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Effect of breed composition in genomic prediction using crossbred pig reference population

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Abstract

In contrast to conventional genomic prediction, which typically targets a single breed and circumvents the necessity for population structure adjustments, multi-breed genomic prediction necessitates accounting for population structure to mitigate potential bias. The presence of this structure in multi-breed datasets can influence prediction accuracy, rendering proper modeling crucial for achieving unbiased results. This study aimed to address the effect of population structure on multi-breed genomic prediction, particularly focusing on crossbred reference populations. The prediction accuracy of genomic models was assessed by incorporating genomic breed composition (GBC) or principal component analysis (PCA) into the genomic best linear unbiased prediction (GBLUP) model. The accuracy of five different genomic prediction models was evaluated using data from 354 Duroc × Korean native pig crossbreds, 1,105 Landrace × Korean native pig crossbreds, and 1,107 Landrace × Yorkshire × Duroc crossbreds. The models tested were GBLUP without population structure adjustment, GBLUP with PCA as a fixed effect, GBLUP with GBC as a fixed effect, GBLUP with PCA as a random effect, and GBLUP with GBC as a random effect. The highest prediction accuracies for backfat thickness (0.59) and carcass weight (0.50) were observed in Models 1, 4, and 5. In contrast, Models 2 and 3, which included population structure as a fixed effect, exhibited lower accuracies, with backfat thickness accuracies of 0.40 and 0.53 and carcass weight accuracies of 0.34 and 0.38, respectively. These findings suggest that in multi-breed genomic prediction, the most efficient and accurate approach is either to forgo adjusting for population structure or, if adjustments are necessary, to model it as a random effect. This study provides a robust framework for multi-breed genomic prediction, highlighting the critical role of appropriately accounting for population structure. Moreover, our findings have important implications for improving genomic selection efficiency, ultimately enhancing commercial production by optimizing prediction accuracy in crossbred populations.

Keywords: Genomic breed composition, Genomic prediction, Multi-breed genomic prediction, Population structure

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INTRODUCTION

Accurate prediction of genomic breeding values is a critical component of successful genomic selection, which requires a sufficiently large reference population to reliably estimate marker effects [1]. However, small populations, such as Jersey cattle, often pose challenges owing to the limited reference populations of progeny-tested bulls, leading to less reliable genomic breeding values [2]. Consequently, genetic progress is restricted in breeds without a large reference population. One approach to addressing this limitation is across-breed prediction, which involves the use of a large reference dataset from another breed [3]. Another approach is multi-breed prediction, which combines data from multiple breeds to create a larger, more comprehensive dataset [3]. Both approaches can enhance prediction accuracy for smaller breeds, helping them become more competitive while minimizing the additional costs associated with genotyping and phenotyping.

Empirical studies have demonstrated that the accuracy of across-breed genomic prediction is often near zero and that combining multiple breeds has not yielded significant improvements in accuracy [3,4]. However, these methods remain promising, particularly when combined with strategies that account for population structure and other sources of variation [5,6]. Addressing population structure, also referred to as population stratification, is critical for genomic prediction across different breeds. Population structure arises from differences in allele frequencies between subpopulations, which may result from geographic separation, or natural or artificial selection [7]. These differences can lead to spurious marker-trait associations [8,9], potentially inflating estimates of genomic heritability [10] and introducing bias into genomic prediction accuracy [6].

To mitigate the effects of population structure, it is important to model it appropriately within genomic prediction models, particularly when combining data from multiple breeds. A common method involves incorporating principal components (PCs) derived from genomic data as a fixed effect in the prediction model [7]. However, incorporating PCs as a fixed effect can result in over-correction, as these components are derived from the genomic relationship matrix used in genomic prediction [11]. To address this limitation, in this study, PCs were modeled as a random effect to capture population structure without confounding the genomic relationship matrix. The prediction accuracy of these models was compared with those of models in which PCs were excluded. Additionally, breed composition, another explanatory factor for population structure, was modeled as either a fixed or random effect to adjust for population structure.

In this study, we evaluated the accuracy of genomic predictions using models that incorporated breed composition and PCs as fixed and random effects and compared the results with those of a baseline model. This study aimed to determine whether accounting for population structure using breed composition or PCs can improve genomic prediction accuracy. The findings of this study may provide valuable insights into optimizing genomic prediction models for populations with complex or diverse structures.

MATERIALS AND METHODS

Animals, genotypes, and phenotypes

The genotype dataset comprised data from 354 Duroc × Korean native pigs (DK), 1,105 Landrace × Korean native pigs (LK), 1,017 Landrace × Yorkshire × Duroc (LYD) crossbreds, along with purebred animals. Crossbred individuals were genotyped using the Illumina PorcineSNP60 Genotyping BeadChip, whereas genotype data for purebred animals were provided by the Centre for Research in Agricultural Genomics [12]. Genotype data for the Korean native pigs (KNPs) among the purebreds were provided by the National Institute of Animal Science in Korea. Details

regarding the number of animals, single nucleotide polymorphisms (SNPs), and average observed heterozygosity rate for each breed are presented in Table 1. The quality control process involved the exclusion of SNPs located on sex chromosomes, with a genotype call rate below 90%, and with a minor allele frequency below 1%. After merging datasets and applying the quality control process, a common set of 24,118 SNPs were retained for analysis.

Phenotypic data revealed differences in backfat thickness and carcass weight among the breeds. The LYD breed exhibited the lowest backfat thickness, whereas the DK breed had the highest backfat thickness. Conversely, the DK breed exhibited the lowest carcass weight, whereas LYD had the highest carcass weight. The carcass performance of the breeds crossed with the KNP was lower than that of LYD. This finding aligns with the known characteristics of the KNP breed, which is known for its good meat quality but poor growth rate [13]. Statistical details for the phenotypes are provided in Table 2.

Principal component analysis

Principal component analysis (PCA) was employed to investigate genetic differences between populations and to correct for population structure. PCA simplifies data complexity while maintaining the underlying relationships among the data points. When applied to biallelic genotype data, PCA identifies the eigenvalues and eigenvectors of the covariance matrix of allele frequencies, thereby reducing the data to a limited number of dimensions known as PCs. Each PC represents a proportion of the total genomic variation. Subsequently, the data are mapped onto the space defined by these PC axes, facilitating the visualization of samples and their distances from each other in a scatter plot. In this visualization, sample overlap indicates shared genetic identity, reflecting common ancestry or origin [14].

Genomic breed composition

Genomic breed composition (GBC) was estimated from genomic data using a maximum likelihood model implemented in ADMIXTURE v1.3.0 [15]. ADMIXTURE uses genotype data to cluster individuals into subgroups based on a predetermined number of groups. The projection extension of

Table 1. Number of animals, SNPs, and average observed heterozygosity rate for each breed

Breed	Number of animals	Number of SNPs	Observed heterozygosity
Duroc × Korean native pig	354	61,565	0.32
Landrace × Korean native pig	1,105	62,163	0.34
Landrace × Yorkshire × Duroc	1,017	52,258	0.39
Duroc	20	46,259	0.27
Korean native pig	25	40,047	0.23
Landrace	20	46,259	0.32
Yorkshire	20	46,259	0.31

SNPs, single nucleotide polymorphisms.

Table 2. Number of animals with record (N), mean, and standard deviation (SD) for backfat thickness and carcass weight

Breed	Backfat thickness (mm)			Carcass weight (kg)		
	N	Mean	SD	N	Mean	SD
Duroc × Korean native pig	295	24.21	5.86	295	69.67	11.62
Landrace × Korean native pig	1,014	22.93	6.9	1,081	79.17	12.48
Landrace × Yorkshire × Duroc	1,017	22.16	5.07	1,017	88.23	5.94

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the ADMIXTURE program allows for estimating ancestry using predefined ancestral population allele frequencies. This extension enables efficient ancestry inference across large genomic datasets, leveraging allele frequencies from reference panels, such as the 1000 Genomes Project. Additionally, the projection approach is particularly advantageous for datasets with significant population distribution imbalances, as such imbalances can adversely affect the accuracy of ancestry inference [16].

The projection extension of the ADMIXTURE program was used to analyze the dataset owing to the imbalance between purebred and crossbred samples. Ancestral population allele frequencies were estimated using the purebred samples, whereas the GBC values of the crossbreds were estimated using the allele frequencies of the purebreds.

Statistical models

First, PCs and GBCs were calculated for each individual, which were subsequently used in five models to predict genomic estimated breeding values (GEBV). Although additional fixed effects such as age and farm were considered, age information was unavailable, and farm data showed high multicollinearity with the PC and GBC values, which precluded their inclusion.

Model 1 (NULL) is defined as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e},$$

where **y** represents the vector of trait records (backfat thickness or carcass weight); **b** indicates the vector of fixed effects, including sex; **X** denotes the design matrix linking fixed effects to the records; **g** represents the vector of random genetic effects, modeled as $\sim N\left(0, \mathrm{G}\sigma_g^2\right)$, with **G** being the genomic relationship matrix and σ_g^2 being the genetic variance captured by the SNPs; **Z** indicates the design matrix linking records to animals; and **e** denotes the vector of random deviations, modeled as $\sim N\left(0, \mathrm{I}\sigma_e^2\right)$, with **I** as an animal-by-animal identity matrix and σ_e^2 representing the error variance. The GEBV for this model was predicted as **GEBV** = $\hat{\mathbf{g}}$. The genomic relationship matrix was constructed using GCTA v1.94.1 software according to the following equation [17]:

$$\mathrm{G}_{jk} = \frac{1}{N}\sum_{i=1}^{N}\frac{\left(x_{ij} - 2p_i\right)\left(x_{ik} - 2p_i\right)}{2p_i\left(1 - p_i\right)}$$

where x_{ij} and x_{ik} represent the genotypes (coded as 0, 1, or 2) of individuals j and k at SNP i. p_i indicates the allele frequency of SNP i, and N denotes the total number of SNPs. The distribution of the diagonal and off-diagonal elements of the genomic relationship matrix is shown in Fig. 1. The mean of the diagonal elements is 1.03, indicating low inbreeding within the population. The mean of the off-diagonal elements is 0, showing that individuals are genetically independent of each other.

Model 2 (PC_F) is defined as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e},$$

where **y** represents the vector of trait records; **b** denotes the vector of fixed effects, which includes PC values (20 PCs) and sex; **X** indicates the design matrix linking fixed effects to records; **g** represents the vector of random genetic effects; **Z** denotes the design matrix linking records to animals; and **e** indicates the vector of random deviations. For this model, **GEBV** = $\hat{\mathbf{g}}$.

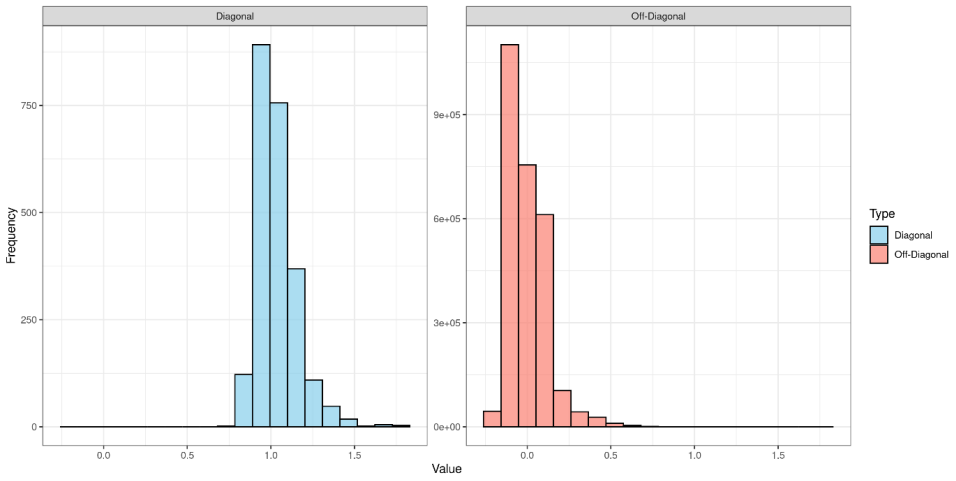

Fig. 1. Distribution of diagonal and off-diagonal elements of the genomic relationship matrix.

Model 3 (GBC_F) is defined as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e},$$

where **y** represents the vector of trait records; **b** denotes the vector of fixed effects, which includes GBC values and sex (here, breed composition values represent the proportion of each individual's genome derived from the four breeds: Duroc, KNP, Landrace, and Yorkshire); **X** indicates the design matrix linking fixed effects to records; **g** represents the vector of random genetic effects; **Z** denotes the design matrix linking records to animals; and **e** indicates the vector of random deviations. For this model, **GEBV** = $\hat{\mathbf{g}}$.

Model 4 (PC_R) is defined as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{Zpc} + \mathbf{e},$$

where **y** indicates the vector of trait records; **b** represents the vector of fixed effects, including sex; **X** denotes the design matrix linking fixed effects to records; **g** indicates the vector of random genetic effects; **pc** denotes the vector of random variables representing groups of PC values, which were clustered using the Gaussian Mixture Model implemented in the 'mclust' R package [18]; **Z** indicates the design matrix linking records to animals; and **e** denotes the vector of random deviations. For this model, $\text{GEBV} = \hat{\mathbf{g}} + \widehat{\mathbf{pc}}$.

Model 5 (GBC_R) is defined as follows:

$$\mathbf{y} = \mathbf{Xf} + \mathbf{Zg} + \mathbf{Zgbc} + \mathbf{e},$$

where **y** represents the vector of trait records; **b** denotes the vector of fixed effects, including sex; **X** indicates the design matrix linking fixed effects to records; **g** represents the vector of random genetic effects; **gbc** denotes the vector of random variables representing groups of GBC values, which were clustered using the Gaussian Mixture Model implemented in the 'mclust' R package [18]; **Z** indicates the design matrix linking records to animals; and **e** represents the vector of random deviations. For this model, $\text{GEBV} = \hat{\mathbf{g}} + \widehat{\mathbf{gbc}}$.

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Variance components were estimated using the restricted maximum likelihood (REML) method, as implemented in MTG2 [19], for each model. Heritability for the traits was estimated using the formula $h^2 = \widehat{\sigma_g^2} / \left(\widehat{\sigma_g^2} + \widehat{\sigma_e^2} \right)$. The accuracy of GEBVs for each of the five models was calculated as $r(\mathbf{GEBV,y})$, where **y** represents the phenotypes corrected for fixed effects [20]. A 5-fold cross-validation approach was used to validate the models. In this method, animals were randomly divided into five groups, with each group treated as the validation set while the remaining groups constituted the reference set.

RESULTS

Principal components analysis

PCA was performed to explore genetic structure across populations. The analysis revealed that the first PC (PC1) accounted for 43.9% of the total genetic variance, whereas the second PC (PC2) constituted 13.6% of the variance (Fig. 2). The PCA plot revealed a clear separation among the crossbred populations, indicating distinct genetic backgrounds. However, the LYD population exhibited greater dispersion along the first two PCs, suggesting more considerable genetic variation within this group. This observed variation is likely attributed to the presence of F1 hybrids in the dataset, which primarily combined Landrace and Yorkshire genetics, thereby increasing the overall diversity observed in this population.

Genomic breed composition

The breed composition of the crossbred populations was evaluated using ADMIXTURE analysis; the results are depicted in Fig. 3. The analysis was conducted in unsupervised mode using genomic

Fig. 2. Population distribution across the first and second principal components. PC, principal components; DK, Duroc × Korean native pigs; LK, Landrace × Korean native pigs; LYD, Landrace × Yorkshire × Duroc.

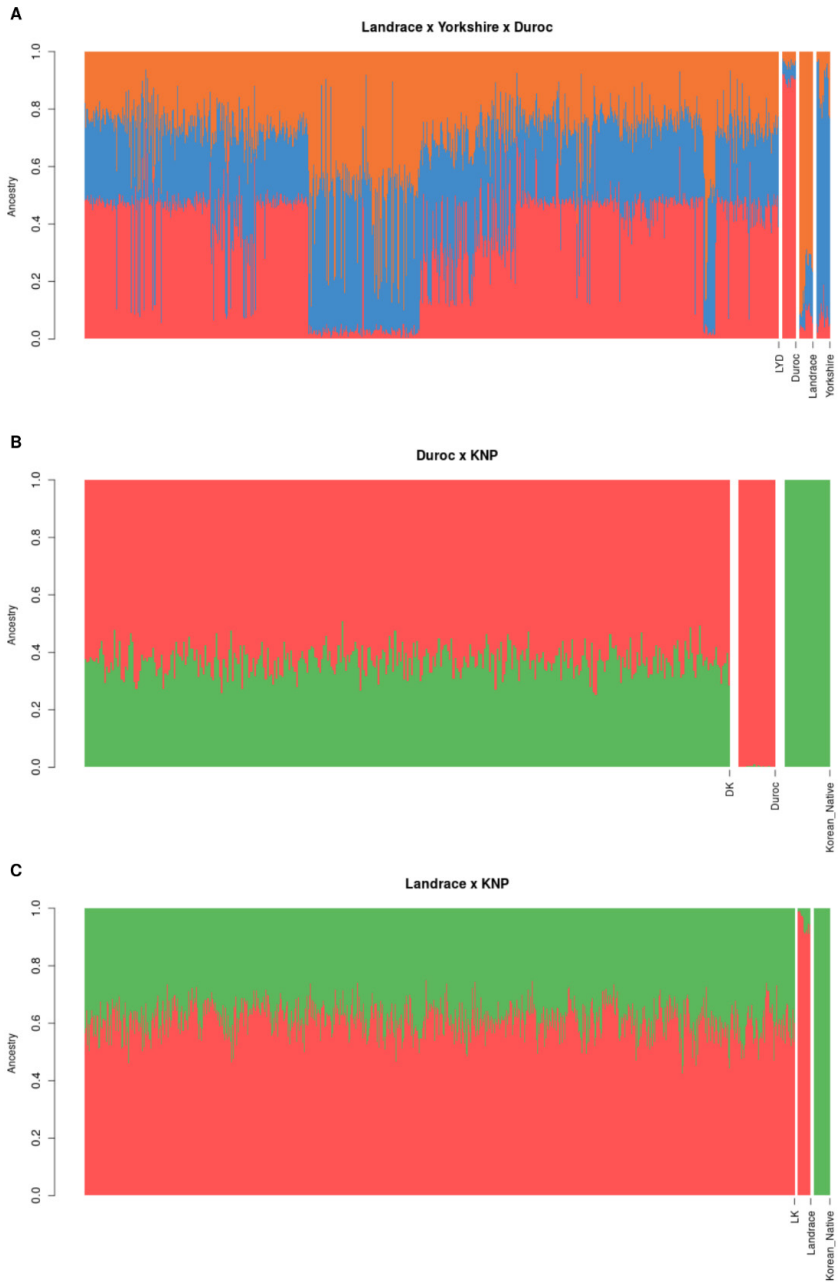

Fig. 3. Bar plot of the *Q* matrix from an ADMIXTURE run, showing the proportion of the genome contributed by each breed. (A) LYD population, (B) DK population, and (C) LK population. Each vertical bar represents an individual. KNP, Korean native pig; DK, Duroc × Korean native pig; LYD, Landrace × Yorkshire × Duroc.

data from purebred samples, and the estimated breed allele frequencies were subsequently used to infer breed membership coefficients for the crossbred individuals.

In the LYD population, the estimated breed composition revealed an average contribution of 31%, 33%, and 36% from Landrace, Yorkshire, and Duroc, respectively (Table 3). The presence of F1 animals, as indicated by the PCA, was corroborated by the breed composition analysis, where the contribution of the Landrace and Yorkshire breeds showed that the F1 crossbreds were indeed hybrids of these two pure breeds. The variation in breed composition within the LYD population

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Table 3. Genomic breed composition by breeds

Population	Breed	Minimum	Median	Maximum	Mean	SD
Landrace × Yorkshire × Duroc	Landrace	0.06	0.27	0.90	0.31	0.13
	Yorkshire	0.05	0.30	0.89	0.33	0.12
	Duroc	0	0.43	0.75	0.36	0.19
Duroc × KNP	Duroc	0.49	0.63	0.75	0.63	0.05
	KNP	0.25	0.37	0.51	0.37	0.05
Landrace × KNP	Landrace	0.43	0.62	0.75	0.61	0.06
	KNP	0.25	0.38	0.57	0.39	0.06

KNP, Korean native pig.

was not substantial, with standard deviations of 0.13, 0.12, and 0.19 for Landrace, Yorkshire, and Duroc, respectively. Similarly, the DK and LK populations exhibited balanced breed compositions. In the DK population, the average breed composition was 63% Duroc and 37% KNP, with minimal variation between individuals (SD = 0.05 for both breeds). The LK population had an average composition of 61% Landrace and 39% KNP, and low variation was also observed across individuals (SD = 0.06 for both breeds). These results suggest that the parental breeds had relatively balanced genetic contributions, as evidenced by the minimal variation in breed composition between individuals within the DK and LK populations.

Genetic parameter estimates

Heritability estimates for backfat thickness and carcass weight were derived from five different models; the associated variance components are detailed in Table 4. The estimates of genetic additive variance (V_g) and error variance (V_e) were used to calculate heritability for each trait.

Model 1 (NULL), which did not account for population structure, yielded the highest heritability estimates, with a heritability value of 0.44 ± 0.03 for backfat thickness and 0.31 ± 0.03 for carcass weight. The elevated heritability estimates for this model may be attributed to its lack of adjustments for potential confounding factors related to breed differences. Models 2 (PCA_F)

Table 4. Variance components and heritability estimates from five models for backfat thickness and carcass weight traits

Model		Variance components		Heritabilities	
		Backfat thickness (mm)	Carcass weight (kg)	Backfat thickness (mm)	Carcass weight (kg)
1 (NULL)	V_g	13.5 ± 1.3	31.4 ± 3.6	0.44 ± 0.03	0.31 ± 0.03
	V_e	17.1 ± 0.8	69.2 ± 2.7		
2 (PC_F)	V_g	12.1 ± 1.3	24.9 ± 3.7	0.41 ± 0.03	0.26 ± 0.03
	V_e	17.5 ± 0.8	71.3 ± 2.8		
3 (GBC_F)	V_g	13.7 ± 1.3	26.0 ± 3.4	0.44 ± 0.03	0.27 ± 0.03
	V_e	17.1 ± 0.8	70.6 ± 2.7		
4 (PC_R)	V_g	13.2 ± 1.3	28.1 ± 3.6	0.41 ± 0.04	0.23 ± 0.04
	V_{pc}	1.6 ± 1.7	23.7 ± 15.1	0.05 ± 0.05	0.19 ± 0.1
	V_e	17.2 ± 0.8	69.9 ± 2.7		
5 (GBC_R)	V_g	13.5 ± 1.3	27.1 ± 3.5	0.44 ± 0.03	0.23 ± 0.04
	V_{gbc}	0.2 ± 0.3	22.3 ± 14.3	0	0.19 ± 0.1
	V_e	17.1 ± 0.8	70.2 ± 2.8		

[1]Variance components are the genetic additive variance (V_g) and the error variance (V_e). In addition, the Model 4 (PC_R) and the Model 5 (GBC_R) estimates additional genetic variance components (V_{pc} and V_{gbc}).

PC, principal components; GBC, genomic breed composition.

and 3 (GBC_F), which incorporated population structure as a fixed effect, yielded lower heritability estimates; Model 2 estimated heritability for backfat thickness at 0.41 ± 0.03 and carcass weight at 0.26 ± 0.03, whereas Model 3 estimated these factors at 0.44 ± 0.03 and 0.27 ± 0.03, respectively. These reductions in heritability suggest that accounting for population structure as a fixed effect can decrease the perceived genetic influence on the traits. Models 4 (PCA_R) and 5 (GBC_R) included additional genetic variance components (V_{pc} and V_{gbc}) to account for population structure as a random effect. In Model 4, the genetic variance (V_g) was estimated at 13.2 ± 1.3 and V_{pc} at 1.6 ± 1.7 for backfat thickness, contributing an additional heritability of 0.05 ± 0.05 to the base estimate of 0.41 ± 0.04. For carcass weight, V_g was estimated at 28.1 ± 3.6 and V_{pc} at 23.7 ± 15.1, contributing an additional heritability of 0.19 ± 0.1 to the base estimate of 0.23 ± 0.04. Model 5 demonstrated similar patterns, although V_{gbc} for backfat thickness was close to zero. These models typically yielded heritability estimates similar to those of Model 1 for backfat thickness; however, for carcass weight, they provided a more nuanced understanding of genetic effects by accounting for population structure as a separate effect.

Accuracy of Genomic Estimated Breeding Values

The accuracy of GEBVs was evaluated using five models; the results are summarized in Table 5 and depicted in Fig. 4. Model 1 (NULL), Model 4 (PCA_R), and Model 5 (GBC_R) exhibited the highest accuracy for predicting both backfat thickness and carcass weight. These models achieved an

Table 5. Mean and standard deviation of GEBV accuracy for five prediction methods

Model	Backfat thickness (mm)		Carcass weight (kg)	
	Mean	SD	Mean	SD
1 (NULL)	0.59	0.01	0.50	0.04
2 (PCA_F)	0.40	0.03	0.34	0.03
3 (GBC_F)	0.53	0.04	0.38	0.02
4 (PCA_R)	0.59	0.01	0.50	0.03
5 (GBC_R)	0.59	0.01	0.50	0.03

GEBV, genomic estimated breeding values; PCA, principal component analysis; GBC, genomic breed composition.

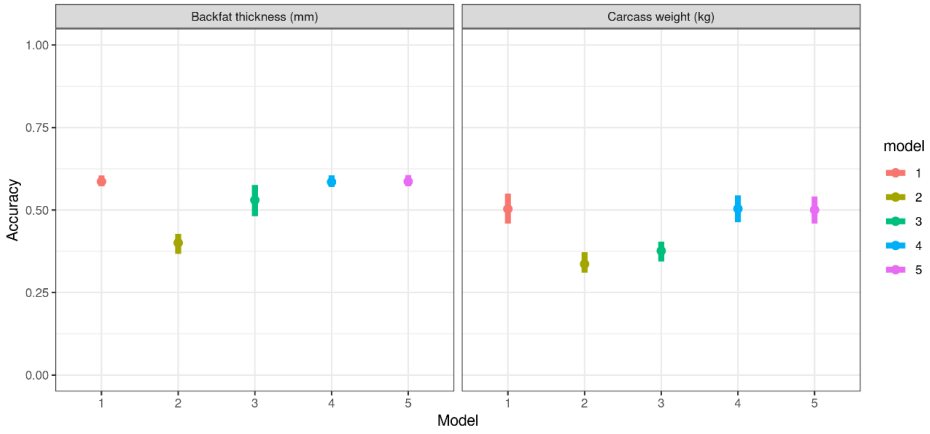

Fig. 4. GEBV accuracy of five prediction models. From left to right, the models are Model 1 (NULL), Model 2 (PCA_F), Model 3 (GBC_F), Model 4 (PCA_R), and Model 5 (GBC_R). The dots represent the average accuracy, and the lines indicate the standard deviation. GEBV, genomic estimated breeding value; PCA, principal component analysis; GBC, genomic breed composition.

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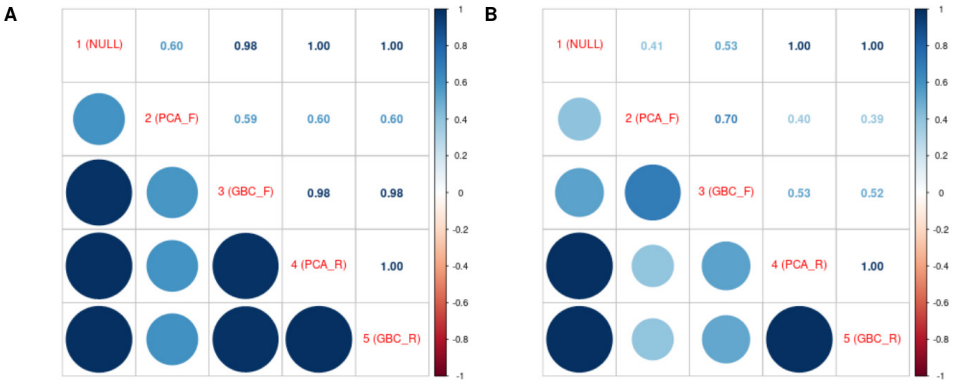

Fig. 5. Spearman correlation between models. (A) Backfat thickness and (B)carcass weight. GBC, genomic breed composition; PCA, principal componant analysis; GBC, genomic breed composition.

average accuracy of 0.59 for backfat thickness and 0.50 for carcass weight, with minimal variation across replicates (SD = 0.01 for backfat thickness and between 0.03 to 0.04 for carcass weight). Models that incorporated population structure as a fixed effect (Models 2 and 3) demonstrated lower accuracies for GEBVs. For backfat thickness, Model 2 (PCA_F) achieved a mean accuracy of 0.40 ± 0.03, whereas Model 3 (GBC_F) yielded a mean accuracy of 0.53 ± 0.04. The accuracy for carcass weight in these models was reduced similarly, with Model 2 achieving an accuracy of 0.34 ± 0.03 and Model 3 yielding an accuracy of 0.38 ± 0.02. These results suggest that modeling population structure as a fixed effect captures population differences but compromises GEBV accuracy. In contrast, modeling population structure as a random effect captures genetic variation due to breed differences without adversely affecting GEBV accuracy.

The Spearman rank correlation coefficient of GEBV between all models showed that all models were highly correlated with each other (except Model 2 in backfat thickness), ranging from 0.59 to 0.60. In carcass weight, Models 1, 4, and 5 had high Spearman correlation coefficients with each other, but models 2 and 3 had low correlation coefficients with the other models, ranging from 0.39 to 0.70 (Fig. 5). Models that did not correct for population structure and models that corrected for population structure as a random effect had similar genomic prediction patterns.

DISCUSSION

In multi-breed genomic predictions, using a reference population that encompasses multiple breeds inevitably introduces differences in population structure across these breeds. Therefore, this study aimed to assess prediction accuracy while adjusting population structure as either a fixed or random effect in multi-breed genomic predictions. The findings revealed that adjusting for population structure as a fixed effect resulted in decreased accuracy, whereas treating it as a random effect did not yield any improvements in accuracy. These results suggest that in multi-breed genomic predictions, the genomic relationship matrix sufficiently accounts for population structure, indicating that a model without adjustments for population structure is the most efficient.

Genotypic versus pedigree-based breed composition

GBC highlights the superior accuracy of genotypic data over that of pedigree information in determining breed composition. Pedigree records often contain inaccuracies or are incomplete, which can result in erroneous breed composition estimates [21,22]. In contrast, using genomic

data with tools such as ADMIXTURE provides a more precise assessment [23]. The findings of this study revealed that the breed compositions calculated using ADMIXTURE closely aligned with those expected from complete pedigree records, thereby corroborating previous research that emphasizes the reliability of genomic data for estimating breed composition in admixed populations [23].

Effect of population structure on genomic estimated breeding values

The effect of population structure on the estimation of genetic parameters is a well-established concern in genomic studies. Population structure can lead to false-positive associations [24], which may result in inflated heritability estimates [10] and biased accuracies in genomic predictions [6]. To address this issue, this study incorporated PCs and GBCs into GBLUP models as fixed or random effects.

Notably, the inclusion of PCs or GBCs as fixed effects resulted in decreased accuracy of GEBVs compared to those of models that excluded these factors. This reduction in accuracy may stem from the redundancy between the information provided by these variables and that captured by the genomic relationship matrix. Essentially, the genomic relationship matrix already encompasses much of the population structure information; therefore, adding PCs or breed composition as fixed effects could result in double-counting, leading to overcorrection and reduced model accuracy [11,25]. In contrast, treating PCs and GBC as random effects did not yield any improvement in prediction accuracy. This result suggests that the additional genetic variance components captured by these random effects did not provide significant new information beyond what was already accounted for by the genomic relationship matrix. Similarly, previous studies have demonstrated that incorporating population structure as a random effect does not enhance the accuracy of genomic predictions [25]. However, the advantage of including breed as a random effect within the model, as GEBVs are divided into two components. Specifically, a model with a random effect splits the genetic variance into within-breed and across-breed GEBVs, thereby facilitating the understanding of how predictions differ within and across breeds [25].

These findings hold significant implications for the optimal design of genomic prediction models. Although accounting for population structure is crucial to avoid biases, these results indicate that the genomic relationship matrix within the GBLUP framework sufficiently captures the required information. Consequently, additional adjustments for population structure, whether as fixed or random effects, may be unnecessary and could even negatively affect prediction accuracy. These findings support the growing consensus that simpler models that rely on the genomic relationship matrix without further correction for population structure are often the most effective [25].

This study focused on carcass traits and therefore did not explicitly include heterozygosity, even though crossbred animals were used. However, recent findings suggest that including heterozygosity in genomic predictions for maternal traits can improve prediction accuracy [26]. Therefore, future research on maternal traits in genomic prediction models may benefit from considering heterozygosity as a factor to further enhance prediction accuracy.

Implications for multi-breed genomic prediction

Our findings have significant implications in the field of multi-breed genomic prediction. This study demonstrated that the genomic relationship matrix alone could effectively capture breed differences within multi-breed populations, thereby eliminating the necessity for additional corrections for population structure. This circumvention is particularly advantageous in multi-breed contexts, where genetic relationships among breeds can vary widely, facilitating accurate predictions of breeding values for selection decisions.

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Given the observed decrease in accuracy when population structure was included as a fixed effect, future studies and practical applications of genomic prediction should prioritize models that incorporate the genomic relationship matrix as the primary tool for capturing genetic variance. This approach is more straightforward and ensures higher accuracy in predicting breeding values, which is crucial for effectively managing and improving crossbred populations.

In conclusion, this study underscores the robustness of the genomic relationship matrix in accounting for population structure within multi-breed genomic prediction. The findings suggest that, although population structure is an important consideration, the genomic relationship matrix is sufficient for capturing the relevant genetic variance, modeling additional corrections unnecessary. This insight is valuable for optimizing genomic prediction models in crossbred populations and enhancing the accuracy of GEBV predictions.

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