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# The Evolving Landscape of Genomic Selection: Insights and Innovations in Quantitative Genetics

Xiaojun Li ✉, Shuiji Zhang
Biotechnology Research Center, Cuixi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China
✉ Corresponding author: xiaojun.li@cuixi.org

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**Abstract** Genomic selection (GS), as a key technology in modern breeding programs, has significantly advanced crop and livestock breeding. By integrating quantitative genetics and genome prediction models, GS has improved the accuracy of predicting complex traits and accelerated the cultivation of high-yield and stress resistant varieties. This study explores the historical evolution, technological innovation, and practical applications of genome selection in breeding. It analyzes the advantages brought by innovative technologies such as high-density genotyping and whole genome prediction, especially their widespread application in multi trait and multi environment models. Although GS has great potential in modern breeding, it still faces challenges such as genotype environment interaction, prediction accuracy, and data complexity. I hope to summarize the latest progress of GS through case analysis and provide direction for future research, in order to promote the application of quantitative genetics and genome selection in a wider range of fields, and provide support for global food security and sustainable agricultural development.

**Keywords** Genomic selection; Quantitative genetics; Genomic prediction; Marker-assisted selection; Complex traits

## 1 Introduction

Genomic Selection (GS) has emerged as a significant breakthrough in the field of breeding in recent years. Unlike traditional marker-assisted selection, which relies on a limited number of markers associated with specific traits, GS utilizes genome-wide marker data to predict the breeding values of individuals. By estimating the effects of all markers comprehensively, GS captures the small-effect alleles that influence complex traits, thereby improving breeding efficiency and accuracy (Meuwissen et al., 2016; Crossa et al., 2017). With advances in high-density genotyping technologies, GS has been widely applied in both plant and animal breeding, significantly accelerating genetic improvement (Heslot et al., 2015; Rice and Lipka, 2021).

GS plays a crucial role in modern breeding programs. By integrating genome-wide marker information, GS significantly increases selection accuracy, shortens breeding cycles, and enhances genetic gains per unit time. This method is particularly effective in improving quantitative traits controlled by multiple genes, especially in addressing challenges related to climate change and enhancing crop yields and livestock production (Liu et al., 2019; Merrick et al., 2022). Additionally, GS reduces the need for large-scale phenotyping, lowers breeding costs, and, through advanced statistical models and high-throughput phenotyping technologies, improves breeding efficiency (Larkin et al., 2019; Cappetta et al., 2020).

This study systematically reviews the latest developments and innovations in the field of GS. By analyzing the development history, various application models, and methods of GS, this study explores the actual effects of GS in different breeding programs and evaluates its impact on genetic gain and breeding efficiency. In addition, challenges and limitations in the implementation of GS were identified, and possible solutions to address these issues were proposed. In the future, GS is expected to continue promoting the sustainable development of global agriculture by integrating emerging technologies and improving prediction accuracy.

## 2 Evolution of Genomic Selection

### 2.1 Historical development of GS

The concept of genomic selection (GS) was first introduced by Meuwissen et al. in 2001, marking a significant departure from traditional marker-assisted selection (MAS) methods. Prior to this, agricultural genomics primarily focused on detecting quantitative trait loci (QTL) using experimental crosses or existing family relationships. The innovative approach proposed by Meuwissen et al. required a high density of genomic markers to ensure that every QTL affecting a relevant trait would be in linkage disequilibrium with at least one marker. This allowed for selection decisions to be based on the joint merit of all markers across the genome, rather than a few significant ones. This breakthrough laid the foundation for the rapid advancements in GS, particularly in livestock breeding, where it has led to unprecedented improvements in genetic gain per generation (Koning et al., 2016; Meuwissen et al., 2016).

### 2.2 Early applications in crop and livestock breeding

The initial applications of GS were predominantly in livestock breeding, driven by the high individual value of livestock and the significant reduction in generation intervals achievable through GS. Dairy cattle breeding, in particular, saw a dramatic shift from traditional progeny testing to GS, resulting in a doubling of genetic improvement per generation (Koning et al., 2016; Meuwissen et al., 2016). The success in livestock spurred interest in applying GS to crop breeding. Early applications in crops such as rice, maize, and wheat have demonstrated that GS has resulted in significant genetic gains, thanks to the large international efforts led by organizations like the International Maize and Wheat Improvement Center (CIMMYT) (Crossa et al., 2017; Li and Jiong, 2022).. The integration of GS in plant breeding has been further enhanced by advances in field management, heritability estimation, and the development of robust GS models that account for genotype-by-environment interactions (Burri, 2017; Xu et al., 2019).

### 2.3 Technological advances driving GS evolution

The evolution of GS has been propelled by several key technological advancements. The development of high-density single nucleotide polymorphism (SNP) chips around 2006 made it feasible to routinely genotype animals and plants for thousands of markers in a cost-effective manner. This was complemented by improvements in statistical modeling approaches, including the Bayesian methods (BayesA and BayesB) introduced by Meuwissen et al., which have been extensively refined over the years (Koning et al., 2016). The advent of high-throughput sequencing technologies has further revolutionized GS by enabling the use of whole-genome sequence data, which offers higher accuracy in predicting breeding values (Meuwissen et al., 2016; VanRaden, 2020). Additionally, the integration of new technologies such as hyperspectral imaging and digital breeding platforms is poised to further enhance the efficiency and accuracy of GS in both plant and animal breeding (Crossa et al., 2017; Jeon et al., 2023).

## 3 Quantitative Genetics and Its Integration with Genomic Selection

### 3.1 Basic principles of quantitative genetics

Quantitative genetics is the study of traits that are influenced by multiple genes and environmental factors. These traits, known as quantitative traits, exhibit continuous variation and are typically measured on a numerical scale. The fundamental principles of quantitative genetics involve the partitioning of phenotypic variance into genetic and environmental components, the estimation of genetic parameters such as heritability, and the prediction of breeding values. Traditional methods like Best Linear Unbiased Prediction (BLUP) have been widely used to estimate breeding values by leveraging pedigree information and phenotypic data (Koning, 2016; Li et al., 2017).

### 3.2 Genomic prediction models

Genomic prediction models have revolutionized the field of quantitative genetics by incorporating dense marker information to predict the genetic potential of individuals. These models can be broadly categorized into linear models, Bayesian approaches, and machine learning or non-linear models.

#### 3.2.1 G-blup and other linear models

Genomic Best Linear Unbiased Prediction (G-BLUP) is a widely used linear model that extends the traditional BLUP by incorporating genomic information. G-BLUP assumes that all markers contribute equally to the genetic variance and uses a genomic relationship matrix to capture the genetic similarities between individuals (Koning, 2016; Li et al., 2017). Other linear models, such as Ridge Regression BLUP (RR-BLUP), have also been employed for genomic prediction, particularly when dealing with traits controlled by a large number of small-effect loci (Wang et al., 2015; Liu et al., 2018).

#### 3.2.2 Bayesian approaches

Bayesian methods offer a flexible framework for genomic prediction by allowing the incorporation of prior information and the estimation of marker effects with different distributions. Notable Bayesian models include BayesA, BayesB, and BayesC, each differing in their assumptions about the distribution of marker effects (Wang et al., 2015; Koning, 2016). Bayesian regularized quantile regression (BRQR) has been proposed as a robust alternative for dealing with skewed data, showing comparable or superior prediction ability to traditional Bayesian ridge regression (BRR) (Pérez-Rodríguez et al., 2020). Additionally, Bayesian models can be extended to account for genotype-by-environment interactions, enhancing prediction accuracy in multi-environment trials.

#### 3.2.3 Machine learning and non-linear models

Machine learning and non-linear models have gained traction in genomic prediction due to their ability to capture complex genetic architectures. Methods such as reproducing kernel Hilbert space (RKHS) and Gaussian kernel models have been used to model non-additive genetic effects and interactions between markers (Covarrubias-Pazaran, 2016; Liu et al., 2018). These models are particularly useful for traits with low heritability or those influenced by a large number of minor genes.

### 3.3 Integration of genomics with quantitative genetics

The integration of genomics with quantitative genetics has led to significant advancements in the accuracy and efficiency of breeding programs. By combining genome-wide association studies (GWAS) with genomic selection (GS), researchers can identify quantitative trait loci (QTL) and improve the precision of genomic predictions. For instance, the Stepwise Linear Mixed Model (StepLMM) unifies GWAS and GS, enhancing both QTL mapping and genomic prediction accuracy (Li et al., 2017). The iterative method GBC, which incorporates aspects of both G-BLUP and Bayes-C, has shown marginally superior prediction accuracy compared to using either method alone (Iheshiulor et al., 2017).

Empirical studies have demonstrated that factors such as marker density, population size, and heritability significantly influence the prediction accuracy of genomic models. Increasing marker density and population size generally improves prediction accuracy (Figure 1), while the choice of statistical model should consider the genetic architecture of the trait (Liu et al., 2018). The development of software tools like the R package sommer facilitates the application of mixed models for genomic prediction, allowing for the inclusion of multiple variance components and complex covariance structures (Covarrubias-Pazaran, 2016).

The integration of quantitative genetics with genomic selection has transformed breeding strategies, enabling more precise and efficient selection of superior individuals. The continuous development and refinement of genomic prediction models will further enhance the potential of genomic selection in various agricultural and human genetic studies.

Comparison of marker prediction accuracy based on association and linkage maps under different marker density conditions. The results indicate that increasing marker density can significantly enhance the predictive accuracy of models, especially for traits with low heritability. Additionally, the figure illustrates the performance differences between randomly selected markers and feature markers in the model, supporting the view that "factors such as marker density, population size, and heritability significantly affect the prediction accuracy of genomic models.

## 4 Innovations in Genomic Selection Techniques

### 4.1 High-density genotyping and sequencing

High-density genotyping and sequencing have revolutionized genomic selection by providing a comprehensive view of the genetic architecture of traits. The use of single nucleotide polymorphism (SNP) arrays and next-generation sequencing (NGS) technologies has enabled the identification of thousands of genetic markers across the genome. This dense marker information is crucial for accurate genomic predictions, as it ensures that all quantitative trait loci (QTLs) are in linkage disequilibrium with at least one marker (Meuwissen et al., 2016). The transition from medium-density SNP chips to whole-genome sequencing has further enhanced the resolution of genomic data, allowing for more precise selection decisions. However, the computational burden associated with high-density data remains a challenge, necessitating the development of efficient algorithms and models to handle the vast amount of information (Wang et al., 2016).

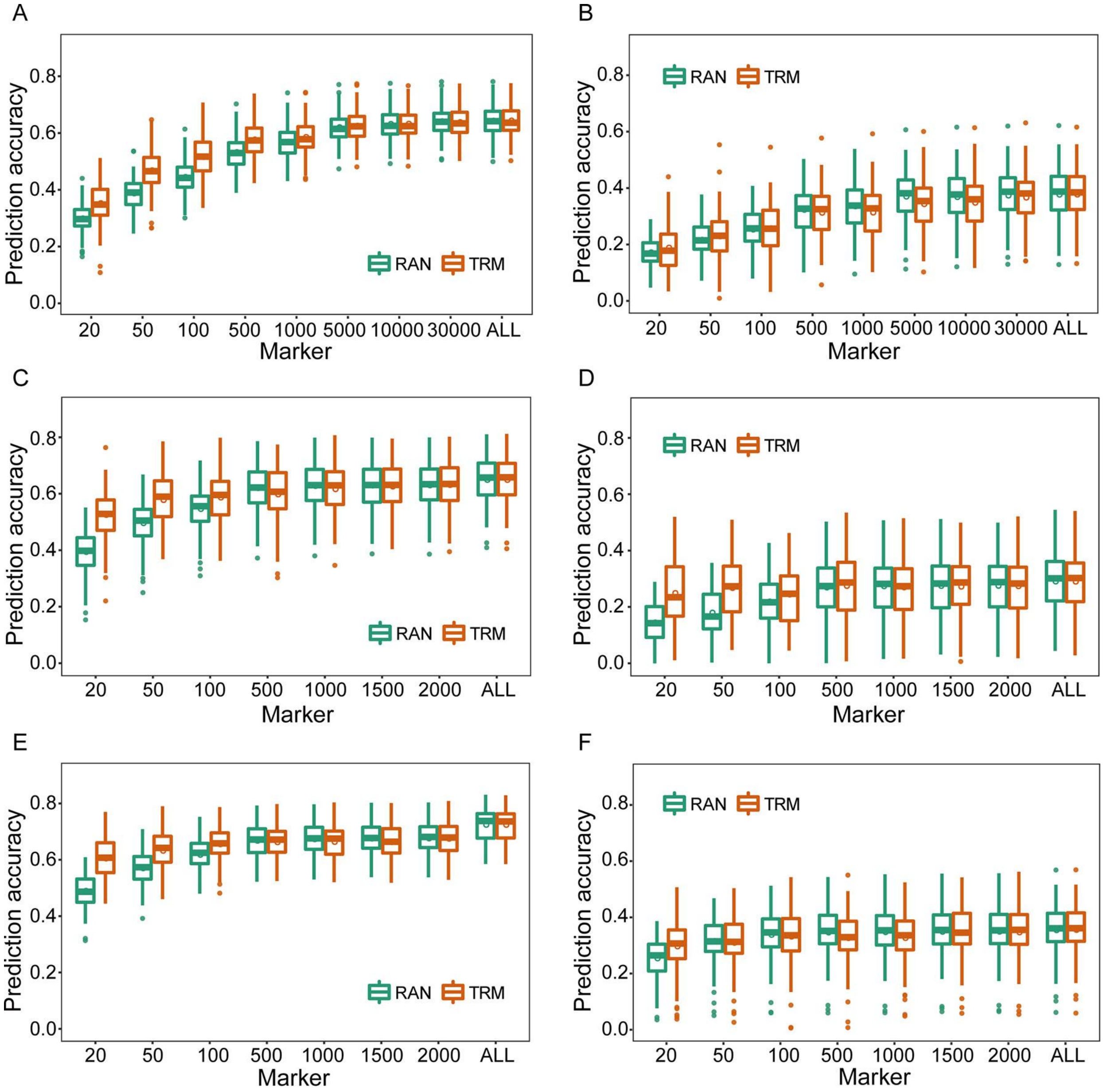

Figure 1 Comparison of prediction accuracies between trait-relevant markers (TRMs) and randomly selected markers based on the results of association and linkage mapping using genotypic and phenotypic data of the training set within the experimental populations. (A) and (B) Plant height (PH) and grain yield per plant (GYP) in the natural population (N = 435); (C) and (D) PH and GYP in the RIL population (N = 212); (E) and (F) PH and GYP in the F2:3 population (N = 304). N is the number of individuals in each population. TRM: the prediction accuracy based on TRMs in the general genomic best linear unbiased prediction (GBLUP) model; RAN: the prediction accuracy based on randomly selected markers in the general GBLUP model. ALL: total of 38,299 single nucleotide polymorphisms (SNPs), 2,450 and 2,826 bin markers were used to perform the scheme of cross-validation in natural, recombinant inbred line (RIL), and F2:3 populations, respectively. The fivefold cross-validation scheme was implemented in this case (Adopted from Liu et al., 2018)

## 4.2 Whole-Genome Prediction and Marker-Assisted Selection

### 4.2.1 Advantages over traditional marker-assisted selection

Traditional marker-assisted selection (MAS) has been limited by its focus on a few significant markers, often missing the polygenic nature of complex traits (Koning, 2016). In contrast, whole-genome prediction (WGP) leverages the effects of all markers across the genome, providing a more comprehensive and unbiased estimate of genetic values (Bradshaw et al., 2016). This approach captures the cumulative effect of numerous small-effect QTLs, which are often overlooked in MAS. As a result, WGP offers higher accuracy in predicting breeding values, leading to more effective selection and faster genetic gains (Meuwissen et al., 2016).

#### 4.2.2 Application in complex trait prediction

The application of WGP in predicting complex traits has shown significant promise in both plant and animal breeding. By incorporating all available marker information, WGP models can predict the genetic potential of individuals with high accuracy, even for traits with low heritability (Bradshaw et al., 2016; Varshney et al., 2017). This has been particularly beneficial in livestock breeding, where traits such as milk production and disease resistance are influenced by many genes with small effects (Meuwissen et al., 2016). In crop breeding, WGP has enabled the selection of lines with superior agronomic performance, accelerating the breeding cycle and enhancing genetic gains per unit time (Unêda-Trevisoli et al., 2017).

### 4.3 Use of multi-trait and multi-environment models

The integration of multi-trait and multi-environment models in genomic selection has further improved the accuracy and robustness of predictions. These models account for the genetic correlations between traits and the interactions between genotypes and environments, providing a more holistic view of an individual's genetic potential. By leveraging data from multiple traits and environments, breeders can make more informed selection decisions, optimizing genetic gains across diverse conditions (Figure 2). This approach is particularly valuable in plant breeding, where environmental variability can significantly impact trait expression and selection outcomes (Merrick et al., 2022).

The advancements in high-density genotyping, whole-genome prediction, and the use of multi-trait and multi-environment models have significantly enhanced the effectiveness of genomic selection. These innovations have addressed the limitations of traditional MAS, providing more accurate and comprehensive predictions of genetic values, and ultimately accelerating the pace of genetic improvement in both plant and animal breeding (Wang et al., 2016; Meuwissen et al., 2016; Varshney et al., 2017).

Merrick et al. (2022) demonstrated the use of multi-trait and multi-environment models in genomic selection, showing how different methods integrate data from multiple traits and environments to improve prediction accuracy. Figure 2 highlights how the integration of environmental variables and multiple traits enhances model accuracy, confirming that multi-trait and multi-environment models can provide more robust prediction results in complex breeding environments.

## 5 Challenges and Limitations of Genomic Selection

### 5.1 Genotype-environment interactions

Genotype-environment interactions (GEI) present a significant challenge in genomic selection (GS) as they can drastically affect the prediction accuracy of GS models. Traditional models often struggle to account for the complexity of GEI, leading to poor phenotype predictions in unobserved environments. To address this, novel models such as the 3GS model have been developed, which integrate genotype plus genotype × environment (GGE) analysis with GS. This model has shown higher prediction accuracy, especially in environments with low to negative correlations to other environments, and can predict new genotypes in unobserved environments with high accuracy. Additionally, the computational complexity of 3GS increases linearly with the number of environments and population size, making it significantly faster than standard models for large datasets (Jighly et al., 2021). Other approaches, such as the BGGE package, also aim to improve computational efficiency while accounting for GEI by using Bayesian linear mixed models and special genetic covariance matrices (Granato et al., 2018). These advancements highlight the importance of incorporating GEI into GS models to enhance prediction accuracy and computational efficiency.

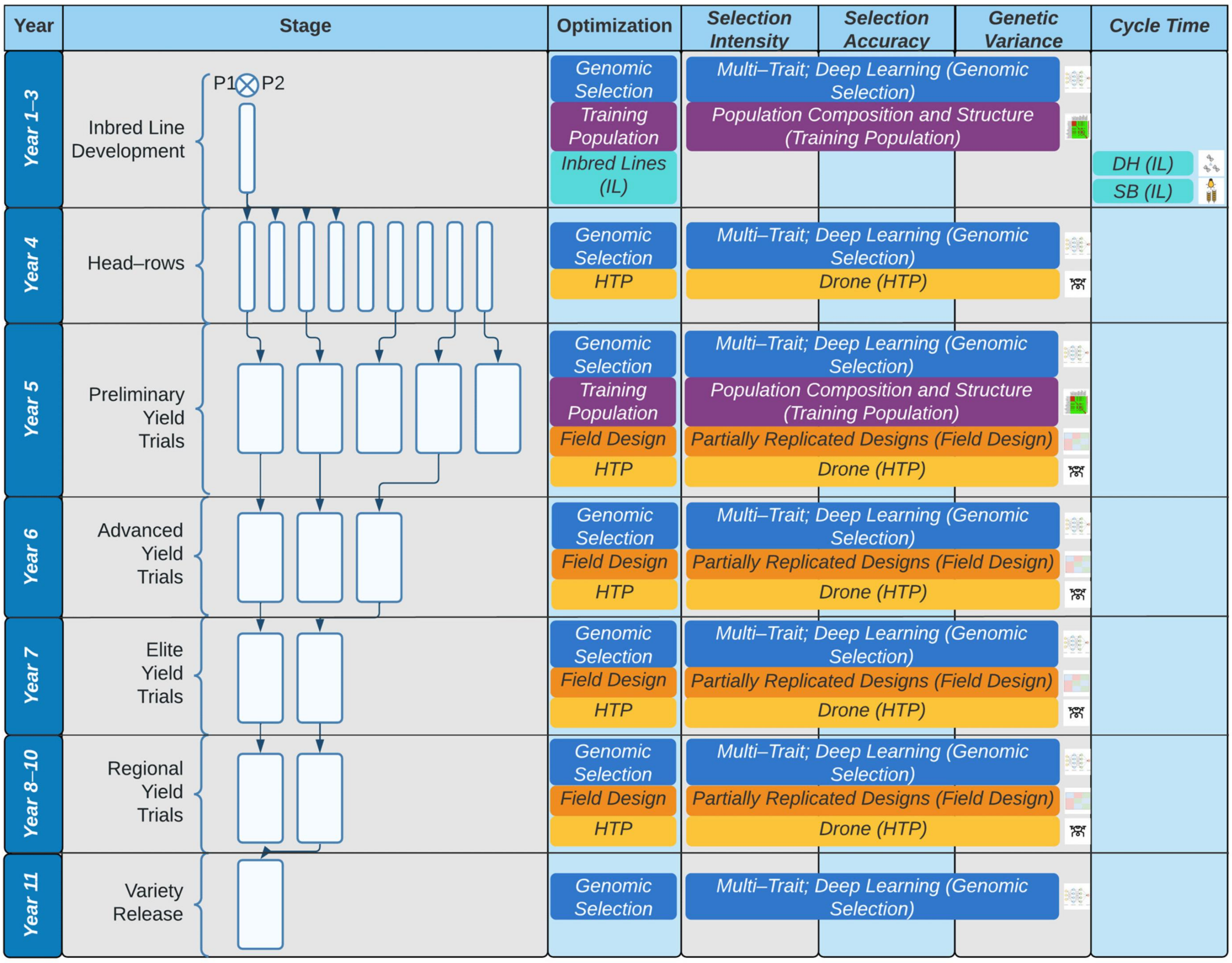

Figure 2 Optimization of the traditional breeding pipeline and product development based on an 11–year breeding program from parental crossing to variety release. The effect of each component of optimization (genomic selection, training population design, inbred line development, field design, high-throughput phenotyping (HTP) on different aspects of the breeder's equation (selection intensity, selection accuracy, genetic variance, and cycle time) is shown by the coverage of the method of optimization within the respective column of the different factors of the breeder's equation. For example, for Years 1-3 of the breeding cycle, the composition and structure of the training population (purple) affect both selection accuracy and genetic variance, whereas the choice of genomic selection models affects the intensity of selection, prediction accuracy, and genetic variance (Adopted from Merrick et al., 2022)

### 5.2 Accuracy of genomic predictions

The accuracy of genomic predictions is a critical factor in the success of GS. The correlation between predicted and true breeding values is influenced by several factors, including the density of markers and the size of the reference population. Increasing the size of the reference set and using denser markers can improve prediction accuracy. However, this often comes at the cost of increased computational burden, particularly with non-linear Bayesian models, which, while providing higher accuracy for some traits, require significant computational resources (Wang et al., 2016). Theoretical advancements have introduced new proxies for accuracy that outperform existing ones, particularly in configurations of linkage disequilibrium (LD) between quantitative trait loci (QTLs) and markers (Rabier et al., 2016). Despite these improvements, challenges remain in maintaining the stability of genomic predictions, as fluctuations in evaluations can lead to a crisis of confidence in GS (Misztal et al., 2021). Therefore, ongoing research is needed to develop models that balance accuracy and computational efficiency while ensuring stable predictions.

### 5.3 Data complexity and computational demands

The complexity of data and the computational demands associated with GS are significant limitations. The integration of high-density SNP and whole-genome sequence data into GS models has transformed breeding practices but also introduced substantial computational challenges. Non-linear Bayesian models, while accurate, are computationally intensive, necessitating strategies to improve efficiency (Wang et al., 2016). The development of ensemble learning algorithms, such as Gradient Boosted Decision Trees (GBDT), offers a promising alternative by providing high computational efficiency and competitive prediction accuracy compared to traditional Bayesian models (Yu et al., 2022). Additionally, the use of sparse covariance matrices and block diagonal matrices in models like BGGE can reduce computational time significantly (Granato et al., 2018). These innovations are crucial for managing the large-scale, high-dimensional data typical in modern breeding programs and ensuring that GS remains a viable and efficient tool for genetic improvement.

## 6 Case Studies and Practical Applications

### 6.1 Successful implementation in crop breeding

Genomic selection (GS) has revolutionized crop breeding by enabling the rapid selection of superior genotypes and accelerating breeding cycles. The concept, initially proposed by Meuwissen et al. in 2001, has been widely adopted in crop breeding programs, particularly for crops like maize and wheat, due to large international efforts by organizations such as the International Maize and Wheat Improvement Center (CIMMYT) (Koning, 2016). GS has shown significant promise in improving quantitative traits controlled by multiple genes with small effects, which traditional marker-assisted selection (MAS) struggled to address (Varshney et al., 2017; Budhlakoti et al., 2022).

The integration of GS with other breeding tools and platforms has further enhanced genetic gain. For instance, refining field management to improve heritability estimation and prediction accuracy, and developing optimum GS models that consider genotype-by-environment interactions and non-additive effects, have been crucial (Xu et al., 2019). Additionally, the use of high-throughput genotyping and phenotyping technologies has accelerated the breeding process, making GS a powerful tool for developing climate-resilient crop varieties (Wang et al., 2018; Krishnappa et al., 2021).

### 6.2 Application in livestock improvement

In livestock breeding, GS has led to unprecedented advances, particularly in dairy cattle, where it has almost entirely replaced traditional selection methods based on progeny testing. This shift has resulted in a doubling of genetic improvement per generation compared to traditional methods (Koning, 2016). The success of GS in livestock is attributed to the significant reduction in generation intervals and the higher individual values of livestock, which make the investment in GS more economically viable (Xu et al., 2019).

The application of GS in livestock has been facilitated by the development of medium-density SNP chips, which became routinely available for main livestock species around 2006. This technological advancement allowed for the widespread adoption of GS in the industry, leading to remarkable improvements in genetic gain and selection accuracy . Current methods for GS in livestock include linear regression, Best Linear Unbiased Selection (BLUP), and Bayesian approaches, with the latter being extensively refined over the years (Meuwissen et al., 2016).

### 6.3 Insights from emerging research

Emerging research in GS continues to push the boundaries of what is possible in both crop and livestock breeding. For instance, studies have shown that integrating GS with speed breeding and other novel technologies can significantly enhance the efficiency and pace of breeding programs. Additionally, the development of improved statistical models that leverage genomic information to increase prediction accuracies is critical for the effectiveness of GS-enabled breeding programs (Budhlakoti et al., 2022).

In the context of human genetics, insights into the genetic architecture of complex traits are informing GS approaches in livestock. For example, understanding the genetic mechanisms underlying variation in complex traits, such as height, can help improve the accuracy of genomic predictions in livestock (Kemper, 2021). This cross-disciplinary approach highlights the potential for GS to benefit from advances in other fields of genetics, further enhancing its application in agricultural breeding programs.

Overall, the evolving landscape of GS is characterized by continuous innovation and integration of new technologies, making it a cornerstone of modern quantitative genetics and breeding strategies (Koning, 2016; Krishnappa et al., 2021; Xu et al., 2019).

## 7 Concluding Remarks

Genomic selection has brought significant innovations to the field of quantitative genetics, utilizing single-nucleotide polymorphisms (SNPs) and other genomic markers to enable the early identification of genetically superior individuals. This approach has greatly improved selection accuracy, particularly in animal breeding, by calculating breeding value indexes that encompass almost all quantitative trait loci (QTLs). The application of high-throughput sequencing technologies has further enhanced our ability to identify genomic regions related to adaptation and species differentiation, and to deepen our understanding of the genomic structure of diversity. Emerging methods like deep learning and convolutional neural networks have provided critical support for uncovering the role of natural selection from large-scale genomic data.

The future of quantitative genetics lies in the continued integration of genomic data with advanced computational methods. Genome-wide association studies (GWAS) and population genetics will help us understand the evolutionary mechanisms that maintain genetic variation for quantitative traits. Additionally, genomic selection holds great promise in plant breeding for improving agricultural productivity, though it must be carefully adapted to different breeding systems and environmental conditions. Furthermore, exploring the importance of balancing selection in genetic diversity will provide more insights into species evolution.

To further advance genomic selection and quantitative genetics, future research should focus on several key areas. First, integrating multivariate selection will be crucial for understanding how correlational selection shapes genomic architecture. Second, more accurate prediction models are needed to account for the complex interactions between genetic and environmental factors, especially in breeding value predictions. Additionally, genomic selection methods should be expanded to include a wider range of species, particularly those with complex breeding systems or those underrepresented in current research. The potential of deep learning and artificial intelligence is vast, and future research should explore how these tools can be applied in genomics. Finally, developing new methods to identify and quantify balancing selection in genomes will help us better understand its role in maintaining genetic diversity within populations.

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### Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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