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Effect of Breed Composition in Genomic Prediction Using Crossbred Pig Reference Population

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 predictive 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 predictive 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

Introduction

35

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

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

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

62 In this study, we evaluated the accuracy of genomic predictions using models that incorporated breed

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

67

68 **Materials and Methods**

69 **Animals, genotypes, and phenotypes**

70 The genotype dataset comprised data from 354 Duroc × Korean native pigs (DK), 1,105 Landrace × Korean
71 native pigs (LK), 1,017 Landrace × Yorkshire × Duroc (LYD) crossbreds, along with purebred animals. Crossbred
72 individuals were genotyped using the Illumina PorcineSNP60 Genotyping BeadChip, whereas genotype data for
73 purebred animals were provided by the Centre for Research in Agricultural Genomics [12]. Genotype data for the
74 Korean native pigs (KNPs) among the purebreds were provided by the National Institute of Animal Science in
75 Korea. Details regarding the number of animals, single nucleotide polymorphisms (SNPs), and average observed
76 heterozygosity rate for each breed are presented in **Supplementary Table 1**. The quality control process involved
77 the exclusion of SNPs located on sex chromosomes, with a genotype call rate below 90%, and with a minor allele
78 frequency below 1%. After merging datasets and applying the quality control process, a common set of 24,118
79 SNPs were retained for analysis.

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

86

87 **Principal Component Analysis**

88 Principal component analysis (PCA) was employed to investigate genetic differences between populations and

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

96

97 **Genomic Breed Composition**

98 Genomic breed composition (GBC) was estimated from genomic data using a maximum likelihood model
99 implemented in ADMIXTURE v1.3.0 [15]. ADMIXTURE uses genotype data to cluster individuals into
100 subgroups based on a predetermined number of groups. The projection extension of the ADMIXTURE program
101 allows for estimating ancestry using predefined ancestral population allele frequencies. This extension enables
102 efficient ancestry inference across large genomic datasets, leveraging allele frequencies from reference panels,
103 such as the 1000 Genomes Project. Additionally, the projection approach is particularly advantageous for datasets
104 with significant population distribution imbalances, as such imbalances can adversely affect the accuracy of
105 ancestry inference [16].

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

110

111 **Statistical Models**

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

116 · Model 1 (NULL) is defined as follows:

$$117 \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e},$$

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

$$125 \quad \mathbf{G}_{jk} = \frac{1}{N} \sum_{i=1}^N \frac{(x_{ij} - 2p_i)(x_{ik} - 2p_i)}{2p_i(1 - p_i)},$$

126 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
127 allele frequency of SNP i , and N denotes the total number of SNPs. The distribution of the diagonal and off-
128 diagonal elements of the genomic relationship matrix is shown in **Supplementary Figure 1**. The mean of the
129 diagonal elements is 1.03, indicating low inbreeding within the population. The mean of the off-diagonal elements
130 is 0, showing that individuals are genetically independent of each other.

131 · Model 2 (PC_F) is defined as follows:

$$132 \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e},$$

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

137 · Model 3 (GBC_F) is defined as follows:

$$138 \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e},$$

139 where \mathbf{y} represents the vector of trait records; \mathbf{b} denotes the vector of fixed effects, which includes GBC values
140 and sex (here, breed composition values represent the proportion of each individual's genome derived from the

141 four breeds: Duroc, KNP, Landrace, and Yorkshire); \mathbf{X} indicates the design matrix linking fixed effects to records;
142 \mathbf{g} represents the vector of random genetic effects; \mathbf{Z} denotes the design matrix linking records to animals; and \mathbf{e}
143 indicates the vector of random deviations. For this model, $\mathbf{GEBV} = \hat{\mathbf{g}}$.

144 · Model 4 (PC_R) is defined as follows:

$$145 \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{Zpc} + \mathbf{e},$$

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

151 · Model 5 (GBC_R) is defined as follows:

$$152 \quad \mathbf{y} = \mathbf{Xf} + \mathbf{Zg} + \mathbf{Zgbc} + \mathbf{e},$$

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

158 Variance components were estimated using the restricted maximum likelihood (REML) method, as
159 implemented in MTG2 [19], for each model. Heritability for the traits was estimated using the formula $h^2 =$
160 $\widehat{\sigma}_g^2 / (\widehat{\sigma}_g^2 + \widehat{\sigma}_e^2)$. The accuracy of GEBVs for each of the five models was calculated as $r(\mathbf{GEBV}, \mathbf{y})$, where \mathbf{y}
161 represents the phenotypes corrected for fixed effects [20]. A 5-fold cross-validation approach was used to validate
162 the models. In this method, animals were randomly divided into five groups, with each group treated as the
163 validation set while the remaining groups constituted the reference set.

164

165

Results

166 **Principal Components Analysis**

167 PCA was performed to explore genetic structure across populations. The analysis revealed that the first PC
168 (PC1) accounted for 43.9% of the total genetic variance, whereas the second PC (PC2) constituted 13.6% of the
169 variance (**Figure 1**). The PCA plot revealed a clear separation among the crossbred populations, indicating distinct
170 genetic backgrounds. However, the LYD population exhibited greater dispersion along the first two PCs,
171 suggesting more considerable genetic variation within this group. This observed variation is likely attributed to
172 the presence of F1 hybrids in the dataset, which primarily combined Landrace and Yorkshire genetics, thereby
173 increasing the overall diversity observed in this population.

174

175 **Genomic Breed Composition**

176 The breed composition of the crossbred populations was evaluated using ADMIXTURE analysis; the results
177 are depicted in **Figure 2**. The analysis was conducted in unsupervised mode using genomic data from purebred
178 samples, and the estimated breed allele frequencies were subsequently used to infer breed membership coefficients
179 for the crossbred individuals.

180 In the LYD population, the estimated breed composition revealed an average contribution of 31%, 33%, and
181 36% from Landrace, Yorkshire, and Duroc, respectively (**Table 1**). The presence of F1 animals, as indicated by
182 the PCA, was corroborated by the breed composition analysis, where the contribution of the Landrace and
183 Yorkshire breeds showed that the F1 crossbreds were indeed hybrids of these two pure breeds. The variation in
184 breed composition within the LYD population was not substantial, with standard deviations of 0.13, 0.12, and
185 0.19 for Landrace, Yorkshire, and Duroc, respectively. Similarly, the DK and LK populations exhibited balanced
186 breed compositions. In the DK population, the average breed composition was 63% Duroc and 37% KNP, with
187 minimal variation between individuals (SD = 0.05 for both breeds). The LK population had an average
188 composition of 61% Landrace and 39% KNP, and low variation was also observed across individuals (SD = 0.06
189 for both breeds). These results suggest that the parental breeds had relatively balanced genetic contributions, as
190 evidenced by the minimal variation in breed composition between individuals within the DK and LK populations.

191

192 **Genetic Parameter Estimates**

193 Heritability estimates for backfat thickness and carcass weight were derived from five different models; the
194 associated variance components are detailed in **Table 2**. The estimates of genetic additive variance (V_g) and error
195 variance (V_e) were used to calculate heritability for each trait.

196 Model 1 (NULL), which did not account for population structure, yielded the highest heritability estimates,
197 with a heritability value of 0.44 ± 0.03 for backfat thickness and 0.31 ± 0.03 for carcass weight. The elevated
198 heritability estimates for this model may be attributed to its lack of adjustments for potential confounding factors
199 related to breed differences. Models 2 (PCA_F) and 3 (GBC_F), which incorporated population structure as a
200 fixed effect, yielded lower heritability estimates; Model 2 estimated heritability for backfat thickness at $0.41 \pm$
201 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 ,
202 respectively. These reductions in heritability suggest that accounting for population structure as a fixed effect can
203 decrease the perceived genetic influence on the traits. Models 4 (PCA_R) and 5 (GBC_R) included additional
204 genetic variance components (V_{pc} and V_{gbc}) to account for population structure as a random effect. In Model 4,
205 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
206 additional heritability of 0.05 ± 0.05 to the base estimate of 0.41 ± 0.04 . For carcass weight, V_g was estimated at
207 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
208 ± 0.04 . Model 5 demonstrated similar patterns, although V_{gbc} for backfat thickness was close to zero. These
209 models typically yielded heritability estimates similar to those of Model 1 for backfat thickness; however, for
210 carcass weight, they provided a more nuanced understanding of genetic effects by accounting for population
211 structure as a separate effect.

212

213 **Accuracy of Genomic Estimated Breeding Values**

214 The accuracy of GEBVs was evaluated using five models; the results are summarized in **Table 3** and depicted
215 in **Figure 3**. Model 1 (NULL), Model 4 (PCA_R), and Model 5 (GBC_R) exhibited the highest accuracy for
216 predicting both backfat thickness and carcass weight. These models achieved an average accuracy of 0.59 for
217 backfat thickness and 0.50 for carcass weight, with minimal variation across replicates (SD = 0.01 for backfat
218 thickness and between 0.03 to 0.04 for carcass weight).

219 Models that incorporated population structure as a fixed effect (Models 2 and 3) demonstrated lower accuracies

220 for GEBVs. For backfat thickness, Model 2 (PCA_F) achieved a mean accuracy of 0.40 ± 0.03 , whereas Model 3
221 (GBC_F) yielded a mean accuracy of 0.53 ± 0.04 . The accuracy for carcass weight in these models was reduced
222 similarly, with Model 2 achieving an accuracy of 0.34 ± 0.03 and Model 3 yielding an accuracy of 0.38 ± 0.02 .
223 These results suggest that modeling population structure as a fixed effect captures population differences but
224 compromises GEBV accuracy. In contrast, modeling population structure as a random effect captures genetic
225 variation due to breed differences without adversely affecting GEBV accuracy.

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

232

233

Discussion

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

241

Genotypic versus pedigree-based breed composition

242
243 GBC highlights the superior accuracy of genotypic data over that of pedigree information in determining breed
244 composition. Pedigree records often contain inaccuracies or are incomplete, which can result in erroneous breed
245 composition estimates [21, 22]. In contrast, using genomic data with tools such as ADMIXTURE provides a more

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

250

251 **Effect of population structure on genomic estimated breeding values**

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

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

269 These findings hold significant implications for the optimal design of genomic prediction models. Although
270 accounting for population structure is crucial to avoid biases, these results indicate that the genomic relationship
271 matrix within the GBLUP framework sufficiently captures the required information. Consequently, additional
272 adjustments for population structure, whether as fixed or random effects, may be unnecessary and could even
273 negatively affect prediction accuracy. These findings support the growing consensus that simpler models that rely

274 on the genomic relationship matrix without further correction for population structure are often the most effective
275 [25].

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

281 **Implications for multi-breed genomic prediction**

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

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

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

297

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356 **Tables**357 **Table 1. Genomic breed composition by breeds.**

Population	Breed	Min	Median	Max	Mean	SD
Landrace ×	Landrace	0.06	0.27	0.90	0.31	0.13
Yorkshire ×	Yorkshire	0.05	0.30	0.89	0.33	0.12
Duroc	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

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360 **Table 2. Variance components and heritability estimates from five models for backfat thickness**
 361 **and carcass weight traits. Variance components are the genetic additive variance (V_g) and the**
 362 **error variance (V_e). In addition, the Model 4 (PC_R) and the Model 5 (GBC_R) estimates**
 363 **additional genetic variance components (V_{pc} and V_{gbc}).**

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		

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366 **Table 3. 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

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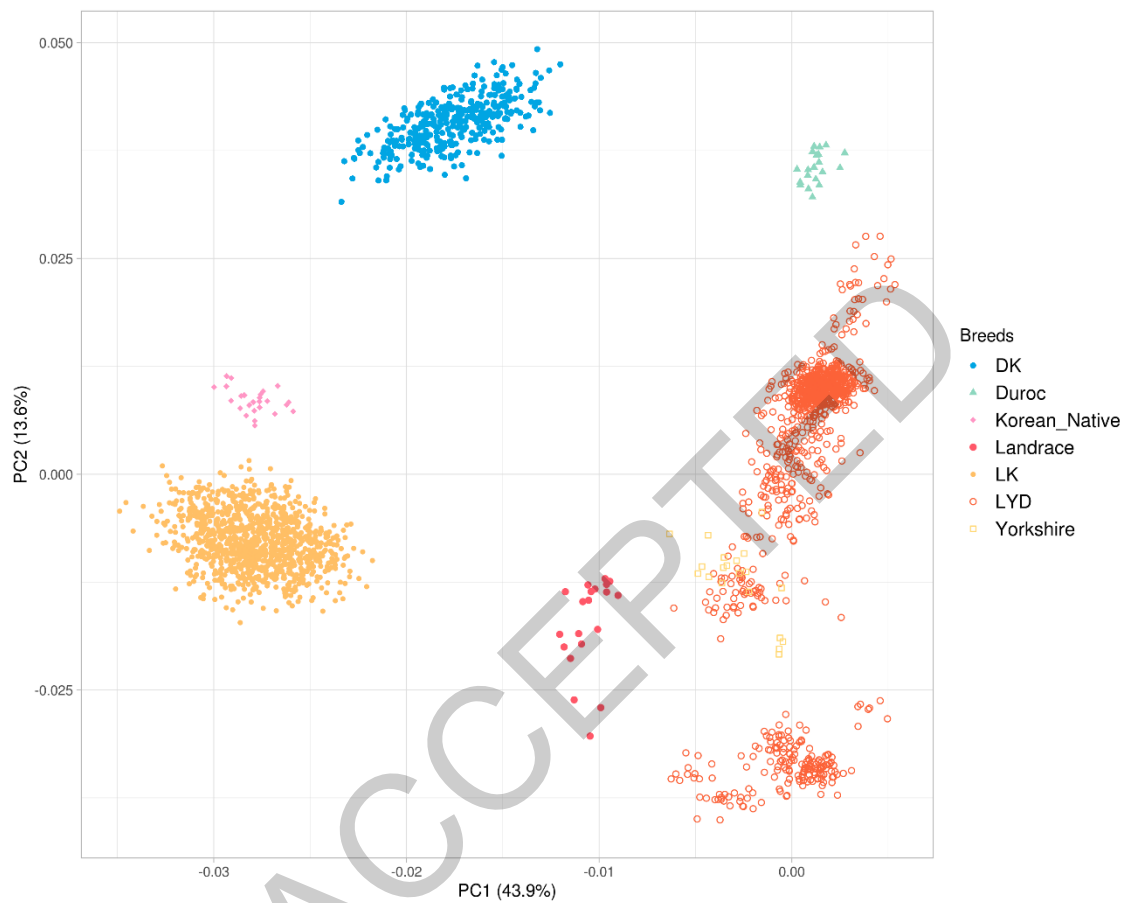
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370 **Figures**

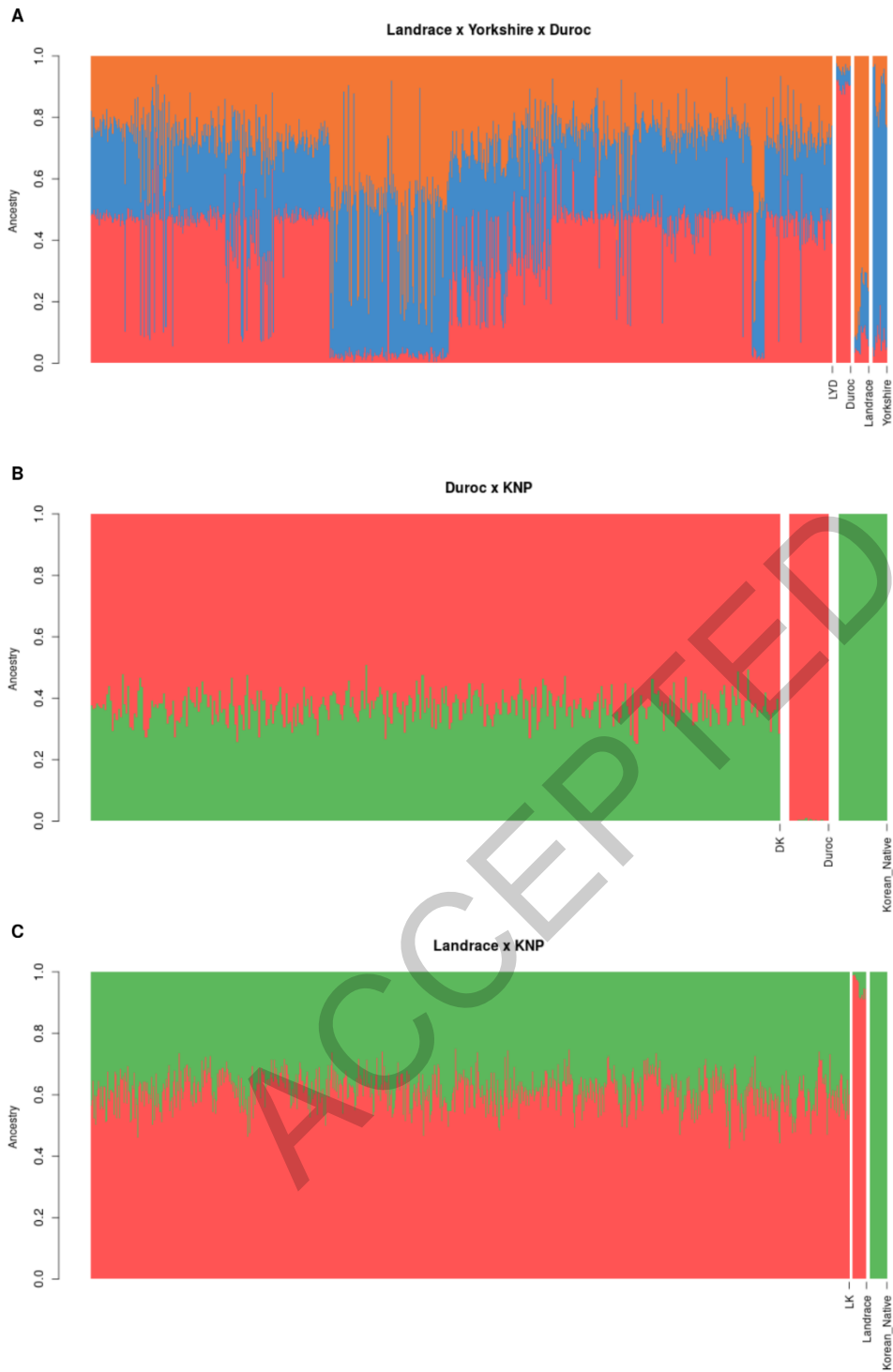
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373 **Figure 1. Population distribution across the first and second principal components.**

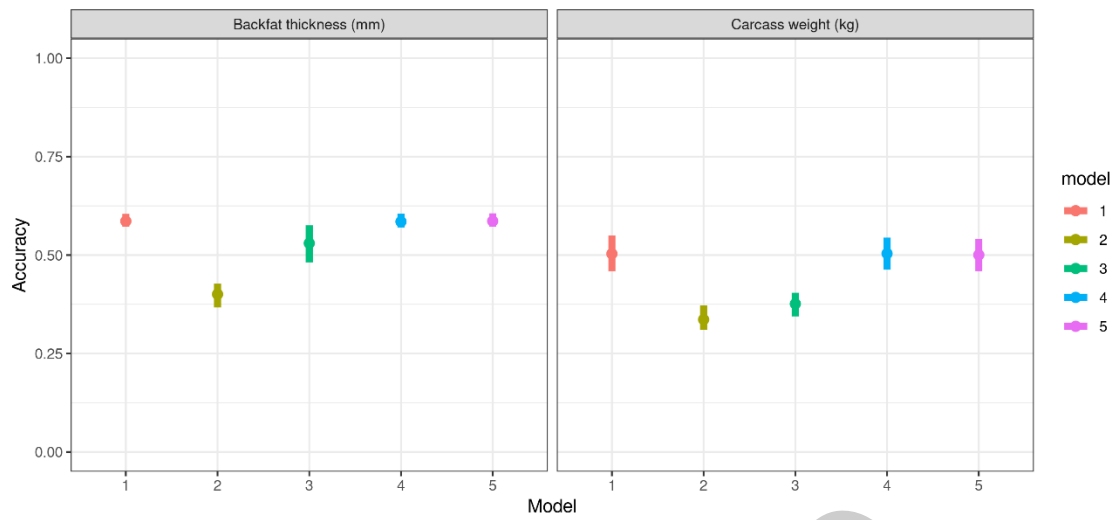
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376 **Figure 2. Bar plot of the Q matrix from an ADMIXTURE run, showing the proportion of the genome**
 377 **contributed by each breed. A shows the LYD population, B shows the DK population, and C shows the LK**
 378 **population. Each vertical bar represents an individual.**

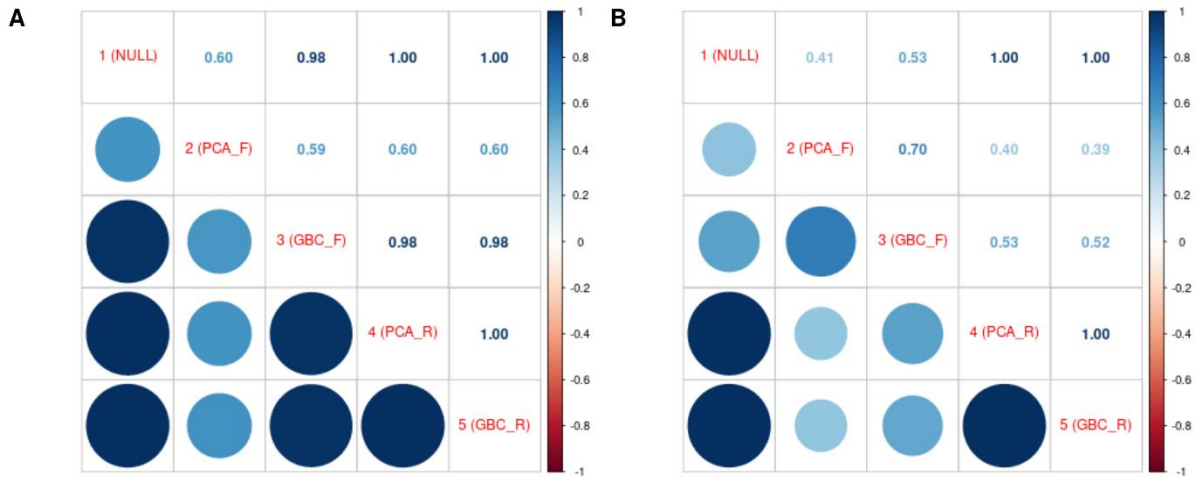
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381 **Figure 3. GEBV accuracy of five prediction models. From left to right, the models are Model 1 (NULL),**
 382 **Model 2 (PCA_F), Model 3 (GBC_F), Model 4 (PCA_R), and Model 5 (GBC_R). The dots represent the**
 383 **average accuracy, and the lines indicate the standard deviation.**

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386 **Figure 4. Spearman correlation between models. A represents backfat thickness and B**
 387 **represents carcass weight.**

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