

ORIGINAL ARTICLE

The role of agro-ecological factors and transboundary transhumance in shaping the genetic diversity in four indigenous cattle populations of Benin

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Abstract

The indigenous cattle population of Benin is a diverse mix of taurine and hybrid breeds shaped by diverse ecological and climatic conditions with eight agro-ecological zones (AEZ). Presumably, the taurine breeds face current endangerment due to ongoing indicine introgression following climate change and transboundary transhumance. The aim of the study was to investigate the genetic diversity and population structure of the indigenous breeds Lagune, Somba, Pabli and Borgou considering spatial agro-ecological and socio-economic factors (transhumance) based on 50k SNP and microsatellite data. Among the four sampled breeds, six genetic clusters were identified using model-free (discriminant analysis of principal components) and model-based (TESS and ADMIXTURE) methods separating taurine from hybrid breeds. Results based on an extension with publicly available historic SNP data sets from taurine and indicine West African cattle and additional outgroups provided additional insight into changes of genetic structure in the sampled breeds over time. Both taurine breeds, Somba and Lagune, showed a stable foundation but also spatially limited partial indicine introgression associated with transhumance leading to high genetic diversity. In addition, we found evidence for spatial diversity and changes in genetic structure over time in the Borgou breed in comparison of our samples with the historic samples which could be explained by potential continuous indicine introgression into the Borgou breed in two sample regions. Results for the Pabli breed do not conclusively point to full absorbance by the Borgou in comparison with all available Borgou samples. Further research is needed in this regard.

KEYWORDS

animal genetic resources, Borgou, indicine introgression, Lagune, Pabli, Somba, transhumance

1 | INTRODUCTION

About 180 cattle breeds, excluding extinct and international transboundary distributed ones, have been recognized in sub-Saharan Africa (FAO, 2015). Among these, 150 are indigenous and grouped into taurine *Bos taurus*, indicine *Bos indicus* (zebus) and intermediate (Taurine × Zebu) types (Kim et al., 2017; Mwai, Hanotte, Kwon, & Cho, 2015). While the taurine longhorn cattle arrived from the Middle East through the Nile Delta around 7000 B.C (Epstein & Mason, 1971), taurine Shorthorn cattle originated within the African continent since 2750–2500 B.C (Hanotte et al., 2002). The Zebu populations (*Bos indicus*) came to the African continent in two waves about 1500 B.C. associated with the Arab invasion of Africa about 699 A.D (Epstein & Mason, 1971; Hanotte et al., 2002). In West Africa, the two cattle subspecies coexist but occupy two ecologically distinct regions. The zebu subspecies, naturally adapted to heat, poor feeding

and long-distance walks, is predominant in the semi-arid and arid regions (Bradley et al., 1994). The taurine subspecies is widely distributed in the humid and subhumid regions characterized by a hot and humid climate and endemic for tsetse flies which transmit trypanosomiasis (Bradley et al., 1994). Hence, in contrast to zebus, most taurine cattle are tolerant or resistant to trypanosomiasis due to adaption and selective breeding (Murray & Trail, 1984; Smetko et al., 2015). The West African taurine populations are further divided into two main categories: the Shorthorn (*B. taurus brachyceros*) and longhorn (*B. taurus longifrons*). Within the Shorthorn cattle, the savannah type and the Dwarf type are distinguished (FAO, 1987; Thévenon & Belemsaga, 2005).

The current cattle population in the West African country of Benin, estimated to about 2.3 million heads (FAO, 2017), reflects the mentioned diversity of cattle breeds in sub-Saharan Africa with two indigenous Shorthorn taurine breeds, namely the Somba and Lagune, a stabilized hybrid breed (i.e.,

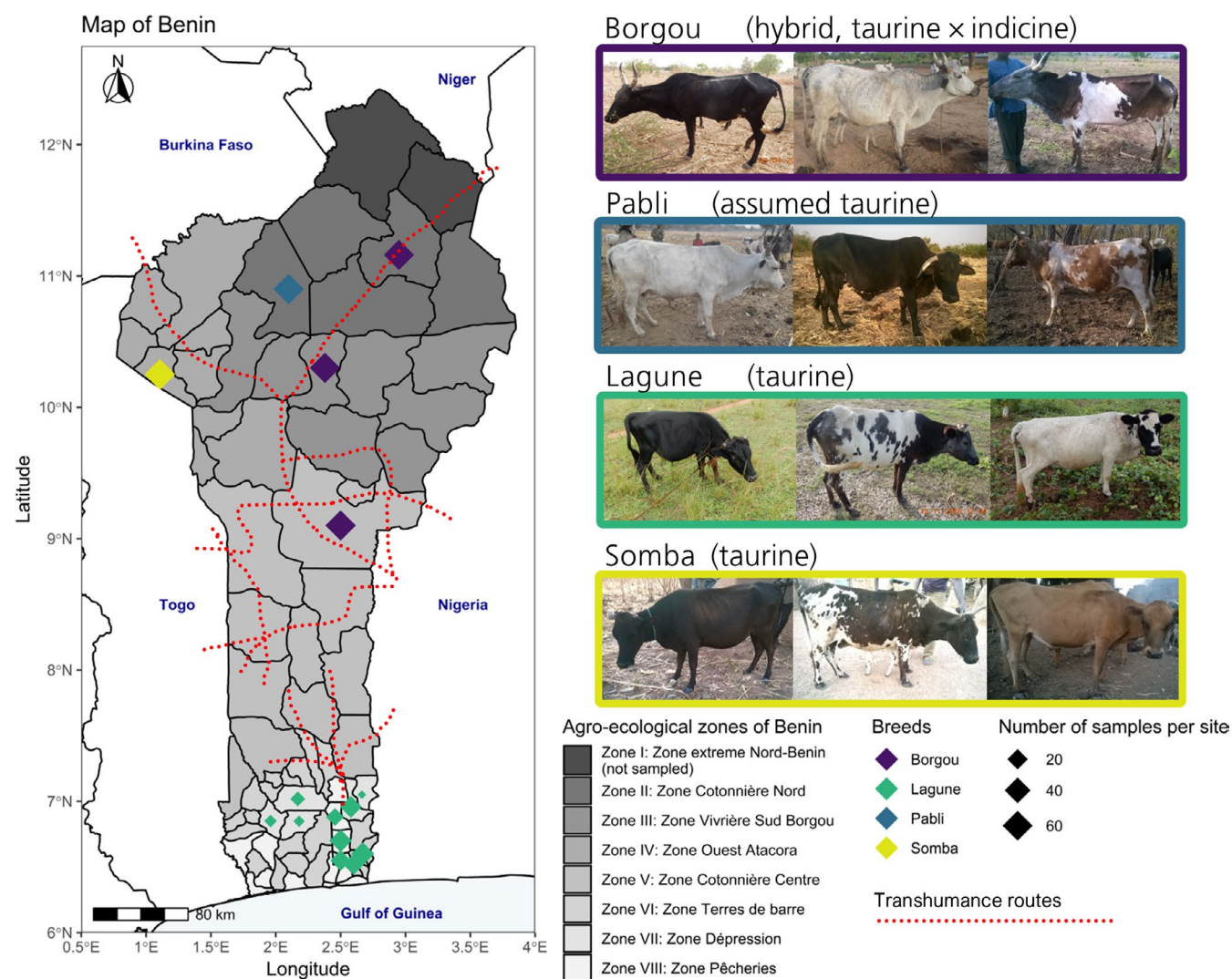


FIGURE 1 Map of Benin and surrounding countries including information on sampling locations, sample sizes, agro-ecological zones, transhumance routes as well as photographic characterization of the sampled breeds. Transhumance routes were included based on information from Alimi, Gbedomon, Bekpa-Kinhou, Bisous, and Egboou (2015) and ACF (2018) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

taurine $\times$ zebu) named Borgou and further various zebu and undefined or unstabilized hybrids (Figure 1). The term stabilized hybrid breed refers to a breed that is bred in a closed population after a phase of deliberate crossbreeding. The Lagune breed, a taurine Dwarf Shorthorn type, is one of the smallest cattle breeds of the world (see also Table 1 for the distribution of phenotypic characteristics of all sampled breeds). Lagune are well adapted to the hot and humid climatic conditions of South Benin and resistant to various endemic diseases, especially to trypanosomiasis (Berthier et al., 2015). It is mainly kept in smallholdings in the Oueme Valley (Comlan & Ibrahim, 2015). The main distribution area of Somba cattle, also a taurine Shorthorn type, is the Boukombe district in the north-western part of Benin, around the Atacora mountain region. Despite its strong cultural value among the Otammari, the indigenous people, the population of this trypanotolerant breed has sharply decreased over the last two decades, mainly because of indiscriminate crossbreeding with zebus (Dossa & Vanvanhossou, 2016). The Borgou breed, which belongs to the group of Sanga cattle, is one of the several genotypes which originated from deliberate crossbreeding between cervico-thoracic-humped or thoracic-humped zebu cattle and humpless longhorn taurine cattle during the first wave of Zebu introgression in Africa around 1500 B.C (Epstein & Mason, 1971; Manwell & Baker, 1980; Mwai et al., 2015; Porter, Alderson, Hall, & Sponenberg, 2016). Results from studies on zebu specific alleles on the bovine Y-Chromosome suggest that the Borgou were mainly bred by mating zebu bulls with taurine cows (Hanotte et al., 2000). The Borgou breed is currently considered as a stabilized hybrid breed (Rege, 1999). Flori et al. (2014) were able to confirm this status using a formal test of ancestry and dated the time of the admixture between African taurine (e.g., N'Dama) and African indicine (e.g., Zebu Fulani) ancestors that formed the Borgou breed to 130 years ago. The Borgou breed is phenotypically significantly taller and wider than the two Shorthorn breeds but not necessarily longer in body length (Table 1).

In addition to the three indigenous cattle populations aforementioned, the Pabli breed an indigenous humpless longhorn breed of N'Dama type (Porter et al., 2016) was previously observed in the regions of Kouande and Kerou in the north-western part of the country until it has been

reported as extinct. The breed is assumed to be absorbed by the Borgou in an undocumented process at an unknown but very recent date (Porter et al., 2016). Absorption in this regard could be defined as continuous deliberate as well as undeliberate crossbreeding of Pabli animals with Borgou animals leading to a change in the ancestral composition of the remaining Pabli population similar to a replacement crossing in structured breeding programmes. Consequently, this development would be characterized by a significant raise of indicine ancestry proportions in the formerly predominantly taurine composition of the Pabli breed up to a point where the ancestral composition of sampled Pabli and Borgou would be not distinguishable anymore. Local farmers in the region still refer to a Pabli breed, and the extinction hypothesis has not been tested empirically in the framework of a population genetics study so far to the knowledge of the authors. The animals referred to as Pabli sampled in this study show similar phenotypic characteristics in comparison with the sampled Borgou animals (Table 1). Figure 1 displays the distribution of the aforementioned cattle breeds in Benin highlighting the sample sites used in the present study and presents a first impression on the phenotypic diversity of the cattle population in Benin.

The presence of trypanosomiasis-transmitting tsetse flies had for long been considered as the factor curbing the conquest of humid and subhumid regions by trypanosome-sensitive breeds. Yet, the current climatic changes combined with deforestation processes caused by the expansion of farmlands in these zones and the availability of trypanocidal drugs have significantly contributed to reducing the risk of contracting trypanosomiasis and other diseases (Ayantunde, Asse, Said, & Fall, 2014; Blench, 1999). As a consequence, there is an increase in the number of zebu cattle at the expense of taurine trypanotolerant populations. Furthermore, thousands of zebu cattle herds are annually trekked in a seasonal and cyclical movement between countries in the semi-arid regions of Niger, Burkina Faso, Nigeria and Benin (FAO, 2012). This transboundary back and forth movement, termed as cross-border transhumance, is an important element of pastoralists' adaptation to the drylands ecosystem. It gives them the opportunity to optimize weight gain and milk production in the wet season and limit weight loss in the dry season (Krätli

TABLE 1 Descriptive statistics for three conformation traits for the four sampled cattle breeds from Benin

Breed	Samples	Conformation traits (all traits measured in cm)											
		Heart girth				Body length				Height at withers			
		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Borgou	177	150	9	121	177	103	7	86	122	117	6	100	132
Lagune	156	122	12	88	153	102	10	71	130	93	7	76	113
Pabli	61	146	9	115	168	106	7	90	123	111	7	93	140
Somba	62	132	10	103	150	95	8	72	117	96	7	84	107

& Schareika, 2010; Moritz, 2010). Furthermore, it allows to minimize possible impacts of climate change and variability mainly due to rising temperatures and consequently heat stress on livestock production (Zampaligré, Dossa, & Schlecht, 2014) and facilitates regional livestock trade between Sahelian and coastal countries (Corniaux, Thébaud, & Gautier, 2012; Quarles van Ufford, 1999). Hence, from an economically driven perspective it can be considered as an opportunity for local herders in Benin to enhance their herds' productivity through deliberate crossbreeding. On the other hand, possible uncontrolled and accidental matings typical for the unstructured breeding practices in Western Africa could lead to untraced gene flow potentially endangering important local animal genetic resources. The annual transhumance movement routes traverse the breeding areas of the Lagune, Somba and Borgou breeds. However, there are also regions which are distant from the routes and are therefore isolated from the potential direct effects of transhumance, such as the Kouande and Kerou regions where animals referred to as Pabli were sampled for this study. A continued introgression of trypano-sensitive zebu breeds in the natural environment of the taurine trypanotolerant breeds represents a considerable risk of genetic dilution of the latter and thus a threat to their genetic integrity (Ayantunde et al., 2014).

Long-distance mobility of cattle in the West African region since the precolonial period still remains an important way of transporting livestock to meet the growing demand for meat in the coastal cities (Bassett & Turner, 2007) and has been used to argue for better attention by policy-makers recognizing it as an effective strategy for enhancing livestock productivity in the region. Therefore, the Economic Community of West African States (ECOWAS) has set up regional agreements and policies and put in place frameworks to regulate this practice. However, while the ECOWAS protocol is meant to facilitate cross-border transhumance in the region, it fails to clearly define how to protect the untapped genetic diversity of the indigenous cattle breeds along the transhumance routes and prevent its loss through dilution.

It is assumed that the observed genetic diversity in a breed can be explained by ancestral diversity, geographical isolation and natural selection, but is of course mostly dependent on farmers' breeding practices like selection and animal exchange (Dumasy, Daniaux, Donnay, & Baret, 2012). The genetic structure of domestic animal populations is therefore expected to reflect patterns of animal exchanges between different populations. Previous genetic characterization studies among West African cattle breeds used Y-chromosomal markers (Bradley et al., 1994; Hanotte et al., 2000), microsatellites (MS) (e.g., Dayo et al., 2009; Freeman et al., 2004; Ibeagha-Awemu, Jann, Weimann, & Erhardt, 2004) or SNP data (Decker et al., 2014; Gautier et al., 2009). The results synthesize growing knowledge of genetic relationships among West African cattle breeds and show high levels of

introgression of zebu in taurine cattle. However, the roles of livestock mobility and of animal exchange networks have never been explicitly addressed or tested but are important for their sustainable use and for minimizing the risks of epidemic livestock disease outbreaks in the West African region (Dean et al., 2013).

The use of neutral molecular markers is a well-established method to describe the genetic diversity between populations. In contrast to MS, SNP markers have the advantage of fast, reliable and reproducible high density genotyping at substantially lower costs per data point. It is estimated that ten to hundred biallelic SNP are as informative as one microsatellite (Gärke et al., 2012; Schopen, Bovenhuis, Visker, & van Arendonk, 2008). Furthermore, the results of SNP chip genotyping offer the opportunity of haplotype analyses. The availability of high-throughput SNP chip genotyping technology established during the last decade has enhanced the potential for studies of complex factors influencing the genetic structure of populations with sufficiently high resolution. Nonetheless, it is discussed if the measurement of genetic distances based on neutral genetic variation is sufficient to determine conservation priority among different breeds (Hall, Lenstra, & Deeming, 2012).

The aim of the present study was to analyse the genetic diversity of indigenous cattle breeds of Benin using genome-wide SNP and microsatellite data to clarify:

(a) the genetic structure of the indigenous breeds Lagune, Somba, Pabli and Borgou in terms of genetic diversity and distance as well as ancestral composition, (b) if there is any traceable remnant of the Pabli breed, (c) if spatial separation or proximity within and between breeds across the agro-ecological zones (AEZ) lead to genetic differences and (d) if socio-economic aspects reflected by special management practices such as transhumance have a measureable impact on genetic diversity in the Lagune, Somba and Borgou breeds.

2 | MATERIAL AND METHODS

2.1 | Study area and geographical distribution of cattle populations

The republic of Benin is a long stretched country in West Africa and lies between 6° and 13°N, and 0° and 4°E (Figure 1). Its human population was estimated to about 10 million inhabitants in 2013 (INSAE, 2015). Next to its western and eastern neighbour countries Nigeria and Togo, it is bordered in the north by the Sahelian countries of Niger and Burkina Faso and in the South by the Atlantic Ocean (i.e., the Gulf of Guinea).

Benin covers four climatic zones: (a) a littoral humid tropical zone (1,200–1,400 mm rainfall per year), (b) a littoral and inland subhumid zone (900–1,200 mm rainfall per year),

TABLE 2 Selected characteristics of AEZs in Benin and overview of sampling design for the four breeds

Agro-ecological zones		CCB	CNB	D	OA	P	TB	VS
a) Selected characteristics for all sampled AEZs								
Avg. annual rainfall (in mm)		1,124	1,032	1,083	1,090	1,165	1,300	1,105
Avg. Temperature (Min-Max)		26.4 (18.0–35.8)	27.3 (15.7–38.9)	27.4 (20.8–35.7)	28.0 (19.4–38.2)	27.5 (21.9–35.1)	27.4 (22.5–33.0)	26.6 (17.4–36.9)
Max. elevation (in m)		335	310	86	230	42	31	362
b) Sampling design stratified by AEZ (Transhumance influence for samples is presented in brackets: yes no)								
Borgou		60 (41 19)	60 (27 33)					61 (27 34)
Lagune				39 (17 22)		59 (36 23)	59 (9 50)	
Pabli			61 (0 61)					
Somba					62 (36 26)			

Abbreviations: CCB, Cotonnière Centre; CNB, Cotonnière Nord; D, Dépression; OA, Ouest Atacora; P, Pêcherie; TB, Terre de Barre; VS, Vivrière Sud Borgou.

(c) a wetter inland zone (1,200–1,400 mm rainfall per year) and (d) a continental dry northern zone (900–1,200 mm rainfall per year) (Faure & Volkoff, 1996). In South Benin, the rainfall regime is bimodal, with a short dry season during August and a longer dry season from November to March. In central and northern Benin, only one dry season occurs lasting from October to March (Faure & Volkoff, 1996). Along the south–north gradient, the country has been divided in four main vegetation zones: (a) the coastal zone, (b) the Guinea-Congolian zone characterized by ferrallitic soils with savannah and shrubs as well as mangrove, (c) the Guinean zone characterized by ferruginous soils with a vegetation dominated by moist woodland and savannahs and (d) the Sudanian zone characterized by ferruginous soils with savannah and dry woodlands (Sinsin & Kampmann, 2010). As rainfed agriculture is the mainstay of the country's economy and contributed about 32.5% to the Gross Domestic Product in 2012 (INSAE, 2015), the four main vegetation zones were further subdivided into eight smaller AEZs: Pêcherie (P), Dépression (D), Terre de Barre (TB), Cotonnière Centre (CCB), Vivrière Sud Borgou (VS), Cotonnière Nord (CNB), Ouest Atacora (OA) and Extrême Nord based on the main crop grown (see also Figure 1 for the geographical distribution and Table 2 for a summary of characteristics of all AEZs).

The Lagune breed is distributed across the AEZs P, D and TB. The Borgou breed is generally distributed across the country but widely found in a belt which encompasses the AEZs CCB, VS and CNB. The Somba breed is endemic to the OA AEZ. The presumed remnants of the Pabli breed were mainly found in the Kouande–Kerou region in the AEZ CNB.

2.2 | Sample collection, sampling design and DNA extraction

Hair samples from animals representing four cattle breeds from different regions of Benin were collected between October 2016 and June 2017: Lagune ($n = 157$), Borgou ($n = 181$), Somba ($n = 62$) and Pabli ($n = 61$). Figure 1 shows the precise sampling locations for each breed. The sampling design was set up to assess the influence of different ecological and socio-economic factors such as climate and transhumance on the genetic structure in the sampled breeds. Hence, the established sampling design described hereafter allows stratified analysis and interpretation based on sample specific descriptor variables such as AEZ, location (i.e., precise spatial coordinates of sample sites in UTM format) and transhumance in order to answer the main research questions of the study as presented in the introduction.

Samples for the Lagune population were collected from three different AEZ (P, D and TB) in the Southern part of Benin. Samples for the Borgou breed were also collected from three different AEZ (CCB, VS and CNB) in the northern

and orth-eastern part of Benin. Sampling for the Somba and Pabli breeds was restricted to one AEZ per breed (i.e., OA for Somba, CNB for Pabli) in the north-western part of Benin. In sample regions, samples were evenly collected at villages with sample sizes of one to ten animals per village.

To evaluate the influence of transhumance on the genetic structure in the sampled populations, the final sampling scheme in the Lagune, Borgou and Somba breeds at the village level implemented a balanced design of roughly equal numbers of villages either influenced or not influenced by transhumance. All sampling locations for the Pabli breed were not influenced by transhumance. The sampled animals were unrelated as per consultation of farmers before sampling. Table 2b gives a detailed overview of the distribution of factors considered for sampling in the four sampled breeds. Table 1 gives an overview of the descriptive statistics of three representative conformation traits in all four sampled breeds.

Genomic DNA was extracted from hair roots using the NucleoSpin Tissue Kit (Macherey Nagel) following manufacturer's instructions. The DNA quality and quantity were checked by ND-1000 NanoDrop spectrophotometer (NanoDrop Technologies, Inc.).

2.3 | SNP genotyping and quality control

In total, 461 animals were genotyped using the Illumina BovineSNP50 BeadChip v.3 SNP genotyping array. After excluding SNPs positioned on sex chromosome (1,181) and SNPs with unknown location (759), 51,278 SNPs were subjected to quality control (QC) and further analysis. Individual and marker-based QC of SNPs was conducted using the PLINK software package, version 1.90 (Purcell et al., 2007). One individual with more than 90% of missing genotypes (sample call rate <0.90) was removed from further analysis. SNPs were removed based on marker call rate (<0.95, 1,908 SNPs), minor allele frequency (MAF < 0.01, 862 SNPs), and Hardy–Weinberg equilibrium (HWE-test p -value < $1e-6$, 2,666 SNPs). After QC, the number of SNPs remaining for further analysis was 45,866.

LD pruning was performed in PLINK to limit a potential overrepresentation of SNPs containing the same biased information due to ascertainment bias (Kijas et al., 2009; Malomane et al., 2018). Hence, SNPs in high LD to each other were removed based on r^2 values greater than 0.2 in a sliding window approach (PLINKs—indep-pairwise command with window size: 50, SNPs shifted per step: 5 and r^2 threshold: 0.2). After LD pruning, the final data set contained 23,994 SNPs for statistical analysis.

2.4 | Additional Microsatellite analysis

In addition to SNP genotyping, the following 13 MS were chosen from the MS panel recommended by the FAO for

genetic diversity studies (FAO, 2011) to extend the data set: BM1818, BM2113, ETH003, ETH010, ETH225, ILSTS005, ILSTS006, INRA023, INRA032, INRA035, MM12, TGLA53, TGLA122. PCR reactions were performed for each MS using 12.5 μ l Quiagen® PCR Master Mix (Qiagen), 0.5–0.25 μ l of each primer, 7.5–6.5 μ l H₂O and 1 μ l DNA. The reverse primer was labelled with a fluorescent dye at the 5' end. Microsatellite genotype analysis was performed on an ABI automated sequencer 3130 (Applied Biosystems) using the Gene Mapper software version 4.0 (Applied Biosystems). All animals with available SNP data were also genotyped for the chosen panel of 13 MS. MS genotype data were subjected to the same QC criteria as SNP data mentioned above. QC for MS data was performed using the software R, version 3.5.0 (R Core Team, 2019) and the R package adegenet (Jombart, 2008; Jombart & Ahmed, 2011). After QC, the MS genotype data set was integrated into the SNP data set based on genomic position to build a final hybrid SNP/MS data set for statistical analysis.

2.5 | Statistical analysis

The hybrid SNP/MS data set was used for all analysis except methods unsuitable for multi-allelic marker types. Analysis relying only on SNP data is denoted explicitly hereafter. All postprocessing of results and generation of graphics were performed using the software R. A detailed list of all R packages used in the course of this study is available in Appendix S1. R scripts for postprocessing and graphics are available on a GitHub page (https://github.com/ca-sche/Div_Cattle_Breeds_Benin).

2.5.1 | Basic measures of genetic diversity

To initially explore the basic genetic differentiation among the four sampled breeds, pairwise fixation indices (F_{st}) were estimated according to Weir and Cockerham (Weir & Cockerham, 1984) using the R package adegenet (Jombart, 2008; Jombart & Ahmed, 2011). Additionally, genetic distances between breeds were estimated based on the formula in Nei (1973) and a neighbour-joining tree was computed to visualize the results. F_{st} values and genetic distances were estimated using adegenet. Three measures of genetic variability within each sampled breed were estimated: mean allelic richness, expected heterozygosity and mean inbreeding coefficients (F). Mean allelic richness and expected heterozygosity were calculated using the R package hierfstat (Goudet, 2005). In addition, the mean inbreeding coefficients were calculated by initially estimating individual inbreeding coefficients using PLINK (Purcell et al., 2007) based solely on SNP data and subsequently averaging individual inbreeding coefficients per breed.

2.5.2 | Unsupervised clustering and DAPC

As a first step in the assessment of the genetic structures in the comprised data set, the R package *adeigenet* was used for unsupervised clustering and a discriminant analysis of principal components (DAPC) (Jombart, Devillard, & Balloux, 2010). This approach was chosen particularly with regard to the variety of factors potentially influencing the genetic structure (i.e., classical factors such as artificial selection/breeding as well as socio-economic, spatial and ecological factors). Thus, DAPC does not rely on a specific population genetics model in contrast to other popular software packages [e.g., ADMIXTURE (Alexander, Novembre, & Lange, 2009)] in population genetics and is free of assumptions about, for example Hardy–Weinberg equilibrium or linkage disequilibrium.

Genetic clusters in the data set of four breeds were initially inferred using the *k*-means clustering algorithm (*find.clusters* function in *adeigenet*). The optimal value of *k*, that is the actual number of genetic clusters in the full data set, was inferred based on comparisons of the Bayesian information criterium (BIC) by identifying the *k* value corresponding to the lowest BIC. Following this, DAPC comprises a principal component analysis (PCA) with a subsequent linear DAPC in a multivariate approach (Jombart et al., 2010). Compared to the traditional PCA approach to infer genetic clusters, DAPC results in clustering the data in a way that maximizes the variation between and minimizes variation within clusters. For the DAPC, 100 principal components accounting for around 45% of the total variance in the data set and five discriminant eigenvalues corresponding to six inferred genetic clusters were retained as determined using the *xvalDAPC* and *find.clusters* procedures in *adeigenet* (see Figure S2a-d and g for all diagnostic graphics associated with the unsupervised clustering and cross-validation for DAPC).

2.5.3 | Ancestry coefficients: TESS and ADMIXTURE

We applied two different model-based methods to analyse the composition and admixture of the sampled breeds or more specifically genetic groups in relation to the chosen ecological and socio-economic descriptors such as AEZ, transhumance and sampling location on a broader basis. ADMIXTURE models the ancestry of observed genotypes based on estimation of ancestry proportions and population allele frequencies similar to STRUCTURE (Pritchard, Stephens, & Donnelly, 2000).

ADMIXTURE was initially run with varying levels of *k* (i.e., 1–20) in a cross-validation approach to improve model fit and infer the optimal value of *k* genetic clusters based on the ancestry model. The optimal number of ancestral populations

in ADMIXTUREs cross-validation procedure is selected by choosing the level of *k* with the lowest cross-validation error. Furthermore, the algorithm implemented in the TESS program family (Caye, Deist, Martins, Michel, & François, 2016) extends the ancestry model by incorporating spatial proximity information based on geographical coordinates of the studied individuals. Thus, individual ancestry proportions and their corresponding parameters are modelled from genetic and geographic data. The TESS model was implemented using the R package *tess3r* (Caye & François, 2016). Analogous to the approach with ADMIXTURE, the cross-validation procedure implemented in *tess3r* was used to infer the optimal value of *k* genetic clusters (i.e., the model with the lowest root-mean-square error). Results for the cross-validation procedures in ADMIXTURE and TESS are displayed in Figure S1e-f. Geographical coordinates for sampled individuals were provided in longitude-latitude format after conversion of the originally recorded UTM formats. The *tess3r* package also includes a plotting function to interpolate the major ancestry coefficients of the sampled individuals on the spatial scale, that is a geographic map of Benin, to visualize the spatial distribution of ancestries and inferred genetic groups (see Figure 5). ADMIXTURE as well as TESS is not suitable for multi-allelic marker types, and the respective results were therefore obtained exclusively from analysis of SNP data.

2.5.4 | Spatial analysis of genetic structure

The results from the initial analysis of genetic structure especially considering geographical information (i.e., using the TESS approach) suggested patterns of genetic structure associated to the spatial distribution of samples within the Lagune breed as well as between the Borgou and the sampled animals referred to as Pabli. A common method for a first evaluation in the context of spatial genetics is to map the most important principal components from a PCA or DAPC analysis on a given spatial reference to visualize spatial patterns of genetic structure (Jombart, 2008). Colourplots combine up to three scores or measures (i.e., principal components in our case) at the same time by transforming each principal component into the scale of a RGB colour channel (red, green and blue) to compose a specific colour representing a multivariate distribution using the RGB system (Menozzi, Piazza, & Cavalli-Sforza, 1978). Visible patterns associated with spatial autocorrelation of principal components can be easily visualized in this way (Figure 6). The visual inspection is complemented by a statistical test of spatial autocorrelation, for example a Moran's *I* test (Cliff & Ord, 1981). To further assess spatial patterns of genetic structure in the mentioned breeds Lagune, Borgou and Pabli, we performed the aforementioned visualization approach using colourplots for the first three principal components from the DAPC and

complemented this with a Moran's I test as implemented in the R package *spdep* (Bivand, Pebesma, & Gómez-Rubio, 2013).

2.5.5 | Refined ancestry coefficient estimation using an extended data set and supervised ADMIXTURE analysis

Considering that the sampling focused on stationary herds and excluded mobile transhumant herds due to a lack of practicability, we searched for opportunities to extend the data set with publicly available SNP data preferably from breeds typically used in transhumant herds, namely indicine breeds from West African origin. Available SNP genotypes from previous studies (Flori et al., 2014; Gautier et al., 2009) for the same breeds as sampled in our study and additional West African taurine and hybrid breeds also provided opportunities to study the dynamic of the genetic structure over time and include further genetically close breed groups. In addition, we also sought to extend the data set to achieve a more representative sample of the genetic diversity of the bovine species (i.e., European and African taurine as well as indicine breeds).

Gautier et al. (2009) studied selection signatures in West African cattle based on 50k SNP data (Illumina BovineSNP50 BeadChip v.1) from 288 animals of eight breeds including the Lagune, Somba and Borgou sampled in Benin (Gautier et al., 2009). The other sampled breeds were N'Dama (two populations) and Baoulé from Burkina Faso, Sudanese Fulani from Benin, Kuri and Choah zebu or Zebu Bororo from Chad. We therefore used this data set as a basis for extending our own data. See Gautier et al. (2009) for further details on sample collection and genotyping. In addition, we also included samples from further 158 Borgou individuals originating from Flori et al. (2014), 25 N'Dama individuals from Matukumalli et al. (2009). To complement the extended data set, additional outgroups for European taurine breeds and Asian indicine breeds were also incorporated. The outgroup data were comprised of additional 135 samples (62 Angus, 25 Brahman, 24 Gir, 24 Nellore) from Matukumalli et al. (2009), 50 samples (20 Charolais, 30 Holstein) from Gautier et al. (2009) and 55 samples (20 Ongole, 35 Shorthorn) from Decker et al. (2014). The corresponding data sets used for the extension are freely available in the public domain under a Creative Commons license (<https://creativecommons.org/licenses/by-nc/4.0/>) for scientific purposes from the WIDDE database (Sempéré et al., 2015). Hence, we complemented our data set including 461 animals with the mentioned 711 animals in order to enhance the assessment of the ancestral composition of the current cattle population in Benin and gene flows originating from transhumance. Furthermore, the extension also allowed us to evaluate the development and dynamic of genetic

structures in the Lagune, Borgou and Somba breeds. The data sets were merged using PLINK followed by the same QC and LD pruning procedures mentioned above for the initial SNP data set. The extended data set finally consisted of 1,172 individuals from 17 breeds and 14,607 genome-wide SNP markers. We also used the framework for DAPC (i.e., unsupervised clustering) and unsupervised ADMIXTURE (i.e., cross-validation and ancestry coefficient estimation) as described above to estimate the number of genetic groups also in the extended data set. Diagnostic graphics for DAPC and unsupervised ADMIXTURE analysis of the extended data set are included in Figure S2.

In addition, estimation of ancestry coefficients in an additional ADMIXTURE run was based on a supervised analysis. The supervised analysis included reference samples for ancestral European taurine (EUT, Breeds: ANG, HOL, CHA), ancestral African taurine (AFT, Breeds: BAO, LA4, ND3) and ancestral Asian indicine (IND, Breeds: BRM, GIR, ONG, NEL) populations retrieved from the WIDDE database as described above. All other samples entered the estimation with unknown ancestry.

To assess a potential influence of transhumance on ancestry composition and genetic structure, we calculated a mean individual indicine ancestry proportion estimated from the supervised ADMIXTURE run. The individual indicine ancestry proportion was calculated from the ancestry component associated with the ancestral indicine reference samples for all non-reference samples. Individual results were then averaged stratified by breed, sampling location indicated by breed code and influence of transhumance at the sampling location (i.e., for all samples we recorded if the specific sampling location is regularly influenced by transhumant herds or not). In addition, the standard deviation and extrema (maximal and minimal values) were also calculated.

3 | RESULTS

3.1 | Basic measures of genetic diversity

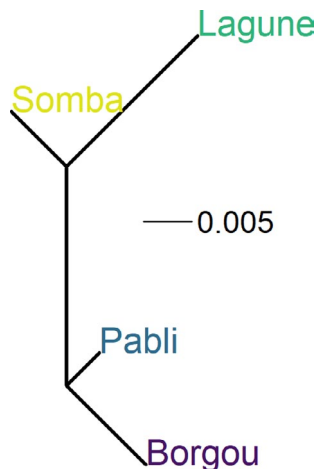
The estimated genetic distances and pairwise F_{st} values (see Table 3 and Figure 2) largely reflect the geographical distribution (i.e., isolation by distance), the phenotypic diversity (see also Table 1) and the diverging breed histories of the sampled breeds. Genetic distances of the Borgou breed to the Lagune and Somba breeds are relatively high. The estimated genetic distance between the Pabli and the Borgou breed in contrast is remarkably small. However, the estimated genetic distances from the Pabli to the Lagune and Somba are smaller in comparison with the genetic distances of the Borgou to the Lagune and Somba. Given the measures of genetic diversity, the Somba and Pabli breed show higher within breed diversity based on mean allelic richness and expected heterozygosity

TABLE 3 Basic measures of genetic diversity for the four sampled indigenous cattle breeds from Benin

	Lagune	Somba	Pabli	Borgou
Lagune	1.306 ¹ 0.283 ² 0.097 ^{3,a}	0.026	0.035	0.057
Somba	0.027	1.327 ¹ 0.305 ² 0.006 ^{3,a}	0.026	0.035
Pabli	0.038	0.025	1.307 ¹ 0.324 ² 0.064 ^{3,a}	0.005
Borgou	0.052	0.043	0.007	1.284 ¹ 0.305 ² 0.039 ^{3,a}

Note: Nei's genetic distances below the diagonal, pairwise F_{st} are given above diagonal. In diagonal: 1. Mean allelic richness, 2. Expected heterozygosity, 3. mean inbreeding, as referenced by numeric superscripts.

^aEstimation based only on SNPs.

**FIGURE 2** Neighbour-joining tree based on Nei's genetic distances for the four sampled indigenous cattle breeds from Benin [Colour figure can be viewed at wileyonlinelibrary.com]

compared to the Lagune and Borgou breeds. The Lagune and Pabli breeds additionally show relatively high values of estimated genomic inbreeding.

3.2 | Unsupervised clustering and DAPC results

According to the unsupervised k -means clustering prior to DAPC, the optimal number of k (i.e., the lowest overall BIC value) was 6, reflecting 6 distinguishable genetic groups (see the inset plot in Figures 3 and S1c). However, all k values from five to ten result in comparably low BIC values and therefore all potentially provide useful descriptions of the data. After inspection of DAPC plots and group membership

probabilities for k values from five to ten (see Figure S5), it becomes clear that higher k values above $k = 6$ (the run associated with the lowest BIC value) typically lead to division of small inner-breed clusters. Those smaller inner-breed clusters show close proximity rather than distinctive discrimination of between-breed structure. We therefore concluded that based on the model-free exploratory DAPC approach a number of six genetic groups provides a meaningful and sufficient description of the genetic structure in our sample. The graphical representation of the two most important principal components of the respective DAPC shows great accordance to the results from the basic measures of genetic diversity (see especially Figure 2 in comparison with Figure 3) while concurrently reflecting the between- and inner-breed relationships in much better detail.

The inferred clusters based on $k = 6$ are in general accordance with the initial breed assignments (see Table 4 for a detailed overview of cluster-breed assignments). The two taurine breeds Somba and Lagune form separated genetic groups clearly distant from Borgou and Pabli as expected. Whereas the Somba breed builds a homogenous cluster (cluster six, see Figure 3) with only a very limited number of out-grouped individuals originally assigned to the breed (i.e., 3 of 62 animals), the Lagune population appears to be much more diverse with two main and quite distant genetic groups (clusters four and five). Cluster four shows significantly less distance to the Borgou and Pabli breed, with equal distances to the core Lagune cluster and the Borgou and Pabli clusters. In proximity to cluster four, DAPC also identifies a small (13 animals) cluster with no clear breed association including individuals from Somba, Lagune and Pabli (Table 4) that might have a similar potential background of influences.

The sampled individuals referred to as Pabli are less distant to the taurine breeds compared to the majority of the Borgou breed. This leads to two separate clusters for both breeds with substantial overlap. A considerable part of the sampled Borgou individuals (42 of 139 animals) clusters with the Pabli.

3.3 | Estimated ancestry coefficients from TESS and ADMIXTURE

While the DAPC analysis indicated six genetic Clusters ($k = 6$) as shown above, the results of the model-based approaches slightly deviated in this regard. The cross-validation-based selection procedures for TESS and ADMIXTURE indicated six to seven and four clusters. While the TESS analysis shows a high degree of agreement with the results of the DAPC, the ADMIXTURE analysis, on the other hand, points to a lower number of genetic groups.

Figure 4 presents the estimated ancestry coefficients for the two different model-based approaches in direct context to

FIGURE 3 Scatterplot for the first two principal components of each individual estimated from DAPC for the four sampled indigenous breeds from Benin. The colouring is based on the original breed assignment of samples. Clusters inferred in unsupervised k -means clustering are visualized using dashed ellipses. Inset plots depict the number of optimal clusters based on BIC and the F -Statistic value for the estimated five linear discriminants within DAPC [Colour figure can be viewed at wileyonlinelibrary.com]

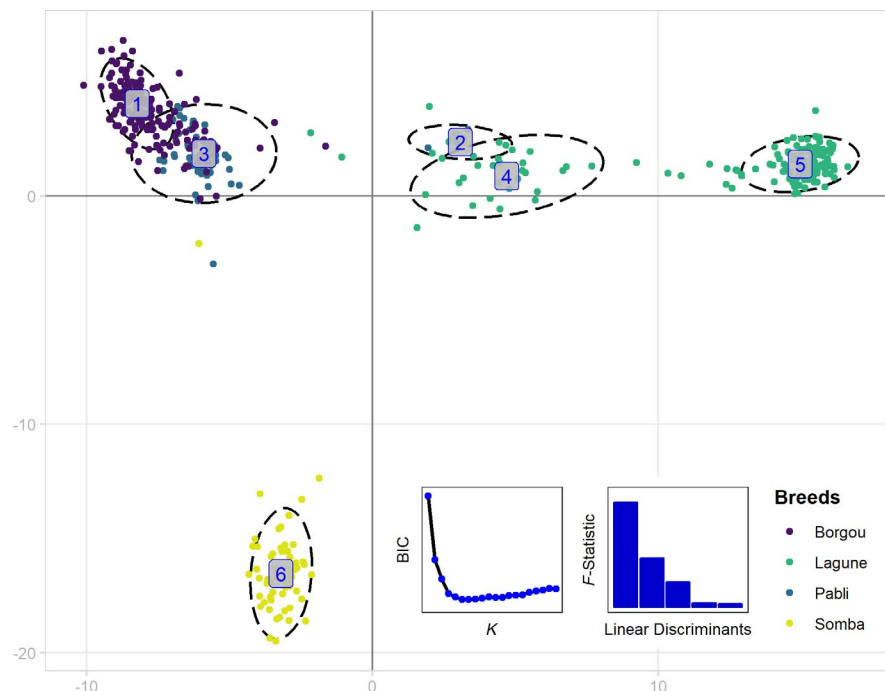


TABLE 4 Contingency table depicting the relationship between inferred clusters from unsupervised clustering in the DAPC framework and the original breed assignments at sampling

Breeds	Inferred clusters					
	1	2	3	4	5	6
Borgou	139	0	42	0	0	0
Lagune	0	8	3	27	119	0
Pabli	2	3	56	0	0	0
Somba	0	2	1	0	0	59

each other. The samples in the barplots are ordered by AEZ and community within AEZ to visualize patterns of genetic structure associated with the sampling design.

The animals in cluster two, which subsumes individuals from three different breeds, are consistently outgrouped by both methods with only small deviations. Apart from the 13 animals which are part of this cluster, no other animals were identified with significant proportions of ancestry from this cluster.

The estimated ancestral composition for the Somba breed is in good accordance between ADMIXTURE and TESS. Both model-based approaches capture apparent genetic diversity (i.e., two separate genetic groups and potential crossbreeding) in the Lagune population at $k = 6$. Animals assigned to cluster four show substantially higher proportions of ancestry from cluster three associated with Borgou and Pabli samples and taurine (i.e., cluster six associated with Somba) ancestry. In context of the AEZs, it becomes clear that this effect is not restricted to a single AEZ. Animals from cluster four appear in all three AEZs of the Lagune breed with emphasis on the AEZs Depression

and Terre de Barre. Instead, the effect appears to be associated with either regional spatial factors limited to some communes or transhumance effects, or both. This becomes visually evident as highly admixed samples in the barplots appear in blocks representing municipalities (Figure 4). Although the degree of admixture (i.e., proportion of ancestries from genetic groups not mainly associated with the Lagune breed) in all Lagune individuals is profoundly higher in the TESS model, both models show accordance for highly admixed individuals in general.

The Borgou population can be characterized by heterogeneity between AEZs. The samples from the AEZ VSB show higher taurine ancestry components compared to samples from the AEZs CCB and CNB in the ADMIXTURE estimation while remaining in the same genetic cluster altogether. In this context, the Pabli samples clustering with the Borgou samples display the highest amounts of taurine ancestry components. In contrast, the Borgou samples from the AEZ VSB form a separate cluster with the Pabli samples slightly apart from the Borgou samples from AEZs CCB and CNB using TESS and DAPC. The estimated ancestry composition of the assumed Pabli and the Borgou breed in both model-based approaches indicates a larger-scale spatial pattern associated with the sampled AEZs and their spatial proximity. The respective pattern is further reflected in the interpolated projection of the ancestry coefficient matrix estimated using the TESS model onto the map of Benin in Figure 5.

3.4 | Spatial analysis of genetic structure

The colourplot for the Lagune population shows no visible general spatial pattern of genetic structure but points

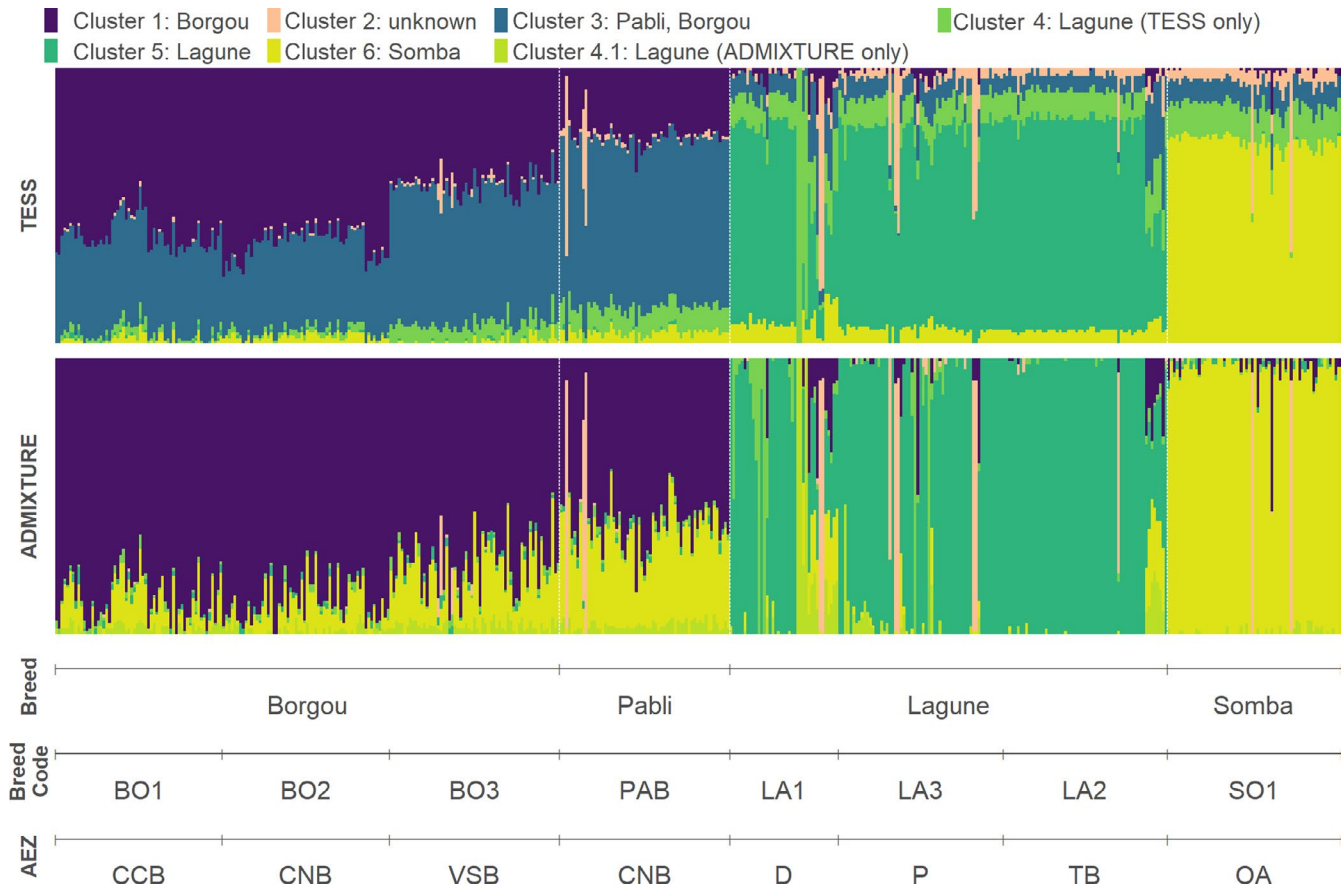


FIGURE 4 Barplots for ancestry coefficients estimated with TESS and ADMIXTURE for the four sampled breeds from Benin [Colour figure can be viewed at wileyonlinelibrary.com]

to outgrouped individuals which were sampled mostly apart from the core sampling region around Porto-Novo and Sakété (Figure 6b, see also Figure S4). The results of Moran I tests for the first two principal components of the DAPC however significantly ($p < .05$) reflected a spatial genetic pattern. Outgrouped individuals are associated with the cluster of unknown origin that is not clearly associated with one of the sampled breeds based on the results above (Figures 4 and 5). Apart from this, no general spatial pattern associated with the different AEZs or transhumance influence was found.

In contrast, the colourplot (Figure 6 a, see also Figure S3) for the sample locations of Pabli and Borgou points to a rather clear spatial pattern in the genetic structure and connection between and within these breeds supported by significant Moran I tests for the first three principal components ($p < .05$). Consequently, the sampled Pabli animals show a distinctively different colour than all three Borgou sample locations representing numerical differences in the first three PCs between the Pabli and Borgou samples. A closer connection between the Pabli samples and the Borgou samples from AEZ VSB is less distinct compared to the ancestry coefficient estimation with ADMIXTURE.

3.5 | Refined ancestry coefficient estimation using the extended data set

ADMIXTURE and DAPC results from the unsupervised analysis using DAPC and ADMIXTURE point to seven distinguishable genetic groups or clusters in the data set of 17 different breeds (Figures 7 and S2). The cluster of unknown origin from the analysis of the smaller data set (cluster two, see Figures 3 and 4) is clearly associated with the EUT ancestry of the included breeds HOL, ANG, SHO and CHA proving admixture of a small number of Beninese animals with exotic EUT breeds. Some aspects from the analysis of the smaller data set were further confirmed using the extended data set (Figure 7): i) the genetic structure of the Somba breed and its AFT foundation appears stable over time comparing our samples (SO1) with the samples from Gautier et al. (2009) (SO2). The results from unsupervised as well as supervised ADMIXTURE indicate only a slight rise in proportions of indicine ancestry in a small number of cases next to the sampled individuals admixed with EUT breeds. Nevertheless, a single sampled SO1 individual showed an estimated indicine ancestry proportion of 39% in the supervised analysis. In contrast, the sampled Lagune populations (LA1, LA2, LA3) appeared

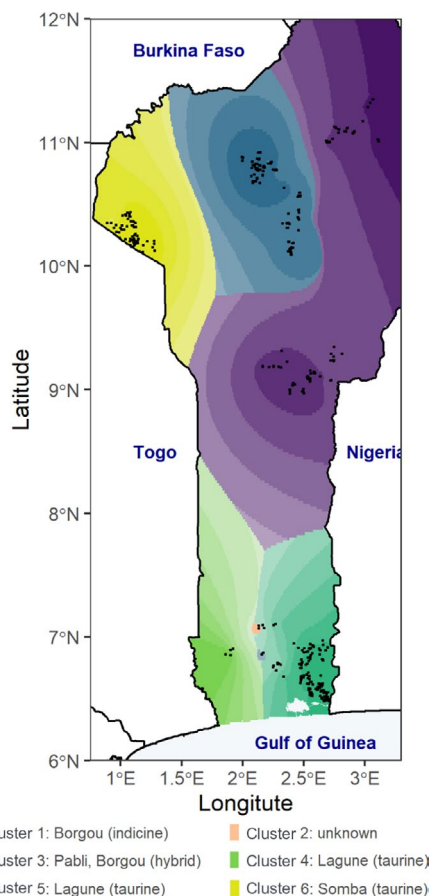


FIGURE 5 Spatial Interpolation of ancestry coefficients for the four sampled indigenous cattle breeds estimated with TESS on the map of Benin [Colour figure can be viewed at wileyonlinelibrary.com]

much more diverse and heterogeneous compared to the samples taken in 2009 (LA4). Hence, next to a small number of sampled animals admixed with EUT breeds, we could identify a small but noticeable group of individuals with indicine ancestry proportions of up to 35%. Almost all sampled individuals assumed to be the remnants of the Pabli breed show a balanced mixture of indicine and taurine ancestry components in the unsupervised as well as supervised ADMIXTURE analysis comparable to the older samples from the Borgou breed (BO4, BO5 and BO6). As for Lagune and Somba, we also identified a small number of individuals admixed with EUT breeds. The taurine ancestry components for the sampled Pabli animals are associated with AFT ancestry with only small amounts of EUT ancestry comparable to NDama (ND1 and ND2) and Somba (SO1 and SO2) samples. The results for the Borgou breed reflect substantial diversity in the breed between sample locations and time of sampling. All sampled populations

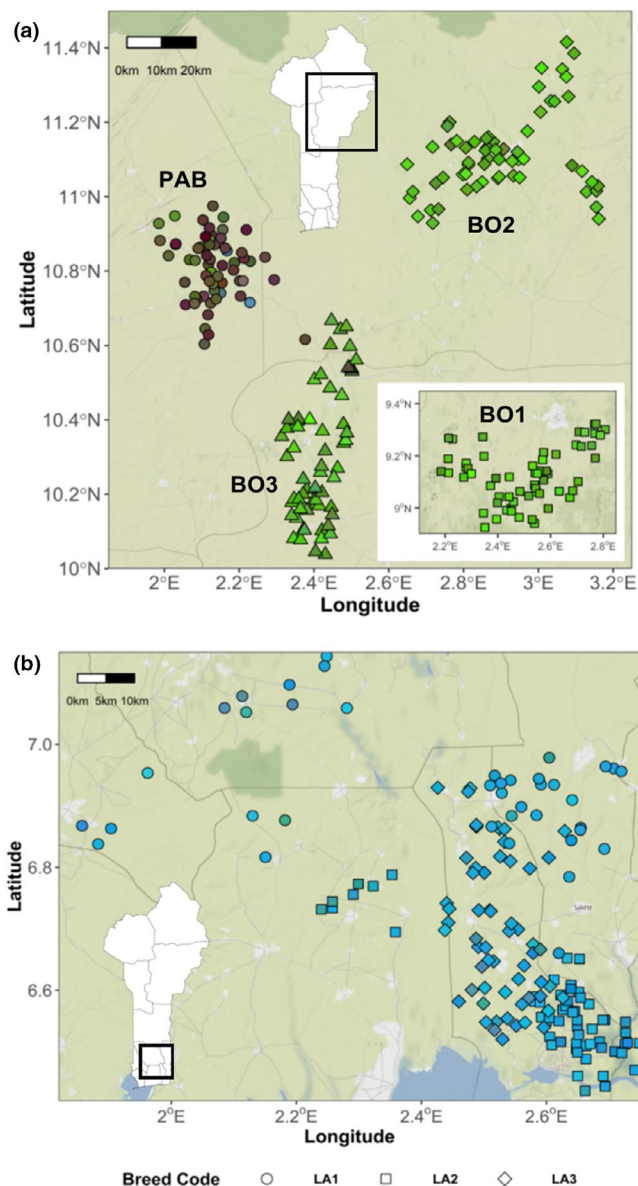
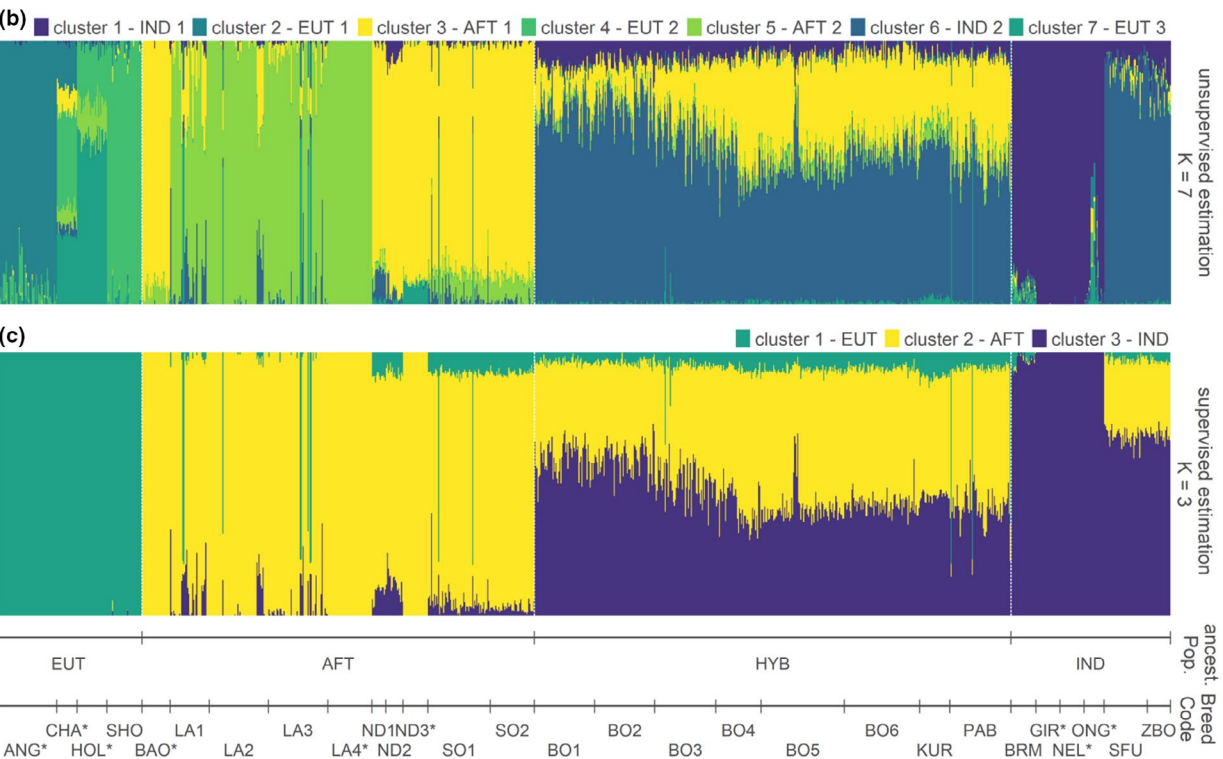
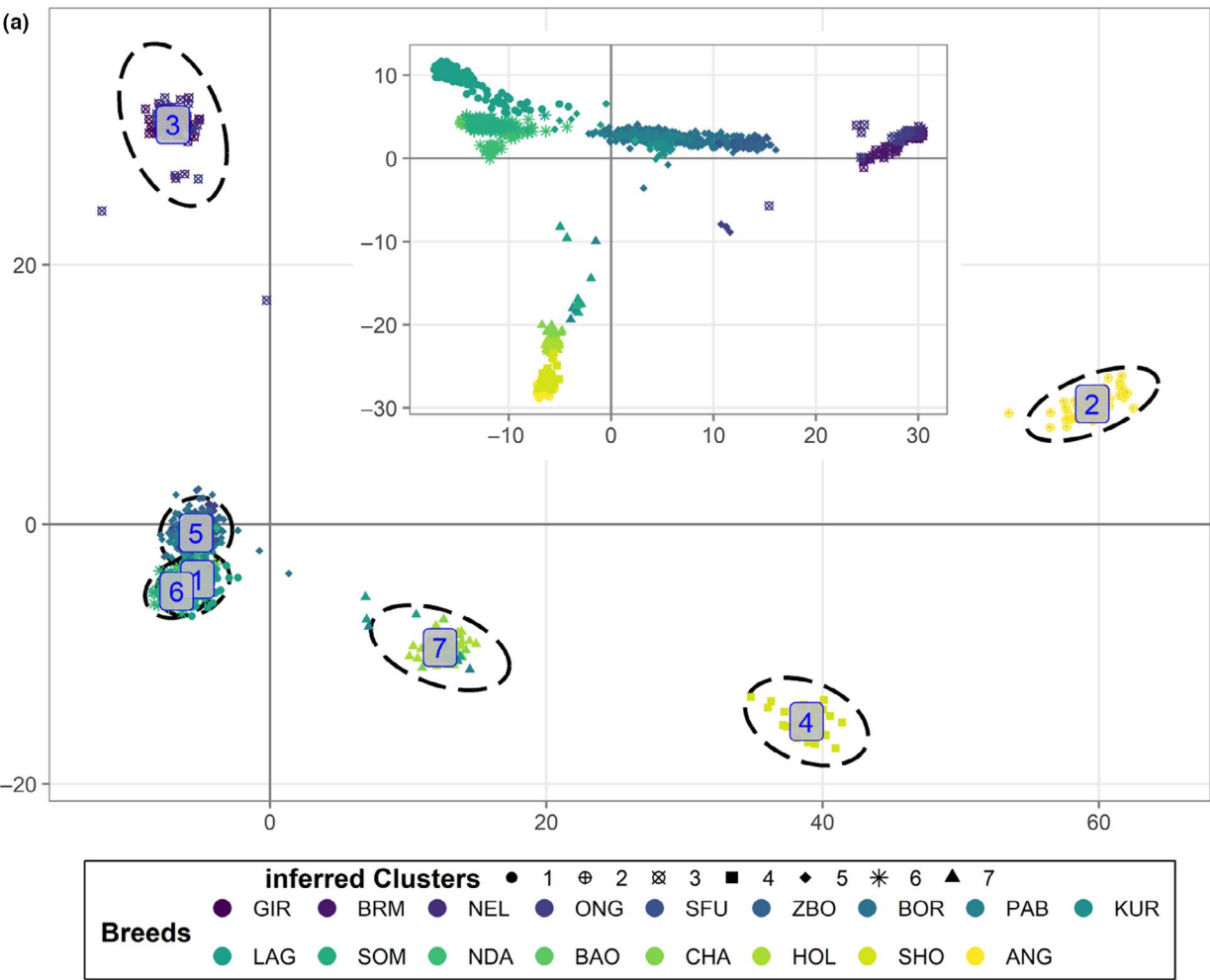


FIGURE 6 Colourplots for the first three principal components estimated with DAPC analysis for sampled individuals from three indigenous breeds of Benin. a) Colourplots for the sampled Borgou and Pabli individuals; b) Colourplots for the sampled Lagune individuals [Colour figure can be viewed at wileyonlinelibrary.com]

during this study (BO1, BO2, BO3) show higher mean indicine ancestry proportions compared to previously sampled populations (BO4, BO5 and BO6, Flori et al., 2014; Gautier et al., 2009). Comparing sample locations in our study, samples from AEZ VSB (BO3) display lower mean indicine ancestry proportions (Figure S3), compared to samples from the AEZs CCB and CNB (BO1 and BO2)

FIGURE 7 a) Scatterplot for the first two principal components of each individual estimated from DAPC for the extended data set including 17 different breeds. The inset plot shows a scatterplot of the raw PCA results; b) Barplot for ancestry coefficients estimated with ADMIXTURE in an unsupervised estimation run for the extended data set including 17 different breeds; c) Barplot for ancestry coefficients estimated with ADMIXTURE in a supervised estimation run for the extended data set including 17 different breeds [Colour figure can be viewed at wileyonlinelibrary.com]



confirming the results from the initial analysis using the smaller data set (Figure 4).

The supervised ADMIXTURE analysis based on reference samples for ancestral European taurine (ANG, HOL, CHA), ancestral African taurine (BAO, LA4, ND3) and ancestral Asian indicine (BRM, GIR, ONG, NEL) populations further confirms the results from the unsupervised analyses.

Finally, Table 5 depicts mean ancestry proportions of indicine origin from the supervised ADMIXTURE analysis for the sampled breeds stratified for sample locations known to be influenced by transhumant herds compared to sample locations not influenced by transhumant herds. The Borgou breed, which is already influenced by indicine ancestry reflected in its hybrid character, does not show any noticeable influence of transhumance based on means and extrema. This is consistent for all sample regions and for both methods. The comparison of sample region BO1 and the Pabli samples (during sampling only sample locations without any transhumance effect were considered) to sample regions BO2 and BO3 further quantifies the finding of lower indicine ancestry proportions.

However, the results indicate a potential transhumance effect particularly in the Lagune breed and to a lesser extent also in the Somba breed. Accordingly, there is only a slight average effect associated with transhumance in the Somba (i.e., slightly higher mean indicine ancestry proportions in locations influenced by transhumance), but the individual maximal values in Somba and Lagune indicate a much higher individual probability for admixture due to crossbreeding in locations influenced by transhumance. Maximal values of 0.23–0.39 compared to 0.09–0.26 in locations influenced by transhumance show that there are most likely single cases of recent crossbreeding with indicine or hybrid cattle while the majority of the population remains unaffected. The values for the Lagune breed also reflect a regionally differing effect of transhumance in two of the three sampled AEZs. While the locations around the core area of Porto-Novo and Sakété in AEZ P remain rather unaffected by transhumance with only slightly higher maximal individual values, LA1 and LA2 in AEZs D and TB indicate systematic effects. The mean indicine ancestry proportions as well as individual maximal proportions in these sampling regions are noticeably higher in sampling locations influenced by transhumance compared to locations not influenced by transhumance in both methods. This complements the prior observed spatial patterns displayed in the colourplots confirmed by the Moran tests.

4 | DISCUSSION

Since the risk of over-interpretation of results from genetic cluster algorithms is high (Lawson, van Dorp, &

Falush, 2018), we wanted to add robustness to our conclusions by comparing different methods in the context of potential environmental and socio-economic factors and by extending the data set with additional genotype data. The inference of a certain number of genetic clusters (i.e., k genetic groups) using genetic cluster algorithms depends on features such as sample size and the number of genotyped markers which are independent of the population history (Lawson et al., 2018). As both sample size as well as the number of genotyped markers in our study are only moderate, the results for the inferred genetic groups should be seen explicitly as useful descriptions of firstly our data set, while general conclusions should only be drawn carefully. The extension of our data set however successfully substantiated the results from the smaller data set.

Cattle populations in Benin, especially in smallholder farms, are managed in a semi-natural framework compared to more restrictive and highly structured breeding practices for example in Western Europe (i.e., purebreds, restrictive mating). This most likely leads to more dynamic in gene flow and admixture (e.g., due to unrestricted mating during grazing) between different breeds, although to a lesser extent as in fully natural or wild populations. Spatial (i.e., isolation by distance) and environmental factors then are more likely to have higher effects on genetic structure compared to intensively and restrictively bred populations. The DAPC and TESS approaches appear to be able to depict apparent small scale spatial genetic patterns in our data set in this regard most likely related to recent genetic exchanges and selection. ADMIXTURE on the other hand appears to rather explicitly depict the historical context of breed formations and admixture reflected by African and European taurine and African Indicine ancestors. In our view, the mixture of methods therefore enables different perspectives to the current genetic structure of the Beninese cattle population.

Overall, we did not find any uniform and large-scale spatial genetic patterns associated to the tested environmental or socio-economic factors AEZ and transhumance. While the overall climatic conditions (i.e., precipitation and elevation) have most likely shaped the large-scale distribution of bovine subspecies and breeds over time, the rather small environmental gradients between neighbouring AEZs do not lead to distinct within- and between-breed spatial patterns in genetic structure in our data set. Based on the results of unsupervised clustering and model-based analysis as well as the specific spatial analysis, we conclude that environmental factors like the climate represented by AEZ are not the only drivers of genetic change and diversity in the cattle populations of Benin. In comparison, local spatial factors, that is isolation by distance, as well as socio-economic factors such as transhumance practices also determine the level of genetic exchange between breeds. This reflects the current rather unstructured character of

cattle breeding in Benin compared to for example European conditions mainly driven by purebred breeding and highly controlled gene flows.

The genetic structure of the Somba breed with its African taurine foundation appears stable over time comparing our samples with the samples from Gautier et al. (2009). However, we identified a small number of individuals highly admixed with African indicine or European taurine breeds. Those individuals admixed with African indicine breeds were sampled in communities influenced by transhumance. Due to the small number of admixed individuals, we conclude that the breed has a solid foundation with only little signs for a progressing dilution due to the existing presence of transhumance in its core breeding region.

In contrast, the current Lagune population appears much more diverse compared to the samples taken in 2009 pointing to a potential rise in crossbreeding from taurine as well as indicine sources. However, this could also be a sampling effect. Gautier et al. (2009) sampled a much lower number of individuals from the Porto-Novo region. Samples from the same region in our data set also show only very low levels of admixture. It is likely that Gautier et al. (2009) were not able to capture the full diversity in the Lagune population then, due to the small sample size and restricted sample region. We are confident that our balanced sampling design and the results of the spatial analysis help to paint a more complete picture of the diversity in the Lagune breed in this regard. Hence, there is sufficient evidence of a broad and pure African taurine, stable basis for the Lagune breed in the core breeding region around Porto-Novo in the AEZs TB and P. Nonetheless, we also found evidence for ongoing admixture with African indicine breeds associated with transhumance which could facilitate a potential dilution of the breed foundation in the Lagune in the future. Our results in the Lagune breed indicate that a higher degree of admixture with indicine donors in places apart from the core region is certainly due to crossbreeding with transhumant herds leading to a spatial pattern in genetic structure (Figure 6b). Results from the unsupervised ADMIXTURE analysis point to West African zebu breeds (represented by ZBO and SFU in our study) as the source of indicine introgression in the context of transhumance in Lagune as well as Somba (Figure 7b). Next to the effects of importing foreign exotic European taurine cattle, we therefore conclude that transhumance also plays a significant role in the high genetic diversity in some parts of the Lagune population. Furthermore, this presents further evidence that the foundation of the breed is not endangered as those effects are restricted to certain specific locations while most core breeding regions are unaffected by these diversifying effects. Livestock markets in Benin are known to be a source for the introduction of either local or imported exotic and indicine breeds (Kinkpé, Diogo, Kpade, Yabi, & Dossa, 2019). These authors reported three different livestock market locations

near the Lagune core sampling region. Due to the fact, that we did not find any uniform spatial effects associated to the tested environmental or socio-economic factors AEZ and transhumance, introduction of exotic and indicine individuals based on market trades could offer an explanation for those unexplained sources of genetic diversity and admixture especially in the Lagune breed.

In this context, Freeman et al. (2004) concluded that hybridization is the major influence on allelic diversity in African cattle breeds. Our results confirm this statement by showing that genetic diversity due to crossbreeding is also present in breeds without a general history of hybridization, most clearly visible in the Somba breed. We could show that one driver of this effect is transhumance which most likely leads to undeliberate crossbreeding. This is an important aspect from a conservation standpoint, as especially the African taurine breeds are likely to face growing threats in the future and need a broad and diverse genetic basis to remain healthy and productive if the population declines. Based on our results, we suggest that socio-economic effects such as transhumance practices need to be considered in future conservation programs in Benin. In addition, guidelines for pastoralists, especially for smallholder farms, should include precise information on risks of undeliberate crossbreeding associated with transhumance practices from the perspective of stationary herds to sustainably protect animal genetic resources. Also, the uncontrolled import of exotic European taurine breeds should be monitored.

The current Borgou population in Benin is historically seen as a result of crossbreeding between local *B. taurus* and *B. indicus* strains during breed formation roughly one century ago (Flori et al., 2014). For our rather small data set, we could ascertain a profound diversity between sampling locations with higher indicine ancestry proportions in the AEZs CCB and CNB compared to the samples from VSB. This finding was confirmed in the extended data set. The samples from location BO3 (AEZ VSB) show a high similarity to the older samples from 2009 and 2014 with balanced AFT and IND ancestry. These findings are an interesting addition to the results from Flori et al. (2014) who concluded that the Borgou samples they collected, which are also part of our analysis (BO4, BO5 and BO6), support a stabilized hybrid status due to equally partitioned indicine and taurine ancestry composition based on ADMIXTURE analysis and formal tests of admixture. These samples were mainly collected on national farms (Flori et al., 2014; Gautier et al., 2009) from three different locations in 2013 and 2002, whereas the samples collected for our study originate from a large number of smallholder farms in a spatially greater sampling region in 2015 and 2016.

Therefore, the apparent heterogeneity in the genetic structure of samples from the Borgou breed might be due to a sampling effect reflecting a difference in genetic structure

TABLE 5 Mean proportion of indicine ancestry components for the four sampled indigenous breeds from Benin comparing sampling locations based on transhumance influence

	Influenced by transhumance								Not influenced by transhumance							
	Supervised				Unsupervised				Supervised				Unsupervised			
	Mean	SD	Max	Min	Mean	SD	Max	Min	Mean	SD	Max	Min	Mean	SD	Max	Min
BO1	0.59	0.06	0.69	0.43	0.81	0.09	0.97	0.62	0.61	0.06	0.70	0.50	0.85	0.08	0.97	0.70
BO2	0.59	0.06	0.68	0.45	0.83	0.08	0.95	0.65	0.61	0.06	0.73	0.47	0.85	0.08	0.96	0.65
BO3	0.49	0.07	0.61	0.34	0.69	0.10	0.86	0.49	0.52	0.07	0.65	0.38	0.72	0.09	0.90	0.51
PAB	–								0.40	0.08	0.59	0.15	0.56	0.13	0.82	0.07
LA1	0.11	0.11	0.33	0.00	0.15	0.14	0.46	0.00	0.04	0.07	0.24	0.00	0.06	0.09	0.33	0.00
LA2	0.13	0.08	0.23	0.00	0.18	0.12	0.33	0.00	0.00	0.02	0.14	0.00	0.00	0.01	0.07	0.00
LA3	0.04	0.07	0.35	0.00	0.05	0.09	0.48	0.00	0.03	0.07	0.26	0.00	0.03	0.08	0.37	0.00
SO1	0.07	0.07	0.39	0.00	0.07	0.09	0.52	0.00	0.03	0.02	0.09	0.00	0.02	0.03	0.11	0.00

Note: Means are estimated based on individual ancestry coefficients from supervised and unsupervised ADMIXTURE analysis using the extended data set with 17 breeds.

over different farm types. Smallholder farms run by part-time farmers without a strict and professional management are more likely to be affected by influences of transhumance or indeliberate crossbreeding leading to further indicine introgression compared to state-owned professional farms, pointing to another interesting socio-economic aspect potentially driving the genetic structure in cattle in Benin. In addition, considerably higher mean indicine ancestry proportions for BO1 and BO2 compared to BO4, BO5 and BO6 are potentially contrasting the perception that the Borgou breed is a stabilized hybrid breed (Flori et al., 2014; Rege, 1999). The discrepancy in ancestry suggests spatially driven ongoing local gene flow from West African zebu breeds such as Fulani (SFU) and Bororo (ZBO) in regions near the border to Nigeria and Niger into the Beninese Borgou population or potentially a selection effect over time favouring indicine allele variants for example due to climate change.

The picture surrounding the main question if a Pabli breed still exists is complex and rather inconclusive. Compared to the historic descriptions of the Pabli breed as a taurine breed of N'Dama type or descent (Porter et al., 2016), we can confidently state that the samples collected for our study assumed to be the remnants of the Pabli breed are not dominantly taurine and therefore do not resemble the traditional breed. In fact, the reported admixture with the Borgou breed in the past is evident in the results from our data set and further confirmed in the extended data set. The obvious proximity and similarity of the animals assumed to be Pabli and parts of the Borgou samples (BO4 in particular) from previous studies supports the theory of absorption. However, the comparison with the more recently taken Borgou samples from our study indicate a stronger taurine component in both ADMIXTURE and TESS analysis for the animals assumed to be Pabli. This is further reflected by the fact that the Pabli and Borgou samples are assigned to different genetic clusters

in DAPC. Given the questions surrounding the heterogeneity of the Borgou population over time as discussed above, we conclude that the actual fate of the Pabli breed cannot be fully answered based on the used explanatory methods and requires further research. Formal tests of admixture as used by Flori et al. (2014) could be suitable to study the history and dynamic in genetic structure of the Borgou breed and the sampled animals assumed to be Pabli in this regard. Nonetheless, in the meantime, we suggest adding the affix Kerou indicating the sampling location to any samples associated with the term Pabli, which leads to a proposed breed/population notation Borgou/Pabli-Kerou.

5 | CONCLUSIONS

Based on the aims of our study we conclude that (a) the genetic structure and diversity of the Beninese indigenous breeds Lagune, Somba, Pabli-Kerou and Borgou is associated with ecological and socio-economic factors (transhumance) leading to spatial genetic patterns. We found good evidence for a stable and broad breed foundation of the taurine Somba and Lagune breeds. The Lagune breed however shows a much higher inner-breed diversity with local hotspots of admixture associated with transhumance effects. In contrast, the Borgou breed is genetically heterogeneous, especially when considering also older samples, as expected for a stabilized hybrid breed. Samples from smallholder farms collected in this study in AEZs CCB and CNB show higher mean indicine ancestry compared to older samples collected in previous studies from commercial farms. (b) The sampled assumed Pabli individuals show some differentiation in ancestry compared to the sampled current Borgou individuals, in the extended data set however they show similar ancestry patterns as older Borgou samples from previous studies. Based on our results,

we cannot fully conclude that the sampled Pabli animals are true remnants of the former Pabli breed. (c) Spatial separation or proximity reflects recent gene flow between the sampled Pabli and Borgou individuals leading to local spatial genetic patterns and also contributes to diversity in the Lagune breed. Hence, next to large-scale ecological factors represented by AEZ, local small scale effects also affect the specific breed distribution. (d) Transhumance has a traceable influence in the taurine breeds Somba and Lagune based on the estimated ancestry composition. The influence is limited in the Somba with some cases of crossbreeding in sampling locations influenced by transhumance without evidence for substantial effects on the breed foundation. In the Lagune breed however, we found evidence for substantial regional effects with higher amounts of indicine admixture and crossbreeding in sampling locations influenced by transhumance in two of the four sampling locations. Nonetheless, the breed foundation for the Lagune in the other two sampling locations is also stable.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in a DRYAD repository at <https://doi.org/10.5061/dryad.59zw3r238> (Scheper, 2019). The SNP data sets used to extend the original data set in this study are available from the WIDDE database (<http://widde.toulouse.inra.fr/widde/#>). The SNP data sets obtained in this study for the four cattle breeds from Benin will also be submitted to the WIDDE database.

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SUPPORTING INFORMATION

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