the following aspects: (1) systematically outlining the necessary conditions for comparability between SNP-based and pedigree-based heritability; (2) clarifying the statistical target of heritability estimated by GREML and the conceptual boundaries of "missing heritability"; (3) proposing a unified comparison template for common methodological extensions; and (4) providing a standardized workflow and diagnostic checklist for practical interpretation. Through theoretical derivation and empirical analysis, this study aims to offer a clearer understanding of the GCTA framework and its extensions, thereby providing a theoretical foundation and methodological reference for the application of heritability in complex trait research and crop breeding practice.

2 Basic Concepts and Classification of Heritability

Heritability is defined as a variance ratio under a specified statistical model, which depends on both the population and environmental conditions, and quantifies the proportion of phenotypic variation attributable to genetic variation. Therefore, heritability estimates are not directly comparable across different populations, environments, or modeling assumptions.

2.1 Narrow-sense and broad-sense heritability

Heritability is a core parameter in quantitative and statistical genetics, used to characterize the relative contribution of genetic factors to phenotypic variation under a given population, environment, and set of model assumptions (Vinkhuyzen et al., 2013; Yang et al., 2017). From a statistical perspective, heritability is fundamentally a variance ratio, rather than an intrinsic property of a trait or an individual.

Within the classical variance decomposition framework, heritability is typically divided into narrow-sense heritability (h^2) and broad-sense heritability (H^2).

Narrow-sense heritability is defined as the proportion of additive genetic variance (V_a) relative to total phenotypic variance (V_p):

$$h^2=\frac{V_A}{V_P}$$

where V_p represents the overall magnitude of phenotypic variation in the population. Because additive genetic effects are stably transmitted across generations and are cumulative, h^2 plays a central role in predicting the response to selection (e.g., under the Breeder's equation framework), as well as in breeding value estimation and gene mapping studies (Evans et al., 2017; Yang et al., 2017). In practical breeding, narrow-sense heritability is generally regarded as the key indicator of expected selection gain, and its practical relevance often exceeds that of broad-sense heritability (Berry, 2024).

In contrast, broad-sense heritability captures the total contribution of all genetic effects to phenotypic variation, and is defined as:

$$H^2=\frac{V_A+V_D+V_I}{V_P}$$

where V_D denotes dominance variance and V_I denotes epistatic (gene-gene interaction) variance. Although H^2 theoretically reflects the total explanatory power of genetic factors, dominance and epistatic effects depend on allele frequencies and genotype combinations, resulting in limited reproducibility and operability across generations. Therefore, H^2 is generally not suitable for directly predicting selection response (Abney et al., 2001; Zhu et al., 2015).

In most outbred or natural populations, it typically holds that $H^2 \geq h^2$, and the difference between the two reflects the presence and relative magnitude of non-additive genetic variance (Abney et al., 2001; Berry, 2024). Recent studies based on genome-wide marker data have shown that, for many complex traits, dominance variance contributes only modestly to total genetic variation, whereas rare and low-frequency variants may account for part of the "missing heritability" observed in earlier studies (Speed et al., 2012; 2016; Jang et al., 2022; Wainschtein et al., 2022; Srivastava et al., 2023). These findings help establish a consistent and interpretable framework for variance decomposition and prediction across evolutionary genetics and applied breeding (Bérénos et al., 2014; Zimmermann and Distl, 2023).