Improved Ensemble Performance by Weight Optimisation for the Genomic Prediction of Maize Flowering Time Traits

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Abstract

Ensembles of multiple genomic prediction models have demonstrated improved prediction performance over the individual models contributing to the ensemble. The outperformance of ensemble models is expected from the Diversity Prediction Theorem, which states that for ensembles constructed with diverse prediction models, the ensemble prediction error becomes lower than the mean prediction error of the individual models. While a naïve ensemble-average model provides baseline performance improvement by aggregating all individual prediction models with equal weights, optimising weights for each individual model could further enhance ensemble prediction performance. The weights can be optimised based on their level of informativeness regarding prediction error and diversity. Here, we evaluated weighted ensemble-average models with three possible weight optimisation approaches (linear transformation, Nelder-Mead and Bayesian) using flowering time traits from two maize nested associated mapping (NAM) datasets; TeoNAM and MaizeNAM. The three proposed weighted ensemble-average approaches improved prediction performance in several of the prediction scenarios investigated. In particular, the weighted ensemble models enhanced prediction performance when the adjusted weights differed substantially from the equal weights used by the naïve ensemble models. For performance comparisons within the weighted ensembles, there was no clear superiority

among the proposed approaches in both prediction accuracy and error across the prediction scenarios. Weight optimisation in ensembles warrants further investigation to explore the opportunities to improve their prediction performance; for example, integration of a weighted ensemble with a simultaneous hyperparameter tuning process may offer a promising direction for further research.

Introduction

Plant breeders have a long history of research into technologies for predictive modelling to accelerate genetic improvement of crops for agricultural systems (Cooper et al., 2009, 2021, 2025; Crossa et al., 2017, 2024). Genomic prediction (Meuwissen et al., 2001; Bernardo and Yu, 2007) has enhanced crop breeding programs by reducing breeding cycle length and consequently costs (Crossa et al., 2017; Voss-Fels et al., 2019). Instead of full dependency on phenotype records for selection, genomic prediction identifies potential candidates by predicting trait phenotypes from corresponding genomic marker values (Heffner et al., 2009; Escamilla et al., 2025). The performance of genomic prediction models is influenced by the complexity of the genetic architecture controlling target traits and prediction algorithms, and hence various algorithms have been introduced to achieve higher prediction performance (Hammer et al., 2006; Riedelsheimer et al., 2012; Technow et al., 2015; Messina et al., 2018; Voss-Fels et al., 2019; Negus et al., 2024).

The success of each genomic prediction model has motivated the investigation of ensembles that aggregate the strengths of multiple genomic prediction models (Kick and Washburn, 2023; Cooper et al., 2025; Messina et al., 2025; Washburn et al., 2025). A range of ensemble-based prediction approaches have been introduced, employing both simple arithmetic averaging (Wallach et al., 2018; Kick and Washburn, 2023) and more complex aggregations (McCormick et al., 2021; Yan et al., 2021). The evaluation of these ensemble approaches revealed successful performance improvement across various traits and datasets. The potential of ensembles can be explained by the framework of the Many-model Diversity Prediction Theorem (Hong and Page, 2004; Page, 2007; Page, 2014; Page, 2018), which states that the prediction error of an ensemble becomes lower than the mean error of individual prediction models, assuming that the ensemble consists of diverse prediction models. This theoretical framework provides a logical basis for the potential of ensemble

58 approaches, explaining the improved genomic prediction performance in previous studies and thereby
59 motivating the further investigation of ensemble algorithms.

60 In our previous investigations of ensembles (Tomura et al., 2025a, b, c), we demonstrated the
61 framework of the Diversity Prediction Theorem as a foundation for constructing ensembles of prediction
62 models that equally weigh the contributions of individual models. The observed results indicated inconsistent
63 levels of performance improvement for different scenarios generated by various combinations of traits and
64 datasets. The Diversity Prediction Theorem provides a possible interpretation of such inconsistency by
65 emphasising the importance of model diversity in the construction of ensembles, when the individual models
66 are given equal weight in their contribution to the ensemble. While the theorem does not directly inform the
67 optimal weightings for models when their contributions to ensembles differ, it does provide a framework for
68 exploring alternative weightings that can improve prediction performance relative to that of the naïve
69 ensemble. This application of the Diversity Prediction Theorem is investigated as a novel contribution with
70 broad applications for genomic prediction.

71 The weight adjustment problem of the ensembles shares a structural similarity with the framework of
72 other optimisation problems. By adjusting key variables, optimisation approaches aim to achieve the best
73 value of the performance criteria (highest benefit or lowest cost) in target complex problems. In the ensemble,
74 a weight assigned to each individual prediction model can be a key variable, and the optimum weight values
75 can be estimated based on performance criteria defined in the respective prediction algorithms. Through
76 weight optimisation of individual models, the predictive ability of ensembles was further improved for
77 genomic prediction in animal breeding applications (Liang et al., 2021a, b; Yu et al., 2021; Liang et al., 2023;
78 Wang et al., 2023). However, the potential of weight optimisation to improve performance of ensembles has
79 not been well investigated in crop breeding applications.

80 Here, we investigated the potential to construct weighted ensemble-average models for genomic
81 prediction in crop breeding using three different weight optimisation methods, two of which directly use the
82 Diversity Prediction Theorem as a framework to identify weightings. The prediction performance was
83 evaluated by extending our previous studies (Tomura et al., 2025a, b, c) in maize flowering time traits (Buckler
84 et al., 2009; Chen et al., 2019). Three objectives motivated this study: (1) Compare the prediction performance

of the proposed weighted ensemble-average models against the benchmark ensemble using equal weights (naïve ensemble-average model) following the Diversity Prediction Theorem. (2) Analyse how the diversity in the individual genomic prediction models affected the prediction performance of the ensembles by applying the framework of the Diversity Prediction Theorem. (3) Compare the prediction performance of the three weighted ensemble-average models to identify which weighting approach consistently improved the prediction performance. Combining these three objectives, we apply the Diversity Prediction Theorem as a framework to investigate which weight optimisation method can outperform the naïve ensemble-average model by adjusting weights in proportion to the diversity of prediction performance at the individual prediction model level.

Materials & Methods

1. Datasets

In this study, two maize nested association mapping (NAM) datasets were used to investigate the proposed ensemble approaches: the TeoNAM (Chen et al., 2019) and MaizeNAM (Buckler et al., 2009) datasets. The total number of recombinant inbred lines (RILs) and genomic markers (SNPs) was summarised in Table S1.

The TeoNAM dataset provides the genotype (genomic markers in the form of single nucleotide polymorphisms, SNPs) and trait phenotype records of RILs from five subpopulations, developed from hybrids between the maize inbred line W22 and five teosinte lines (*Z. mays ssp. parviglumis* for TIL01, TIL03, TIL11 and TIL14 and *Z.mays ssp. mexicana* for TIL25). Following the initial cross, the F1 was backcrossed once with W22. Subsequently, four generations were created through controlled self-pollination. The five RIL populations were evaluated twice through a randomised complete block design at the University of Wisconsin West Madison Agricultural Research Station. For W22TIL01, W22TIL03 and W22TIL11, the RILs were evaluated in the summers of 2015 and 2016. For W22TIL14, the RILs were evaluated in the summers of 2016 and 2017. W22TIL25 was evaluated at two different blocks in the summer of 2017. Since each subpopulation dataset consists of two record sets due to the evaluation of each RIL twice, both record sets were concatenated into one dataset by adding a factor column representing the respective environments in each subpopulation.

The MaizeNAM (Buckler et al., 2009) dataset provides genotype (SNPs) and trait phenotype records from RILs in 25 hybrid populations of the B73 maize line and 25 inbred lines generated from breeding programs operating in temperate and tropical regions. Following the initial cross to create the F1 generation, the F1 individual was self-pollinated to create the F2 generation. Each RIL population was generated by controlled self-pollination of a sample of F2 individuals until the generation was advanced to F5. The F5 RILs were tested twice in each of the four locations (Aurora in New York, Clayton in North Carolina, Columbia in Missouri and Urbana in Illinois) with a randomised design for each test. The scored phenotypes for each RIL across the environments were used to calculate best linear unbiased predictors (BLUPs) with ASReml (v2.0) per population. The estimated BLUPs were linked to their corresponding genotypes as phenotype values.

The genetic diversity of the founders of the TeoNAM and MaizeNAM datasets was investigated by Hufford et al. (2012). The TeoNAM dataset is expected to have higher genetic diversity due to crosses with the ancestor species of maize (teosinte), introducing variation at loci that have become fixed during the domestication process. In contrast, the MaizeNAM dataset is expected to have less genetic diversity due to crosses involving elite lines created post domestication. The dataset diversity broadens the range of scenarios considered and is expected to affect the predictive performance of the individual genomic prediction models and the proposed weighted ensemble approaches. Hence, the difference in genetic marker pattern diversity between the TeoNAM and MaizeNAM datasets is advantageous for the objectives of this study.

Two flowering time-related traits (days to anthesis (DTA) and anthesis to silk interval (ASI)) were targeted for evaluation of the ensemble approaches. For DTA, the genetic architecture has been well-studied (Dong et al., 2012; Wisser et al., 2019), and hence it is possible to assess the model features for each ensemble approach at the genome level by comparing the estimated genetic architecture from each proposed approach with the well-known key gene regulators of DTA. ASI is a secondary trait that is measured as the difference between DTA and days to silk (DTS) flowering traits, potentially generating a more complex genetic architecture that is controlled by both traits and other developmental processes (Messina et al., 2019). Greater biological complexity of ASI might affect the prediction performance of the individual prediction models and proposed weighted ensemble approaches. The two maize NAM datasets and traits were used to investigate the predictive characteristics of the proposed weighted ensemble-average approaches.

2. Data preprocessing

Prior to the prediction performance evaluation of the ensembles, the two NAM datasets were processed by applying the three approaches leveraged in Tomura et al. (2025b). For the TeoNAM dataset, missing genetic markers were imputed using flanking markers. For the MaizeNAM dataset, Buckler et al. (2009) applied the flanking marker-based imputation, and hence no missing genomic markers were observed. RILs with missing phenotypes were removed from the TeoNAM dataset, while Buckler et al. (2009) had already removed RILs with missing phenotypes during the BLUP calculation process in the MaizeNAM dataset. Genomic markers were then filtered to mitigate the curse of dimensionality (Bellman, 1957; Ramstein et al., 2019), which can negatively affect the prediction patterns by containing an excessively large number of attributes (genomic markers, SNPs) compared to data points (RILs) for trait phenotype. Genomic markers with linkage disequilibrium (LD) higher than 0.8 were removed, applying a window size of 30,000 and a step size of 5 using PLINK (v1.9) (Chang et al., 2015) for the TeoNAM and MaizeNAM datasets.

3. Genomic prediction models

Three classical genomic prediction models (ridge regression BLUP (rrBLUP), BayesB and reproducing kernel Hilbert Space regression (RKHS)) and three machine learning models (random forest (RF), support vector regression (SVR) and multi-layer perceptron (MLP)) were developed as individual genomic prediction models in this study using the computational tool EasiGP (Tomura et al., 2025c) in Python (v3.11.10) (Figure 1). rrBLUP and BayesB (Meuwissen et al., 2001) were implemented through a linear mixed model (Pérez and de Los Campos, 2014). These models are grounded in different assumptions regarding the distribution of genomic marker effects: normally distributed with the same variance for rrBLUP (Endelman, 2011), and a mix of zero effects and values from a t-distribution for BayesB. Such a difference in these assumptions is typically represented as shrinking a large amount of genomic marker effects to zero in BayesB, but not in rrBLUP. RKHS regression (Gianola and Van Kaam, 2008) uses a kernel based on squared Euclidean distance that implicitly maps data points (RILs) into a Hilbert space (de los Campos et al., 2009). RF (Breiman, 2001) is a

tree-based approach consisting of a collection of decision trees that predict values through a series of decision conditions from provided attributes (SNPs). The mean predicted values from each tree are calculated to determine the final prediction values. SVR (Drucker et al., 1996) optimises the location of a hyperplane by including the maximum number of data points between the hyperplane and support vectors (epsilon tube). By optimising the hyperplane location based on data points mapped to higher dimensions using a kernel, SVR returns predicted values with nonlinear prediction patterns. MLP (Rosenblatt, 1962) predicts target values by mimicking the structure of the information transmission system in human brains. Numerous neurons are fully connected across several layers to aggregate information from others that were converted nonlinearly by applying an activation function. Consequently, the final prediction values are expected to be the sequential results of captured complex nonlinear prediction patterns.

Following the Diversity Prediction Theorem, the naïve ensemble-average model (Tomura et al., 2025b) calculated the arithmetic mean of predicted trait phenotypes from all individual genomic prediction models with equal weights (Figure 1). The prediction performance of the naïve ensemble-average model is used as a benchmark for evaluating that of the weighted ensemble-average models.

For classical genomic prediction models (rrBLUP, BayesB and RKHS), the number of iterations was set to 12,000 and the burn-in was set to 2,000 in both datasets. The values for the other parameters were not adjusted from default settings. The number of decision trees was set to 1,000 in RF. Radial Basis Function (RBF) kernel was used in SVR. For the remaining hyperparameters in RF and SVR, the default hyperparameter values were leveraged for both datasets. In both datasets, MLP contained one hidden layer. For the TeoNAM dataset, 50 neurons were developed in the hidden layer with a dropout of 0, which were nonlinearly transformed using the Rectified Linear Unit (ReLU; Nair and Hinton, 2010) activation function. The constructed model was trained 200 times iteratively with a learning rate of 0.005 using the Adaptive Moment Estimation with decoupled weight decay (AdamW; Loshchilov and Hutter, 2017) optimiser. For the MaizeNAM dataset, the number of neurons was set to 10 with a dropout of 0.1. ReLU was also used as the activation function. The prediction model was trained with 2,500 iterations with a learning rate of 0.005 using the Root Mean Square Propagation (RMSprop; Tieleman, 2012) optimiser. Different hyperparameter settings were used for each dataset since the selected hyperparameter setting for one dataset achieved considerably

low prediction performance on the other. These hyperparameter settings for each prediction model were previously demonstrated to provide stable results for applications of these prediction methods in the TeoNAM and MaizeNAM datasets (Tomura et al., 2025a, b, c). The combinations of hyperparameter values were selected heuristically from a range of options, and hence other hyperparameter value combinations might possibly achieve higher prediction performance. Hyperparameter tuning in consideration with weight optimisation methods can be a research extension for weighted ensemble studies, as mentioned later in the Discussion.

4. Weight optimisation

Three weight optimisation approaches (linear transformation, Nelder-Mead and Bayesian) were implemented to construct weighted ensembles as a part of the EasiGP software pipeline (Tomura et al. 2025c) operation in this study (Figure 1).

The linear transformation ensemble-average model was implemented to discover the set of optimum weights that minimises the mean square error (MSE) objective function using the neural network approach. A set of predicted phenotypes from each individual genomic prediction model was multiplied by a corresponding trainable weight. The weighted predicted trait phenotypes from all individual genomic prediction models were summed as the final predicted phenotypes. The optimum value for the weights was determined through the iterative training process as performed in MLP training. The weight values were adjusted in each iteration to minimise the difference between the predicted and observed trait phenotype values. However, the randomness in the initial weight values affected the ideal number of training iterations, and hence the standard training approach could not effectively identify the optimum weights. To mitigate this problem, the linear transformation ensemble-average model was equipped with an early stop. If the prediction error (MSE) for the validation set did not improve after M iterations (defined as patience), the training process was terminated. After the development of the N independent ensemble models with the early stop, the one that reached the lowest prediction error in the validation set was selected as the final linear transformation ensemble-average model. The total number of neurons was set to six (the total number of individual genomic prediction models

in this study was six). In both datasets, the total number of epochs was 150 with the optimiser of Adaptive Moment Estimation (Adam, Kingma and Ba, 2014). The learning rate was 0.005 with the weight decay of 0.01. The size of each batch was set to 2. The number of the independent linear transformation ensemble-average model (N) and patience (M) were set to 30 and 10, respectively.

The Nelder-Mead ensemble-average model heuristically determined the optimum set of weights that minimised an objective function using the Nelder-Mead algorithm (Nelder and Mead, 1965). The algorithm randomly selected sets of values for the vertices (weights in this study) prior to the implementation. Those sets were defined as Simplex, and an output value from the objective function using each vertex was returned. Subsequently, the vertices were ranked by the value of the returned output, and the one returning the worst performance in relation to the objective function was replaced with another vertex calculated based on the concept of reflection, expansion and contraction (Singer and Nelder, 2009). This replacement process was repeated until the output values from the objective function converged or until the defined number of iterations was reached. The objective function used in this study was derived from the Diversity Prediction Theorem (Page, 2018) defined below:

$$(\bar{M} - V)^2 = \sum_{i=1}^{N} \frac{(M_i - V)^2}{N} - \sum_{i=1}^{N} \frac{(M_i - \bar{M})^2}{N} \tag{1}$$

where M_i is the predicted value from the prediction model i, $\bar{M}$ is the mean predicted value from the i individual prediction models calculated from the arithmetic mean operation with the same weight, V is the true value and N is the total number of prediction models included in the ensemble mechanism. The Many-model error (first term) is estimated by the subtraction of the prediction diversity (third term) from the mean error of individual prediction models (second term). In this study, observed phenotypes were defined as the true value V, and the Many-model error was leveraged as the ensemble error. The Diversity Prediction Theorem indicates that the diversity in the predicted values can reduce the ensemble prediction error compared to the mean prediction error of individual prediction models. The minimisation of Equation (1) can improve the prediction performance of the ensemble, achieved by adjusting the predicted phenotype (M_i) from each

individual genomic prediction model using weights. Hence, the objective function for the Nelder-Mead ensemble-average model can be represented below:

$$\min_{w_i} \sum_{i=1}^{N} w_i * (M_i - V)^2 - \sum_{i=1}^{N} w_i * (M_i - \bar{M})^2 \tag{2}$$

where w_i is the weight allocated to the individual prediction model i. When the weights were equal as applied in the naïve ensemble-average model, the weights were represented as constant: $w_i = \frac{1}{N}, \forall_i$. In the weight ensembles, the weights were adjusted to minimise Equation (2). The weight values were optimised to increase the prediction diversity values for minimising the ensemble error in relation to the mean error of the individual prediction models. In both datasets, the total number of weights was six (the total number of individual genomic prediction models). Weight values were sought within the range of 0 and 10 and then normalised. The threshold for the convergence was $1*10^{-8}$. The other parameters were set to default.

The Bayesian ensemble-average model statistically estimated the optimum variable (weight) values to maximise an objective function. Using the values of the objective function based on the random sets of weight values, the algorithm estimated the ranges of potential sets of weight values that are likely to be the optimum by developing a surrogate model. An acquisition function converted the information from the surrogate model to estimate the next set of weights that was likely to maximise the objective function. This process of sampling and updating was iterated until the returned value converged or reached the end of the iteration process. The objective function for the Bayesian ensemble-average model was defined below based on Equation (2):

$$\max_{w_i} \frac{1}{\sum_{i=1}^{N} w_i * (M_i - V)^2 - \sum_{i=1}^{N} w_i * (M_i - \bar{M})^2} \tag{3}$$

The weights (w) were adjusted to maximise Equation (3). Since Equation (3) is the inverse of Equation (2), the maximisation of Equation (3) leads to the minimisation of Equation (2). In both datasets, the total number of weights was six, which were optimised within the range of values 0 and 10 with normalisation. The expected improvement was used as the acquisition function with the exploration-exploitation trade-off hyperparameter of $1*10^{-6}$. The other hyperparameters were set to default.

265 5. Genomic marker and marker-by-marker interaction effect inference

266 Genomic marker (SNP) effects were extracted from the individual genomic prediction models and the
267 ensemble models using the back-calculation functions in EasiGP (Tomura et al. 2025c). For rrBLUP and
268 BayesB, the allele substitution effects were used as the SNP effects. For RKHS, SVR, MLP and pairwise SNP
269 effects (genomic marker-by-marker interaction effects) from RF, Shapley scores (Shapley, 1953; Lundberg
270 and Lee, 2017) were used to compare the causal effect of a specific SNP represented in an accumulative
271 conditional effect. Shapley scores from the 50 randomly chosen data points (RILs) were leveraged as the SNP
272 effects in the absolute value format for each prediction scenario. For RF, the impurity-based approach
273 (Ishwaran, 2015) was applied to extract SNP effects. A higher importance (SNP effect size) value was allocated
274 to the corresponding attribute (SNP) if the SNP value clearly clusters data points (RILs) with similar target
275 (trait phenotype) values. The SNP effects for the naïve ensemble-average model were estimated by calculating
276 the mean value of the normalised SNP effects from the individual genomic prediction models. For the
277 weighted ensemble models, the mean value of the normalised SNP effects from all the individual genomic
278 prediction models was calculated with weights estimated in each method.

279

280 6. Trait genetic architecture comparison

281 The extracted genomic marker SNP effects and interactions from the genomic prediction models were mapped
282 to respective genomic marker regions using circos plots (Krzywinski et al., 2009) to visualise the genetic
283 architecture derived from each prediction model and the four ensemble-based models as the final phase in
284 EasiGP operations (Tomura et al., 2025c). The first few rings of the circos plot represented key gene regions
285 identified in the previous studies. For the circos plots of DTA, the innermost ring indicated QTL regions from
286 Chen et al. (2019) for the TeoNAM dataset and Buckler et al. (2009) for the MaizeNAM dataset. The second
287 innermost ring showed the location of each QTL from Wisser et al. (2019). The third and fourth rings
288 represented the key gene locations that operate on the leaf and shoot apical meristem (SAM), respectively,
289 from Dong et al. (2012). The subsequent rings represented the estimated SNP effects from each genomic
290 prediction model. For ASI, QTL information (Chen et al. (2019) for the TeoNAM dataset and Buckler et al.

(2009) for the MaizeNAM dataset) was used as the key gene region ring, and the SNP genomic marker effect rings followed afterwards. For the TeoNAM and MaizeNAM datasets, the range of each SNP genomic marker on the circos plot was extended by 0.2 cM and 1 cM, respectively, on each side for visualisation purposes. Internal links between SNP positions illustrated genomic marker pairs with the top 0.01% of the highest pairwise Shapley scores in both datasets.

7. Genomic prediction model evaluation

Two metrics were used to evaluate the prediction performance of each genomic prediction model. Pearson correlation measured the prediction accuracy, whereas MSE measured the prediction error. For the calculation of the diversity level in each proposed ensemble approach, the ratio of the prediction diversity (third term) over the mean error of individual prediction models (second term) from the Diversity Prediction Theorem was leveraged by updating Equation (1):

$$ratio = \frac{\sum_{i=1}^{N} w_i * (M_i - \bar{M})^2}{\sum_{i=1}^{N} w_i * (M_i - V)^2} \quad (4)$$

Since the scale of each phenotype differed from traits and datasets, the direct comparison of the third term in Equation (1) did not allow for a fair comparison of the diversity observed in each ensemble approach. Additionally, the level of diversity needs to be analysed in relation to the mean error of individual genomic prediction models. The Many-model error (first term) would still be high even if the prediction diversity (third term) was high when the mean error of individual prediction models (second term) was also high. A higher ratio value in Equation (4) indicated more diversified phenotypes in relation to the second term in Equation (1).

The prediction performance and the diversity level of the four ensemble models were iteratively evaluated under various prediction scenarios (Figure 1). For the TeoNAM dataset, each subpopulation data was sampled 500 times, and hence 2,500 (5 populations * 500 samples) different prediction scenarios were generated per trait. For the MaizeNAM dataset, each subpopulation data was sampled 50 times, and hence 1,250 (25 populations * 50 samples) different prediction scenarios were generated per trait. The data was split

316 into training, validation and test sets with the ratio of 0.5-0.25-0.25 (Figure 1). The optimum weights were
317 estimated from the validation set. The prediction performance of each ensemble approach was evaluated using
318 the test set in each prediction scenario. The SNP genomic marker and marker-by-marker interaction effects
319 for the circos plots were estimated by calculating the mean values across all the prediction scenarios in each
320 trait.

321

322 Results

323 1. The weighted ensemble-average models improved prediction performance for DTA but not for ASI

324 The prediction ability of the proposed weighted ensemble models depended on the target traits. For DTA, all
325 weighted ensemble-average models reached higher median prediction accuracy and lower median prediction
326 error than the naïve ensemble model, especially for the TeoNAM dataset (Figure 2; Table S2). In the TeoNAM
327 dataset, the Nelder-Mead ensemble model reached the highest median prediction accuracy (Pearson
328 correlation = 0.879) and the lowest median prediction error (MSE = 8.448). Similarly, the Nelder-Mead
329 ensemble model achieved the highest median prediction accuracy (0.625) and lowest median prediction error
330 (2.436) in the MaizeNAM dataset, with a small performance difference compared to other ensemble-average
331 models. This result indicates that the weighted ensemble-average models can improve prediction performance
332 for DTA in both the TeoNAM and MaizeNAM datasets.

333 For ASI, however, such outperformance of the weighted ensemble-average models was not clearly
334 observed. The naïve and weighted ensemble methods performed similarly (Figure 2; Table S2). In the
335 TeoNAM dataset, while the naïve ensemble-average model reached the highest median prediction accuracy
336 and lowest median prediction error, the difference from the other models was subtle (prediction accuracy
337 ranging from 0.469 to 0.477; prediction error ranging from 4.476 to 4.555). In the MaizeNAM dataset, the
338 prediction performance difference between the naïve ensemble-average model and the weighted ensemble-
339 average models was negligible in both median prediction accuracy (ranging from 0.432 to 0.436) and
340 prediction error (ranging from 4.461 to 4.666). The weighted ensemble-average model did not clearly improve

341 the prediction performance of the naive ensemble average model for ASI in either the TeoNAM or MaizeNAM
342 dataset.

343

344 2. Individual models contributed differently to the weighted ensembles across the traits and datasets

345 The contribution level of each individual genomic prediction model for the proposed weighted ensemble
346 models highly depended on the traits. For DTA, the parametric and semiparametric genomic prediction models
347 (rrBLUP, BayesB and RKHS) were assigned heavier weights with more diverse weighting patterns compared
348 to the machine learning models (RF, SVR and MLP) (Figure 3; Table S3). For the TeoNAM dataset, the mean
349 sum of weights from the parametric and semiparametric genomic prediction models across the weighted
350 ensembles (0.773) was considerably higher than that from the machine learning models (0.227). The
351 differences between the highest and lowest normalised mean weights for the parametric and semiparametric
352 genomic prediction models were also higher than the machine learning models (rrBLUP = 0.173, BayesB =
353 0.323, RKHS = 0.287, RF = 0.102, SVR = 0.014, MLP = 0.050). The same trend was observed in the
354 MaizeNAM dataset, showing heavier mean summed weights from the parametric and semiparametric genomic
355 prediction models across the three weighted ensembles (0.687) than the machine learning models (0.313),
356 with higher weight value differences (rrBLUP = 0.210, BayesB = 0.084, RKHS = 0.340, RF = 0.127, SVR =
357 0.087, MLP = 0.082). This comparison indicates that the proposed weighted-ensemble approaches emphasised
358 predictive information from the parametric and semiparametric genomic prediction models more with diverse
359 weighting patterns for DTA.

360 In contrast, heavier weights were assigned to the machine learning models with similar weighting
361 patterns across the three weighted ensemble-average models for ASI (Figure 3; Table S3). The mean summed
362 weight of parametric and semiparametric genomic prediction models across the weighted ensemble models
363 (0.446) became smaller than that of machine learning models (0.555) for the TeoNAM dataset. The weight
364 value differences in the parametric and semiparametric genomic prediction models became smaller for ASI
365 compared to DTA (rrBLUP = 0.041, BayesB = 0.043, RKHS = 0.060, RF = 0.008, SVR = 0.153, MLP =
366 0.085). The same trend was observed for the MaizeNAM dataset, with increased mean summed weight from
367 the machine learning models (0.472) that was comparable to that from the parametric and semiparametric

368 models (0.528), with less diverse weighting patterns than DTA (rrBLUP = 0.128, BayesB = 0.191, RKHS =
369 0.111, RF = 0.033, SVR = 0.029, MLP = 0.003). These observed results indicate that the predictive information
370 from the machine learning models was emphasised more for ASI, and the naïve ensemble-average model
371 weights were within the range of values identified by all three weighted ensemble algorithms. A smaller
372 deviation in the weight combination identified by the weighted ensemble-average models from that of the
373 naïve ensemble-average model led to similar prediction performance in both naïve and weighted ensemble-
374 average models for ASI (Figure 2, 3; Table S3).

375

376 3. The Diversity Prediction Theorem provided insight into when the weight optimisation reduces prediction
377 error

378 The framework of the Diversity Prediction Theorem revealed that the effect of the weight optimisation on
379 diversity at the individual level was highly trait-dependent. The Many-model error (first term) for the weighted
380 ensemble-average models was lower than that of the naïve ensemble-average models for DTA across the
381 datasets (Table 1). This lower Many-model error was attributed to reduced mean prediction error (second term)
382 and enhanced model diversity (third term) at the individual level compared to those of the naïve ensemble-
383 average models. Consequently, the ratio of the third term over the second term tended to be higher for DTA,
384 especially in the TeoNAM dataset. The Bayesian ensemble-average model achieved the highest ratio value in
385 both datasets. In contrast, no notable differences in the values of each term were observed for the ASI of both
386 datasets. While the naïve ensemble-average and the Bayesian ensemble-average models achieved the highest
387 ratio values for the TeoNAM and MaizeNAM datasets, respectively, the differences among the ensemble
388 models were subtle. These results indicated that when the three weighted ensemble-average models did not
389 diversify the individual genomic prediction models more than the naïve ensemble-average model, they failed
390 to improve prediction performance relative to the naïve ensemble-average model.

391

392 4. The ensemble models returned similar predicted phenotypes and trait genetic architecture

393 The differences between naïve ensemble-average and the three weighted ensemble-average models were small
394 at both predicted phenotype and genome levels. The pairwise comparison of the ensemble models at the
395 predicted phenotype level showed a strong mean Pearson correlation across pairs, especially in the
396 MaizeNAM dataset (DTA = 0.990, ASI = 0.982) compared to the TeoNAM (DTA = 0.939, ASI = 0.931) dataset
397 for both traits (Figure 4). The stronger correlation for the MaizeNAM dataset was highlighted when the mean
398 correlation was calculated for the pairs with the naïve ensemble-average model, especially for DTA
399 (MaizeNAM = 0.985, TeoNAM = 0.901) rather than ASI (MaizeNAM = 0.973, TeoNAM = 0.953). While the
400 observed correlations between the naïve ensemble-average model and the weighted ensemble-average models
401 were high for both datasets and traits, the lower correlation with the naïve ensemble-average model for DTA
402 in the TeoNAM dataset corresponded to the larger improvement of prediction performance using the weighted
403 ensemble-average models for DTA in the TeoNAM dataset.

404 Similarly, the mean correlation values for the genomic marker effects in the MaizeNAM (DTA = 0.926,
405 ASI = 0.921) and TeoNAM (DTA = 0.929, ASI = 0.931) datasets were high. This strong correlation between
406 the ensemble pairs was observed as clear positive associations for genomic markers with small effect sizes,
407 while weaker correlations between the pairs were observed for genomic markers assigned larger effect sizes
408 (Figure 4). These association patterns indicate that more variation in quantification patterns for genomic
409 markers with large effect sizes resulted in slightly more contrasting predicted phenotypes, especially in the
410 TeoNAM dataset. Nonetheless, both predicted phenotypes and genomic marker effects of the ensemble
411 approaches were similar, considering the high mean correlation values.

412 The similarity of the weighted ensemble-average models at the genome level was also observed in the
413 constructed circos plots representing the inferred genetic architecture of DTA and ASI (Figure 5). Each
414 weighted ensemble-average model highlighted similar genome regions as highly influential to the target traits
415 across the chromosomes. These consistent quantification patterns were emphasised when compared with the
416 inferred trait genetic architecture from the individual genomic prediction models that showed highly diverse
417 patterns of genomic marker effects, especially for the TeoNAM dataset (Figure 5). Additionally, several
418 highlighted genomic marker regions in the genetic architecture of each ensemble model overlapped with key
419 gene regulators identified in previous studies. This trend was more recognisable in the MaizeNAM dataset

420 (Figure 5). This indicates that the proposed ensemble models captured similar genetic architectures across the
421 chromosomes for both traits, especially in the MaizeNAM dataset, while capturing the large marker effects of
422 several well-known key gene regions to improve their prediction performance.

423

424 Discussion

425 1. Weighted ensemble performance is affected by the precision and diversity of the inferred trait genetic
426 architecture at the individual level

427 This study investigated the possibility of improving the prediction performance using weighted ensemble
428 approaches over the naïve ensemble-average methodology through weight optimisation. We clarify that the
429 naïve ensemble-average model is a specific weighting pattern in weighted ensemble-average models, where
430 the contributing individual models are given equal weight (Figure 3). In a number of cases, the prediction
431 accuracy and error results from the naïve ensemble-average model were also observed within the results of
432 the weighted ensemble-average models, particularly for ASI (Figure 2). In contrast, the three weighted
433 ensemble-average models frequently achieved higher prediction performance for DTA than the naïve
434 ensemble-average model across the datasets. The observed result indicates that the proposed weighted
435 ensemble-average models were more effective in finding improvements over the naïve ensemble-average
436 model for DTA rather than ASI. The equally weighted scenario of the naïve ensemble model might have
437 already been close to the optimal weights for ASI in both datasets. Therefore, the weighted ensemble models
438 could not find improvements in the weights for the individual prediction models.

439 The lower accuracy in the inferred trait genetic architecture at the individual level might have reduced
440 the predictive ability of the weighted ensemble-average models for ASI. Such lower accuracy might have been
441 attributed to the potential complexity of the trait genetic architecture. ASI is a secondary trait controlled by
442 two quantitative flowering time traits (DTA and DTS) (Lu et al., 2010; Mhike et al., 2012; Messina et al.,
443 2019), potentially increasing the complexity level of nonlinearity in the regulatory network. The component
444 of nonlinearity was emphasised by the increased weights of the machine learning models for ASI in both
445 datasets (Figure 3; Table S3), since machine learning models primarily focus on capturing complex nonlinear

interactions between SNP genomic markers. However, the complex genetic architecture might have challenged the accurate detection of key genomic marker regions and their interactions by the individual genomic prediction models, including the machine learning models in this study. Such complexity in the regulatory network can also be further strengthened by the high sensitivity of ASI to genotype-by-environment (GxE) interactions (Buckler et al., 2009; Silva et al., 2022). Detailed environmental information can help prediction models learn key predictive patterns in environmental factors, possibly mitigating the negative effects of the complexity. However, the datasets used in this study did not include details of the environmental attributes. The difficulty in segregating environmental factors from the genetic architecture might have been amplified. The precision of the inferred trait genetic architecture at the individual level and thereby their prediction performance might have been reduced (Cooper et al., 2022; Arenas et al., 2025). Since the prediction information from the individual level might have been inaccurate, it might have been difficult for the weighted ensemble-average models to optimise and diversify weights (Figure 3; Table S3). Consequently, the proposed weighted ensemble-average models might have failed to improve the prediction performance (Table 1) (Holland, 2007; Yang et al., 2011). Hence, high accuracy in the captured genetic architecture at the individual level can be a critical factor in improving the prediction performance of the weighted ensemble-average models. The inferred genetic architecture can be verified through comparative analysis using the true trait genetic architecture defined from simulation datasets as a future research area.

The diversity of the individual genomic prediction models can be another factor influencing the prediction performance of ensembles. The inferred genetic architecture of both traits from the individual genomic prediction models for the TeoNAM dataset was more diverse compared to that for the MaizeNAM dataset (Figure 5). As implied by the Diversity Prediction Theorem (Hong and Page, 2004; Page, 2007; Page, 2014; Page, 2018), higher information diversity reduces the ensemble error by offsetting the weaknesses of individual genomic prediction models (Washburn et al., 2025). Assuming that the captured genetic architecture of DTA was more accurate than ASI, as discussed above, this higher diversity of the individual genomic prediction models at the genomic level might have contributed to the greater improvement in prediction performance with the weighted ensembles for DTA in the TeoNAM dataset compared to the MaizeNAM dataset. The diversity analysis using the two traits and datasets revealed that the diverse genetic architecture,

473 in combination with the accuracy of the individual genomic prediction models, can be critical factors
474 influencing the potential to amplify the predictive ability of ensembles through weight optimisation.

475

476 2. Multiple optimum weight combinations imply the absence of a consistent winner among the weighted
477 ensembles

478 The prediction performance of the proposed weighted ensemble approaches was similar across the traits and
479 datasets (Figure 2). Strong positive associations between the weighted ensemble approaches were observed at
480 both predicted phenotype and genomic marker effect levels (Figure 4). Despite such high similarity at both
481 levels, the weights assigned to each individual genomic prediction model were diverse, especially for DTA
482 (Figure 3; Table S3). This suggests that multiple weight combinations can optimise prediction performance
483 under the prediction scenarios in this study. The observed prediction performance among the weighted
484 ensemble-average models implies the No Free Lunch Theorem (Wolpert and Macready, 1997), stating that the
485 average performance of each prediction model becomes equivalent to others across all prediction scenarios.
486 The effect of the No Free Lunch Theorem for genomic prediction in crop breeding has been widely observed
487 and discussed at the individual genomic prediction level (Heslot et al., 2012; Haile et al., 2021; Merrick et al.,
488 2021; Lourenço et al., 2024; Montesinos-Lopez et al., 2024; Crossa et al., 2025). The results from this study
489 emphasise the No Free Lunch Theorem for genomic prediction in crop breeding at a higher prediction
490 performance level by demonstrating no "best" weighted ensemble-average model when using similar
491 objective functions.

492 The integration of the trait genetic architecture into ensemble models as prior knowledge can be an
493 alternative approach to mitigate the effect of the No Free Lunch Theorem. The customisation of the prediction
494 model into a problem-specific structure can mitigate the effect of the theorem (Montgomery, 2002). Traits are
495 regulated by complex interactions between genetic markers, forming a genetic architecture (Hammer et al.
496 2006; Cooper et al., 2009). Hence, inferring the genetic architecture beforehand and integrating such
497 information as prior knowledge can effectively supervise genomic prediction models to be problem-specific,
498 especially when the training set size is small (Von Rueden et al., 2021). The genetic architecture can be

represented as a graph, and graph-oriented prediction models such as graph neural networks can directly integrate such graphical information into their prediction mechanisms to predict phenotypes (Xing et al., 2022). The incorporation of graph-based models into weighted ensemble-average models can be investigated to identify opportunities for further enhancing prediction performance.

3. A combined pipeline of hyperparameter tuning and weight optimisation may improve prediction performance

The diversity of individual genomic prediction models has been demonstrated and discussed as a critical factor in improving the prediction performance of the proposed weighted ensemble-average models in this study (Figures 3, 4). However, the current weighted ensemble approaches do not explicitly coordinate between the individual genomic prediction models and the weighting algorithms to maximise the diversity without compromising the prediction accuracy, potentially hindering the reach of the global optimum. As one approach addressing this problem, the hyperparameters of the developed individual genomic prediction models can be tuned to maximise the improvement level of prediction performance using weight optimisation algorithms. The simultaneous optimisation of both weights and hyperparameters has improved prediction performance in several research studies (Lévesque et al., 2016; Wenzel et al., 2020; Shahhosseini et al., 2022). Hence, the prediction mechanisms of each individual genomic prediction model can be further adjusted to increase the diversity through hyperparameter tuning, combined with the weight optimisation incorporated into the weighted ensemble-average model (Shahhosseini et al., 2022).

The combined prediction pipeline can be created by seamlessly connecting the individual genomic prediction models and the weighted ensemble-average models by updating Equation (2) as follows:

$$\min_{w_i,h_i} \sum_{i=1}^{N} w_i * (f_i(X,Y,h_i) - V)^2 - \sum_{i=1}^{N} w_i * (f_i(X,Y,h_i) - \bar{M})^2 \quad (5)$$

where X is the vector of genomic marker values, Y is the phenotype value, $f_i(\cdot)$ is an individual prediction model and h_i is the set of hyperparameters related to the prediction model ($f_i(\cdot)$). The hyperparameters of each individual genomic prediction model can be optimised using the validation set as well as the weights

allocated to each. This pipeline can simultaneously optimise hyperparameters to diversify genomic prediction models with the consideration of the subsequent weight adjustment process, potentially further improving prediction performance. This is a promising area for further investigation that is highlighted by the current investigation of weighted ensemble prediction.

Conclusion

In this study, the prediction performance of the three weighted ensemble-average models based on different optimisation strategies (linear transformation, Nelder-Mead and Bayesian algorithms) was evaluated against the prediction performance of the naïve ensemble-average model that calculates the arithmetic mean with equal weights. In agreement with the expectations of the Diversity Prediction Theorem, the naïve ensemble-average model performed well across traits and datasets. Our experimental results indicate the potential for performance improvement using the proposed weight optimisation approaches for several prediction scenarios. However, the observed improvements were not achieved for all traits and dataset scenarios, suggesting the need for further investigation. We suggest that the weighted ensemble approaches can be further refined by developing a pipeline that can optimise both weights and hyperparameters of the individual genomic prediction models simultaneously.

Data and code availability

The TeoNAM dataset (Chen et al., 2019) used in this study is located at https://datacommons.cyverse.org/browse/iplant/home/shared/panzea/genotypes/GBS/TeosinteNAM for the genotypes and https://gsajournals.figshare.com/articles/dataset/Supplemental_Material_for_Chen_et_al_2019/9250682 for the phenotypes. The MaizeNAM dataset (Buckler et al., 2009) used in this study is located at https://cbsusrv04.tc.cornell.edu/users/panzea/download.aspx?filegroupid=10 for the genotypes and phenotypes. The computational tool, EasiGP, used in this study is located at https://github.com/ShunichiroT/EasiGP.

Author contribution

ST designed the experiment, analysed data, visualised the results and wrote the manuscript. OP, MJW and JL provided feedback on the analysis, results and manuscript draft. MC formalised the concept, introduced the datasets, designed the experiment and provided feedback on the analysis, results and manuscript draft. All authors discussed the results and contributed to the writing and editing of the final version of the manuscript.

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Conflicts of interest

The authors declare no conflicts of interest.

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Figures and tables

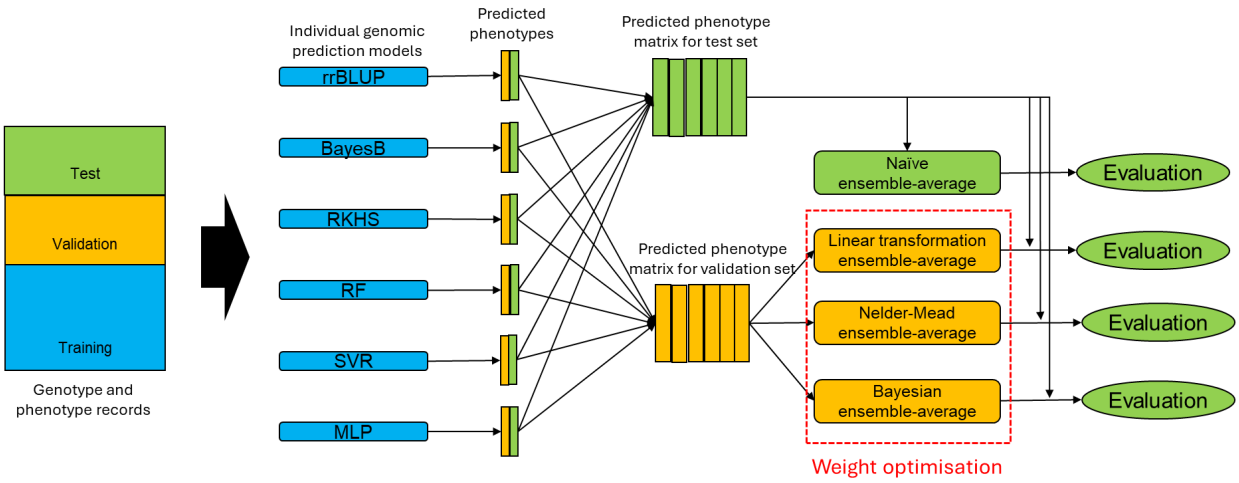

Figure 1: Model development and evaluation flow in this study. Genotype and phenotype records for each prediction scenario were split into training, validation and test sets, represented in blue, orange and green, respectively. The six individual genomic prediction models (rrBLUP, BayesB, RKHS, RF, SVR and MLP) were trained independently using the training set, followed by phenotype prediction on the validation and test sets. As a benchmark prediction performance, the naïve ensemble-average model was developed by calculating the mean predicted phenotypes for the test set using equal weights. The weights allocated to the individual genomic prediction models were optimised using the validation set through three optimisation approaches (linear transformation, Nelder-Mead and Bayesian ensemble-average). These weight optimisation approaches were expected to adjust weights assigned to each prediction model by maximising or minimising their objective function (Figure 3). The predicted phenotypes for the test set were weight-averaged using the identified weights. The three weighted ensemble-average models were evaluated against the naïve ensemble-average model (Figure 2).

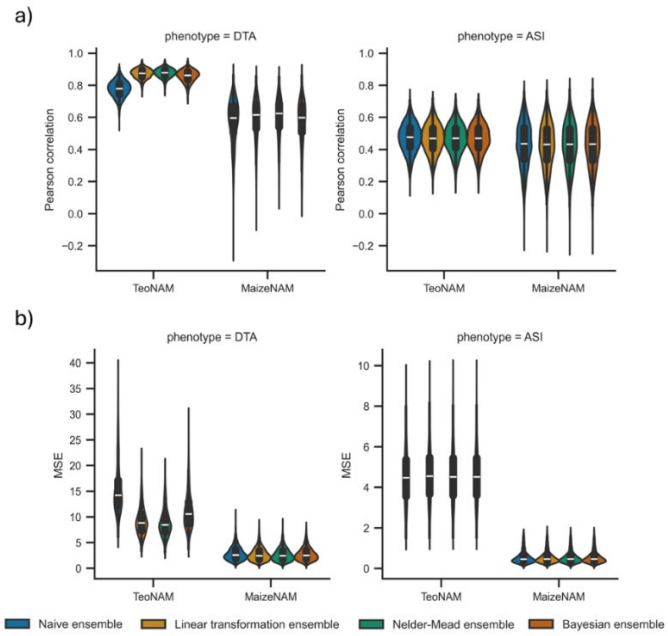

Figure 2: Comparison of prediction performance between the three proposed weighted ensemble-average models (linear transformation ensemble, Nelder-Mead ensemble and Bayesian ensemble) and the naïve ensemble-average model (naïve ensemble) for the days to anthesis (DTA) and anthesis to silking interval (ASI) traits in the TeoNAM and MaizeNAM datasets. The prediction performance was measured using the two metrics: a) Pearson correlation and b) mean square error (MSE). The prediction metrics were calculated from 2,500 prediction scenarios for the TeoNAM dataset and 1,250 prediction scenarios for the MaizeNAM dataset for each trait. The width of the violins represents the distribution of performance metrics. The

white horizontal lines on the black box plots show the median value for each metric. The whiskers extend 1.5 times the interquartile range. The median value of each metric is recorded in Table S2.

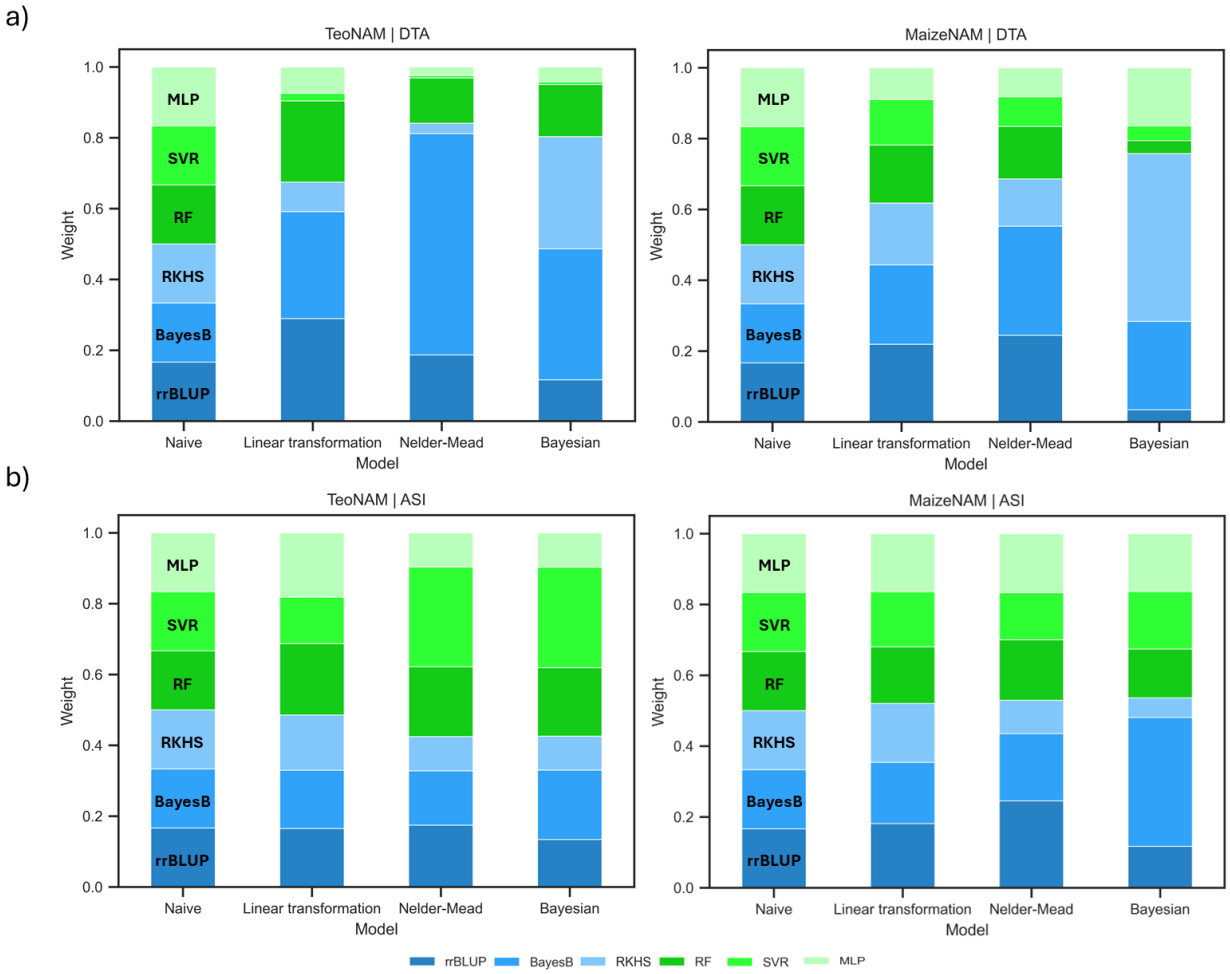

Figure 3: The comparison of mean weights allocated to the six individual genomic prediction models (rrBLUP, BayesB, RKHS, RF, SVR and MLP) by the naïve ensemble-average model and the three weighted ensemble-average models (linear transformation, Nelder-Mead and Bayesian) for a) the days to anthesis (DTA) and b) anthesis to silking interval (ASI) traits in the TeoNAM and MaizeNAM datasets. The blue colours represent weights for parametric and semiparametric models (rrBLUP, BayesB and RKHS), while the green colours indicate weights for machine learning models (RF, SVR and MLP). The weights were extracted from 2,500 prediction scenarios for the TeoNAM dataset and 1,250 prediction scenarios for the MaizeNAM dataset. The actual mean weight and standard error values are reported in Table S3.

Table 1: Association analysis between the diversity level of individual prediction models and prediction error of ensembles. The mean value of each term in the Diversity Prediction Theorem from the three proposed weighted ensemble-average models (linear transformation, Nelder-Mead and Bayesian) was compared with that of the naïve ensemble average model. The first, second and third represent the Many-model (ensemble) error, average-model error and diversity of model predictions, respectively. The third/second term is the ratio of the mean prediction diversity over the mean average error of the individual prediction models. For the first and second terms, the lowest value was highlighted in bold in each trait-by-dataset prediction scenario. For the third and third/second term, the highest value was highlighted in bold in each trait-by-dataset prediction scenario. The mean value for each term was calculated for the days to anthesis (DTA) and anthesis to silking interval (ASI) traits in the TeoNAM and MaizeNAM datasets.

Trait	Term	TeoNAM				MaizeNAM			
		Naïve	Linear transformation	Nelder-Mead	Bayesian	Naïve	Linear transformation	Nelder-Mead	Bayesian
DTA	First	22.090±0.044	10.515±0.037	4.822±0.032	**3.631±0.026**	3.618±0.019	**2.703±0.018**	2.831±0.018	3.143±0.018
	Second	33.544±0.053	24.391±0.047	18.424±0.038	**16.351±0.028**	5.975±0.023	**4.269±0.022**	4.391±0.021	5.322±0.023
	Third	11.455±0.014	**13.876±0.022**	13.602±0.021	12.720±0.019	**2.357±0.010**	1.566±0.008	1.560±0.007	2.179±0.010
	Third / Second	0.341	0.569	0.738	**0.778**	0.394	0.367	0.355	**0.409**
ASI	First	5.227±0.015	**5.213±0.015**	5.255±0.015	5.292±0.016	0.597±0.003	0.582±0.003	0.583±0.003	**0.576±0.003**
	Second	6.122±0.015	**6.033±0.015**	6.058±0.015	6.088±0.016	0.667±0.003	0.653±0.003	0.655±0.003	**0.649±0.003**
	Third	**0.895±0.002**	0.819±0.002	0.803±0.002	0.796±0.002	0.071±0.000	0.071±0.000	0.072±0.000	**0.073±0.000**
	Third / Second	**0.146**	0.136	0.133	0.131	0.106	0.109	0.109	**0.112**

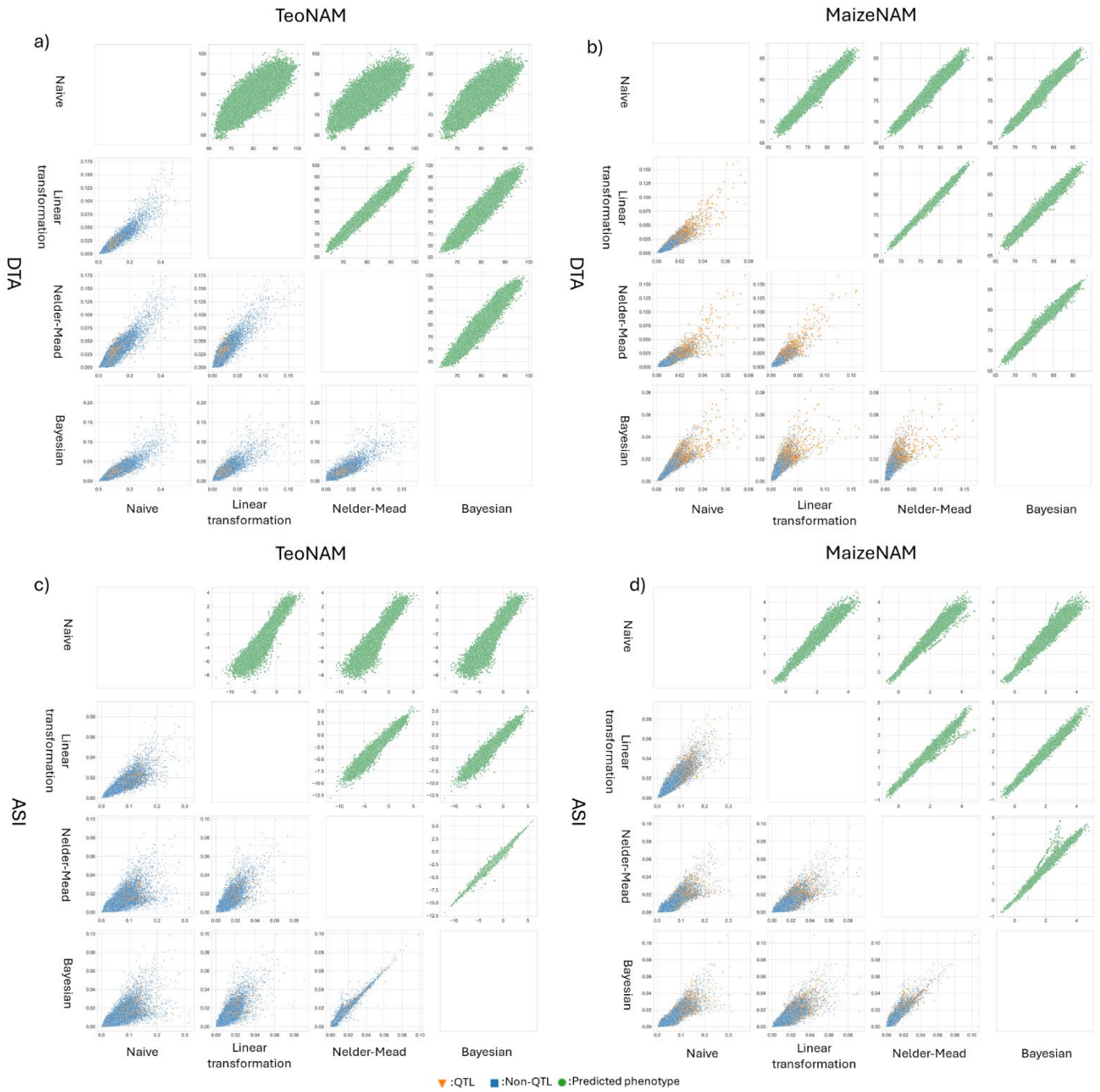

Figure 4: Pairwise comparisons of the ensemble models (naïve ensemble, linear transformation, Nelder-Mead and Bayesian) for the days to anthesis (DTA) and anthesis to silking interval (ASI) trait across all the prediction scenarios for the TeoNAM (2,500 prediction scenarios) and MaizeNAM (1,250 prediction scenarios) datasets; a) DTA for the TeoNAM dataset, b) DTA for the MaizeNAM dataset, c) ASI for the TeoNAM dataset and d) ASI for the MaizeNAM dataset. Within each scatter plot matrix, the ensemble models were compared at the predicted phenotypes (top right triangle) and genomic marker effects (the bottom left triangle) levels. The green dots represent a pair of predicted phenotypes for RIL samples in the test sets for each prediction scenario. The blue squares and orange triangles represent pairs of inferred effects of genomic markers in each sample scenario for non-QTL and QTL, respectively. Non-QTL and QTL markers were identified by Chen et al. (2019) for the TeoNAM dataset and Buckler et al. (2009) for the MaizeNAM dataset.

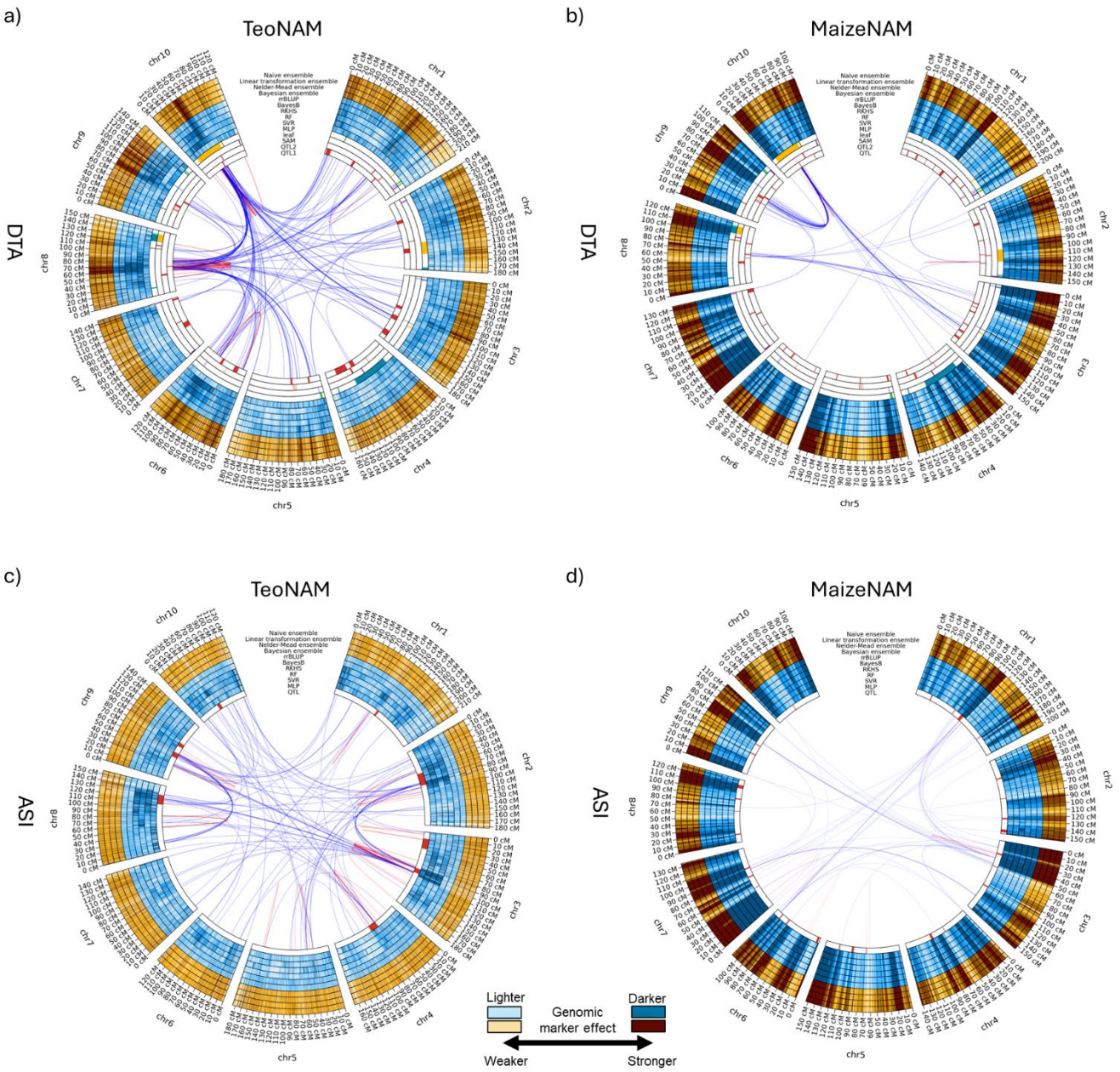

Figure 5: Circos plots for the days to anthesis (DTA) and anthesis to silking interval (ASI) trait in the TeoNAM and MaizeNAM datasets; a) DTA for the TeoNAM dataset, b) DTA for the MaizeNAM dataset, c) ASI for the TeoNAM dataset and d) ASI for the MaizeNAM dataset. For DTA, the innermost (QTL 1) ring represents the QTL gene regions estimated by Chen et al. (2019) for the TeoNAM dataset and by Buckler et al. (2009) for the MaizeNAM dataset, respectively. The second innermost ring (QTL 2) represents the QTL gene regions identified by Wisser et al. (2019). For ASI, the innermost (QTL) ring shows the QTL gene regions estimated by Chen et al. (2019) for the TeoNAM dataset and by Buckler et al. (2009) for the MaizeNAM dataset. The blue rings indicate genomic marker effects across the gene regions estimated by MLP, SVR, RF, RKHS, BayesB and rrBLUP. The subsequent four orange rings outwards are the genomic marker effects estimated by Bayesian, Nelder-Mead, linear transformation and naïve ensemble. The darkness level of the blue and orange colours indicates the strength of the genomic marker effects, sectioned into ten levels using the quantiles. Darker colours represent higher genomic marker effect sizes. The red and blue lines between genome regions show the genomic marker interaction effects calculated from pairwise Shapley scores from RF (top 0.01%; red = within chromosome and blue = between chromosomes).

Supplementary Materials

Table S1: The total number of genomic markers (SNPs) at the original and after linkage disequilibrium (LD) filtering and the records of recombinant inbred lines (RILs) for the TeoNAM and MaizeNAM datasets.

Dataset	SNPs		RIL Records
	Original	LD Filtering	
TeoNAM	11,396 - 16,110	268 - 342	438 - 616
MaizeNAM	1,106	170 - 251	126 - 196

Table S2: The median prediction accuracy (Pearson correlation) and error (mean squared error; MSE) of each ensemble model in the days to anthesis (DTA) and b) anthesis to silking interval (ASI) traits in the TeoNAM and MaizeNAM datasets. The prediction performance was measured across 2,500 prediction scenarios for the TeoNAM dataset and 1,250 prediction scenarios for the MaizeNAM dataset, respectively, for each trait. The sign "±" indicates the standard error of the corresponding mean weight value. For prediction accuracy, the highest value in each prediction scenario was highlighted in bold, while for prediction error, the lowest value in each prediction scenario was highlighted in bold. This table corresponds to the violin plots in Figure 2.

Trait	Metric	TeoNAM				MaizeNAM			
		Naïve	Linear transformation	Nelder-Mead	Bayesian	Naïve	Linear transformation	Nelder-Mead	Bayesian
DTA	Pearson correlation	0.780±0.001	0.875±0.001	**0.879±0.001**	0.863±0.001	0.596±0.004	0.616±0.004	**0.625±0.004**	0.598±0.004
	MSE	14.239±0.095	8.838±0.051	**8.448±0.051**	10.559±0.070	2.599±0.037	2.449±0.035	**2.436±0.034**	2.523±0.035
ASI	Pearson correlation	**0.477±0.002**	0.469±0.002	0.471±0.002	0.470±0.002	**0.436±0.004**	0.432±0.004	0.433±0.004	0.434±0.004
	MSE	**4.476±0.026**	4.555±0.026	4.523±0.026	4.522±0.026	**0.461±0.009**	0.466±0.009	0.466±0.009	0.466±0.009

Table S3: The mean weight and standard error values allocated to the six individual genomic prediction models (rrBLUP, BayesB, RKHS, RF, SVR and MLP) by the three optimisation approaches (linear transformation, Nelder-Mead and Bayesian ensemble-average approaches), along with naïve ensemble-average approach as the reference, for a) the days to anthesis (DTA) and b) anthesis to silking interval (ASI) traits in the TeoNAM and MaizeNAM datasets. The weights were extracted from 2,500 prediction scenarios for the TeoNAM dataset and 1,250 prediction scenarios for the MaizeNAM dataset for each trait. The sign "±" indicates the standard error of the corresponding mean weight value. This table corresponds to Figure 3.

a)

	TeoNAM				MaizeNAM			
	Naïve	Linear transformation	Nelder-Mead	Bayesian	Naïve	Linear transformation	Nelder-Mead	Bayesian
rrBLUP	0.17±0	0.29±0.0020	0.19±0.0027	0.12±0.0039	0.17±0	0.22±0.0007	0.24±0.0038	0.03±0.0075
BayesB	0.17±0	0.30±0.0040	0.63±0.0028	0.37±0.0049	0.17±0	0.22±0.0057	0.31±0.0038	0.25±0.0079
RKHS	0.17±0	0.08±0.0030	0.03±0.0013	0.32±0.0009	0.17±0	0.18±0.0032	0.13±0.0034	0.47±0.0057
RF	0.17±0	0.23±0.0023	0.13±0.0024	0.15±0.0025	0.17±0	0.16±0.0010	0.15±0.0035	0.04±0.0057
SVR	0.17±0	0.02±0.0004	0.01±0.0003	0.01±0.0004	0.17±0	0.13±0.0009	0.08±0.0029	0.04±0.0043
MLP	0.17±0	0.07±0.0008	0.02±0.0011	0.04±0.0005	0.17±0	0.09±0.0029	0.08±0.0020	0.16±0.0026

b)

	TeoNAM				MaizeNAM			
	Naïve	Linear transformation	Nelder-Mead	Bayesian	Naïve	Linear transformation	Nelder-Mead	Bayesian
rrBLUP	0.17±0	0.16±0.0043	0.17±0.0024	0.13±0.0050	0.17±0	0.18±0.0063	0.25±0.0034	0.12±0.0095
BayesB	0.17±0	0.16±0.0052	0.15±0.0025	0.20±0.0046	0.17±0	0.17±0.0096	0.19±0.0033	0.36±0.0087
RKHS	0.17±0	0.16±0.0040	0.10±0.0025	0.10±0.0040	0.17±0	0.17±0.0039	0.09±0.0033	0.06±0.0063
RF	0.17±0	0.20±0.0047	0.20±0.0028	0.19±0.0046	0.17±0	0.16±0.0069	0.17±0.0034	0.14±0.0078
SVR	0.17±0	0.13±0.0057	0.28±0.0019	0.28±0.0056	0.17±0	0.16±0.0070	0.13±0.0033	0.16±0.0068
MLP	0.17±0	0.18±0.0021	0.10±0.0026	0.10±0.0021	0.17±0	0.16±0.0066	0.17±0.0035	0.16±0.0066