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Dynamics of genomic architecture during composite breed development in cattle

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Summary

Some livestock breeds face the challenge of reduced genetic variation, increased inbreeding depression owing to genetic drift and selection. Hybridization can reverse these processes and increase levels of productivity and adaptation to various environmental stressors. Samples from American Brangus were used to evaluate the indicine/taurine composition through nine generations (~45 years) after the hybridization process was completed. The purpose was to determine how hybridization alters allelic combinations of a breed over time when genetic factors such as selection and drift are operating. Furthermore, we explored genomic regions with deviations from the expected composition from the progenitor breeds and related these regions to traits under selection. The Brangus composition deviated from the theoretical expectation, defined by the breed association, of 62.5% taurine, showing taurine composition to be $70.4 \pm 0.6\%$. Taurine and indicine proportion were not consistent across chromosomes. Furthermore, these non-uniform areas were found to be associated with traits that were probably under selection such as intermuscular fat and average daily gain. Interestingly, the sex chromosomes were predominantly taurine, which could be due to the composite being formed particularly in the final cross that resulted in progeny designated as purebred Brangus. This work demonstrated the process of new breed formation on a genomic level. It suggests that factors like genetic drift, selection and complementarity shift the genetic architecture into a uniquely different population. These findings are important to better understand how hybridization and crossbreeding systems shape the genetic architecture of composite populations.

Keywords *Bos indicus*, *Bos taurus*, generations, haplotypes, hybridization

Introduction

Domesticated cattle consist of two subspecies, *Bos taurus indicus* (indicine or zebu) and *Bos taurus taurus* (taurine), derived from independent domestication events of the same progenitor species, the aurochs (*Bos taurus primigenius*) (McTavish *et al.* 2013). Composite beef breed development using subspecies hybridization that combines environmental adaptability and desirable performance for meat production has resulted in the successful formation of several breeds, like Brangus (Gregory & Cundiff 1980). However, after formation and subsequent *inter-se* mating over time, it is unclear if progenitor breed composition is stable in the composite breed. Knowing such information may be useful in determining future uses and management of the composite breed, especially under conditions of climate variability.

Depending on its use, hybridization can solve or create problems in conservation biology (vonHoldt *et al.* 2018; Harrisson et al. 2016). For example, hybridization can be

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used for genetic rescue to increase the fitness of a small and inbred population (Bay *et al.* 2014). However, hybridization can also cause genetic erosion and outbreeding depression, when hybrid individuals have reduced fitness, owing to masking of adaptive genetic variants or noncompatible genetic backgrounds, as well as the loss of locally adapted alleles through swamping (Frankham 2015; Harrison & Larson 2014).

Significant numbers of livestock breeds have effective population sizes below 50, thereby compromising selection and/or long-term viability (Kristensen *et al.* 2015). Nowadays, intensive reproductive technologies and genomic selection strategies can speed up the loss of genetic variation (Goddard *et al.* 2010; Taberlet *et al.* 2011). Therefore, hybridization can be used to increase effective population size and genetic variance, and reduce inbreeding in small populations (Kristensen *et al.* 2015; FAO 2013).

Specific genomic regions of the hybrid may represent a specific founder subspecies composition that differs from the expected composition computed from pedigree analysis (McTavish & Hillis 2014), which is based upon Mendelian sampling (Gobena *et al.* 2018). Differential introgression refers to alleles at some loci that increase in frequency more than others in the newly hybridized population, and may confer adaptive advantage (Harrison & Larson 2014). For example, Goszczynski et al. (2017) demonstrated the increase in indicine haplotypes in the bovine leucocyte antigen region of Brangus cattle raised in Argentina, potentially owing to selection for adaptation to the environment.

The International Brangus Breeders Association (IBBA) started the Brangus registry in 1949 with a goal of making the hybrid 62.5% Angus (*B. taurus taurus*) and 37.5% Brahman (*B. taurus indicus*), retaining heterosis and maintaining a steady combination of the progenitor genotypes (Koger 1980). IBBA has maintained the original 1949 definition in their registration process. The current study sampled foundational and subsequent generations of US Brangus cattle to understand the dynamics of the hybridization process and breed formation within the IBBA definition of the breed.

Material and methods

Animals

Genotypic data (777 962 SNP, BovineHD Beadchip, Illumina, San Diego, CA, USA) from 68 Brahman, 95 Angus and 59 Brangus prominent sires born from 1970 to 2010 were evaluated. Thirty-six Brahman and 20 Brangus samples were acquired from the National Animal Germplasm Program's (NAGP-ARS-USDA) gene bank, Fort Collins, CO, USA. The other samples were genotyped by USMARC Research Center (ARS-USDA), Clay Center, NE, USA.

The Brangus pedigree, provided by the IBBA, consisted of 1 152 050 individual animal records from which the genetic relationship coefficients were computed. The coefficient of genetic relationship was used in clustering the current Brangus population into 17 clusters (Fig. S1). The Brangus animals sampled for genotyping represented all clusters. These sampled Brangus bulls were born in 12 states in the southern USA from 1970 to 2010 and these bulls had 43 393 progeny recorded by IBBA.

Pedigree evaluation and inbreeding calculations

The IBBA pedigree file was evaluated using the optiSel package (Wellmann 2017) in R 3.4.2 software (R Core Team 2017). The Angus, Brahman and crossbred animals (with pedigree breed composition other than the 5/8 Angus, 3/8 Brangus) were considered as ancestors, totaling 75 449 ancestors in the whole pedigree file of the Brangus breed. The number of equivalent generations of each Brangus animal was calculated by the equation: $g = \sum \left(1/2\right)^n$, where g is the generation number and n is the number of generations separating the individual from each known ancestor, equivalent to the equation described by Welsh *et al.* (2010).

Expected progeny differences (EPD) and respective accuracies of Brangus bulls were downloaded from the IBBA website (https://gobrangus.com/) in March 2018. The accuracy of all EPD was 0.68 ± 0.206 (mean $\pm$ standard deviation). Pearson correlation analyses among birth year, generations, pedigree inbreeding, EPD and accuracies were performed.

Filtering and quality control of genomic data

Markers with call rate lower than 95% or not physically mapped to the bovine genome assembly Btau5.0.1 were removed from the analyses. The remaining genotypes were 698 282 SNP markers on the autosomes and 38 581 SNP on the sex chromosomes (37 538 in X and 1043 in Y). Markers with MAF lower than 1% were removed. One animal with a call rate lower than 90% was removed.

For PCA and model-based clustering (ADMIXTURE), a LD pruned dataset with 158 264 autosomal SNPs was used. The expectation-maximization algorithm (EM method) was used to perform LD pruning with a moving window of 50 SNP with increments of five SNP and $r^2 = 0.5$ as the LD threshold.

PCA

The PCA analyses were conducted in SNP AND VARIATION SUITE® version 8.7 (Golden Helix Inc., Bozeman, MT, USA; www.goldenhelix.com) to verify the genetic distance between Angus, Brahman and Brangus cattle. In addition, we evaluated the relationship of Brangus animals stratified by generations. These analyses were performed using all filtered SNPs in the autosomes and by each chromosome,

including the X and Y (without pseudo-autosomal region) chromosomes.

The PCA analyses were performed with up to 10 components using an additive genetic model with normalization based on theoretical sigma at HWE. The PCA components were recomputed up to five times after removing outliers (more than 6 standard deviations from the mean).

Simulation model

We performed a population genetics simulation using an online tool (http://popgensimulator.pitt.edu/graphs/allele). The initial parameters were set to an initial allele frequency of 62.5% (representing the Angus allele in the first generation of Brangus); 10 generations; effective population size of 100; and no selection, mutation, migration and inbreeding (similar to a neutral model). We performed 50 simulations for each generation. The raw data were used to calculate the summary statistics (mean and standard deviation) and to determine the expected lower and upper values (within 99% of the Gaussian distribution) of the expected founder composition for each locus. These lower and upper values were applied as thresholds in the visualization of chromosome painting results to identify regions with significant enrichment of alleles coming from one of the founders. Moreover, one simulated random value from the same generation was chosen for each animal in the Brangus dataset. These values were used thereafter for the statistical comparison with the ADMIXTURE results for K equal to 2.

Model-based clustering

Clustering analyses of all autosomes, and each chromosome separately, were performed using maximum likelihood estimates of the underlying admixture coefficients and ancestral allele frequencies (ADMIXTURE version 1.3.0; Alexander *et al.* 2009). First, all autosome markers were tested with varying K from 2 to 10. The X and Y chromosomes (36 607 and 95 SNPs respectively) were evaluated similarly using the haploid function (as all data came from bulls). Individual coefficients of K cluster membership were visualized using CLUMPAK with the feature DISTRUCT for many Ks (Kopelman *et al.* 2015). Subsequently, we repeated these analyses for each chromosome using K equal to 2 and 3. The objective of these analyses was to ascertain the breed composition of each chromosome to the founder breeds ($K = 2$; Angus and Brahman) and to observe the formation of the new cluster for Brangus ($K = 3$). Three different t-test analyses, using the ggpubr package in R version 3.4.2 (R Core Team 2017; Kassambara 2017), were performed to evaluate the following: (1) Angus proportion in all autosomes and each chromosome to the theoretical composition in Brangus (based on the simulation model); (2) the composition of Angus proportion to each chromosome of the whole genome; and (3) using the K equal to 3 cluster assignment, the proportion of each cluster by chromosome compared with the proportion of the cluster in the whole genome.

Pearson correlations were estimated between the Angus proportion in the whole genome and each chromosome, as well as the generation, pedigree inbreeding and EPD. Linear regression analyses of ADMIXTURE proportional assignments on Brangus generations (whole genome and by each chromosome) were also performed. In addition, linear regression analyses of the cluster's proportions with EPD were conducted. For correlation analyses, we used the Hmisc package (Harrell Jr. et al. 2018) and, for linear regression analyses, we used the *lm* function in R version 3.4.2 software (R Core Team 2017).

Chromosome painting

We used the copying model implemented in CHROMOPAINTER (Lawson et al. 2012) to estimate the ancestry of regions across each chromosome. This copying model related the patterns of LD across chromosomes to the underlying recombination process. The method used a hidden Markov model to reconstruct a sampled haplotype.

We used the founder breeds, Angus and Brahman, as haplotype donors to the Brangus haplotypes. The CHROMOPAINTER analyses were performed twice (allowing or not allowing self-copying) using the linked model. The recombination files were created using the Perl scripts provided on the CHROMOPAINTER website (http://www.paintmychromosomes.com/). BEAGLE3.3 (Browning & Browning 2007) was used to phase the genotypes (using 20 iterations).

Identification of genes and QTL in candidate regions

Genes in the regions of founder deviation were identified in Golden Helix GenomeBrowse® visualization tool version 2.1 (Golden Helix Inc., Bozeman, MT, USA; www.goldenhelix.com). The genes were identified based on the NCBI *Bos taurus* Annotation Release 105 and Btau5.0.1 genome assembly. Thereafter, a search in the literature and in the AnimalQTL database (https://www.animalgenome.org/cgi-bin/QTLdb/index) was executed to identify traits related to genes located in each significant genomic region.

Results

Using IBBA pedigree records, we calculated the mean number of generations for each animal from the first purebred Brangus in the pedigree (Fig. 1). The average number of generations (±standard deviation) was 6.8 ± 1.85 with a maximum of 9.52 (Fig. S2). The generation interval in beef cattle is generally close to 5 years (Jonas & de Koning 2015);

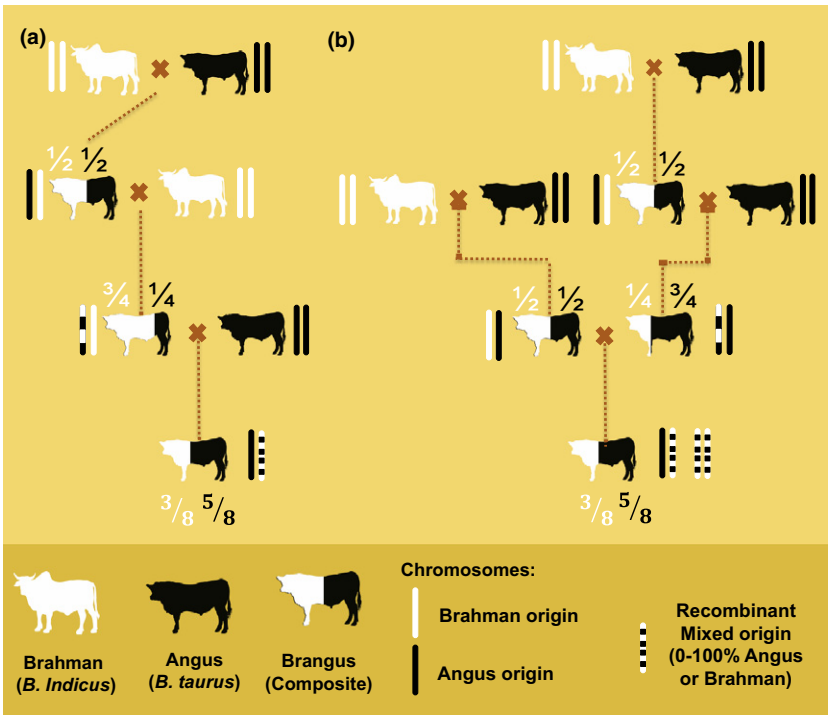

Figure 1 Illustration of two (a and b) cross-breeding schemes to establish the Brangus breed, a composite (hybrid) cattle breed of 5/8 Angus and 3/8 Brahman. The bars at the side of each animal represent possible chromosome pairs.

therefore, our samples trace back close to the beginning of Brangus registration (Fig. 1).

Genetic structure

PCA from 158 264 SNPs revealed substantial divergence between Angus and Brahman whereas Brangus was intermediate for the first principal component (Fig. 2) (Bovine HapMap Consortium et al. 2009; Decker *et al.* ; Gobena *et al.* 2018). The second principal component represented variation within breeds. Brangus cattle with a generation assignment of less than 3 were positioned between Angus and Brahman whereas advanced generations of Brangus (>5) diverged in the second principal component when evaluating all autosome markers, suggesting that Brangus, as a breed, was becoming a distinct cluster (Blackburn et al. 2014).

On a chromosome-by-chromosome basis, principal component analyses suggested that Brangus were closer to Angus, except for chromosomes 5, 16, 25 and 29, which were uniformly distributed between the two progenitor breeds (Fig. 2). PCA based on sex chromosomes also showed Brangus placed closely to Angus (Fig. 2). Among Brahman there were two separate groups for both the X and Y chromosomes; the same pattern was found in some Brangus animals.

ADMIXTURE analysis was performed with K ranging from 2 to 10. The lowest CV error was when K equaled 3 (Fig. S3) suggesting that Brangus cattle have become a unique breed. Using K equal to 2 among all chromosomes, Brangus were shown to be $70.4 \pm 0.6\%$ (mean $\pm$ standard error of the mean) Angus, and statistically different from the theoretical expectation of 62.5% Angus based upon breed definition and simulated data ($62.1 \pm 1.3\%$; Fig. 3). Autosomal chromosomes 5 and 15 showed the lowest and highest Angus proportions, 56.3 ± 2.2 and $84.7 \pm 1.6\%$ respectively. Both sex chromosomes (Fig. S4) had a high percentage of Angus ($X = 86.6 \pm 2.1\%$ and $Y = 90.3 \pm 3.7\%$).

The proportional cluster assignments for Brangus, Angus and Brahman were regressed on Brangus generation number and found to be significant for all clusters (Fig. 4). After the fifth generation, for Brangus more than 50% of the cluster assignment was in the newly formed 'Brangus' cluster.

In order to investigate if the cluster assignment had a relationship with traits used in typical Brangus breeding programs, we performed a regression analysis between EPD data and proportion of assigned clusters. Chromosome 3, which had a high Angus assignment, had a positive linear regression coefficient with backfat thickness (FAT) and rib eye area (REA) (Fig. S5), whereas Angus assignment of chromosome X had a positive linear regression with scrotal circumference EPD ($\beta = 0.094$, $R^2_{adj} = 0.08$).

Chromosome painting

The chromosomes with a high Angus or Brahman proportion in the clustering analyses were evaluated with chromosome painting to identify the breed composition throughout the chromosomes (Figs 5 and S6–S8). When allowing the 'self-copying' model in chromosome painting (which allows identification of haplotypes derived from

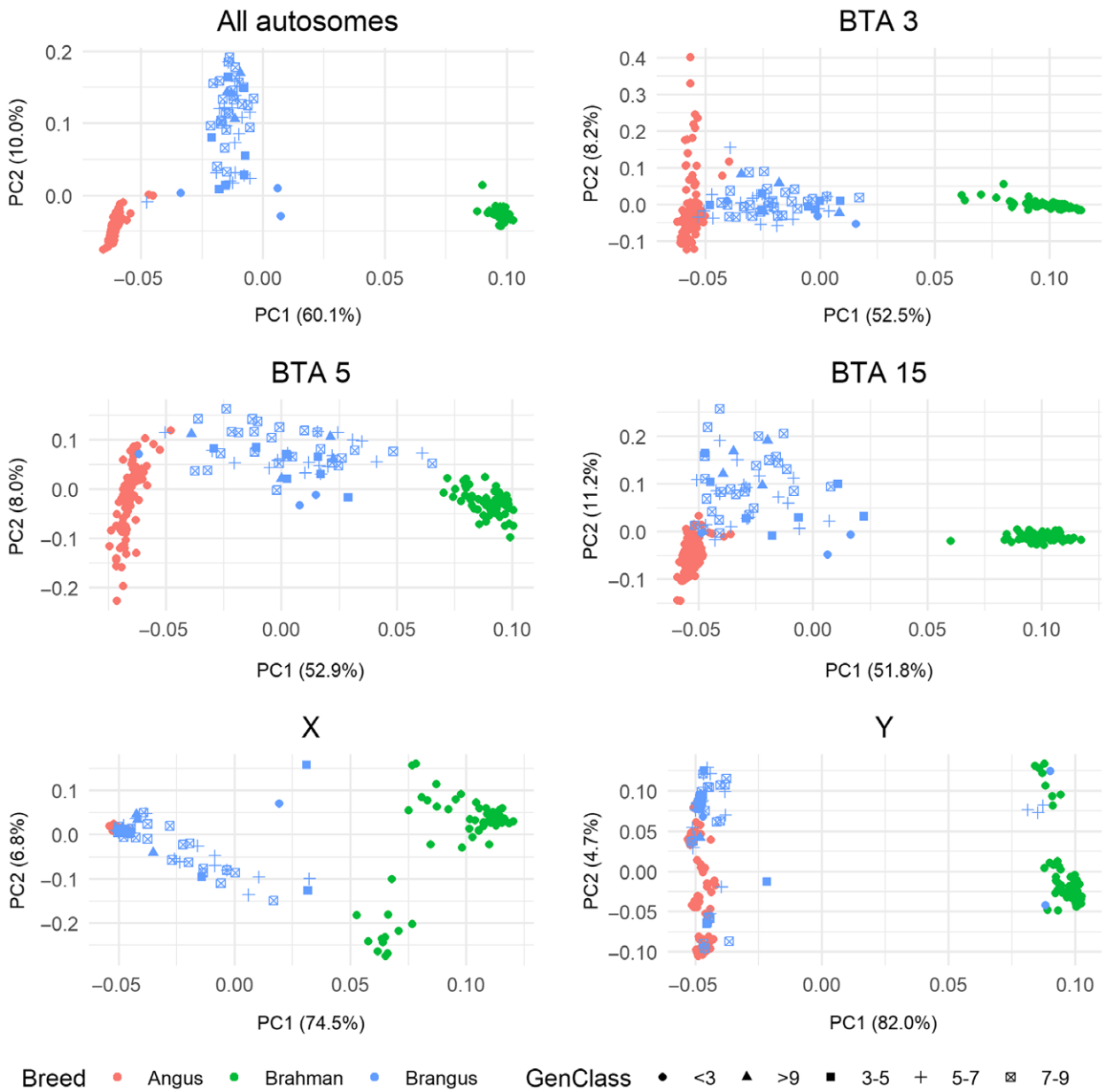

Figure 2 PCA plots for Brangus, Angus and Brahman cattle using genotypes from all autosomes and *Bos taurus* autosomes (BTA) 3, 5 and 15, and sex chromosomes (X and Y). The classes of equivalent complete generations (GenClass) of Brangus pedigrees are shown as different shapes. The number in parentheses on each axis represents the proportion of variance explained by each principal component.

within a breed), the chromosomes with more Brahman composition in the clustering analyses showed some Brahman haplotypes maintained across generations and also higher haplotype diversity (Fig. S9). However, chromosomes with larger Angus composition showed a low number and size of Brahman haplotypes and longer haplotypes of the other ancestors (Fig. S10).

In general, the number of genomic segment copies from the donor populations (allowing 'self-copying' or not) decreased at approximately the same rate across generations for the two founder breeds whereas the length of Brangus DNA segments increased across generations (Fig. S11). The chromosome painting also revealed new haplotypes evolving during new breed formation, reducing the number of segments copied from the founder breeds and increasing the length of segments copied from the new breed itself. Moreover, we identified founder breed contributions for selected regions.

Discussion

Simulations have demonstrated that gene flow between subspecies is essential for maintenance of some species (Bay *et al.* 2014). The growth of composite breeds like Brangus in

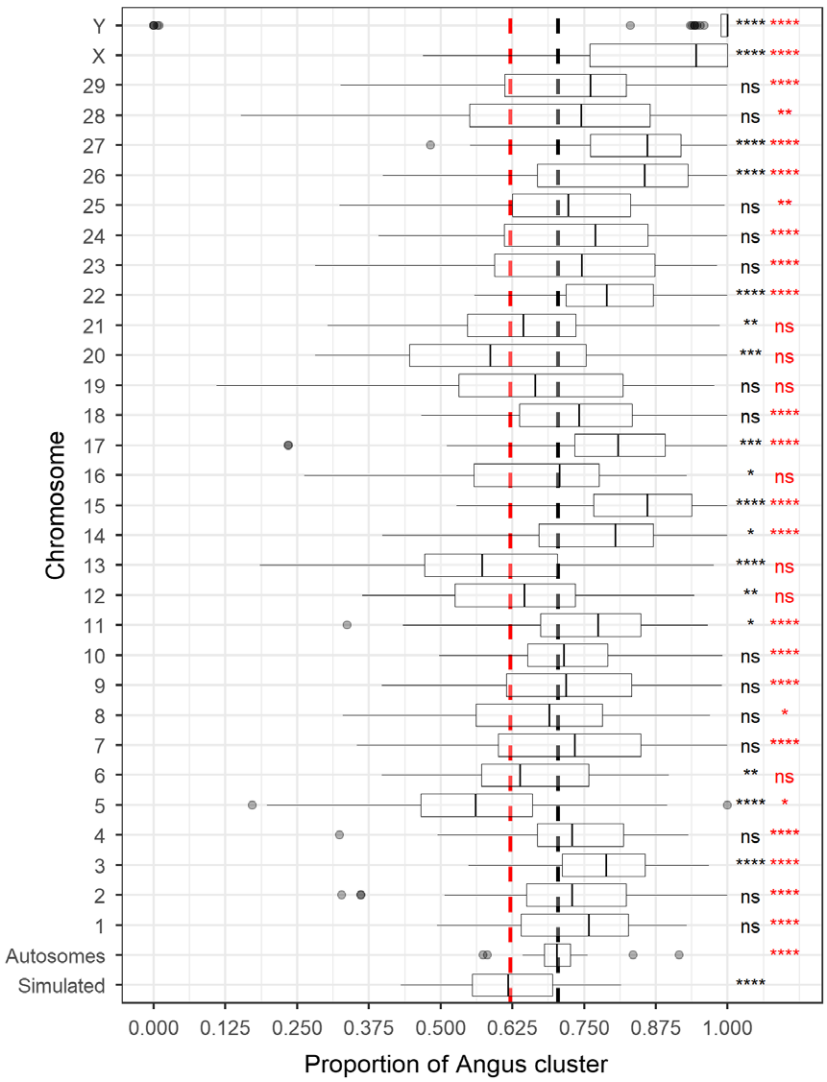

Figure 3 Box plot of distribution of Angus cluster assignment in Brangus cattle from the ADMIXTURE results using genotypes from all autosomes and each chromosome (1–29, X and Y). 'Simulated' represents the distribution of the proportions estimated by the simulated data based on a null model. The dashed line in red represents the mean Angus proportion based on simulated data (62.1%), and the dashed line in black is the average Angus composition using all autosomes (70.38%). On the right are the *t*-tests for each chromosome (black indicates comparison with the proportion observed in all autosomes and red indicates comparison with the expected Angus proportion from simulated data). n.s., Not significant. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

the Gulf Coast Region of the USA demonstrated that livestock breeders have taken advantage of the hybridization process (Thomas et al. 2002; Shirley et al. 2006; Peters et al. 2012). The long-term ramifications of this process have not been explored over generations at the genomic level before now.

The results of the current study provide a view into how genomic architecture changes with hybridization and subsequent *inter se* mating during the formation of a composite breed (Fig. 4). The disproportionate representation of progenitor breeds and the mating design used to develop the breed have important ramifications on the overall genetic architecture reported.

After initial breed formation, assignment to the Brangus cluster increased at 11.5% per generation, and by the sixth and seventh generations, some animals attained 100% assignment to the Brangus cluster. The UN Food and Agriculture Organization (FAO) Guidelines for *in vivo* conservation of animal genetic resources (FAO 2013) stated that three generations of *inter se* mating are required to establish a new composite breed. Here, we observed that a minimal of five generations are required for forming a new genomic profile in a two-breed composite. The emergence of the new genomic cluster across generations of *inter se* mating and the uneven distribution of the founder contributions on chromosomes and specific genomic regions showed the consequences of the genetic events (as drift, selection and complementarity) shaping the genetic architecture of the hybrids.

Brangus cattle in this study exhibited a higher proportion of Angus when compared with the theoretical expectation (70.4 vs 62.5%) and previous studies (Goszczynski et al. 2017; Gobena *et al.* 2018). However, the previous studies used experimental herds in Florida and Argentina. In addition, other differences between the current and previous studies included the facts that this study's bulls were widely

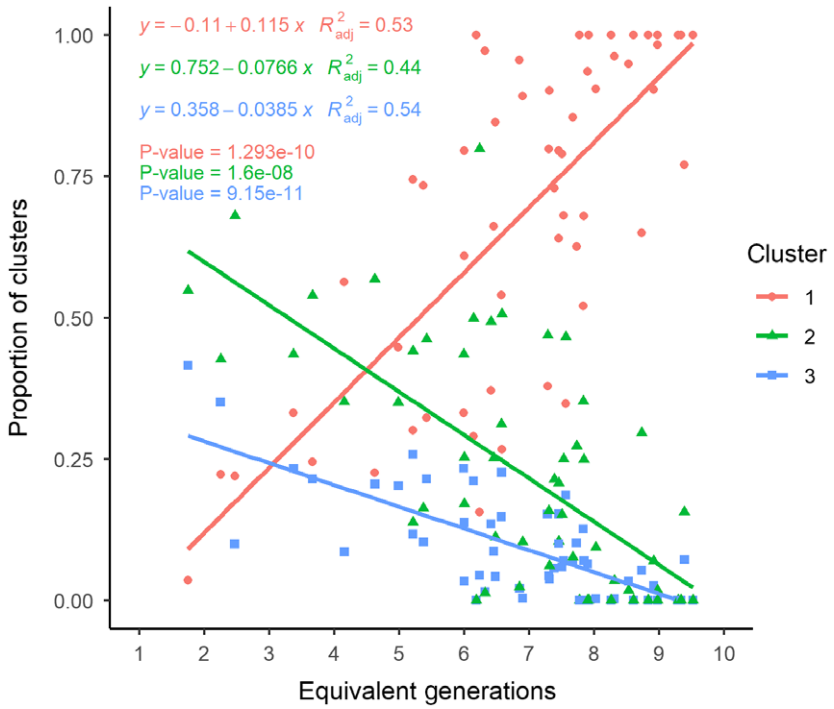

Figure 4 Linear regression analyses between ADMIXTURE clusters assignments and number of equivalent generations from pedigree data in Brangus. Cluster 1 represents Brangus, cluster 2 represents Angus and cluster 3 represents Brahman.

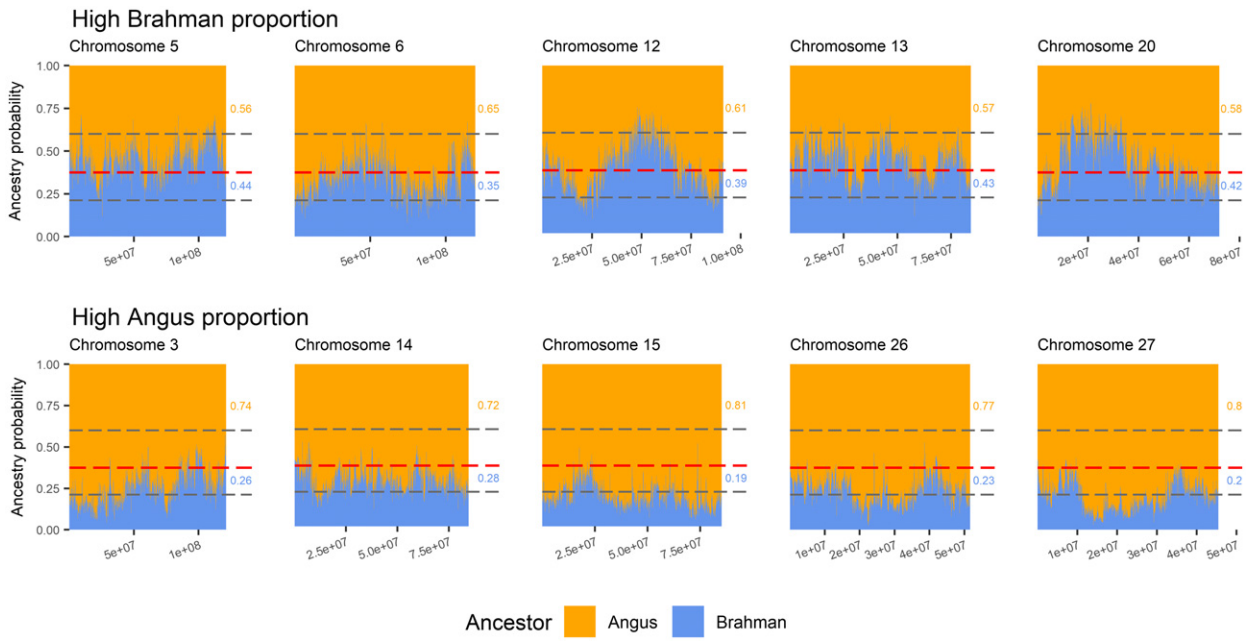

Figure 5 Average ancestry probability (from chromosome painting results) of the chromosomes identified as containing high Brahman proportion (top) and high Angus proportion (bottom) compared with the results from all autosomes (choosing the five with the highest *P*-values). For each chromosome, the number on the right-hand side displays the mean ancestry for each ancestor over all of the chromosome. The horizontal dashed line in red represents the expected Brahman ancestry (0.375). The horizontal dashed line in gray represents the expected maximum (top 1%) and minimum (bottom 1%) thresholds for Brahman ancestry according to simulated data.

used by industry (over 44 000 progeny) vs. relatively small experimental populations and that the bulls from this study came from breeders in 12 states of varying environments.

Breed proportion of an individual estimated by averaging the breed proportion of its parents can be inaccurate, especially when estimates cross many generations (Basarab

et al. 2018). There is no definitive explanation for the increased proportion of Angus, but there are several plausible theories. There is a variation in the proportion of actual genotype passed from one generation to the next owing to Mendelian sampling, genetic recombination rate and LD (Basarab et al. 2018). Therefore, artificial selection for traits more prevalent in Angus (e.g. carcass, growth, feed efficiency) can favor some alleles which can sweep more 'Angus' haplotypes to further generations. An explanation could be that, as Brangus cattle have a higher proportion of Angus and share long haplotypes as observed here, during each recombination event there is a higher probability in Mendelian sampling that alleles derived from Angus will be selected. In this manner the population moves away from the theoretical expectation; in essence genetic drift is an important driver. Despite the cause, Brangus breeders should be aware of this shift as over time the complementarity of Brahman and Angus could become diminished.

The results presented in this study also provide insight for conserving livestock breeds, an internationally recognized issue of concern (Pertoldi et al. 2014; FAO 2013; Welsh *et al.* 2010). These results suggest that endangered breeds can be hybridized in an effort to maintain viable populations capable of improving productivity.

Founder composition across the genome of the new composite

The magnitude of chromosome-by-chromosome variability (Fig. 3) for progenitor breed composition provides new insights into the formation of composite breeds. Furthermore, as Fig. 5 illustrates on a within-chromosome basis, the proportion contributed by the progenitor breeds varies substantially. Evaluation of haplotypes for chromosomes 15 and 5 that were predominantly Angus (Fig. S10) or Brahman (Fig. S9) respectively suggests that relatively large segments of chromosomes associated with the progenitor breeds persist in advanced generations of Brangus. Haplotypes from Brahman look long on chromosome 12 (Fig. S7) and 20 (Fig. S8), for example, whereas on most chromosomes Angus haplotypes are more prevalent. These differences may reflect an array of genetic functionalities that both progenitor breeds are contributing to the Brangus. In addition, these results suggest how complementarity can persist in a composite after heterosis has diminished with advancing generations (Goszczynski et al. 2017).

In general, among chromosomes exhibiting a high Angus proportion in ADMIXTURE, the Angus origin was uniformly distributed across chromosomes based on chromosome painting results. This suggests that multiple favorable alleles were spread across the chromosome and/or that there is selection pressure with strong hitchhiking effects (Jacobs *et al.* 2016; McTavish & Hillis 2014).

Among chromosomes with greater Brahman contribution, the breed proportions were not uniformly distributed, which is potentially a function of the original mating design, the lower initial Brahman composition and/or potentially selection advantage or lack thereof (Fig. 5). Chromosomes 5, 6 and 13 contained a mixed origin of the haplotypes consistently throughout the chromosome. Some regions on chromosome 12 (40–60 Mb) and 20 (10–20 Mb) showed more Brahman origin (≥60%), confirming these can be considered as indicine enriched regions (Goszczynski et al. 2017). The existence of such haplotypes may be related to the exploitation of complementarity with selection of the favorable alleles of each subspecies.

Two pleiotropic QTL identified in Brangus were located on *B. taurus* autosomes (BTA) 12 at 88 Mb (weaning and yearling weight, and rib eye area) and BTA 20 at 7–8 Mb (birth, yearling and mature weight) (Weng et al. 2016). These two regions had a high Angus assignment as observed in chromosome painting (Fig. 5), whereas in general the two chromosomes had a high Brahman assignment. These examples suggest that selection and complementarity are working on favorable alleles for the traits of interest in various regions of the genome and persist as the new breed continues to develop its own signature.

Sex chromosomes

The manner in which the parents of the first Brangus generation were mated impacted the breed composition of the X and Y chromosomes. Under mating plan A (Fig. 1), sires at the last crossbreeding were most likely to have been purebred Angus. There is a well-known effect of a higher birth weight and dystocia rate when mating a Brahman sire to a taurine female (Dillon *et al.* 2015), which contributed to the Angus sire preference. In mating plan B there would have been potential opportunities for Brahman Y chromosomes be maintained through breed development.

Despite aspects of mating design, there were elements of sex chromosome structure worthy of further discussion in relation to composite breed development. Chromosome X harbors several QTL associated with calving ease, age at puberty and scrotal circumference (Cole et al. 2011; Fortes *et al.* 2013). Therefore, favorable alleles originating from Angus may have been selected in Brangus, probably during the early crossbreeding phase because we did not observe a relationship between the Angus proportion in this chromosome over generations. The commercial practice of culling animals that had not bred by a specific age and did not show pregnancy at weaning during the crossbreeding scheme may have favored the Angus X chromosome. From a practical perspective, it is well documented that Angus reach puberty before Brahman (Lopez et al. 2006; Fortes et al. 2010; Cánovas et al. 2014), and calve at 2 years of age, which is a highly desired trait for US beef production systems (Cammack *et al.* 2009; Peters et al. 2013).

Therefore, this may lead to differential sex selection (Mank 2012). According to this hypothesis, the selected males in the new population would carry a Y chromosome from Angus and the selected females would have a higher proportion of Angus on the X chromosome.

Conservation of genetic diversity in sex chromosomes can be challenging (Yue *et al.* 2015). In this case, we observed that the crossbreeding scheme favored the sex chromosomes from one founder breed; however, two sources of Y diversity for alleles from indicine origin were observed. Important genetic variation from the other founder can be quickly lost because of the lack of recombination and more efficient selection for X- and Y-linked loci in males (hemizygous). American Holsteins, for example, have minimal genetic diversity on the Y chromosome (only two independent Y chromosomes have survived in the population) owing to strong use of artificial insemination in the last 40 years, which can compromise male reproduction and other important traits for the future of the breed (Yue *et al.* 2015).

In summary, hybridization can be an effective genetic management practice by controlling inbreeding levels, combining unique attributes from the progenitor populations and promoting hybrid vigor (Kristensen *et al.* 2015). With increased variability among the hybrid progeny, it is possible to develop populations capable of more quickly adapting to climate variability (Becker et al. 2013). As presented herein, the adaptive alleles (with selective advantage) from the founder breeds tend to remain present in the composite population. Thus, the selection program applied in the composite population should be carefully designed to avoid the loss of important alleles, such as those related to environmental adaptability.

Conclusions

Brangus had a higher proportion of Angus than expected. Brangus breeders should be aware of this situation if they want to maintain the Brahman component of the breed. Plausible explanations for the shift in founder breed composition including the manner in which the composite was developed, genetic drift and/or selection for traits for which Angus excel. We identified portions of various chromosomes where QTL were related to traits strongly associated with Angus, suggesting that a portion of the shift towards Angus has been due to artificial selection and facilitated by the crossbreeding scheme used to form the hybrid. Importantly, the results suggest these issues should be considered if complementarity is an important component to maintain in a new breed.

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Conflict of interest

No conflict to declare.

Data availability

All genotypic data used in this study are available from the website of The Animal Genetic Resources Information Network (Animal-GRIN) (https://nrrc.ars.usda.gov/A-GRIN).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig S1. Cluster of Brangus population based on pedigree using Ward method. Red line represents the point with the minimal variance within the clusters.

Fig S2. Density distribution of number of equivalent generations of Brangus bulls used. Dashed line represents the average.

Fig S3. Plot of ADMIXTURE results using markers in all autosomes (each bar represents one animal), evaluating *K* from 2 to 5.

Fig S4. Plot of ADMIXTURE results using markers on sex chromosomes, X at the top and Y at the bottom (each bar represents one animal), evaluating *K* from 2 to 5 on the left.

Fig S5. Linear regression analyses between ADMIXTURE clusters assignments in each chromosome and EPDs in Brangus.

Fig S6. Plot of haplotypes (each row is one haplotype) according to the ancestor (founder breed) of each position on chromosome 5.

Fig S7. Plot of haplotypes (each row is one haplotype) according to the ancestor (founder breed) of each position on chromosome 12. Similar to Fig. S5.

Fig S8. Plot of haplotypes (each row is one haplotype) according to the ancestor (founder breed) of each position on chromosome 20. Similar to Fig. S5.

Fig S9. Plot of haplotypes (each row is one haplotype) according to the ancestor (founder breed) of each position on chromosome 5.

Fig S10. Plot of haplotypes (each row is one haplotype) according to the ancestor (founder breed) of each position in chromosome 15. Similar to Fig. S8.

Fig S11. Linear regression analyses between number of equivalent generations and expected number of segments copied from each donor population (founder breed) on the left and expected total genetic length of DNA copied from each donor population on the right for chromosome 15.