

Research Report

Open Access

## Genomic Prediction: Enhancing Breeding Strategies for Complex Traits in Livestock

Xiao Zhu, Siping Zhang ✉

Tropical Animal Medicine Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572024, Hainan, China

✉ Corresponding author: [2495757304@qq.com](mailto:2495757304@qq.com)

Animal Molecular Breeding, 2024, Vol.14, No.1 doi: [10.5376/amb.2024.14.0012](https://doi.org/10.5376/amb.2024.14.0012)

Received: 06 Jan., 2024

Accepted: 16 Feb., 2024

Published: 26 Feb., 2024

**Copyright** © 2024 Zhu and Zhang, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

**Preferred citation for this article:**

Zhu X., and Zhang S.P., 2024, Genomic prediction: enhancing breeding strategies for complex traits in livestock, *Animal Molecular Breeding*, 14(1): 95-105 (doi: [10.5376/amb.2024.14.0012](https://doi.org/10.5376/amb.2024.14.0012))

**Abstract** Genomic prediction has become a cornerstone in livestock breeding programs, aiming to enhance the selection process for complex traits. This approach leverages dense single nucleotide polymorphism (SNP) genotypes to estimate breeding values, which are pivotal for making informed selection decisions. The accuracy of genomic predictions is influenced by the genetic architecture of the trait, including the number and effect distribution of loci involved. Studies have shown that traits with a mix of large and small effect loci, such as coat color and milk-fat percentage in Holstein cattle, tend to yield higher prediction accuracies than traits governed solely by small effect loci. Incorporating biological priors, such as gene ontology terms, into prediction models can further refine these estimates, particularly when considering traits with immunological relevance like mastitis. The effectiveness of genomic selection is also dependent on the statistical models employed, with whole-genome regression methods demonstrating significant promise in both plant and animal breeding. Moreover, the integration of genome-wide association study (GWAS) results into prediction models has been proposed to enhance the accuracy of whole genome predictions, especially for traits with lower heritability. The application of genomic selection is not without challenges, including the management of inbreeding and the need for large reference populations to achieve accurate predictions. Nonetheless, the paradigm shift towards genomic selection in animal breeding is anticipated to continue evolving, with the potential inclusion of whole-genome sequence data to capture all genetic variance.

**Keywords** Genomic prediction; Complex traits; Livestock breeding; Genetic architecture; SNP genotypes

The advent of genomic selection (GS) has marked a transformative period in the field of animal breeding, particularly in the context of complex traits in livestock. Traditional breeding methods, which have been the cornerstone of genetic improvement for centuries, rely on phenotypic selection and pedigree information to estimate breeding values. However, these methods have limitations, particularly when it comes to the accuracy and efficiency of selection for complex traits, which are typically influenced by many genes with small effects (Meuwissen et al., 2016).

The development of genomic selection has been driven by significant technological advancements, including the discovery of a vast number of genetic markers known as single nucleotide polymorphisms (SNPs) and the ability to genotype animals at a high throughput and reduced cost (Meuwissen et al., 2016). Genomic selection assumes that all markers are linked to genes affecting the trait and focuses on estimating their effects rather than testing for significance, a paradigm shift from traditional marker-assisted selection (MAS) (Meuwissen et al., 2016).

Genomic prediction technologies leverage dense SNP genotypes to estimate breeding values, with the accuracy of these predictions depending on the genetic architecture of the trait in question (Hayes et al., 2010). For instance, traits like coat color in Holstein cattle and fat concentration in milk have been shown to have a mix of large-effect loci and many loci with small effects, while other traits like overall type are affected only by loci with small effects (Hayes et al., 2010). The application of whole-genome regression (WGR) models allows for the concurrent regression of phenotypes on thousands of markers, enhancing the prediction of complex traits (Campos et al., 2013).

The potential impact of genomic prediction on the livestock industry is substantial. It offers the possibility of increasing the accuracy of selection, reducing the generation interval, and enabling the selection for traits that are difficult to measure or can only be measured late in life or post-mortem (Bolormaa et al., 2013; Lopes et al., 2020). Moreover, the integration of genomic information with traditional breeding values can lead to more accurate genetic evaluations, as demonstrated in Nelore cattle for carcass and meat quality traits (Lopes et al., 2020).

Despite the promise of genomic prediction, challenges remain. The accuracy of genomic breeding values (GEBVs) can vary widely between traits and breeds, and the effectiveness of genomic selection is influenced by factors such as the size of the reference population and the number of markers used (Hayes and Goddard, 2010; Bolormaa et al., 2013). Additionally, the integration of biological priors, such as gene ontology (GO) terms, into genomic prediction models has been shown to improve predictive ability for certain traits, suggesting that a better understanding of the genetic architecture can enhance genomic prediction (Fang et al., 2017).

In conclusion, genomic prediction technologies represent a significant advancement in the field of animal breeding, offering a means to overcome the limitations of traditional breeding methods and to accelerate genetic progress for complex traits in livestock. As research continues to refine these technologies, their integration into breeding programs is likely to become increasingly widespread, with profound implications for the livestock industry.

## **1 Theoretical Foundations of Genomic Selection**

### **1.1 Principles of genomic selection**

Genomic selection is a revolutionary approach in livestock breeding that leverages dense single nucleotide polymorphism (SNP) genotypes to predict the genetic merit of animals. The relationship between genetic markers and phenotypes is a cornerstone of this method, as it allows for the estimation of breeding values which are essential for the selection process (Hayes et al., 2010). The accuracy of these genomic predictions is contingent upon the genetic architecture of the trait in question, such as the number of loci affecting the trait and the distribution of their effects (Hayes et al., 2010; Swami, 2010; Kemper and Goddard, 2012). For instance, traits like coat color in Holstein cattle have been found to be influenced by a few loci of large effect, as well as many loci of small effect (Hayes et al., 2010). This contrasts with other traits, such as overall type, which are affected only by loci of small effect (Hayes et al., 2010).

Hayes et al. (2010) presented a study that demonstrates the relationship between F values and genomic positions of three gene loci (Figure 1). Figure A shows the distribution of the KIT gene locus, which has a clear peak in F value at approximately 72 Mb. Figure B displays the MITF gene locus, which has a higher F value at about 32 Mb. Figure C shows the PAX5 gene locus, where there is a slightly prominent F value at about 64 Mb. These data can be used to reveal the associations between specific gene variations and phenotypic traits.

Genome-wide selection is another aspect of genomic selection that involves regressing phenotypes on thousands of markers concurrently. This method has been applied in both plant and animal breeding and is critical for improving the accuracy of predictions for complex traits (Campos et al., 2013). The accuracy of genomic predictions is higher for traits with a proportion of large effects, provided that the method of analysis capitalizes on the distribution of loci effects (Hayes et al., 2010).

### **1.2 Statistical models and algorithms**

The Best Linear Unbiased Prediction (BLUP) and Bayesian models are statistical tools used to enhance genomic predictions. BLUP|GA, a variant of BLUP, has been proposed to incorporate genome-wide association study (GWAS) results into genomic predictions, thereby improving the accuracy of predictions for certain traits (Zhang et al., 2014). Bayesian models, on the other hand, assume that marker effects are random variables drawn from a specified prior distribution, which has been shown to achieve high accuracy in predicting genetic values (Kemper and Goddard, 2012).

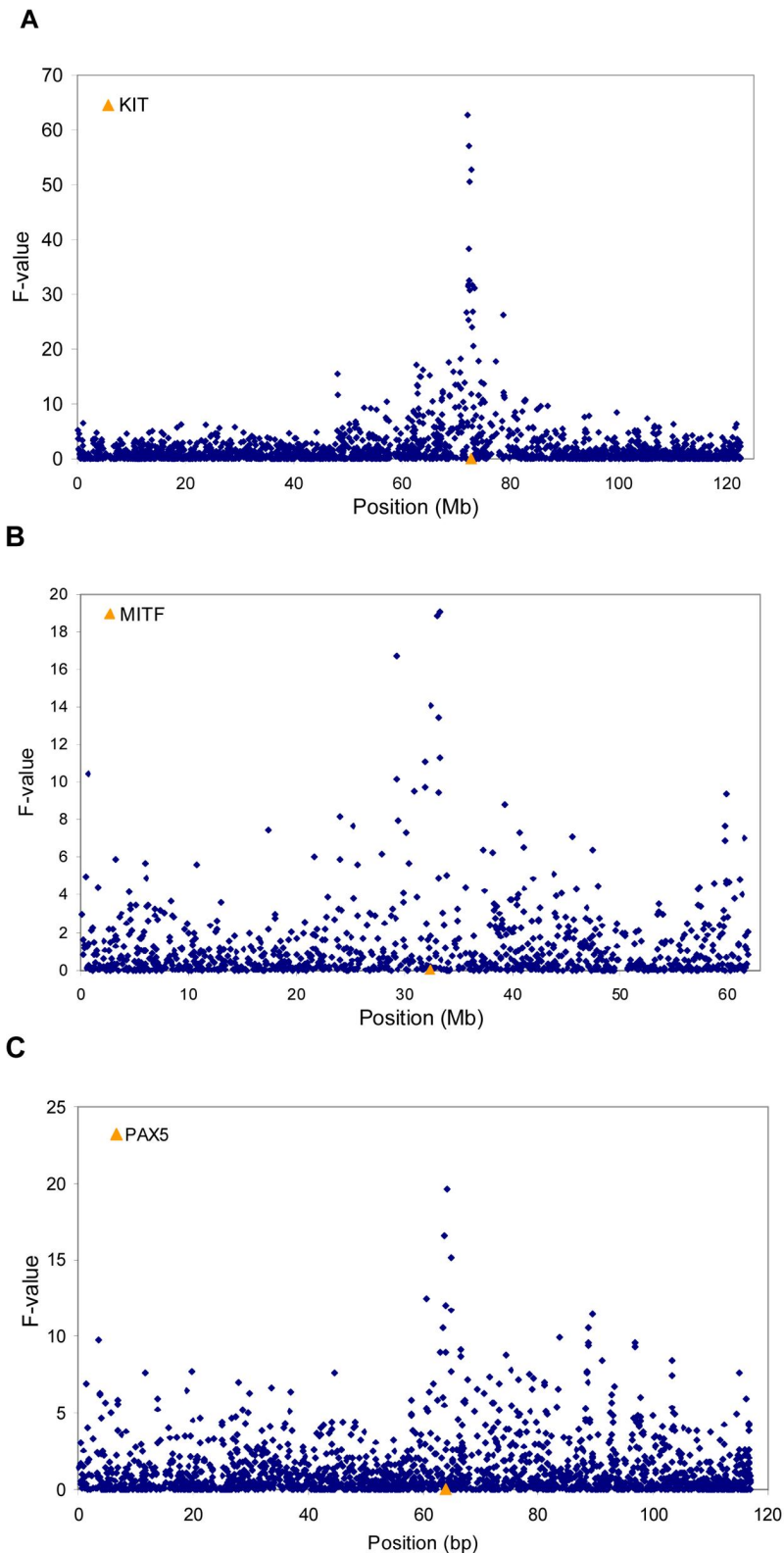


Figure 1 Genome-wide association study for proportion of black bulls (Photo credit: Hayes et al., 2010)

The application of machine learning methods in genomic prediction is an emerging field that offers potential improvements in the prediction of complex traits. These methods can handle large datasets and complex patterns in the data, which are common in genomic selection (Fang et al., 2017; Lopes et al., 2020). For example, the use of genomic feature BLUP (GFBLUP) models, which incorporate biological priors such as gene ontology terms, has demonstrated improvements in predictive ability for complex traits (Fang et al., 2017).

Srivastava et al. (2021) demonstrated the results of predictive correlation and mean squared error (MSE) for four carcass traits of Korean cattle using GBLUP and three machine learning methods (RF, XGB, SVM) (Figure 2). XGB showed the highest predictive correlation for CWT and MS, followed by GBLUP, SVM, and RF. GBLUP exhibited the greatest predictive correlation for BFT and EMA, followed by SVM, RF, and XGB. In terms of measuring prediction performance, although predictive correlation is a commonly used straightforward approach, MSE is a preferable parameter considering prediction bias and variance. Among all traits, GBLUP performed best in terms of MSE, while among the machine learning methods, XGB performed optimally for CWT and MS, and SVM was best for BFT and EMA.

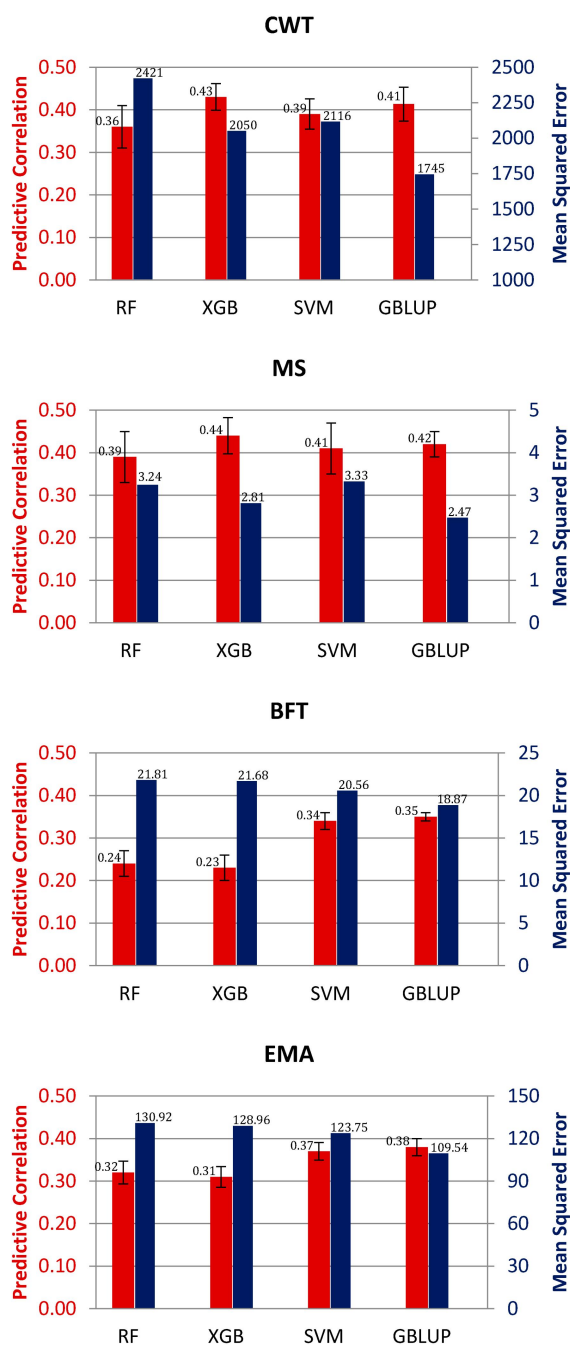


Figure 2 Predictive correlation (red color) and mean squared error (blue color) of prediction obtained using different statistical methods for carcass weight (CWT), marbling score (MS), backfat thickness (BFT), and eye muscle area (EMA) (Photo credit: Srivastava et al., 2021)

Image caption: RF: random forest; XGB: extreme gradient boosting; SVM: support vector machine; GBLUP: genomic best linear unbiased prediction (Adopted from Srivastava et al., 2021)

In summary, the theoretical foundations of genomic selection are built upon the intricate relationship between genetic markers and phenotypes, the implementation of genome-wide selection models, and the utilization of advanced statistical and machine learning algorithms. These foundations are crucial for enhancing breeding strategies and improving the selection of livestock with desirable complex traits.

## **2 Practical Applications of Genomic Prediction Technologies**

### **2.1 Cattle breeding**

Genomic prediction technologies have significantly advanced cattle breeding by enabling more precise selection for desirable traits. One of the key applications is in increasing milk production and improving milk quality. By using genomic selection, breeders can identify and select for alleles that are associated with higher milk yield and better milk composition. This is achieved through methods such as whole-genome regression (WGR) models, which allow for the prediction of complex traits by regressing phenotypes on thousands of markers concurrently (Campos et al., 2013). Additionally, genomic information has been utilized to optimize genetic resistance to diseases in cattle. This not only improves the health and welfare of the animals but also reduces economic losses due to illness. The integration of genomic, pedigree, and phenotype information into a one-step procedure for genomic prediction has been shown to result in more accurate estimated breeding values (EBVs), which is particularly beneficial for disease resistance traits (Christensen and Lund, 2010).

### **2.2 Swine and poultry breeding**

In swine and poultry breeding, improvements in growth rate and meat quality are paramount. Genomic selection has been applied to enhance these traits by predicting genomic estimated breeding values (GEBVs) for economically important traits such as carcass weight, live weight, and meat quality (Liang et al., 2020). The use of ensemble learning algorithms, which combine multiple machine learning methods, has shown to outperform traditional genomic best linear unbiased prediction (GBLUP) methods, leading to higher prediction accuracy (Liang et al., 2020). Furthermore, genomic selection aids in identifying genotypes that are better suited to cope with environmental stresses. This is crucial for maintaining productivity and animal welfare in varying climatic conditions (Meuwissen et al., 2016).

### **2.3 Rare and economically valuable animals**

For rare and economically valuable animals like alpacas and water buffalos, genomic prediction offers a way to achieve genetic improvement while preserving genetic diversity. The application of genomic selection in these species can help identify individuals with superior traits for breeding programs, ensuring the sustainability and profitability of these niche markets. Although genomic selection is more established in common livestock species, its principles are equally applicable to rare breeds, and its implementation can be tailored to the specific needs and challenges associated with these animals (Georges, 2001).

In conclusion, genomic prediction technologies have provided breeders with powerful tools to enhance breeding strategies for complex traits in livestock. These advancements have led to significant improvements in cattle, swine, and poultry breeding, and they hold promise for the genetic improvement of rare and economically valuable animals.

## **3 Case Studies in Genomic Prediction**

### **3.1 Enhancing dairy cattle productivity through genomic selection**

Genomic selection has revolutionized dairy cattle breeding programs by enabling the accurate selection of superior candidates for productivity traits. The use of genomic estimated breeding values (GEBVs) based on intensive progeny testing for production and reproductive traits has been crucial in increasing dairy cattle productivity. Key genes and haplotypes have been identified as markers for productivity traits, improving the strategies for dairy cattle selection. Genome-wide association studies (GWAS), quantitative trait loci (QTL), single nucleotide polymorphisms (SNPs), and single-step genomic best linear unbiased prediction (ssGBLUP) methods have been incorporated into global dairy programs to estimate marker-assisted selection effects. Despite the progress, inbreeding depression remains a challenge due to closed bloodlines in several milk breeds. Genomic

tools are being used to mitigate the negative effects of inbreeding and to facilitate precision management on modern dairy farms. Novel genome editing methodologies also hold promise for the future of dairy cattle selection (Figure 3) (Ding et al., 2013; Gutierrez-Reinoso et al., 2021).

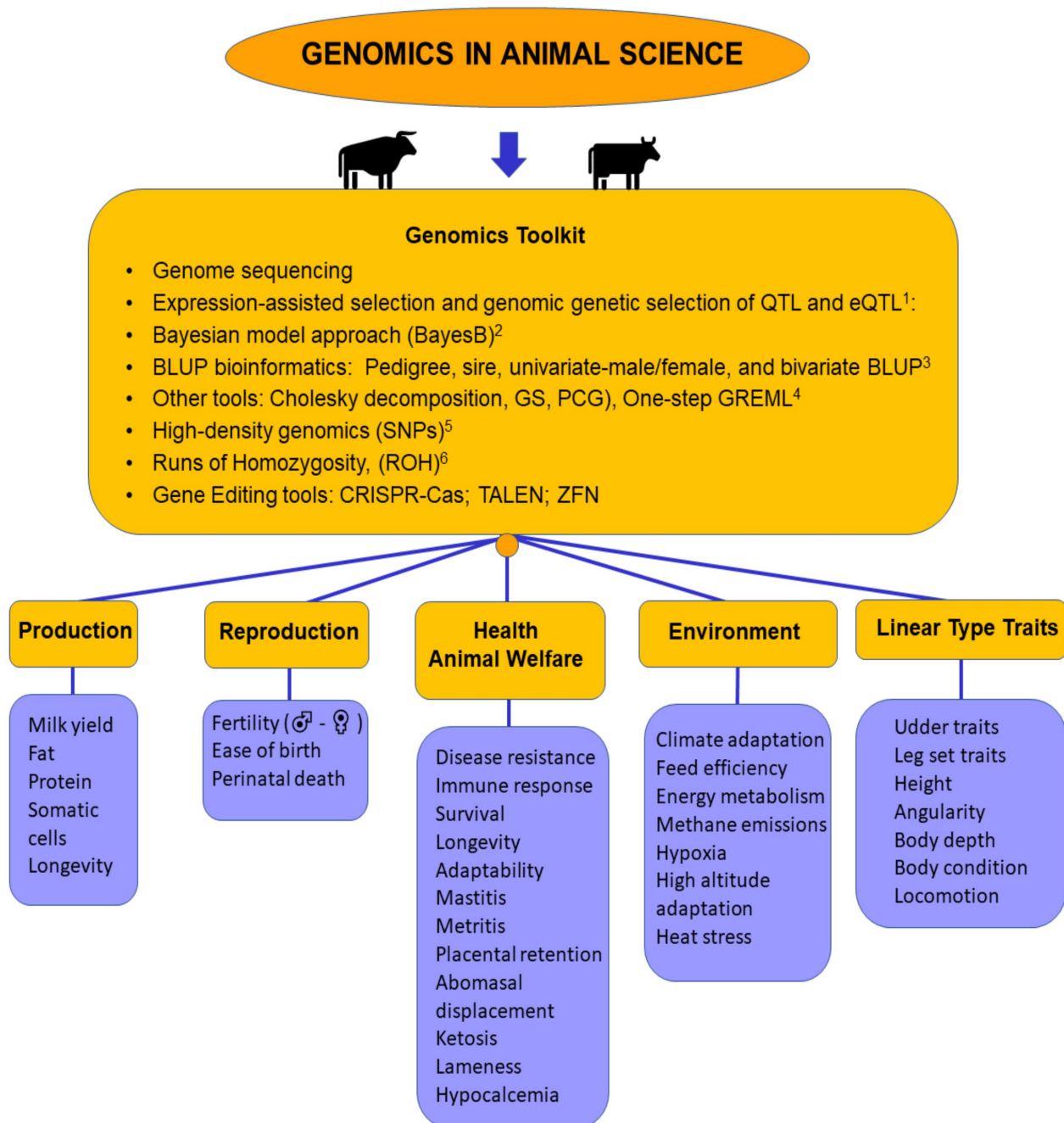


Figure 3 Overview of the impact of genomics on several dairy science topics (Photo credit: Gutierrez-Reinoso et al., 2021)  
 Image caption: (1) Method used for the direct selection of heritable measures of gene expression. (2) A statistical framework for genomic estimations. (3) Genomic relationship matrices for highly accurate estimation of genomic estimated breeding values (GEBV). (4) Unique data resolution methods in very large animal populations; GS = iterative Gauss–Seidel; PCG = preconditioned conjugate gradient; one-step GREML = genome-based restricted maximum likelihood used for >50,000 genotyped animal populations. (5) Analysis of the genetic diversity determining population structure, performing high-density genetic maps and providing genotypes for genome-wide association analysis. (6) Determination of the genomic inbreeding footprint for a specific subpopulation by estimating the individual autozygosity. Under each dairy science topic (production, reproduction, health and animal welfare, environment, linear type traits) examples of relevant traits studied through genomic tools to date are listed (Adopted from Gutierrez-Reinoso et al., 2021)

### 3.2 Genetic optimization in swine for enhanced meat quality

In swine, genomic prediction has been applied to improve traits related to feed efficiency, growth, carcass, and meat quality. The accuracy of genomic predictions varies by trait and method, with traits having a large number of recorded and genotyped animals and high heritability showing the greatest accuracy. Methods such as BayesR and genomic BLUP (GBLUP) have been used to calculate GEBVs, with BayesR often providing higher accuracies for traits with known genes of moderate to large effect mutations. Genomic selection is beneficial for traits that are difficult to improve by conventional selection, such as tenderness and residual feed intake. The study of genomic predictions in beef cattle, including *Bos taurus* and *Bos indicus*, has shown that genomic selection can still be beneficial despite lower accuracies compared to dairy cattle (Bolormaa et al., 2013; Lopes et al., 2020).

Lopes et al. (2020) presented descriptive statistics involving different traits such as Ribeye Area (REA), Back Fat (BF), Rump Fat (RF), and Warner-Bratzler Shear Force (WBSF) in the Nelore cattle breeding program (Table 1). Data for Ribeye Area and Back Fat were derived from cross-sectional images of the longissimus muscle between the 12<sup>th</sup> and 13<sup>th</sup> ribs. Rump Fat was measured at the intersection of the biceps femoris and the gluteus medius between the ilium and ischium. Warner-Bratzler Shear Force was measured after the meat samples had been stored for seven days. These data reflect the diversity in genetic and phenotypic information and their statistical characteristics in Nelore cattle.

Table 1 Descriptive statistics for rib eye area, back fat thickness, rump fat and meat tenderness for genotyped in Nelore cattle (Lopes et al., 2020)

| Statistics         | REA   | BF    | RF    | WBSF |
|--------------------|-------|-------|-------|------|
| Contemporary group | 381   | 383   | 384   | 13   |
| Number of animals  | 3 675 | 3 680 | 3 660 | 524  |
| Number of sires    | 425   | 426   | 426   | 93   |
| Number of dams     | 3 118 | 3 105 | 3 116 | 318  |
| Mean               | 51.93 | 2.69  | 4.11  | 4.07 |
| Standard deviation | 12.94 | 1.91  | 2.23  | 1.41 |
| CV                 | 0.25  | 0.71  | 0.54  | 0.35 |

Note: REA: rib eye area; BF: back fat thickness; RF: rump fat; WBSF: Warner-Bratzler shear force

### 3.3 Conservation and improvement of rare livestock breeds

Genomic selection also offers tools for the conservation and improvement of rare livestock breeds. By integrating genomic information, breeding programs can maintain genetic diversity while improving economically important traits. For example, in Gyr (*Bos indicus*) dairy cattle, genomic selection has been used to predict breeding values for milk yield, fat yield, protein yield, and age at first calving. The use of different SNP chips and the effect of imputed data on genomic prediction accuracy have been studied, showing that a reduced panel of markers can yield similar accuracies to high-density markers. This suggests that genomic selection can be effectively implemented in indicine breeds to accelerate genetic progress. Additionally, the integration of cow information into the reference population can increase the reliability of genomic predictions, which is particularly beneficial for breeds with limited reference populations (Boison et al., 2017).

Boison et al. (2017) demonstrated the reliability estimates (R<sup>2</sup>PEV) for milk production, fat content, protein content, and age at first calving in dairy cattle using the genomic BLUP model with only bulls (TR1) and with both bulls and cows (TR2) as reference populations (Figure 4). The reliability of each trait was calculated from data obtained using chips with different genetic marker densities (such as 50K, 20Ki, 75Ki). The graph shows the reliability for all traits in both TR1 and TR2, and error bars indicate the standard deviation of reliability calculated per animal. This data reflects the variation in prediction accuracy under different testing conditions.

In summary, genomic prediction is a powerful tool for enhancing breeding strategies in livestock, with applications ranging from improving productivity in dairy cattle to optimizing meat quality in swine and conserving rare breeds. The case studies demonstrate the versatility and impact of genomic selection across different livestock species and traits.

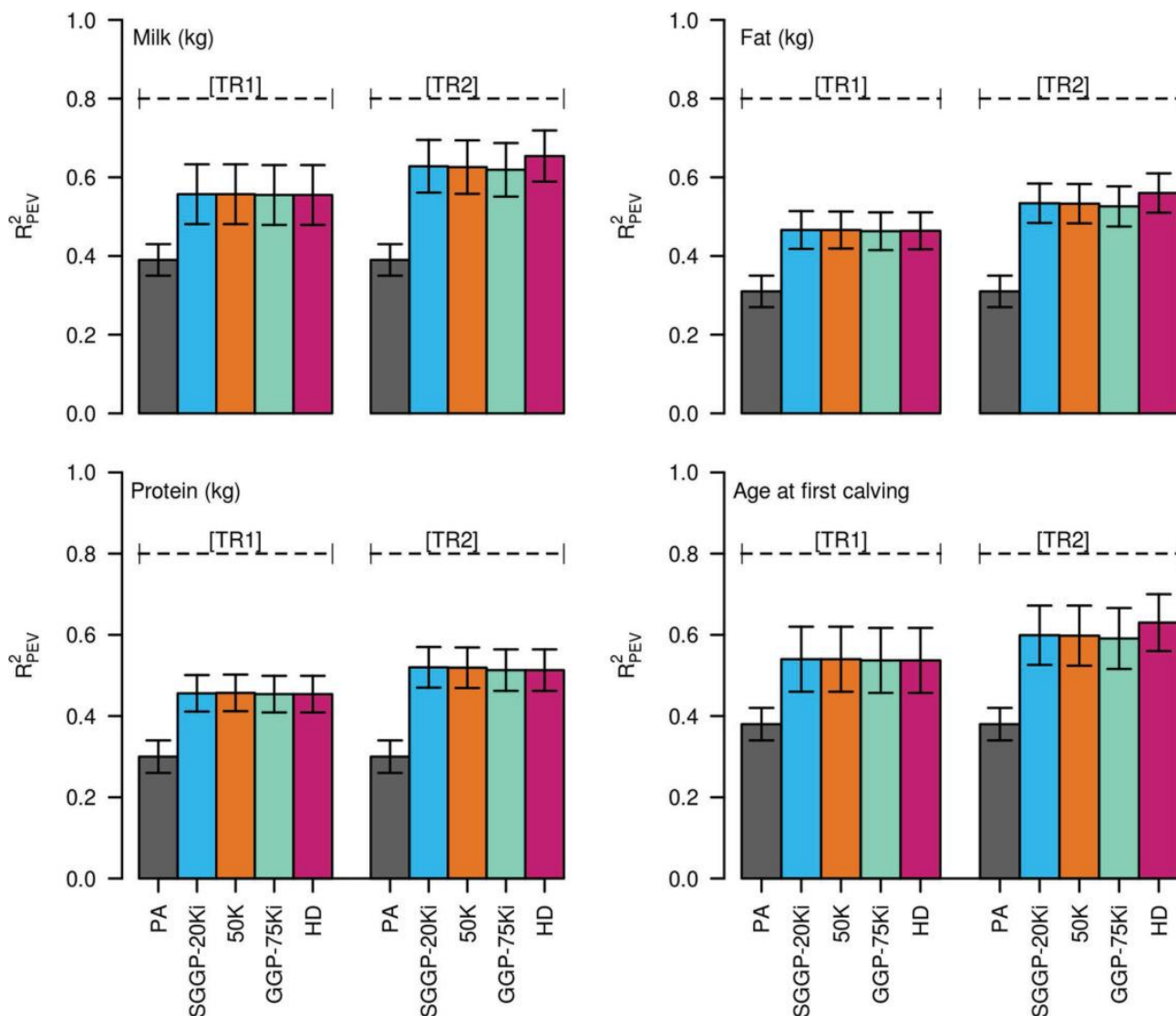


Figure 4 The average reliability (R<sup>2</sup>PEV) using genomic BLUP model with only bulls (TR1) or bulls and cows (TR2) reference population (Photo credit: Boison et al., 2017)

Image caption: Errors bars represent the SD based on the computed reliabilities per animal. PA = parent average EBV computed from pedigree and phenotype data at year 2014; HD = Illumina BovineHD; 50K = Illumina BovineSNP50 (Illumina, San Diego, CA); SGGP-20Ki = GeneSeek SGGP IndicusLD; GGP-75Ki = GeneSeek GGP IndicusHD (Geneseek, Lincoln, NE) (Adopted from Boison et al., 2017)

## 4 Challenges and Solutions

### 4.1 Data acquisition and handling challenges

The acquisition and handling of genomic data present significant challenges in the field of livestock breeding. High-quality genotype data is crucial for accurate genomic predictions, as demonstrated in a study on beef cattle, where the accuracy of genomic predictions was influenced by the density of genetic markers and the statistical methods used (Lu et al., 2016). The importance of high-quality genotype data cannot be overstated, as it directly impacts the reliability of genomic estimated breeding values (GEBVs), which are essential for the genetic improvement of traits such as feed efficiency (Lu et al., 2016).

To address the complexities of analyzing genomic data, the application of big data technologies is essential. These technologies can manage the vast amounts of data generated by high-throughput genotyping platforms, as seen in the utilization of genomic information for livestock improvement (Elsen, 2003). Big data analytics can facilitate the processing and interpretation of genomic data, thereby enhancing the accuracy and efficiency of genomic predictions (Elsen, 2003).



## **4.2 Conservation of genetic diversity**

Balancing the improvement of productive traits with the conservation of genetic diversity is a delicate task. A study on genomic prediction using a reference population of multiple pure breeds and admixed individuals highlights the need to maintain genetic diversity while selecting for desirable traits (Karaman et al., 2021). This balance is critical to avoid the negative consequences of inbreeding and to ensure the long-term sustainability of livestock populations (Karaman et al., 2021).

Strategic crossbreeding and the establishment of genetic diversity databases are potential solutions to this challenge. Crossbreeding can introduce beneficial alleles and increase heterozygosity, which may enhance the robustness and adaptability of livestock (Teng et al., 2019; Karaman et al., 2021). Moreover, the creation of genetic diversity databases can help monitor and manage the genetic variation within and across breeds, as suggested by the genomic analysis of dairy cattle (Gutierrez-Reinoso et al., 2021). These databases can serve as a repository of genetic information that can be used to inform breeding decisions and conservation strategies (Gutierrez-Reinoso et al., 2021).

In conclusion, the challenges of data acquisition and handling, as well as the conservation of genetic diversity, are significant but can be addressed through the use of advanced technologies and strategic breeding practices. High-quality genotype data and big data analytics are key to improving the accuracy of genomic predictions, while crossbreeding and genetic diversity databases play a crucial role in maintaining the genetic health of livestock populations.

## **5 Future Trends**

### **5.1 Precision breeding technologies**

The advent of precision breeding technologies is poised to revolutionize livestock breeding by enhancing the selection process for complex traits. One of the most promising aspects of precision breeding is the application of gene editing and CRISPR technology. These technologies allow for precise modifications of the genome, enabling the introduction or removal of specific genetic traits with unprecedented accuracy. The potential of CRISPR technology in livestock breeding is vast, with the possibility of creating animals that are more resistant to diseases, have improved productivity, and are better adapted to environmental challenges (Hayes and Goddard, 2010; Woolliams, 2011).

Another innovative approach within precision breeding is the use of genetic drive technologies, particularly in pest control. Genetic drives can spread specific genetic alterations through populations at an accelerated rate, which could be utilized to control or eradicate pests that affect livestock health and productivity. While this technology is still in its infancy, it holds significant promise for sustainable livestock management and could greatly reduce the reliance on chemical pest control methods (Woolliams, 2011).

### **5.2 Sustainable breeding strategies**

Sustainable breeding strategies are increasingly important in the context of global environmental challenges and the need for more eco-friendly agricultural practices. Eco-friendly breeding technologies aim to reduce the environmental footprint of livestock farming by selecting for traits that improve feed efficiency and reduce waste. Genomic selection plays a crucial role in this, as it allows for the accurate prediction of breeding values for traits associated with environmental sustainability, such as reduced methane emissions or better utilization of feed resources (Zhang et al., 2014; Meuwissen et al., 2016; Lu et al., 2016).

Moreover, the symbiotic relationship between livestock farming and environmental conservation is gaining attention. By selecting for traits that enhance the adaptability of livestock to various environmental conditions, it is possible to maintain productive farming systems that are in harmony with local ecosystems. This approach not only supports the conservation of biodiversity but also ensures the resilience of livestock populations in the face of climate change and other environmental pressures (Hayes and Goddard, 2010; Gutierrez-Reinoso et al., 2021).

In conclusion, the future of livestock breeding is intricately linked to the development and implementation of precision breeding technologies and sustainable breeding strategies. These advancements will enable breeders to meet the growing demand for animal products while addressing the critical need for environmental stewardship.

## 6 Concluding Remarks

The advent of genomic prediction (GP) technology has revolutionized the field of animal breeding, particularly in the selection for complex traits in livestock. The importance of this technology cannot be overstated, as it has enabled breeders to make more accurate and efficient selection decisions, which are crucial for the improvement of traits that are economically significant in livestock production. Genomic prediction leverages dense single nucleotide polymorphism (SNP) genotypes to estimate breeding values, taking into account the genetic architecture of traits, which often involves a large number of loci with small effects.

The impact of genomic prediction on breeding strategies is evident in various livestock species, including dairy and beef cattle, pigs, and poultry. It has been shown to contribute significantly to increased accuracy in selection decisions, particularly in dairy cattle, where the practical application of GP has been clearly illustrated. Moreover, the integration of genomic data has been successfully applied to local breeds, demonstrating its utility even in populations with smaller sizes.

However, the necessity for continued research and development in this field remains paramount. The genetic architecture of complex traits is intricate, and the identification of causal polymorphisms continues to be a challenge. The use of whole-genome sequence data is anticipated to improve the accuracy of genomic selection, but it also presents new challenges, such as managing inbreeding and ensuring the sustainability of genetic diversity. Furthermore, the design of breeding programs and the optimization of training population structures are critical factors that influence the accuracy of genomic predictors.

The development of new and improved genomic prediction algorithms, including non-linear approaches like artificial neural networks and gradient tree boosting, is an ongoing area of research. Benchmarking these algorithms to identify the most effective ones for specific traits and species is essential for the advancement of genomic prediction. Additionally, the potential of genomic selection to facilitate the introgression of beneficial alleles from exotic germplasm into elite breeding populations is an exciting prospect that warrants further investigation.

In conclusion, genomic prediction technology has already made a substantial impact on livestock breeding strategies for complex traits. To fully realize its potential and to continue enhancing breeding programs, it is crucial to invest in research that addresses the challenges associated with the genetic complexity of these traits, the development of advanced prediction models, and the integration of comprehensive genomic information.

## References

- Boison S., Utsunomiya A., Santos D., Neves H., Carneiro R., Mészáros G., Utsunomiya Y., Carmo A., Verneque R., Machado M., Panetto J., Garcia J., Sölkner J., and Silva M., 2017, Accuracy of genomic predictions in Gyr (*Bos indicus*) dairy cattle, *Journal of dairy science*, 100(7): 5479-5490.  
<https://doi.org/10.3168/jds.2016-11811>
- Bolormaa S., Pryce J., Kemper K., Savin K., Hayes B., Barendse W., Zhang Y., Reich C., Mason B., Bunch R., Harrison B., Reverter A., Herd R., Tier B., Graser H., and Goddard M., 2013, Accuracy of prediction of genomic breeding values for residual feed intake and carcass and meat quality traits in *Bos taurus*, *Bos indicus*, and composite beef cattle. *Journal of animal science*, 91(7): 3088-3104.  
<https://doi.org/10.2527/jas.2012-5827>
- Campos G., Hickey J., Pong-Wong R., Daetwyler H., and Calus M., 2013, Whole-genome regression and prediction methods applied to plant and animal breeding, *Genetics*, 193: 327-345.  
<https://doi.org/10.1534/genetics.112.143313>
- Christensen O., and Lund M., 2010, Genomic prediction when some animals are not genotyped. *Genetics, Selection, Evolution: GSE*, 42: 2.  
<https://doi.org/10.1186/1297-9686-42-2>
- Ding X., Zhang Z., Zhang Z., Li X., Wang S., Wu X., Sun D., Yu Y., Liu J., Wang Y., Zhang Y., Zhang S., and Zhang Q., 2013, Accuracy of genomic prediction for milk production traits in the Chinese Holstein population using a reference population consisting of cows, *Journal of Dairy Science*, 96(8): 5315-5323.  
<https://doi.org/10.3168/jds.2012-6194>

- Elsen J., 2003, Utilization of genomic information in livestock improvement, *Outlook on Agriculture*, 32: 241-245.  
<https://doi.org/10.5367/000000003322740793>
- Fang L., Sahana G., Ma P., Su G., Yu Y., Zhang S., Lund M., and Sørensen P., 2017, Use of biological priors enhances understanding of genetic architecture and genomic prediction of complex traits within and between dairy cattle breeds, *BMC Genomics*, 18: 1-12.  
<https://doi.org/10.1186/s12864-017-4004-z>
- Georges M., 2001, Recent progress in livestock genomics and potential impact on breeding programs, *Theriogenology*, 55(1): 15-21.  
[https://doi.org/10.1016/S0093-691X\(00\)00442-8](https://doi.org/10.1016/S0093-691X(00)00442-8)
- Gutierrez-Reinoso M., Aponte P., and García-Herreros M., 2021, Genomic Analysis, progress and future perspectives in dairy cattle selection: a review, *Animals*, 11(3): 599.  
<https://doi.org/10.3390/ani11030599>
- Hayes B., and Goddard M., 2010, Genome-wide association and genomic selection in animal breeding, *Genome*, 53(11): 876-883.  
<https://doi.org/10.1139/G10-076>
- Hayes B., Pryce J., Chamberlain A., Bowman P., and Goddard M., 2010, Genetic architecture of complex traits and accuracy of genomic prediction: coat colour, milk-fat percentage, and type in holstein cattle as contrasting model traits, *PLoS Genetics*, 6(9): e1001139.  
<https://doi.org/10.1371/journal.pgen.1001139>
- Karaman E., Su G., Croué I., and Lund M., 2021, Genomic prediction using a reference population of multiple pure breeds and admixed individuals, *Genetics, Selection, Evolution: GSE*, 53(1): 46.  
<https://doi.org/10.1186/s12711-021-00637-y>
- Kemper K., and Goddard M., 2012, Understanding and predicting complex traits: knowledge from cattle, *Human Molecular Genetics*, 21(R1): R45-51.  
<https://doi.org/10.1093/HMG/DDS332>
- Liang M., Miao J., Wang X., Chang T., An B., Duan X., Xu L., Gao X., Zhang L., Li J., and Gao H., 2020, Application of ensemble learning to genomic selection in chinese simmental beef cattle, *Journal of Animal Breeding and Genetics*, 2021, 138(3): 291-299.  
<https://doi.org/10.1111/jbg.12514>
- Lopes F., Baldi F., Passafaro T., Brunet L., Costa M., Eifert E., Narciso M., Rosa G., Lôbo R., and Magnabosco C., 2020, Genome-enabled prediction of meat and carcass traits using Bayesian regression, single-step genomic best linear unbiased prediction and blending methods in Nelore cattle, *Animal*, 15(1): 100006.  
<https://doi.org/10.1016/j.animal.2020.100006>
- Lu D., Akanno E., Crowley J., Schenkel F., Li H., Pauw M., Moore S., Wang Z., Li C., Stothard P., Plastow G., Miller S., and Basarab J., 2016, Accuracy of genomic predictions for feed efficiency traits of beef cattle using 50K and imputed HD genotypes, *Journal of Animal Science*, 94(4): 1342-1353.  
<https://doi.org/10.2527/jas.2015-0126>
- Meuwissen T., Hayes B., and Goddard M., 2016, Genomic selection: A paradigm shift in animal breeding. *Animal Frontiers*, 6: 6-14.
- Srivastava S., Lopez B., Kumar H., Jang M., Chai H., Park W., Park J., and Lim D., 2021, Prediction of hanwoo cattle phenotypes from genotypes using machine learning methods, *Animals*, 11(7): 2066.  
<https://doi.org/10.3390/ani11072066>
- Swami M., 2010, Complex traits: Using genetic architecture to improve predictions, *Nature Reviews Genetics*, 11: 748.  
<https://doi.org/10.1038/nrg2888>
- Teng J., Gao N., Zhang H., Li X., Li J., Zhang H., Zhang X., and Zhang Z., 2019, Performance of whole genome prediction for growth traits in a crossbred chicken population, *Poultry Science*, 98: 1968-1975.  
<https://doi.org/10.3382/ps/pey604>
- Woolliams J., 2011, How far and how fast can genomics take us towards precision breeding?, *Journal of Animal Breeding And Genetics*, 128(6): 407-408.  
<https://doi.org/10.1111/j.1439-0388.2011.00974.x>
- Zhang Z., Ober U., Erbe M., Zhang H., Gao N., He J., Li J., and Simianer H., 2014, Improving the accuracy of whole genome prediction for complex traits using the results of genome wide association studies, *PLoS ONE*, 9(3): e93017.  
<https://doi.org/10.1371/journal.pone.0093017>

## Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.