

However, it is essential to recognize that GCTA/GREML estimates rely on a set of statistical assumptions and boundary conditions. First, these methods typically assume that SNP effects follow a multivariate normal distribution and primarily focus on additive genetic variance, with limited consideration of dominance and epistatic effects. Second, the heritability estimates obtained from GCTA/GREML reflect only the variance captured by genotyped or imputed markers, and are therefore influenced by marker density, allele frequency distribution, and the extent of linkage disequilibrium (LD) with causal variants. Consequently, such estimates should not be interpreted as the “true heritability” of a trait, but rather as conditional estimates based on observable genomic variation. Ignoring these underlying assumptions may lead to overinterpretation—for example, incorrectly attributing “missing heritability” to methodological limitations rather than to inherent constraints in data coverage and population characteristics.

In crop genetic improvement and molecular breeding, GCTA and GREML also demonstrate substantial practical value. On the one hand, they enable the characterization of the molecular genetic architecture of complex traits, providing a theoretical basis for quantitative trait locus (QTL) discovery and genomic selection model development. On the other hand, by comparing heritability estimates across traits or environmental conditions, it is possible to identify traits that are highly sensitive to environmental variation, thereby informing precision breeding strategies. In major crops such as rice, maize, and wheat, numerous empirical studies have demonstrated that GREML can effectively distinguish between the selectable and non-selectable components of trait variation, offering critical guidance for breeding target definition and resource allocation.

Overall, the GCTA and GREML family of methods have not only transformed the paradigm of heritability research in quantitative genetics, but have also provided practical tools for dissecting complex traits and advancing molecular breeding. Looking forward, with the continued development of population-scale sequencing, rare variant detection, and large-scale multi-environment datasets, GREML-based heritability estimation is expected to become increasingly refined and comprehensive. This progress will further enhance its role in elucidating the genetic basis of complex traits and in guiding genome-based breeding strategies.

### Author Contributions

Xuanjun Fang conducted this study, including literature review, data analysis, and the drafting and revision of the manuscript. The author has read and approved the final version of the manuscript.

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