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Genetic diversity, population structure, and correlations between locally adapted zebu and taurine breeds in Brazil using SNP markers

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Abstract Genetic diversity is one of the most important issues in studies on conservation of cattle breeds and endangered species. The objective of this study was to estimate the levels of genetic differentiation between locally adapted taurine (*Bos taurus taurus*) and zebu (*Bos taurus indicus*) breeds in Brazil, which were genotyped for more than 777,000 SNPs. The fixation index (F_{ST}), principal component analysis (PCA), and Bayesian clustering were estimated. The F_{ST} highlighted genetic differentiation between taurine and zebu breeds. The taurine lines, Caracu and Caracu Caldeano, had significant genetic differentiation (F_{ST} close to 5%) despite their recent selection for different uses (meat and milk). This genetic variability can be used for conservation of locally adapted animals, as well as for breeding programs on zebu breeds. Introgression of zebu in locally adapted breeds was identified, especially in Curraleiro Pé-Duro breed. The Gyr breed, however, had low breed purity at genomic level due to its very heterogeneous mixing pattern.

Keywords Naturalized bovine · Conservation · Genomic · Introgression

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Introduction

Since the divergence of wild Aurochs (*Bos primigenius*), several types of cattle have accumulated distinct genetic variations, promoting highly differentiated phenotypes. It is estimated that the divergence that originated taurine and zebu cattle occurred long before domestication, between 8000 and 10,000 years ago. Taurine emerged in the Fertile Crescent while zebu cattle emerged in the Indus Valley, Pakistan (Ajmone-Marsan et al., 2010). After domestication, human-oriented selection added more complexity to the evolution of cattle species.

The first bovines arrived in Brazil between the sixteenth and seventeenth centuries, brought by Portuguese to be used as food and traction animals. After successive generations of random crossings, these animals adapted to the local environment and were recognized as locally adapted breed due to their ability to tolerate the high temperatures of the tropics and food shortages (McManus et al., 2009). In the mid-nineteenth century, trade routes between India and Brazil enabled the introduction of zebu cattle, and, as well as the locally adapted taurine breeds, they became naturalized in the country; however, the objective of zebu cattle was to increase the production of domestic herds (Silva et al., 2012).

The genetic variability of locally adapted breeds is mainly related to characteristics of adaptation and resistance to diseases (Bianchini et al., 2006; Nicolau et al., 2004). Thus, the maintenance of genetic diversity of each breed is important to meet the needs of production systems, in terms that it is not possible to assume which characteristics will be needed in the future. In addition, studies on genetic diversity are necessary to understand the available genetic resources and may aid in genetic breeding of animals under conservation (Boettcher et al., 2010).

Although there are studies that evaluated genetic diversity of cattle by pedigree and molecular markers (Porto-Neto et al., 2013; Santana et al., 2016), there is no study of the population genetic structure of large number of commercial and naturalized bovine breeds by single nucleotide polymorphism (SNP) markers. In this context, the objective of this study was to evaluate the genetic divergence between locally adapted breeds (*Bos taurus taurus*) and zebu breeds (*Bos taurus indicus*) using SNP markers.

Material and methods

Genotypes used in this study came from the DNA Bank which was undertaken by Embrapa Gado de Leite, Juiz de Fora, Brazil. All animals were genotyped using the Illumina Bovine HD Genotyping BeadChip, which includes ~777,000 (HD; Illumina, San Diego, CA) by Neogen do Brasil Ltda. Autosomal genotypes were subjected to a quality control procedure, removing SNPs under the following criteria: call rate < 0.98 and lower allele frequency < 0.02. A total of 141 locally adapted taurine animals of Franqueiro (FRA = 41), Pantaneiro (PAN = 18), Curraleiro Pé-Duro (CUR = 17), Caracu (C = 24), and Caracu Caldeano (CC = 41) breeds were compared with 553 zebu animals of Indubrasil (IND = 38), Sindi (SI = 49), Tabapuã (TAB = 24), and Gyr (GI = 442) dairy breeds to assess the level of introgression among these populations. All genotyped animals are from a breeding program in Brazil, where Embrapa is responsible for genetic evaluations.

The global F statistics (F_{IT}, F_{ST}, and F_{IS}) were calculated using the software GENEPOP 4.1.4 (Rousset, 2008). This software was also used to test the Hardy-Weinberg equilibrium deviations in loci at 5% probability. Within the genetic variability of the breed, the proportion of polymorphic loci (PP) and the observed (H_O) and expected (H_E) heterozygosity was estimated using the software ARLEQUIN 3.5.2.2 (Excoffier and Lischer, 2010). The F_{ST}, which measures the population differentiation (pair-to-pair), and the analysis of molecular variance (AMOVA) of breeds were calculated using the software ARLEQUIN 3.5.1.3 (Excoffier and Lischer, 2010) with 10^3 bootstrap permutations.

The genetic structure of the population was inferred by applying a principal component analysis (PCA) for the data set of taurine and another for zebu breeds, using the software SMARTPCA (Patterson et al., 2006). Proportions of individual ancestry for K (assumed number of ancestral populations) were calculated using software STRUCTURE (Pritchard et al., 2000). The ancestry patterns were generated using CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007) and later visualized with DISTRUCT 1.1 (Rosenberg, 2004). For each value of K, ten independent chains were performed for each SNP set, each one consisting of burn-in of 1000 and 10,000 Monte Carlo iterations. These tests were performed for $K = 1$ to N, in which N is the total number of expected subpopulations + 1. The delta K method (DK) was used to determine the number of subpopulations (Evanno et al., 2005).

Results

The evaluated populations had no significant Hardy-Weinberg equilibrium deviations. In all races/lines, the proportions of polymorphic loci (PP) were high and informative for the study of diversity. Genetic variability was identified for all breeds according to estimates of genetic diversity. A F_{IS} greater than 0 was observed only in Sindi breed (Table 1).

The estimated global F_{IT}, F_{ST}, and F_{IS} were 0.1271, 0.1363, and − 0.0106, respectively. The observed F_{IT} (12.71%) revealed the presence of heterozygotes in the population, whereas the F_{IS} (negative) indicated that there was no increase in inbreeding. F_{ST} pair-to-pair estimates ranged from

Table 1 Genetic diversity of locally adapted taurine breeds/lines and zebu breeds

Breeds	PP	H_O[a]	H_E[a]	F_{IS}
Caracu meat	0.9545	0.33505 ± 0.16732	0.33445 ± 0.15070	− 0.00186
Caracu Caldeano	0.8872	0.32327 ± 0.16910	0.31771 ± 0.15685	− 0.01770
Curraleiro Pé-Duro	0.8868	0.33798 ± 0.18498	0.32582 ± 0.15449	− 0.03851
Franqueiro	0.9713	0.35563 ± 0.16555	0.34255 ± 0.14793	− 0.03869
Pantaneiro	0.9355	0.38232 ± 0.18138	0.35618 ± 0.14486	− 0.07570
Gyr milk	0.9936	0.36880 ± 0.15847	0.36660 ± 0.15616	− 0.00600
Indubrasil	0.9647	0.38415 ± 0.16194	0.37256 ± 0.14297	− 0.03155
Sindi	0.9726	0.37092 ± 0.15017	0.37551 ± 0.13970	0.01235
Tabapuã	0.9618	0.39108 ± 0.16304	0.38513 ± 0.13756	− 0.01580

PP proportion of polymorphic loci, H_O observed heterozygosity, H_E expected heterozygosity, F_{IS} coefficient of inbreeding

[a] Mean ± standard deviation

4.39 (Caracu and Caracu Caldeano) to 23.97% (Indubrasil and Caracu Caldeano). Taurine breeds had different isolation levels, ranging from 7.88 (moderate) (Caracu x Franqueiro) and 7.97 (moderate) (Caracu × Pantaneiro) to 15% (high differentiation level) (Curraleiro Pé-Duro × Caracu Caldeano). On the other hand, results for zebu breeds were close to 5%, indicating a low genetic differentiation and a probably greater gene flow between breeds (Table 2).

The variation within all breeds explained 85% of the total genetic variation. This result was confirmed by the F_{ST} (0.15) indicating a low gene flow between taurine and zebu breeds (Table 3). Among taurine, this variation was 89.56% with F_{ST} of 0.10, whereas in zebu animals, almost all variation is explained by differences within breeds (94.66%), which is confirmed by the low F_{ST} (Table 3).

The first two components (PC1 and PC2) explained (12.48%) the variation among breeds/lines locally adapted. The PC1 explained 6.95% of the variation and allowed to discriminate the Curraleira breed from the others, with some animals close to Pantaneira breed. PC2, which explained

5.53% of the variation, discriminated the Franqueira breed of the Curraleira, Pantaneira, Caracu, and Caracu Caldeano. The Caracu lines were closer, presenting homogeneous genetic groups (Fig. 1a).

In the zebu, the first two components explained (6.36%) of the variation (Fig. 1b). It was verified (PC1) that there was separation of the Gyr breed with the Sindi, Tabapuã, and Indubrasil breeds that are destined to the meat production. The second component (PC2) allows visualizing the proximity between Indubrasil, Sindi, and Tabapuã breeds.

Using STRUCTURE analysis, we observed the presence of two clusters, which differentiated the locally adapted taurine from zebu breeds, with $K = 2$ (Fig. 2). Signs of introgression of zebu genes in taurine breeds were identified, except in Caracu Caldeano, originated from the selection of Caracu animals for dairy characteristics.

The genetic structure of taurine breeds indicated the presence of three clusters, with evident differentiation of Caracu Caldeano line from the other breeds (Fig. 3). Pantaneira breed has a greater diversity in its composition due to the proportion

Table 2 Estimates of genetic differentiation (pair-to-pair) between locally adapted taurine breeds/lines and zebu breeds. All F_{ST} estimates were significant ($p < 0.05$)

	C	CC	FRA	PAN	CUR	IND	TAB	SIN	GI
C		0.0439	0.0788	0.0797	0.1203	0.1982	0.1882	0.1926	0.1849
CC	0.0439		0.1126	0.1149	0.1500	0.2397	0.2351	0.2324	0.2130
FRA	0.0788	0.1126		0.1010	0.1439	0.1719	0.1639	0.1685	0.1601
PAN	0.0797	0.1149	0.1010		0.1330	0.1652	0.1542	0.1605	0.1552
CUR	0.1203	0.1500	0.1439	0.1330		0.2132	0.2039	0.2059	0.1950
IND	0.1982	0.2397	0.1719	0.1652	0.2132		0.0502	0.0634	0.0446
TAB	0.1882	0.2351	0.1639	0.1542	0.2039	0.0502		0.0530	0.0505
SIN	0.1926	0.2324	0.1685	0.1605	0.2059	0.0634	0.0530		0.0608
GI	0.1849	0.2130	0.1601	0.1552	0.1950	0.0446	0.0505	0.0608	

C Caracu meat, *FRA* Franqueiro, *IND* Indubrasil, *PAN* Pantaneiro, *CC* Caracu Caldeano, *GI* Gyr milk, *SIN* Sindi, *TAB* Tabapuã, *CUR* Curraleiro Pé-Duro

Table 3 Analysis of molecular variance (*AMOVA*) in the partitioning of genetic variation between and within locally adapted taurine breeds/lines and zebu breeds

Structure	SV	DF	%Var	Fixation index	Nm
Adapted taurine × zebu breeds	Between breeds	1	15.00	$F_{ST} = 0.1500^{**}$	1.4116
	Within breeds	1386	85.00		
Locally adapted taurine breeds	Between breeds	4	10.44	$F_{ST} = 0.1044^{**}$	2.1446
	Within breeds	277	89.56		
Zebu breeds	Between breeds	3	5.34	$F_{ST} = 0.0533^{**}$	4.4400
	Within breeds	1102	94.66		

SV source of variation, *DF* degrees of freedom, *%Var* proportion of total variance, *Nm* estimate of gene flow from the F_{ST}. Nm = $(1 - F_{ST}) / 4 F_{ST}$

[**] Significant at 1% of probability

of alleles of ancestral populations, whereas Curraleiro Pé-Duro and Franqueiro breeds have greater uniformity and low levels of introgression of other breeds. Delta *K* analysis also allowed us to identify an additional peak in *K* = 5 and observe the separation between the five taurine breeds/lines (Fig. 3).

Four clusters were estimated for zebu breeds, with additional peaks in *K* = 6 and *K* = 7 (Fig. 4). The Sindi breed had greater uniformity, while Indubrasil and Tabapuã showed similarities in their composition, with similar proportion of effect of other ancestral animals. Gyr breed had a high mixing level, which is consistent with the history of this breed (Fig. 4).

Discussion

Estimates for the observed heterozygosity (H_O) in all breeds indicate the presence of heterozygous animals in the

population and consequently, greater allelic diversity, which may favor adaptation to changes in climate and productive practices. This heterozygosity is important for zebu breeds, which are raised under different production conditions in Brazil, as well as for locally adapted taurine breeds, which are also raised in different regions of the country and are important and viable targets for conservation. Regarding the taurine breeds, the results indicate that conservation strategies have allowed us to maintain diversity within populations, an unusual condition in animals under conservation, due to their small effective size and inbreeding crossings. Similar results were observed in locally adapted taurine breeds in Brazil using microsatellite markers (Egito et al., 2007) and in Cuban Creole cattle (Acosta et al., 2013).

The identified genetic variation partitioning the taurine breeds was similar to that reported by Líron et al. (2006), which observed 99% of variation within creole breeds of
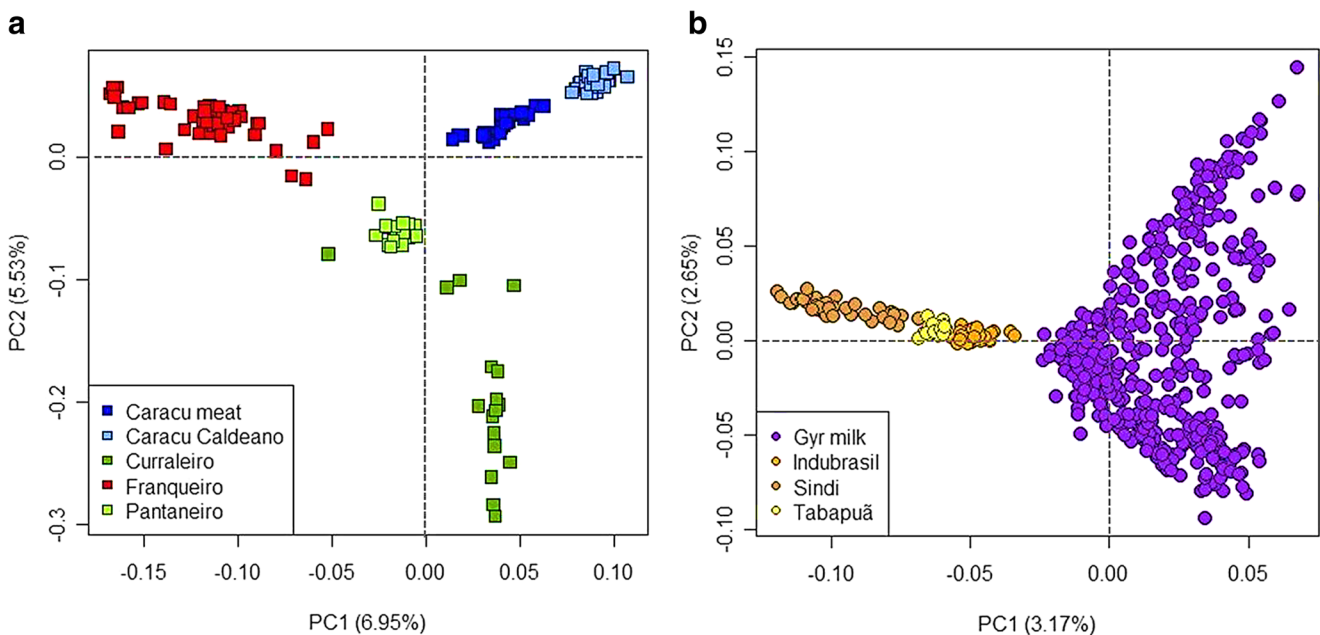
Fig. 1 Principal component analysis (*PCA*) of locally adapted taurine breeds/lineages (**a**) and zebu breeds (**b**)
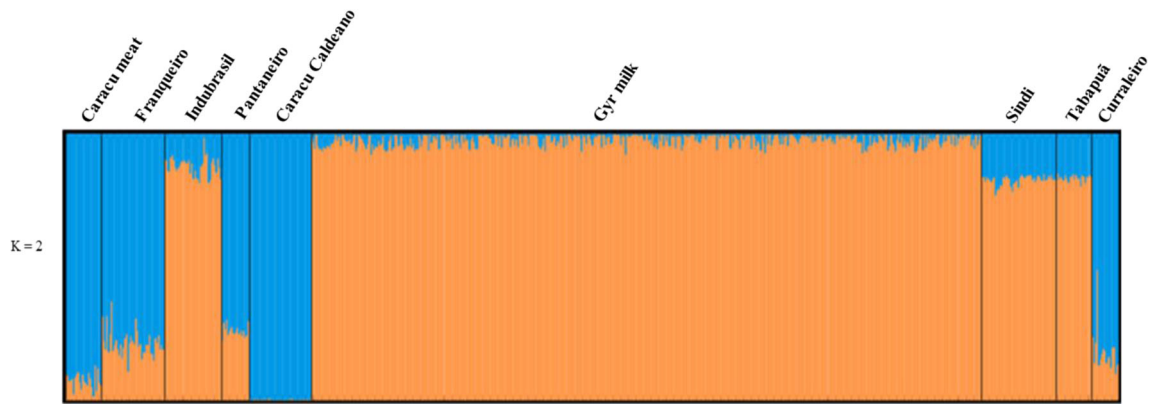
Fig. 2 Estimating the population structure obtained by STRUCTURE analyses for locally adapted taurine breeds/lines and zebu breeds. Each individual is represented by 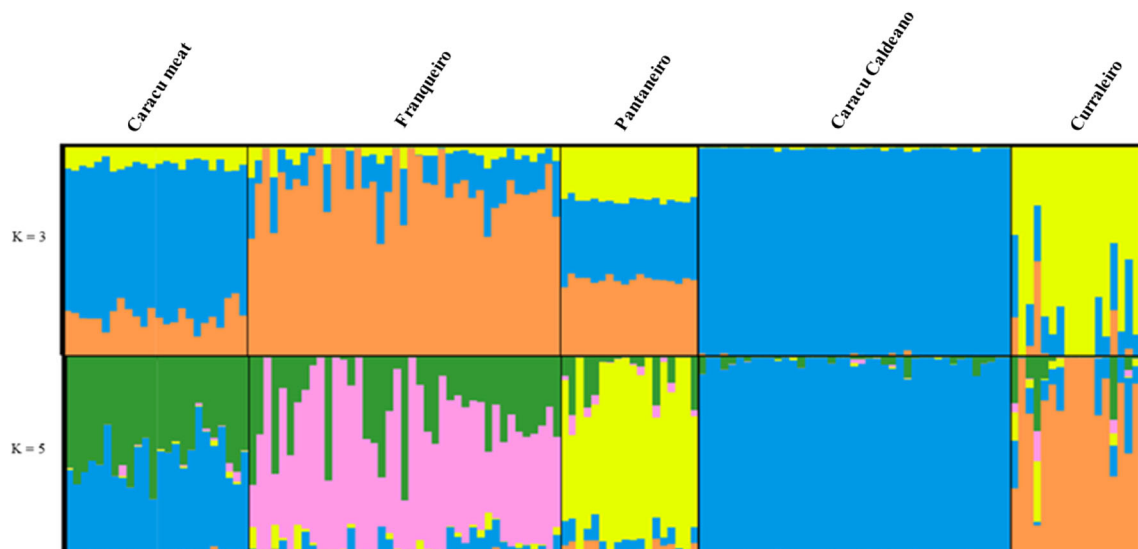a *thin vertical line*, which is partitioned into *colored segments* that represent the proportional contribution of the inferred *K* clusters. The populations are separated by *thin vertical black lines*

Argentina and Bolivia. According to these authors, this variation explains how naturalized breeds adapted to different environments, being an important factor for recovery endangered genetic resources. However, the genetic variation identified on groups' structures (5.24, 10.44, and 15%) may be important due to the benefits of heterosis and complementarity (Toro and Caballero, 2005).

The PCA analysis discriminated all taurine animals and allocated the Curraleiro Pé-Duro distant from the other breeds, probably as a consequence of absorbent crosses with zebu breeds for increasing genetic variability of this endangered breed (Issa et al., 2009). Caracu lines were also allocated distant from the other breeds and close to each other, according to the F_{ST} at 5%. The low percentages explained by the first two principal components in the taurine and zebu breeds did not

allow to reliably evaluate the diversity among the genetic groups. However, Gautier and Naves (2011) separated genetic groups with low percentages of explanation of the principal components, PC1 (8.1) and PC2 (5.91%). The observed discrimination for the locally adapted breeds was similar to those reported by Villalobos-Cortés et al. (2010) in Creole cattle of Panama, which had F_{ST} of 0.10 and Nm lower than 1, indicating that a high F_{ST} and low levels of gene flow may determine the differentiation among populations.

The Gyr breed had greater dispersion and variability than Tabapuã, Indubrasil, and Sindi, possibly due to the type of selection (directed to milk production) and raising in this breed. Differently from taurine, zebu breeds showed less genetic differentiation (F_{ST} close to 5%), due to its greater gene flow between breeds, which

Fig. 3 Estimating the population structure obtained by STRUCTURE analyses for locally adapted taurine breeds/lines. Each individual is represented by a *thin vertical line*, which is partitioned into *colored segments* that represent the proportional contribution of the inferred *K* clusters. The populations are separated by *thin vertical black lines*
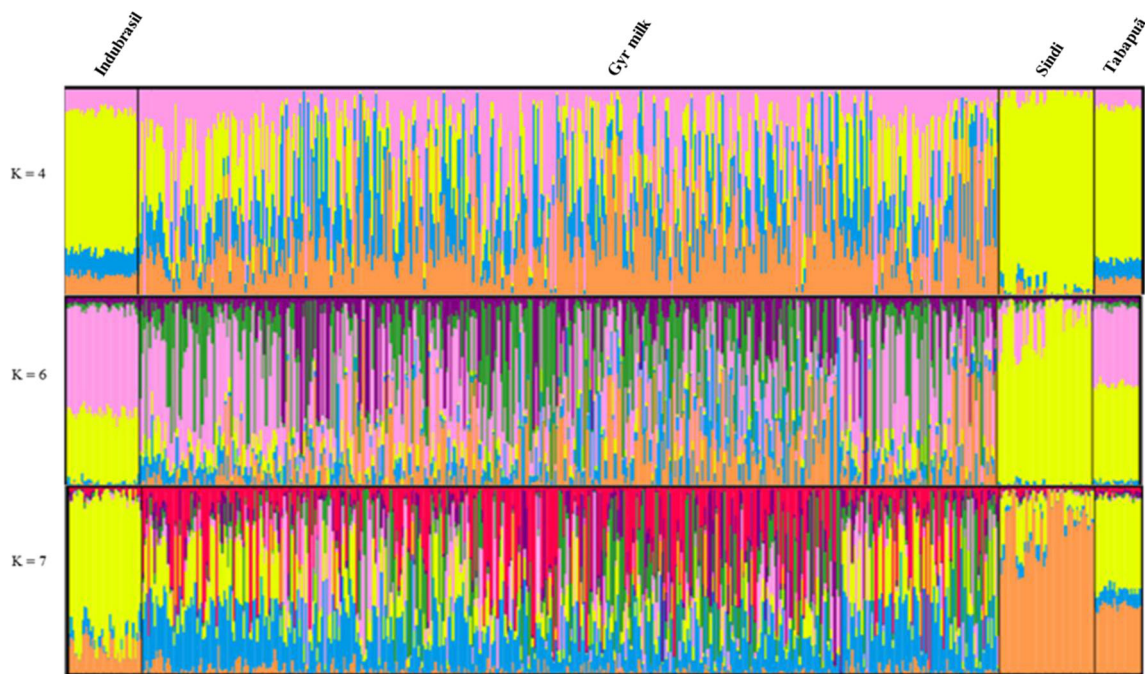
Fig. 4 Estimating the population structure obtained by STRUCTURE analyses for zebu breeds. Each individual is represented by a *thin vertical line*, which is partitioned into *colored segments* that represent the proportional contribution of the inferred *K* clusters. The populations are separated by *thin vertical black lines*

formed other breeds, such as Indubrasil, which has alleles from Nelore, Guzerá, and Gyr breeds (Vercesi Filho et al., 2002), and Tabapuã, which was formed from Nelore and Guzerá breeds (Oliveira et al., 2015). Studies on zebu breeds in the Americas (Villalobos-Cortés et al., 2015) and Sudan (Hussein et al., 2015) identified similar results for F_{ST} and Nm. Dani et al. (2008) observed estimates of 0.0840 (F_{ST}) and 2.7250 (Nm) in Nelore cattle in Brazil.

The introgression of alleles observed between taurine and zebu breeds confirms that the introduction and use of zebu breeds in Brazil was responsible for the mixing in the genetic composition of these animals. Several crosses between zebu breeds and domestic cattle resulted in animals with breed purity masked by the mixture of taurine alleles (Mariante et al., 1999), indicating that locally adapted breeds served as a basis for zebu breeds formation, which formed the largest herds in the country (Euclides Filho, 2009; Primo, 1992). The presence of taurine alleles in Brazilian zebu breeds, such as Nelore and Gyr, was identified by O'Brien et al. (2015) and Egito et al. (2007) on locally adapted taurine and commercial zebu breeds in Brazil.

Caracu Caldeano line differed from the other breeds, probably due to its formation and objective of selection (milk yield) since 1893 (Queiroz et al., 2005). The homogeneity of the sample indicated the base effect as the main precursor of formation of these animals, which allowed us to identify the integrity of their genetic composition (Egito et al., 2014) and

consequently, distinguish them from the other locally adapted breeds and commercial zebu breeds.

Proportion variations of ancestral populations in Franqueira, Pantaneira, and Curraleiro Pé-Duro breeds indicate that, although phenotypically characterized, these animals cannot be considered as breeds at genomic level. The Pantaneira breed showed uniform levels of mixture, which were attributed to its high estimates of genetic diversity. The history of this breed confirms the effect of Franqueiro and Curraleiro Pé-duro breeds in its formation (Mazza et al., 1992; Serrano et al., 2004).

A complex mixing pattern was observed in Gyr breed differing from the other zebu breeds that were more uniform. The genetic variability of Gyr breed can be explained by the formation of pure herds from 1993 with different purposes and selection intensities and subsequent crossings between animals from different herds (Gautier and Naves, 2011; Santana et al., 2014). Moreover, the absorption of characteristics from meat line (Standard Gyr) by Dairy Gyr may have generated more genetic variability (Leão et al., 2013; Reis Filho et al., 2010). Several studies on structure of populations showed reductions of effective population and increases in inbreeding among Gyr animals (Malhado et al., 2010; Faria et al., 2009).

Tabapuã breed had a mixing pattern, with contribution of other ancestor groups. This breed was developed in the early twentieth century from Creole population crosses, called Mocho Nacional, with zebu breeds, mainly Nellore. The

similarity of proportion of ancestral contribution pattern of Tabapuã and Indubrasil breeds confirms the common crosses of Nelore and Guzerá cattle during their formation, which can be proven by their low index of genetic differentiation (Brasil et al., 2013; Vercesi Filho et al., 2002 and Oliveira et al., 2015). Sindi was the only breed probable presenting homogeneity in the population, as observed by the F_{IS} statistic (0.01235), indicating inbreeding among the animals due to the low Ne.

Genetic diversity estimates identified in locally adapted taurine breeds indicate good conservation prospects, while in zebu breeds, the existing variability can be exploited through selection. The presence of structuration in taurine breeds/lines denotes their adaptation to different environments, allowing us to consider them as distinct genetic resources. However, they showed a certain level of mixing with zebu breeds, especially the Curraleiro Pé-Duro breed. Caracu Caldeano line proved to be an extremely homogeneous population. The great gene flow among zebu breeds denotes their common origin and the crosses between these breeds imported from India. Although there is good phenotypic characterization of Gyr, this breed had a very pronounced mixing pattern, revealing little purity at genomic level.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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