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An investigation of machine learning methods applied to genomic prediction in yellow-feathered broilers

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ABSTRACT

Machine learning (ML) methods have rapidly developed in various theoretical and practical research areas, including predicting genomic breeding values for large livestock animals. However, few studies have investigated the application of ML in broiler breeding. In this study, seven different ML methods—support vector regression (SVR), random forest (RF), gradient boosting decision tree (GBDT), extreme gradient boosting (XGBoost), light gradient boosting machine (LightGBM), kernel ridge regression (KRR) and multilayer perceptron (MLP) were employed to predict the genomic breeding values of laying traits, growth and carcass traits in a yellow-feathered broiler breeding population. The results indicated that classic methods, such as GBLUP and Bayesian, achieved superior prediction accuracy compared to ML methods in five of the eight traits. For half-eviscerated weight (HEW), ML methods showed an average improvement of 54.4% over GBLUP and Bayesian methods. Among the ML methods, SVR, RF, GBDT, and XGBoost exhibited improvements exceeding 60%, with respective values of 61.3%, 61.0%, 60.4%, and 60.7%; while MLP improved by 54.4% and LightGBM by 53.7%, KRR had the lowest improvement at 29.4%. For eviscerated weight (EW), ML methods still outperformed GBLUP and Bayesian methods. MLP gained the largest improvement at 19.0%, while SVR, RF, GBDT, XGBoost, LightGBM, and KRR improved by 15.0%, 16.5%, 9.5%, 7.0%, 1.6%, and 15.9%, respectively. Compared to default hyperparameters, the average improvement of ML methods with tuned hyperparameters was 34.0%, 32.9%, 27.0%, 19.3%, 26.8%, 13.2%, 18.9%, and 46.3%, respectively. The prediction accuracy of above algorithms could be optimized using genome-wide association study (GWAS) to select subsets of significant SNPs. This work provides valuable insights into genomic prediction, aiding genetic breeding in broilers.

Introduction

Genomic selection (**GS**) was first proposed by Meuwissen et al. (2001) and has been widely used in animal breeding programs. The basis of genomic selection is to incorporate genomic variants and phenotypic data to predict genomic breeding values or unknown phenotypes. The classic statistical models applied in GS can be divided into direct and indirect methods, based on whether they predict individual breeding values or each marker effect. Direct methods, such as GBLUP and SSGBLUP, straightforwardly predict individual breeding values by solving the mixed model equations (**MME**) from the best linear unbiased prediction, replacing the pedigree relationship matrix (**A matrix**) with the genomic relationship matrix (**G matrix**) or the transformed genomic relationship matrix (**H matrix**). Representative indirect methods are Bayesian methods, which first estimate each marker effect stepwise and obtain the genomic breeding values by summarizing all genetic marker effects. Although GS methods integrate genomic variants into the prediction model, they have higher prediction accuracy than the pedigree-based BLUP model. Factors such as the number and density of markers (Solberg et al., 2008; Zhu et al., 2017; Karimi et al., 2019), the size and structure of the reference population (Makgahlela et al., 2013; Song et al., 2019; Karaman et al., 2021; Nilson et al., 2024; Yin et al., 2024), and the heritability of objective traits (Goddard and Hayes, 2009; Hayes et al., 2009; Karimi et al., 2019; Yin et al., 2024) are critical

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contributors that may affect the predictive outcome of GS. In addition, linear assumptions constrain GS models, making them less adaptable in interpreting the complex interactive relationships in high-dimensional genomic data, thus the traditional GS models may result in lower-than-expected accuracy in some small populations (Gianola et al., 2011).

Machine learning (**ML**) methods offer an alternative for genomic prediction in animal breeding (González-Recio et al., 2014; Bayer et al., 2021; Chafai et al., 2023) and perform as a "black-box" without requiring knowledge of the distribution of variables or the genetic effects of target traits in advance (Li et al., 2018), breaking the limitations of mixed linear models and Bayesian assumptions. Compared with traditional linear models, ML demonstrates superior capability in capturing the complex relationships among genotypes, phenotypes and environment. In recent years, ML methods have been extensively applied to genomic prediction in pigs and cattle. Wang et al. (2022b) found that ML methods outperformed the conventional methods in predicting pig reproductive trait performance by comparing support vector regression (**SVR**), kernel ridge regression (**KRR**), random forest (**RF**), and Adaboost.R2 with traditional methods such as GBLUP, SSGBLUP, and Bayesian Horseshoe (**BayesHE**). Alves et al. (2021) reported that SVR showed the best accuracy compared to other parametric ML models in predicting the reproductive trait performance of Nellore cattle. Liang et al. (2021) also compared different ML methods in predicting genomic breeding values for carcass weight, live weight, and eye muscle area in Chinese Simmental beef cattle, finding that Adaboost.RT performed with the highest reliability and would be an efficient method for genomic prediction. Alves et al. (2023) explored the application of SVR to broiler carcass traits and found that SVR with a nonlinear kernel could improve the prediction accuracy compared to GBLUP and BayesC. Abdollahi-Arpanahi et al. (2020) reported that using simulated data and real cattle datasets, the Multilayer Perceptron (**MLP**) provided better predictive performance than parametric methods for traits with non-additive gene action. In addition, ML algorithms have also been used in the field of broilers to identify SNPs associated with early mortality, revealing risk factors affecting the death upon arrival (Long et al., 2007; Pirompud et al., 2024).

However, there is still a lack of systematical assessments of different ML methods for predicting the genomic effects of important economic traits in broilers. Therefore, in this study, we evaluated the genomic prediction accuracy of classic and ML methods in broiler economic traits, comparing the efficiency and stability of different ML methods to select the optimal algorithm for each specific trait.

Materials and methods

Population and phenotypes

All animal handling procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of Hunan Agricultural University (Changsha, China, Permit No. HAU ACC 2023181).

The experimental broilers were selected from the breeder population of Xiangjia Black Feather chickens (S1 and S2 lines) bred for 7 generations by Hunan Xiangjia Husbandry Co., Ltd (Hunan Province, China). In this study, laying traits of the 5th and 6th generations of the S1 line and growth and carcass traits from the 6th and 7th generations of the S2 line were collected as the experimental phenotypes. The laying traits included age at the first egg (**AFE**), 40-week egg production (**EP40**), and 43-week average egg weight (**EW43**), while the growth and carcass traits included 10-week body weight (**BW10**), 13-week body weight (**BW13**), half-eviscerated weight (**HEW**), eviscerated weight (**EW**), and breast muscle weight (**BRW**). A single-trait animal model was used to estimate heritability for each trait. The fixed effect included generation, batch, and sex, while the random effects were additive genetic effects and random residuals. The response variables used in genomic prediction were the corrected phenotypes ($\mathbf{y_c}$), adjusted by removing the estimated values of the fixed effects.

Genotype data

Genomic DNA was extracted from blood samples collected by needling the wing vein. Two SNP panels, IASCHICK 55K (Liu et al., 2019) and XiangXin 60K, were used for genotyping for each chicken. The PLINK (V1.90) (Purcell et al., 2007a) software was used to control the quality of the genotype data, retaining SNPs with a minor allele frequency (**MAF**) > 5%, SNP detection rate > 90%, and the individuals with genotype detection rate > 90%. All the individuals were imputed to the same SNP density with high fidelity ($DR^2 \geq 0.9$) for the subsequent analysis using Beagle 5.4 software and BCFtools v1.8 (Danecek et al., 2021) software. The descriptive statistics for all traits are shown in Table 1.

Statistical models

Six classical models, including GBLUP, BayesA, BayesB, BayesC, Bayesian Lasso (**BL**), and Bayesian Ridge Regression (**BRR**), as well as seven machine learning methods, such as support vector regression (SVR), random forest (RF), gradient boosting decision tree (**GBDT**), extreme gradient boosting (**XGBoost**), light gradient boosting machine (**LightGBM**), kernel ridge regression (KRR) and Multilayer Perceptron (MLP) were employed for the genomic prediction of eight distinct phenotypes.

GBLUP

$$y_c = 1\mu + Zg + e \quad (1)$$

In the above formula, y_c is the vector of corrected phenotypes, μ is the overall mean, 1 is a vector of 1 s, g is the vector of genomic breeding values following a normal distribution: $g \sim N\left(0, G\sigma_g^2\right)$, and e is the vector of random errors following $e \sim N\left(0, I\sigma_e^2\right)$. Z is a design matrices of g, G was the genomic relationship matrix (G matrix), and σ_g^2 and σ_e^2 were the additive genetic variance and the residual variance, respectively.

Table 1
Summary statistics of eight economic traits from Xiangjia Black Feather chickens.

Trait	Markers	Number of observations	Mean	SD	CV (%)	h^2(SE)
Laying traits						
AFE (d)	31934	1094	158.91	7.68	4.83	0.26 (0.06)
EP40 (n)	31934	1140	91.17	14.35	15.74	0.21 (0.05)
EW43 (g)	31934	989	48.99	3.25	6.63	0.44 (0.06)
Growth and carcass traits						
BW10 (g)	24082	1347	961.13	165.76	17.25	0.48 (0.05)
BW13 (g)	24033	1345	1341.93	169.72	12.65	0.46 (0.05)
HEW (g)	23930	1338	1030.18	145.09	14.08	0.40 (0.05)
EW (g)	24009	1340	852.30	117.37	13.77	0.41 (0.05)
BRW (g)	16962	1036	110.81	34.08	30.75	0.21 (0.05)

Bayesian

The general formula of Bayes A, Bayes B and Bayes C is as follows:

$$y_c = \mu + \sum_{i=1}^{m} Z_i g_i + e \tag{2}$$

where y_c is the vector of corrected phenotypes; $i = 1 \ldots$for the m marker, Z_i is the genotype (0/1/2) of the ith locus; g_i is the effect value of the ith locus; and e is the vector of random residual effects. BayesA assumes that each SNP locus has an effect and the effect variance follows the same prior distribution; BayesB assumes that only a small fraction of SNPs have an effect (a scale of 1-π); and the BayesC approach takes π as an unknown parameter. Park and Casella (2008) proposed Bayesian lasso in 2008, which differs from BayesA in that the marker effect follows Laplace distribution. The Bayesian ridge regression was proposed by Hsiang (1975), which assumes that all markers have effects, and the marker effects follow a normal distribution. In theory, RRBLUP is equivalent to GBLUP with a smoothening parameter λ as the ratio to adjust variance components (Tomar et al., 2021), meaning that Bayesian ridge regression can represent RR-BLUP and GBLUP (Wang et al., 2022a). The five models were implemented based on the BGLR (Pérez and de Los Campos, 2014) package in R. The iterations were set to 12,000, burn-in at 2,000, and the value of π was set to 0.95 for the BayesB method.

Support vector regression

Support vector regression (SVR) is based on the support vector machine (SVM) method and is used in this study because it uses kernel functions to solve nonlinear problems, providing incomparable advantages over other algorithms based on the empirical risk minimization principle (Long et al., 2011). The model expression of SVR is written as follows:

$$f(x) = \beta_0 + h(x)^T \beta \tag{3}$$

in which $h(x)^T \beta$ denotes the kernel function of the SVR, β is the vector of weights, and β_0 is the bias.

Random Forest

Random forest (RF), gradient boosting decision tree (GBDT), and extreme gradient boosting (XGBoost) are typical ensemble learning algorithms applied to predicting genomic breeding values. RF was first proposed by Breiman (2001) and essentially consists of several independent decision trees (Liaw and Wiener, 2002). The combination of the prediction outcomes of each decision tree determines the prediction effect of RF, so the critical step in RF prediction is the formation of decision trees and a forest (Zhang et al., 2023). The expression for RF regression is as follows:

$$y = \frac{1}{M} \sum_{m=1}^{M} t_m(\psi_m(y : X)) \tag{4}$$

where y is the predicted value of RF, $t_m(\psi_m(y : X))$ is each independent decision tree, and M is the number of decision trees in the random forest.

Gradient boosting decision tree

Gradient boosting decision tree (GBDT) is implemented based on the Boosting algorithm. The core idea is to first fit an initial decision tree with training data, then train the next tree based on the residuals of the previous tree, and finally sum up the predictions of a series of trees (Zhang and Jung, 2020). The computational complexity of GBDT is proportional to the number of features and the number of instances, making it very time-consuming to deal with big data. According to the additivity model, the final model of GBDT is expressed as follows:

$$f_M(x) = \sum_{m=1}^{M} T(x; \Theta_m) \tag{5}$$

where $T(x; \Theta_m)$ is the base model represented by the decision tree, Θ_m is the decision tree parameter, and M is the number of decision trees.

Extreme gradient boosting

Extreme gradient boosting (XGBoost) (Chen and Guestrin, 2016) is an improved version of GBDT, superior to GBDT in performance and speed. Similar to GBDT, XGBoost is also an additive model composed of multiple base models. The XGBoost algorithm uses serial dataset training processes to merge decision trees, and the final model is a forest containing several decision trees (Kiangala and Wang, 2021). XGBoost is expressed as follows:

$$\hat{y}_i = \sum_{k=1}^{K} f_k(x_i) \tag{6}$$

where $\hat{y}_i$ is the predicted value of XGBoost, $f_k(x_i)$ is the base model for the decision tree representation, and K is the number of decision trees.

Light gradient boosting machine

Light gradient boosting machine (LightGBM) (Ke et al., 2017) is a new GBDT implementation with Gradient-based One-Side Sampling (**GOSS**) and Exclusive Feature Bundling (**EFB**) developed by Microsoft. Among them, GOSS and EFB algorithms are used to optimize the number of samples and features, respectively. It has been proven that, with the help of GOSS and EFB, LightGBM can significantly outperform XGBoost in computing speed and memory consumption.

Kernel ridge regression

Kernel ridge regression (KRR) is a nonlinear regression method based on ordinary least square (**OLS**) regression and Ridge regression (Exterkate et al., 2016). KRR uses a kernel function to map the original data into high-dimensional space, where the mapped data tend to be linear in the reproducing kernel Hilbert space (**RKHS**). The ridge regression method is then used to analyze and process the data in this high-dimensional feature space (Rosipal, 2001). The final KRR prediction model is written as follows:

$$y(x_i) = k'(K + \lambda I)^{-1} y \tag{7}$$

in which x_i is the individuals in the training set, λ is the regularization parameter, K is the Gram matrix, I is the identity matrix, $k' = K(x_i, x_j)$, j = 1,2,3,…,n, and n is the number of individuals in the training set.

Multilayer perceptron

The Multilayer Perceptron (MLP) is a type of feedforward artificial neural network that has extensive applications in the field of genomic prediction (Abdollahi-Arpanahi et al., 2020; Pedrosa et al., 2024). An MLP consists of an input layer, one or more hidden layers, and an output layer. Each layer is composed of multiple neurons (nodes), and each neuron is connected to all the neurons in the previous layer, receiving and transmitting signals. Input signals are passed through weighted connections. After comparing the input values with the thresholds, an output value is produced by activating the corresponding function.

The seven ML methods, including the MLP which was employed with default parameters, were implemented using the Sklearn package in Python. Based on the Tree-structured Parzen Estimator (**TPE**) algorithm, this study used 10-fold cross-validation (**CV**) to find the most suitable kernel function model and the optimal parameters of the other six ML

algorithms. The key hyperparameters are detailed in Supplementary Table 1. In addition, the optimization process of hyperparameters for the ML methods and the optimal hyperparameters for each trait are detailed in the Supplementary Text and Supplementary Table 2.

Genome-wide association study

Since the integration of trait-related SNPs in GS models may help improve prediction accuracy (Luo et al., 2021), the genome-wide association study (**GWAS**) was performed to sort the SNPs with high association significance. The independent SNPs were extracted by PLINK (V1.90) (Purcell et al., 2007b), and the parameter was set to –indep-pairwise 25 5 0.2. The first two principal component analyses (PCA) were used to correct the population structure. GEMMA (v0.98.5) (Zhou and Stephens, 2012) was used to identify SNPs associated with traits. The SNPs were sorted according to their nominal *P* values after GWAS, and different numbers of SNP sets were selected for the subsequent genome prediction.

Evaluation of the accuracy of genomic prediction

The accuracies of genomic prediction were evaluated by Pearson correlation coefficient between corrected phenotypes (y_c) and predicted value (**PV**). Additionally, root mean square error (**RMSE**) and mean absolute error (**MAE**) were used as evaluation metrics for the regression models. Two more metrics, the coefficient of determination (R^2) and unbiasedness, were also incorporated to further assess the models performance. RMSE is one of the most commonly used performance assessment metrics in regression tasks, indicating the average degree of deviation between the predicted and true values of the model. The calculation formula is given below:

$$RMSE_{(y,y_{pre})} = \sqrt{\frac{1}{N}\sum_{i=1}^{N}\left(y_i - y_{i\_pre}\right)^2} \tag{8}$$

The MAE value reflects the absolute deviation of the true value from the predicted value; the smaller the MAE, the more accurate the model prediction. The calculation formula is provided below:

$$MAE_{(y,y_{pre})} = \frac{1}{N}\sum_{i=1}^{N}\left|y_i - y_{i\_pre}\right| \tag{9}$$

In the above two formulas, y and y_{pre} represent y_c and PV, respectively, and N represents the number of individuals.

The coefficient of determination, denoted as R^2, represents the proportion of the variation in the dependent variable that is predictable from the independent variable(s), indicating the model's explanatory power for the predicted results. The expression for this coefficient is as follows:

$$R^2 = 1 - \frac{SS_{\text{res}}}{SS_{\text{tot}}} \tag{10}$$

Where

$$SS_{\text{res}} = \sum_{i=1}^{N}(\hat{y}_i - \bar{y}_i)^2, SS_{\text{tot}} = \sum_{i=1}^{N}(y_i - \bar{y}_i)^2 \tag{11}$$

Here, N represents the number of individuals, $\hat{y}$ denotes the predicted values by the model, y_i represents the actual values, and $\bar{y}_i$ is the mean of the samples.

Unbiasedness is assessed by regressing the corrected phenotypes onto the predicted values.

The final averages of five metrics were obtained by randomly selecting 10% of the samples as the validation population and the remaining 90% as the reference population. The 10-fold CV was repeated for 10 times.

Time consumption

The runtime for different methods was calculated on a server running CentOS Linux 7, with a 2.5 GHz Intel Xeon processor and 1.0 TB of total memory.

Results

Heritability of eight phenotypic traits

The heritability of the eight traits in this study ranged from 0.21 to 0.48. Among the three laying traits, the heritability of AFE, EP40, and EW43 was 0.26, 0.21, and 0.44, respectively. Except for the low heritability of BRW (0.21), the four growth and carcass traits had relatively high heritability: BW10 (0.48), BW13 (0.46), HEW (0.40), and EW (0.41). The results of the heritability estimates are shown in Table 1.

Fine tuning of ML method hyperparameters

Fig. 1 illustrates the comparison of the ML algorithms before and after hyperparameter optimization. For most of the algorithms, the prediction accuracy significantly improved after parameter optimization, among which SVR had the most significant improvement effect in various traits. For different traits, the average improvement of the ML method with tuned hyperparameters was 34.0%, 32.9%, 27.0%, 19.3%, 26.8%, 13.2%, 18.9%, and 46.3%, respectively. The ratios were determined by dividing the pre-optimization to post-optimization difference by the pre-optimization accuracy.

For laying traits, KRR had the highest prediction accuracy of 0.207 and 0.320 for AFE and EW43, respectively; RF and XGBoost had the highest prediction accuracy for EP40 (0.237 and 0.234). Combined with MAE and RMSE values, it was found that RF and XGBoost had less fluctuation in these three traits. Compared to other ML methods, KRR also showed superior prediction performance in BW13 (0.369), EW (0.381), and BRW (0.197). In the case of BW10, SVR achieved the highest accuracy (0.427), while SVR, RF, GBDT, and XGBoost had very similar prediction accuracies for HEW. In terms of growth and carcass traits, the MAE and RMSE values for SVR were relatively low, indicating that SVR exhibited greater robustness in its predictive ability.

Comparison of the prediction accuracies between 12 GS methods for different traits

Table 2 shows the genomic prediction accuracies of GBLUP, Bayesian methods, and ML methods for the traits of AFE, EP40, EW43, BW10, BW13, HEW, EW, and BRW. Overall, the ML methods showed little advantage in prediction accuracy for the three laying traits, regardless of whether hyperparameters were tuned, compared to GBLUP and Bayesian models. In addition, as shown in Fig. 2, the prediction accuracy of the classical models (GBLUP and Bayesian methods) increased with the heritability of the trait from low to high, but the ML methods showed weak relationships between the prediction accuracy and heritability.

In the prediction of AFE, GBLUP, BayesA, BayesB, BayesC, and BL models had similar performance, among which BL had the highest prediction accuracy of 0.237. Both BayesC and BRR performed the best in the prediction of EP40, with accuracies of 0.246 and 0.242, respectively. In addition, BRR had the highest accuracy in predicting the EW43. As shown in Table 3 and 4, the BRR method had relatively lower MAE values and RMSE compared with other methods.

For the BW10 trait, most of the methods had comparable prediction accuracy close to 0.40, and the SVR with optimized hyperparameters showed the highest prediction accuracy of 0.427. Similar to laying traits, GBLUP and Bayesian models performed better than ML methods in predicting BW13 and BRW traits. BayesA and BL had high prediction accuracy of 0.389 and 0.382 for BW13, and BayesC had the highest prediction accuracy of 0.216 for BRW.

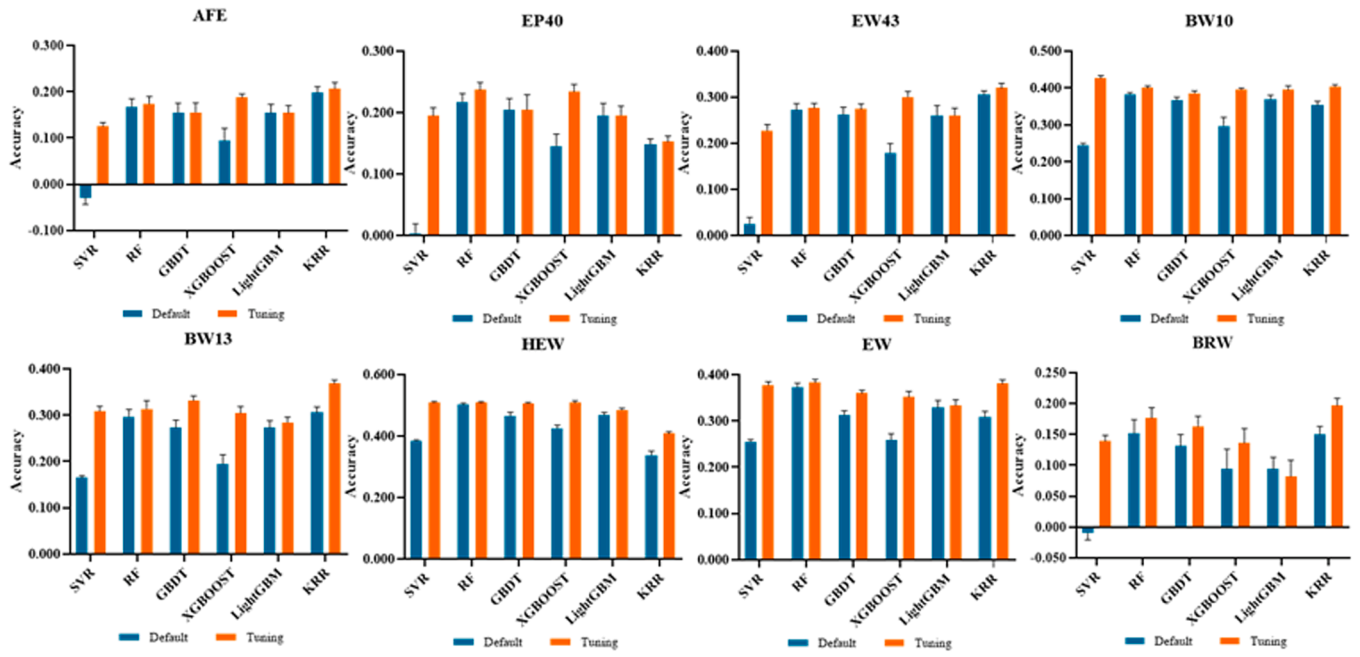

Fig. 1. Prediction accuracies of machine learning methods before and after hyperparameter optimization.

Table 2
Prediction accuracies for 8 traits based on thirteen methods using 10-fold CV.

Method	Laying traits			Growth and carcass traits				
	EP40	AFE	EW43	BRW	HEW	EW	BW13	BW10
GBLUP	0.233	0.233	0.358	0.204	0.304	0.336	0.372	0.401
BayesA	0.224	0.232	0.344	0.183	0.324	0.329	0.389	0.394
BayesB	0.224	0.235	0.343	0.194	0.313	0.328	0.371	0.399
BayesC	0.246	0.223	0.357	0.216	0.311	0.331	0.366	0.395
BL	0.226	0.237	0.344	0.201	0.318	0.330	0.382	0.406
BRR	0.242	0.223	0.364	0.198	0.327	0.319	0.379	0.399
SVR	0.195	0.126	0.228	0.139	0.510	0.378	0.309	0.427
RF	0.237	0.174	0.277	0.177	0.509	0.383	0.314	0.400
GBDT	0.205	0.156	0.274	0.163	0.507	0.360	0.332	0.386
XGBoost	0.234	0.188	0.301	0.136	0.508	0.352	0.305	0.396
LightGBM	0.196	0.155	0.261	0.094	0.486	0.334	0.285	0.395
KRR	0.153	0.207	0.320	0.197	0.409	0.381	0.369	0.404
MLP	0.102	0.174	0.219	0.158	0.488	0.391	0.368	0.413

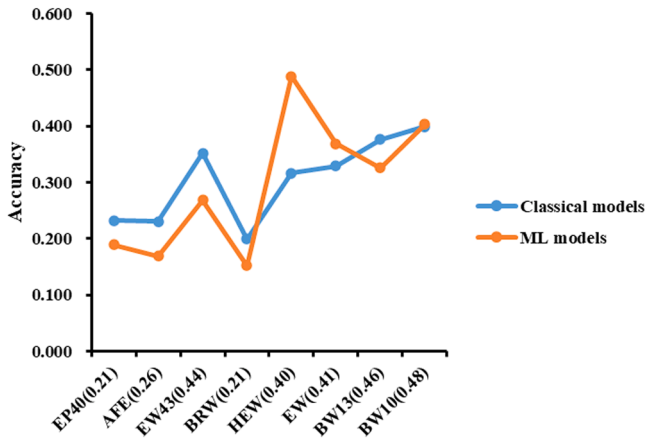

Fig. 2. Average predictive accuracy of models for traits with varying heritability.

The prediction accuracy of ML methods with optimized hyperparameters for HEW and EW is much higher than that of GBLUP and Bayesian models. For two carcass traits HEW and EW, all ML methods except MLP yielded lower MAE and RMSE than GBLUP, BayesA, BayesB, BayesC, BL, and BRR. Compared within the classic models, BayesC had relatively low MAE (103.938) and RMSE (130.915) on HEW, and GBLUP generated a slightly lower MAE (83.584) and RMSE (105.103) on EW. In addition, as shown in Table 5, the unbiasedness indicators calculated by ML methods fluctuated significantly for certain traits, while the unbiasedness of classical methods was generally around 1. The R^2 values indicated an overall low performance in this study (Supplementary Table 3).

Computing time

The average computation time required for each method to complete one round of 10-fold CV is presented in Supplementary Table 4. As expected, the three Bayesian methods—Bayes A, Bayes B, and Bayes C, required approximately 1 hour to complete one round of 10-fold CV, while GBLUP cost 35 minutes to complete. Different ML methods showed distinct running time cost. KRR was the fastest and used only 15s to finish. However, RF spent the longest time about 6.9 hours to

Table 3
Mean absolute error (MAE) for 8 traits based on thirteen methods using 10-fold CV.

Method	Laying traits			Growth and carcass traits				
	EP40	AFE	EW43	BRW	HEW	EW	BW13	BW10
GBLUP	1.075	5.719	2.406	20.682	105.293	83.584	106.219	77.907
BayesA	1.073	5.696	2.428	20.815	104.443	83.798	105.968	78.897
BayesB	1.071	5.663	2.454	20.375	105.172	83.976	106.076	78.407
BayesC	1.074	5.699	2.413	20.379	103.938	84.301	106.590	79.254
BL	1.071	5.713	2.419	20.273	105.272	84.724	106.148	77.465
BRR	1.071	5.653	2.408	20.316	104.008	84.801	105.943	78.708
SVR	1.086	5.774	2.522	20.707	95.179	81.532	108.815	78.268
RF	1.072	5.798	2.524	20.583	95.126	81.539	109.517	79.460
GBDT	1.092	5.849	2.502	20.601	96.901	82.282	107.975	79.447
XGBOOST	1.068	5.795	2.485	20.757	95.170	82.458	108.626	79.270
LightGBM	1.085	5.889	2.547	20.863	96.677	83.322	109.202	79.258
KRR	1.233	6.091	2.623	20.440	100.601	82.044	106.313	78.565
MLP	1.546	6.298	3.160	22.855	99.583	85.134	110.829	81.264

Table 4
Root mean square error (RMSE) for 8 traits based on thirteen methods using 10-fold CV.

Method	Laying traits			Growth and carcass traits				
	EP40	AFE	EW43	BRW	HEW	EW	BW13	BW10
GBLUP	1.386	7.019	2.991	25.937	133.080	105.103	133.311	98.323
BayesA	1.381	7.017	3.022	25.979	131.936	105.046	132.880	99.568
BayesB	1.382	6.969	3.048	25.580	131.988	105.221	133.172	99.130
BayesC	1.382	7.031	3.013	25.558	130.915	105.663	133.916	100.255
BL	1.380	7.040	3.018	25.421	132.843	106.381	133.241	98.394
BRR	1.376	6.951	3.003	25.545	131.223	106.275	133.199	99.534
SVR	1.401	7.188	3.170	26.187	119.970	103.652	137.519	98.233
RF	1.385	7.090	3.154	25.848	120.040	103.300	138.329	99.943
GBDT	1.405	7.211	3.128	25.888	121.932	104.162	136.501	100.116
XGBOOST	1.385	7.074	3.104	26.084	120.077	104.474	137.315	99.750
LightGBM	1.402	7.172	3.188	26.227	121.862	105.217	138.133	99.688
KRR	1.587	7.707	3.267	25.703	127.286	103.186	133.829	99.236
MLP	2.012	8.013	4.346	28.806	125.631	107.532	139.610	102.979

Table 5
Unbiasedness for 8 traits based on thirteen methods using 10-fold CV.

Method	Laying traits			Growth and carcass traits				
	EP40	AFE	EW43	BRW	HEW	EW	BW13	BW10
GBLUP	0.963	0.900	1.010	0.877	0.945	1.052	0.947	1.028
BayesA	0.878	0.843	0.964	0.903	0.979	0.935	1.010	1.046
BayesB	0.813	0.869	0.967	0.963	0.995	0.986	0.972	0.998
BayesC	0.926	0.940	1.038	0.900	1.033	1.036	1.059	1.008
BL	0.933	0.876	0.982	0.938	0.957	0.967	0.986	0.979
BRR	0.933	0.840	1.025	0.862	0.996	0.958	1.020	1.002
SVR	1.750	0.584	0.776	0.488	0.967	0.851	0.794	0.912
RF	1.218	1.126	1.905	1.594	1.044	1.147	1.901	1.297
GBDT	0.604	0.442	0.883	0.755	1.414	1.081	1.401	1.039
XGBOOST	1.031	1.239	1.252	0.590	1.039	1.033	1.244	1.123
LightGBM	1.054	0.778	1.297	0.409	0.974	1.040	1.175	1.082
KRR	0.216	0.331	0.497	0.861	1.081	1.011	0.972	0.999
MLP	0.098	0.281	0.264	0.247	0.681	0.579	0.574	0.609

complete.

Integration of trait-associated SNPs on genomic prediction in different methods

To evaluate the performance of different SNP selection strategies in low and high heritability traits, EP40 and HEW were selected for subsequent analysis. For EP40 and HEW traits, the top 500, 1000, 2000, 5000, and 10000 SNPs that were associated with each phenotype were selected as a subset of genotype data for genomic prediction. The same number of SNPs were also selected from the genome randomly for comparison. A comparison of the effects of the SNP subsets obtained by the two methods on the accuracy of genomic prediction is presented in Figs. 3-6.

The results demonstrated that the prediction accuracies obtained by selecting the top SNPs (**Top SNPs**) through GWAS were much higher than those obtained by randomly selecting the SNPs (**Rand SNPs**). Specifically, for HEW, the average accuracy obtained by GWAS selection at different SNP densities was 0.634 versus 0.360 for random selection, while for EP40, it was 0.538 and 0.205, respectively.

In the Top SNPs scenario, the predictive accuracies of EP40 or HEW by GBLUP, BayesA, BayesB, BayesC, BL, BRR, and KRR methods were consistently higher and more comparable to other ML methods such as SVR, RF, GBDT, XGBoost, and LightGBM. In particular, the BRR model showed to increase the predictive accuracy by 2.8 times when incorporating the Top 2000 trait-associated SNPs (0.696 ± 0.011), compared

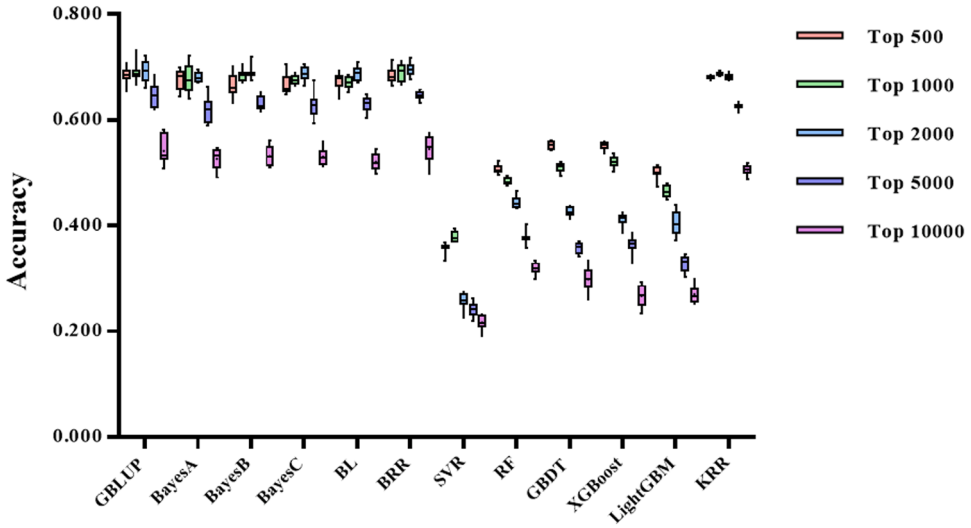

Fig. 3. Accuracy of genomic prediction of EP40 by GWAS selection of different numbers of SNPs.

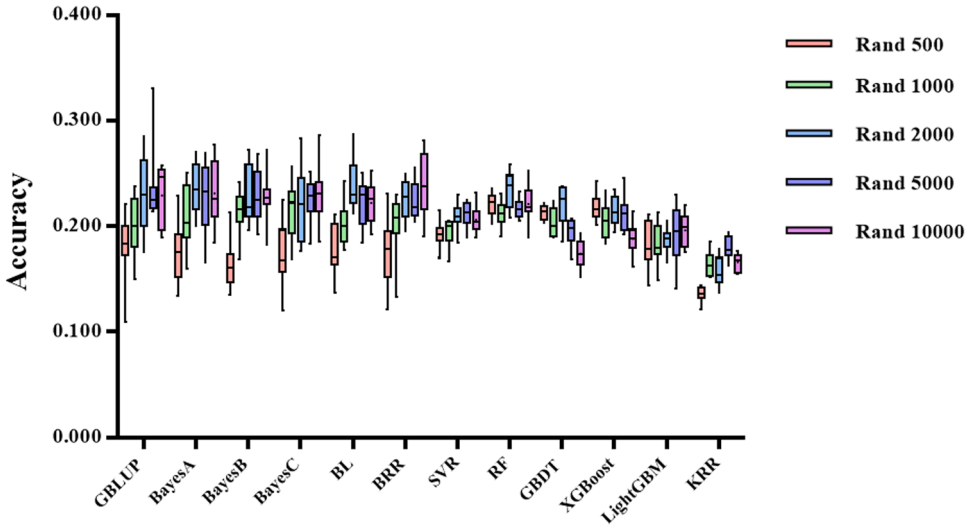

Fig. 4. Accuracy of genomic prediction of EP40 by random selection of different numbers of SNPs.

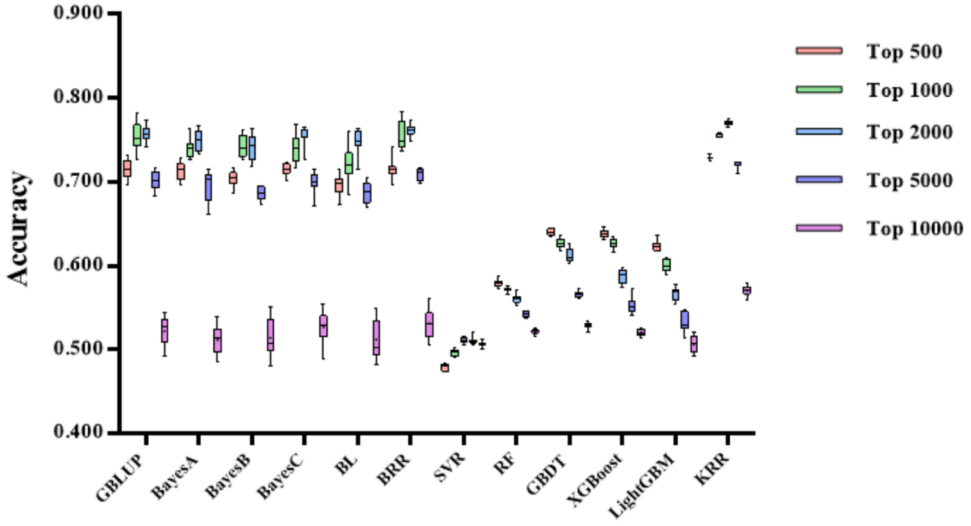

Fig. 5. Accuracy of genomic prediction of HEW by GWAS selection of different numbers of SNPs.

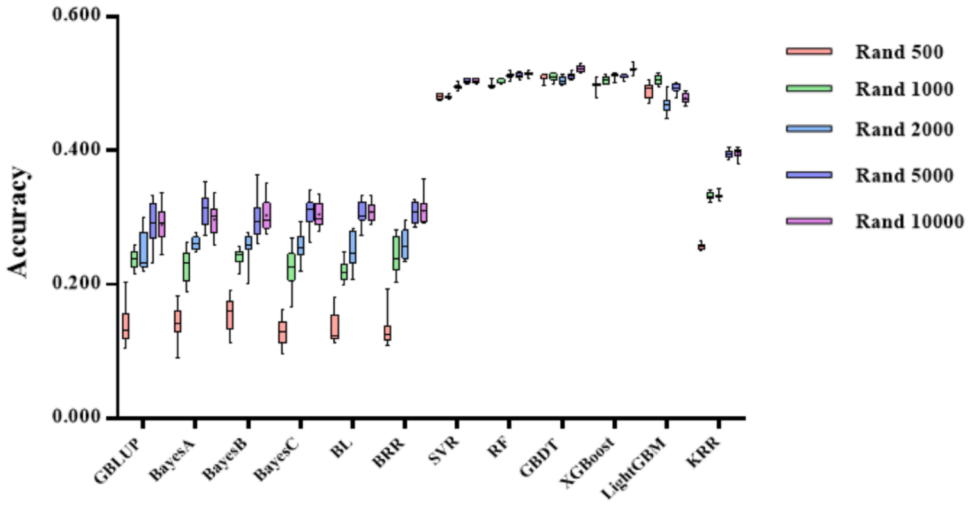

Fig. 6. Accuracy of genomic prediction of HEW by random selection of different numbers of SNPs.

to the accuracy obtained by using all SNPs (0.25 ± 0.008).

For the Rand SNPs situation, most methods have improved prediction accuracy as more SNPs are used in the model. Notably, the improvements in prediction accuracies by classical methods (average 0.418) were slightly larger than those obtained by ML models (average 0.224). Interestingly, in the HEW trait, ML methods even maintained relatively high prediction accuracy when utilizing Rand SNPs, compared to using Top SNPs.

Discussion

GS has been widely used in animal and plant breeding, and its algorithms are continually evolving, but there is no algorithm suitable for all species and traits at present. The characteristics of ML algorithms facilitate the identification of intricate relationships between genes, phenotypes, and environments when dealing with high-dimensional genomic data. To date, there have been studies comparing the application effect of ML algorithms and classic linear models in genome prediction of livestock and aquatic animals (Moser et al., 2009; Alves et al., 2020; Alves et al., 2021; Wang et al., 2022b). The results showed that ML algorithms exhibited superior results in prediction accuracy. Currently, there are few researches on the application of ML algorithms in poultry genome prediction. In this study, we systematically evaluated the application of 12 algorithms for genomic prediction, including GBLUP, Bayesian, and ML methods, using phenotypic and genotypic data of laying traits, growth traits, and carcass traits from two generations of Xiangjia black feather chickens as experimental material.

In our experiments, both BayesC and BRR methods performed well in EP40. Furthermore, BRR also had the highest prediction accuracy for EW43, indicating that BRR may be the optimal algorithm for laying traits. In terms of computational efficiency, BRR consumed less computing time than BayesC. BL had the highest accuracy in predicting AFE. Furthermore, KRR exhibited the highest accuracy in several traits; however, its MAE and RMSE values were not the smallest in comparison to other ML methods. This finding is in accordance with the results of previous research, which indicates that the comparison of different models with varying evaluation criteria will invariably yield disparate ranking outcomes (Nikooienejad et al., 2020; Li et al., 2023). The R^2 value showed negative values in the application of nonlinear models, which may be due to the complexity of nonlinear data and the risk of overfitting. The ML algorithms did not show superior performance in all scenarios, only a huge gain in the prediction of HEW and EW. For HEW traits, compared with that of GBLUP and Bayesian methods, the improvement of ML methods was 54.4% on average. Among ML methods, the improvement of SVR, RF, GBDT, and XGBoost were more than 60%, which was 61.3%, 61.0%, 60.4%, and 60.7%, respectively; MLP achieved an improvement of 54.4%, LightGBM showed an improvement of 53.7%; KRR yielded the lowest improvement of 29.4%. For EW traits, the performance of ML methods was still better than GBLUP and Bayesian methods, MLP gained the largest improvement 16.5%, SVR, GBDT, XGBoost, LightGBM, and KRR were improved by 15.0%, 9.5%, 7.0%, 1.6%, and 15.9%, respectively. The possible reason for this is that the genome prediction accuracy of different algorithms is influenced by many factors, such as population structure and the genetic structure of the traits (Neves et al., 2012). For traits completely regulated by additive effects, the classic linear models showed higher prediction accuracy (Zingaretti et al., 2020). When the target traits are more affected by non-additive effects (such as epistatic effects and environmental effects), ML methods can obtain more accurate predictions (Long et al., 2011; Millet et al., 2019). Therefore, the choice of the appropriate algorithm based on the structural characteristics of the trait is critical for prediction accuracy. Moreover, for complex traits under directed selection, non-additive gene effects such as epistasis also translate into additive genetic variance when allele frequencies are low (Hill et al., 2008; Huang and Mackay, 2016), which may explain to some extent why the ML models performed better on only some traits in this study. Additionally, we found that the SVR model exhibited negative accuracy values for predicting AFE and BRW. This situation may occur when the machine learning model is insufficient to capture the relationship between genotype and phenotype. (Wang et al., 2023; Wang et al., 2024)

It is worth noting that the adjustment of hyperparameters in ML algorithms has a great impact on the calculation accuracy and efficiency of ML algorithms. Currently, there are three mainstream optimization methods. The grid search method is the most commonly used hyperparameter tuning method. Its principle is to combine the parameters within a given range and search for the parameter combination with the highest score through CV. This kind of enumeration search method is the most direct, but it is very resource-intensive, especially when dealing with large datasets or many parameters to optimize, and relies on parameter adjustment experience to determine the appropriate parameter range. The random search method randomly selects a subset from the parameter combination for training and validation, and its operational speed and the parameter space it covers per unit time are better than the grid search method. Whether it is the grid search method or the random search method, its essence is to verify a large number of points in the parameter space and finally obtain the optimal solution, which makes it difficult to achieve both accuracy and efficiency. Using the Bayesian optimization algorithm for hyperparameter optimization is the recommended choice. Some studies have shown that the Bayesian

optimization algorithm based on TPE performs well in hyperparameter optimization (Nguyen et al., 2020; Ozaki et al., 2020; Liang et al., 2022; Shen et al., 2022). The TPE optimization algorithm can handle not only continuous variables but also discrete, classified, and conditional variables which are difficult to solve with Kriging (Ozaki et al., 2020).

ML algorithms are sensitive to user-defined parameters during the training phase (Alves et al., 2021; Wang et al., 2022b). Taking RF as an example, the number of decision trees in the tree model (n_estimators), that is, the number of weak learners, has a great impact on the prediction accuracy, complexity, generalization ability, and computational efficiency of the RF model. The computational time and complexity of the model increase with the number of decision trees. The depth of the decision tree (max_depth) directly determines the overfitting risk of the RF model, and the overfitting of the model can be prevented by lowering the depth of the tree. Liang et al. (2022) determined the optimal parameters of the KRR model by TPE algorithm in Simmental beef. The results showed that compared to the GBLUP model, the prediction accuracy of KRR-TPE was improved by 8.73%. Wang et al. (2022b) compared the prediction effects of different ML methods before and after hyperparameter adjustment for pig offspring. The results showed that compared with the results of using default hyperparameters, the prediction accuracy of ML methods after hyperparameter optimization was improved by 21.8% on average. In summary, the optimization of hyperparameters is necessary for the ML methods to achieve better performance in GS.

Theoretically, the accuracy of genomic prediction increases with the increase of marker density, but not all SNPs in the whole genome are related to traits. Filtering SNPs related to traits is of great significance for GS. Li et al. (2018) explored the effect of three ML methods, such as gradient boosting machine (**GBM**), XGBoost and RF on the genomic prediction of the identified SNPs subsets. The results showed that the prediction effect of the SNP subsets was significantly better than that of the SNPs evenly distributed in the genome. Some studies have shown that the addition of marker effect and *P* value information in GS helps to improve the accuracy of prediction (Su et al., 2014). The common approach is to use the filtered SNPs to weight the relationship matrix (Yin et al., 2020), and directly using SNPs to rank according to *P* value for GS can reduce the cost of subsequent genotyping (Luo et al., 2021). Our study explored the impact of different numbers of SNPs selected by GWAS on the accuracy of genomic prediction. The results showed that the prediction accuracy obtained by the top SNPs was much higher than that of the randomly selected SNPs. Most algorithms achieve the highest prediction accuracy when using the top 2000 SNPs. The construction of low-density SNP chips based on the identification of SNPs related to trait biology has the potential to reduce the cost of genotyping, while it also can facilitate the application of GS in yellow-feathered broilers.

Conclusions

In this study, we explored the efficiency of ML methods such as SVR, RF, GBDT, XGBoost, LightGBM, KRR and MLP for genomic prediction in broilers. The ML methods were evaluated in comparison to the GBLUP and Bayesian methods, focusing on the prediction accuracy, MAE, RMSE, R^2 and unbiasedness of the different models by repeating 10 times 10-fold CV. The results showed that the prediction performance of the classic GS methods was better than that of the ML methods in most traits. For AFE, BL had the highest accuracy. BayesC and BRR had the highest accuracy in predicting EP40 and EW43, respectively. BayesA and BayesC showed the best prediction performance for BW13 and BRW, respectively. ML methods significantly outperformed classic methods in predicting EW and HEW. To explore the effect of the GWAS selection of different numbers of SNPs on the accuracy of genomic prediction, we found that the prediction accuracy obtained by selecting top SNPs was much higher than that obtained by selecting SNPs randomly, with the hierarchy of Top SNPs > All SNPs > Random SNPs. Overall, our findings highlighted the importance of selecting appropriate methods and SNPs while considering the genetic structure of traits, dataset size, and computational efficiency to enhance the accuracy of genomic predictions in broiler breeding. While computational resources limited the efficiency of hyperparameter optimization in ML, future advancements in this area could lead to further improvements in prediction accuracy.

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Declaration of competing interest

No potential conflict of interest was reported by the authors.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.psj.2024.104489.

References

Abdollahi-Arpanahi, R., Gianola, D., Peñagaricano, F., 2020. Deep learning versus parametric and ensemble methods for genomic prediction of complex phenotypes. Genet. Sel. Evol. 52, 1–15.
Alves, A.A.C., da Costa, R.M., Bresolin, T., Fernandes Júnior, G.A., Espigolan, R., Ribeiro, A.M.F., Carvalheiro, R., de Albuquerque, L.G., 2020. Genome-wide prediction for complex traits under the presence of dominance effects in simulated populations using GBLUP and machine learning methods. J. Anim. Sci. 98, skaa179.
Alves, A.A.C., Espigolan, R., Bresolin, T., Costa, R.M.d., Fernandes Júnior, G.A., Ventura, R.V., Carvalheiro, R., Albuquerque, L.G.d., 2021. Genome-enabled prediction of reproductive traits in Nellore cattle using parametric models and machine learning methods. Anim. Genet. 52, 32–46.
Alves, A.A.C., Fernandes, A.F.A., Lopes, F.B., Breen, V., Hawken, R., Gianola, D., Rosa, G. J.d.M., 2023. (Quasi) multitask support vector regression with heuristic hyperparameter optimization for whole-genome prediction of complex traits: a case study with carcass traits in broilers. G3 (Bethesda) 13, jkad109.
Bayer, P.E., Petereit, J., Danilevicz, M.F., Anderson, R., Batley, J., Edwards, D., 2021. The application of pangenomics and machine learning in genomic selection in plants. Plant Genome 14, e20112.
Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.
Chafai, N., Hayah, I., Houaga, I., Badaoui, B., 2023. A review of machine learning models applied to genomic prediction in animal breeding. Front. Genet. 14, 1150596.
Chen, T., Guestrin, C., 2016. XGBoost: a scalable tree boosting system. In: in Proceedings of the 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data MiningAssociation for Computing Machinery. San Francisco, California, USA, pp. 785–794.
Danecek, P., Bonfield, J.K., Liddle, J., Marshall, J., Ohan, V., Pollard, M.O., Whitwham, A., Keane, T., McCarthy, S.A., Davies, R.M., 2021. Twelve years of SAMtools and BCFtools. Gigascience 10, giab008.
Exterkate, P., Groenen, P.J., Heij, C., van Dijk, D., 2016. Nonlinear forecasting with many predictors using kernel ridge regression. Int. J. Forecasting. 32, 736–753.
Gianola, D., Okut, H., Weigel, K.A., Rosa, G.J., 2011. Predicting complex quantitative traits with Bayesian neural networks: a case study with Jersey cows and wheat. BMC Genet 12, 1–14.
Goddard, M.E., Hayes, B.J., 2009. Mapping genes for complex traits in domestic animals and their use in breeding programmes. Nat. Rev. Genet. 10, 381–391.
González-Recio, O., Rosa, G.J., Gianola, D., 2014. Machine learning methods and predictive ability metrics for genome-wide prediction of complex traits. Livest. Sci. 166, 217–231.
Hayes, B.J., Bowman, P.J., Chamberlain, A.J., Goddard, M.E., 2009. Invited review: Genomic selection in dairy cattle: progress and challenges. J. Dairy Sci. 92, 433–443.
Hill, W.G., Goddard, M.E., Visscher, P.M., 2008. Data and theory point to mainly additive genetic variance for complex traits. PLos Genet. 4, e1000008.
Hsiang, T., 1975. A Bayesian view on ridge regression. J. R. Stat. Soc. Ser. D Stat. 24, 267–268.
Huang, W., Mackay, T.F., 2016. The genetic architecture of quantitative traits cannot be inferred from variance component analysis. PLos Genet. 12, e1006421.
Karaman, E., Su, G., Croue, I., Lund, M.S., 2021. Genomic prediction using a reference population of multiple pure breeds and admixed individuals. Genet. Sel. Evol. 53, 46.
Karimi, K., Sargolzaei, M., Plastow, G.S., Wang, Z., Miar, Y., 2019. Opportunities for genomic selection in American mink: a simulation study. PLoS One 14, e0213873.
Ke, G., Meng, Q., Finley, T., Wang, T., Chen, W., Ma, W., Ye, Q., Liu, T.-Y., 2017. Lightgbm: a highly efficient gradient boosting decision tree. Adv. Neural. Inf. Process Syst. 30, 3146–3154.
Kiangala, S.K., Wang, Z., 2021. An effective adaptive customization framework for small manufacturing plants using extreme gradient boosting-XGBoost and random forest

ensemble learning algorithms in an Industry 4.0 environment. Mach. Learn. Appl. 4, 100024.
Li, B., Zhang, N., Wang, Y.-G., George, A.W., Reverter, A., Li, Y., 2018. Genomic prediction of breeding values using a subset of SNPs identified by three machine learning methods. Front. Genet. 9, 237.
Li, Z., Zheng, J., An, B., Ma, X., Ying, F., Kong, F., Wen, J., Zhao, G., 2023. Several models combined with ultrasound techniques to predict breast muscle weight in broilers. Poult. Sci. 102, 102911.
Liang, M., An, B., Li, K., Du, L., Deng, T., Cao, S., Du, Y., Xu, L., Gao, X., Zhang, L., 2022. Improving genomic prediction with machine learning incorporating TPE for hyperparameters optimization. Biology (Basel) 11, 1647.
Liang, M., Miao, J., Wang, X., Chang, T., An, B., Duan, X., Xu, L., Gao, X., Zhang, L., Li, J., 2021. Application of ensemble learning to genomic selection in chinese simmental beef cattle. J. Anim. Breed. Genet. 138, 291–299.
Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. R N 2, 18–22.
Liu, R., Xing, S., Wang, J., Zheng, M., Cui, H., Crooijmans, R.P., Li, Q., Zhao, G., Wen, J., 2019. A new chicken 55K SNP genotyping array. BMC Genomics 20, 1–12.
Long, N., Gianola, D., Rosa, G.J., Weigel, K.A., 2011. Application of support vector regression to genome-assisted prediction of quantitative traits. Theor. Appl. Genet. 123, 1065–1074.
Long, N., Gianola, D., Rosa, G.J., Weigel, K.A., Avendano, S., 2007. Machine learning classification procedure for selecting SNPs in genomic selection: application to early mortality in broilers. J. Anim. Breed. Genet. 124, 377–389.
Luo, Z., Yu, Y., Xiang, J., Li, F., 2021. Genomic selection using a subset of SNPs identified by genome-wide association analysis for disease resistance traits in aquaculture species. Aquaculture 539, 736620.
Makgahlela, M.L., Mäntysaari, E.A., Strandén, I., Koivula, M., Nielsen, U., Sillanpää, M., Juga, J., 2013. Across breed multi-trait random regression genomic predictions in the N ordic R ed dairy cattle. J. Anim. Breed. Genet. 130, 10–19.
Meuwissen, T.H.E., Hayes, B.J., Goddard, M.E., 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics 157, 1819–1829.
Millet, E.J., Kruijer, W., Coupel-Ledru, A., Prado, S.A., Cabrera-Bosquet, L., Lacube, S., Charcosset, A., Welcker, C., van Eeuwijk, F., Tardieu, F., 2019. Genomic prediction of maize yield across European environmental conditions. Nat. Genet. 51, 952–956.
Moser, G., Tier, B., Crump, R.E., Khatkar, M.S., Raadsma, H.W., 2009. A comparison of five methods to predict genomic breeding values of dairy bulls from genome-wide SNP markers. Genet. Sel. Evol. 41, 1–16.
Neves, H.H., Carvalheiro, R., Queiroz, S.A., 2012. A comparison of statistical methods for genomic selection in a mice population. BMC Genet. 13, 100.
Nguyen, H.-P., Liu, J., Zio, E., 2020. A long-term prediction approach based on long short-term memory neural networks with automatic parameter optimization by Tree-structured Parzen Estimator and applied to time-series data of NPP steam generators. Appl. Soft Comput. 89, 106116.
Nikooienejad, A., Wang, W., Johnson, V.E., 2020. Bayesian variable selection for survival data using inverse moment priors. Ann. Appl. Stat. 14, 809–828.
Nilson, S.M., Burke, J.M., Murdoch, B.M., Morgan, J.L., Lewis, R.M., 2024. Pedigree diversity and implications for genetic selection of Katahdin sheep. J. Anim. Breed. Genet. 141, 304–316.
Ozaki, Y., Y. Tanigaki, S. Watanabe, and M. Onishi. 2020. Multiobjective tree-structured parzen estimator for computationally expensive optimization problems. Pages 533-541 in Proceedings of the 2020 genetic and evolutionary computation conference.
Park, T., Casella, G., 2008. The bayesian lasso. J. Am. Stat. Assoc. 103, 681–686.
Pedrosa, V.B., Chen, S.Y., Gloria, L.S., Doucette, J.S., Boerman, J.P., Rosa, G.J.M., Brito, L.F., 2024. Machine learning methods for genomic prediction of cow behavioral traits measured by automatic milking systems in North American Holstein cattle. J. Dairy Sci. 107, 4758–4771.
Pérez, P., de Los Campos, G., 2014. Genome-wide regression and prediction with the BGLR statistical package. Genetics 198, 483–495.
Pirompud, P., Sivapirunthep, P., Punyapornwithaya, V., Chaosap, C., 2024. Application of machine learning algorithms to predict dead on arrival of broiler chickens raised without antibiotic program. Poult. Sci. 103, 103504.
Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A., Bender, D., Maller, J., Sklar, P., De Bakker, P.I., Daly, M.J., 2007a. PLINK: a tool set for whole-genome association and population-based linkage analyses. Am. J. Hum. Genet. 81, 559–575.
Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A., Bender, D., Maller, J., Sklar, P., De Bakker, P.I., Daly, M.J., 2007b. PLINK: a tool set for whole-genome association and population-based linkage analyses. Am. J. Human Genetics 81, 559–575.
Rosipal, R., 2001. PhD thesis. Univ.Paisley, Scotland.
Shen, K., Qin, H., Zhou, J., Liu, G., 2022. Runoff probability prediction model based on natural Gradient boosting with tree-structured parzen estimator optimization. Water 14, 545.
Solberg, T.R., Sonesson, A.K., Woolliams, J.A., Meuwissen, T.H.E., 2008. Genomic selection using different marker types and densities. J. Anim. Sci. 86, 2447–2454.
Song, H., Zhang, J., Zhang, Q., Ding, X., 2019. Using different single-step strategies to improve the efficiency of genomic prediction on body measurement traits in pig. Front. Genet. 9, 730.
Su, G., Christensen, O.F., Janss, L., Lund, M.S., 2014. Comparison of genomic predictions using genomic relationship matrices built with different weighting factors to account for locus-specific variances. J. Dairy Sci. 97, 6547–6559.
Tomar, V., Dhillon, G.S., Singh, D., Singh, R.P., Poland, J., Chaudhary, A.A., Bhati, P.K., Joshi, A.K., Kumar, U., 2021. Evaluations of genomic prediction and identification of new loci for resistance to stripe rust disease in wheat (Triticum aestivum L.). Front. Genet. 12, 710485.
Wang, J., Zong, W., Shi, L., Li, M., Li, J., Ren, D., Zhao, F., Wang, L., Wang, L., 2024. Using mixed kernel support vector machine to improve the predictive accuracy of genome selection. J. Integr. Agric.
Wang, K., Abid, M.A., Rasheed, A., Crossa, J., Hearne, S., Li, H., 2023. DNNGP, a deep neural network-based method for genomic prediction using multi-omics data in plants. Mol. Plant. 16, 279–293.
Wang, K., Yang, B., Li, Q., Liu, S., 2022a. Systematic evaluation of genomic prediction algorithms for genomic prediction and breeding of aquatic animals. Genes (Basel) 13, 2247.
Wang, X., Shi, S., Wang, G., Luo, W., Wei, X., Qiu, A., Luo, F., Ding, X., 2022b. Using machine learning to improve the accuracy of genomic prediction of reproduction traits in pigs. J. Anim. Sci. Biotechnol. 13, 60.
Yin, C., Zhou, P., Wang, Y., Yin, Z., Liu, Y., 2024. Using genomic selection to improve the accuracy of genomic prediction for multi-populations in pigs. Animal 18, 101062.
Yin, L., Zhang, H., Zhou, X., Yuan, X., Zhao, S., Li, X., Liu, X., 2020. KAML: improving genomic prediction accuracy of complex traits using machine learning determined parameters. Genome Biol 21, 1–22.
Zhang, P., Liu, C., Lao, D., Nguyen, X.C., Paramasivan, B., Qian, X., Inyinbor, A.A., Hu, X., You, Y., Li, F., 2023. Unveiling the drives behind tetracycline adsorption capacity with biochar through machine learning. Sci. Rep. 13, 11512.
Zhang, Z., Jung, C., 2020. GBDT-MO: gradient-boosted decision trees for multiple outputs. IEEE Trans. Neural Networks Learn. Syst. 32, 3156–3167.
Zhou, X., Stephens, M., 2012. Genome-wide efficient mixed-model analysis for association studies. Nat. Genet. 44, 821–824.
Zhu, B., Zhang, J.J., Niu, H., Guan, L., Guo, P., Ling-Yang, X.U., Chen, Y., Zhang, L.P., Gao, H.J., Gao, X., 2017. Effects of marker density and minor allele frequency on genomic prediction for growth traits in Chinese Simmental beef cattle. J. Integr. Agric. 16, 911–920.
Zingaretti, L.M., Gezan, S.A., Ferrão, L.F.V., Osorio, L.F., Monfort, A., Muñoz, P.R., Whitaker, V.M., Pérez-Enciso, M., 2020. Exploring deep learning for complex trait genomic prediction in polyploid outcrossing species. Front. Plant Sci. 11, 25.