

**Epistasis** (concept originating from the statistical analysis of phenotypic data)

1. property of genotype to phenotype map, or, if the latter is decomposed, properties „ „ „ „ „ .
2. measure(s) of the effect of those properties on the population phenotypic variance, generally expressed as contributions to that variance.

ad 1. Example: two loci with two alleles each: allele counts  $g_A, g_B = 0, \frac{1}{2}, 1$

If there are no parental or cis-effects: domain contains 9 different genotypes

Polynomial description:

$$\begin{array}{c}
 \text{dominance} \quad \text{additive} \times \text{additive} \\
 \swarrow \quad \searrow \quad \downarrow \\
 \phi = \alpha + \beta_{\phi,A} g_A + \beta_{\phi,B} g_B + \beta_{\phi,A^2} g_A^2 + \beta_{\phi,B^2} g_B^2 + \beta_{\phi,AB} g_A g_B + \\
 + \beta_{\phi,AB^2} g_A g_B^2 + \beta_{\phi,A^2 B} g_A^2 g_B + \beta_{\phi,A^2 B^2} g_A^2 g_B^2 \\
 \nearrow \quad \uparrow \quad \nwarrow \\
 \text{additive} \times \text{dominance} \quad \text{dominance} \times \text{additive} \quad \text{dominance} \times \text{dominance}
 \end{array}$$

ad 2. Ideal case as starting point: known genotypic composition,  
but allow for the phenotypes also to depend on environmental noise.

- Fit polynomial by least squares, starting with the lowest order terms.
- Calculate contributions to the phenotypic variance

Example: additive variance for two loci:

$$V_A = \beta_{\phi,A}^2 \mathbf{Var}(g_A) + \beta_{\phi,B}^2 \mathbf{Var}(g_B) + 2\beta_{\phi,A}\beta_{\phi,B} \mathbf{Cov}(g_A, g_B)$$

- Write the total phenotypic variance as a sum of such contributions plus an environmental variance.

As a result of the least square procedure, generally the terms of higher order (like additive×additive×additive) than the terms shown under ad 1 contribute very little, and can with impunity be considered “environmental”

The experimental trick is that the different variance contributions turn up in the correlations between various kinds of relatives.

Most phenotypic variability comes from unknown genetics. Yet, the various epistatic contributions to the population variance can be determined.

Hence the stress on expressing effects of selection in variance components.