

7.2 Practical implications for plant breeding

For plant breeding, SNP-based heritability estimation has substantial practical relevance. First, it provides a quantitative basis for assessing the predictability of complex quantitative traits. A high SNP-based heritability estimate suggests that the major genetic components of a trait are effectively captured by existing genotyping markers, indicating that genomic selection (GS) models are likely to achieve high predictive accuracy for that trait (Schmidt et al., 2019; Zhu and Zhou, 2020). Conversely, a low estimate implies that a significant portion of genetic variation remains unexplained, highlighting the need for increased marker density, incorporation of rare variants, or improved modeling of gene-environment interactions (Zhu and Zhou, 2020).

Second, SNP-based heritability provides valuable guidance for population design and resource allocation. In major crops such as rice, maize, and wheat, factors such as population size, genetic background, and sample representativeness significantly influence the stability of heritability estimates. By applying GREML in early-stage populations, breeders can rapidly assess whether it is necessary to increase sample size, optimize crossing schemes, or adjust selection strategies for specific traits (Schmidt et al., 2019; Holland et al., 2020). Furthermore, partitioning heritability by functional annotation or allele frequency enables breeders to identify genomic regions or variant classes that should be prioritized for improvement, thereby enhancing selection efficiency (Weissbrod et al., 2019; Zhu and Zhou, 2020).

7.3 Integration with PRS, fine-mapping, and downstream methods

Unlike early marker-assisted breeding approaches centered on QTL mapping and candidate genes (Fang et al., 2001), the GCTA/GREML framework focuses on the genome-wide proportion of genetic variance captured by markers. Its results are therefore more suitable for evaluating the predictive limits of traits, rather than directly identifying functional loci. The value of GREML lies not only in heritability estimation itself, but also in its integrative role within the broader analytical pipeline.

First, GREML is closely related to polygenic risk scores (PRS). SNP-based heritability provides a theoretical upper bound for PRS prediction accuracy. Specifically, if a trait has low SNP-based heritability, improvements in model complexity alone cannot overcome this fundamental limitation (Yang et al., 2017; Zhang et al., 2018; Wang et al., 2023). Recent studies have demonstrated that incorporating functional annotations and LD structure, as well as accounting for uncertainty in individual-level risk estimation, can substantially improve PRS performance (Weissbrod et al., 2019; Ding et al., 2021).

Second, the variance decomposition framework of GREML is highly compatible with fine-mapping approaches. By partitioning heritability across chromosomes, functional annotations, or specific gene sets, GREML can provide prioritization for identifying causal variants, thereby improving both the resolution and biological interpretability of fine-mapping results (Weissbrod et al., 2019; Gazal et al., 2022).

Taken together, GREML is not merely a tool for heritability estimation, but a methodological bridge linking variant discovery, statistical inference, and functional interpretation, thereby offering a systematic framework for future precision breeding and molecular improvement.

8 Conclusion

The development of GCTA and GREML has established a standardized framework for estimating the heritability of complex traits using genome-wide SNP data. Unlike traditional pedigree-based approaches, these methods construct a genomic relationship matrix (GRM) and decompose phenotypic variance within a linear mixed model framework, enabling robust heritability estimation in natural or breeding populations even in the absence of complete pedigree information. This framework represents a fundamental transition from classical quantitative genetics to genotype-driven modern molecular genetics, and demonstrates strong scalability and practical utility as population sizes continue to increase. Furthermore, GCTA/GREML allows heritability to be partitioned by chromosomal segments, functional annotations, or genomic regions, thereby providing a more biologically informative perspective on the genetic architecture of complex traits.