetics Selection Evolution*, *45*, 42.
- Gautier, M., Flori, L., Riebler, A., Jaffrézic, F., Laloë, D., Cut, I., Moazami-Goudarzi, K., & Foulley, J.-L. (2009). A whole genome Bayesian scan for adaptive genetic divergence in West African cattle. *BMC Genomics*, *10*, 550. <https://doi.org/10.1186/1471-2164-10-550>
- Gruber, B., Unmack, P. J., Berry, O. F., & Georges, A. (2017). An R package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Molecular Ecology Resources*, *18*, 691–699. <https://doi.org/10.1111/1755-0998.12745>
- Hayes, B. J., Visscher, P. M., McPartlan, H. C., & Goddard, M. E. (2003). Novel multilocus measure of linkage disequilibrium to estimate past effective population size. *Genome Research*, *13*, 635–643. <https://doi.org/10.1101/gr.387103>
- Ibeagha-Awemu, M. E., Jann, C. O., Weimann, C., & Erhardt, G. (2004). Genetic diversity, introgression and relationships among West/Central African cattle breeds. *Genetics Selection Evolution*, *36*, 673–690. <https://doi.org/10.1051/gse:2004024>
- Jemaa, B. S., Rahal, O., Gaouar, S. B. S., Mastrangelo, S., Boussaha, M., & Ciani, E. (2018). Genomic characterization of Algerian Guelmoise cattle and their genetic relationship with other North African populations inferred from SNP genotyping arrays. *Livestock Science*, *217*, 19–25. <https://doi.org/10.1016/j.livsci.2018.09.009>
- Jombart, T. (2008). A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*, 1403–1405.
- Jombart, T., & Collins, C. (2015). *A tutorial for Discriminant Analysis of Principal Components (DAPC) using adegenet 2.0.0*. Imperial College London, MRC Centre for Outbreak Analysis and Modelling.
- Kassa, S. K., Dayo, G. K. C., Yapi-Gnaore, C. V., Sylla, S., Konkobo, M., & Issaka, Y. A. K. (2019). Genetic diversity of benin cattle populations using microsatellite markers. *International Journal of Animal Science and Technology*, *3*, 7–19. <https://doi.org/10.11648/j.ijast.20190301.12>
- Kim, K., Kwon, T., Dessie, T., Yoo, D., Mwai, A. O., Jang, J., Sung, S., Lee, S., Salim, B., Jung, J., Jeong, H., Tarekegn, G. M., Tijjani, A., Lim, D., Cho, S., Oh, S. J., Le, H.-K., Kim, J., Jeong, C., ... Kim,

- H. (2020). The mosaic genome of indigenous African cattle as a unique genetic resource for African pastoralism. *Nature Genetics*, *52*, 1099–1110. <https://doi.org/10.1038/s41588-020-0694-2>
- Madilindi, M. A., Banga, C. B., Bhebhe, E., Sanarana, Y. P., Nxumalo, K. S., Taela, M. G., Magagula, S. B., & Mapholi, N. O. (2020). Genetic diversity and relationships among three Southern African Nguni cattle populations. *Tropical Animal Health and Production*, *52*, 753–762. <https://doi.org/10.1007/s11250-019-02066-y>
- Madilindi, M. A., Banga, C. B., Bhebhe, E., Sanarana, Y. P., Nxumalo, K. S., Taela, M. G., & Mapholi, N. O. (2019). Genetic differentiation and population structure of four Mozambican indigenous cattle populations. *Livestock Research for Rural Development*, *31*, 47. <http://www.lrrd.org/lrrd31/4/matom31047.html>
- Makina, O. S., Muchadeyi, C. F., van Marle-Köster, E., MacNeil, D. M., & Maiwashe, A. (2014). Genetic diversity and population structure among six cattle breeds in South Africa using a whole genome SNP panel. *Frontiers Genetics*, *5*, 333. <https://doi.org/10.3389/fgene.2014.00333>
- Mastrangelo, S., Tolone, M., Di Gerlando, R., Fontanesi, L., Sardina, M. T., & Portolano, B. (2016). Genomic inbreeding estimation in small populations: Evaluation of runs of homozygosity in three local dairy cattle breeds. *Animal*, *10*, 746–754. <https://doi.org/10.1017/S1751731115002943>
- Mopaté, L. Y. (2015). Caractéristiques, menaces et nécessité de conservation in situ du taurin Baoulé dans les savanes du Sud-Ouest du Burkina Faso. *Journal of Applied Bioscience*, *93*, 8713–8726.
- Nandolo, W., Mészáros, G., Banda, L. J., Gondwe, N. T., Lamuno, D., Mulindwa, H. A., Nakimbugwe, N. H., Wurzinger, M., Utsunomiya, T. Y., Woodward-Greene, M. J., Liu, M., Liu, G., Van Tassell, P. C., Curik, I., Rosen, D. B., & Sölkner, J. (2019). Timing and extent of inbreeding in African goats. *Frontiers Genetics*, *10*, 537. <https://doi.org/10.3389/fgene.2019.00537>
- Nei, M., & Li, W. H. (1973). Linkage disequilibrium in subdivided populations. *Genetics*, *75*, 213–219.
- Orozco-terWengel, P., Barbatto, M., Nicolazzi, E., Biscarini, F., Milanese, M., Davies, W., Williams, D., Stella, A., Ajmone-Marsan, P., & Bruford, M. W. (2015). Revisiting demographic processes in cattle with genome-wide population genetic analysis. *Frontiers Genetics*, *6*, 191. <https://doi.org/10.3389/fgene.2015.00191>
- Ouédraogo, D., Soudré, A., Ouédraogo-Koné, S., Yougbaré, B., Zoma, B. L., Tapsoba, S. A. R., Mészáros, G., Burger, P., Khayatzaadeh, N., Wurzinger, M., Traoré, A., Okeyo, A. M., & Sölkner, J. (2020). Selection of breeding bulls in community-based cattle breeding programs in Burkina Faso. *Bulletin of Animal Health and Production in Africa*, *68*, 103–111.
- Ouédraogo, D., Soudré, A., Ouédraogo-Koné, S., Zoma, B. L., Yougbaré, B., Khayatzaadeh, N., Burger, P. A., Mészáros, G., Traoré, A., Mwai, A. O., Wurzinger, M., & Sölkner, J. (2020). Breeding objectives and practices in three local cattle breed production systems in Burkina Faso with implication for the design of breeding programs. *Livestock Science*, *232*, 103910. <https://doi.org/10.1016/j.livsci.2019.103910>
- Pérez O'Brien, A. M., Mészáros, G., Utsunomiya, T. Y., Sonstegard, S. T., Garcia, F. F., VanTassell, C. P., Carvalheiro, R., daSilva, M. V., & Sölkner, J. (2014). Linkage disequilibrium levels in *Bos indicus* and *Bos taurus* cattle using medium and high density SNP chip data and different minor allele frequency distributions. *Livestock Science*, *166*, 121–132. <https://doi.org/10.1016/j.livsci.2014.05.00>
- Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., Maller, J., Sklar, P., de Bakker, P. I. W., Daly, M. J., & Sham, P. C. (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *American Journal of Human Genetics*, *81*, 559–575. <https://doi.org/10.1086/519795>
- Purfield, C. D., Berry, P. D., McParland, C., & Bradley, D. (2012). Run of homozygosity and population history in cattle. *BMC Genetics*, *13*, 70.
- Saravanan, K. A., Panigrahi, M., Kumar, H., & Bhushan, B. (2019). Advanced software programs for the analysis of genetic diversity in livestock genomics: a mini review. *Biological Rhythm Research*, *1*–11. <https://doi.org/10.1080/09291016.2019.1642650>
- Scheper, C., Bohlouli, M., Brügemann, K., Weimann, C., Vanvanhossou, F. U. S., König, S., & Dossa, L. H. (2020). The role of agro-ecological factors and transboundary transhumance in shaping the genetic diversity in four indigenous cattle populations of Benin. *Journal of Animal Breeding and Genetics*, *137*, 622–640.
- Soudré, A. (2011). *Trypanosomosis, genetic diversity and admixture in cattle breed of Burkina Faso (Doctoral Thesis)*. Vienna, Austria: University of Natural Resources and Life Sciences.
- Soudré, A., Ouédraogo-Koné, S., Wurzinger, M., Müller, S., Hanotte, O., Ouédraogo, A. G., & Sölkner, J. (2013). Trypanosomosis: A priority disease in tsetse-challenged areas of Burkina Faso. *Tropical Animal Health and Production*, *45*, 497–503. <https://doi.org/10.1007/s11250-012-0248-4>
- Szmatola, T., Gurgul, A., Ropka-Molik, K., Jasielczuk, I., Zabek, T., & Bugno-Poniewierska, M. (2016). Characteristics of runs of homozygosity in selected cattle breeds maintained in Poland. *Livestock Production Science*, *188*, 72–80. <https://doi.org/10.1016/j.livsci.2016.04.006>
- Tijjani, A., Utsunomiya, T. Y., Ezkwe, G. A., Nashiru, O., & Hanotte, O. (2019). Genome sequence analysis reveals selection signatures in endangered Trypanotolerant west Africa Muturu cattle. *Frontiers Genetics*, *10*, 442. <https://doi.org/10.3389/fgene.2019.00442>
- Traoré, A., Koudandé, D. O., Fernandez, I., Soudré, A., Granda, V., Alvarez, I., Diarra, S., Diarra, F., Kaboré, A., Sanou, M., Tamboura, H. H., & Goyache, F. (2015). Geographical assessment of body measurements and qualitative traits in West African cattle. *Tropical Animal Health and Production*, *47*, 1505–1513. <https://doi.org/10.1007/s11250-015-0891-7>
- Zavarez, B. L., Utsunomiya, T. Y., Camo, S. A., Neves, R. H. H., Carvalheiro, R., Ferenčaković, M., Pérez O'Brien, M. A., Curik, I., Cole, B. J., Van Tassell, P. C., da Silva, B. G. M., Sonstegard, S. T., Sölkner, J., & Garcia, F. J. (2015). Assessment of autozygosity in Nellore cows (*Bos indicus*) through high-density SNP genotypes. *Frontiers Genetics*, *6*, 5. <https://doi.org/10.3389/fgene.2015.00005>
- Zhang, J., Nie, C., Li, X., Ning, Z., Chen, Y., Jia, Y., Han, J., Wang, L., Lv, X., Yang, W., & Qu, L. (2020). Genome-wide population genetic analysis of commercial, indigenous, game, and wild chickens using 600K SNP microarray data. *Frontiers Genetics*, *11*, 543294. <https://doi.org/10.3389/fgene.2020.543294>
- Zhang, L., Orloff, S. M., Reber, S., Li, S., Zhao, Y., & Eng, C. (2013). cgaTOH: extended approach for identifying tracts of homozygosity. *PLoS One*, *8*, e57772. <https://doi.org/10.1371/journal.pone.0057772>

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