Coheritability and Coenvironmentability as Concepts for Partitioning the Phenotypic Correlation

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List of Symbols

(■ denotes subscript to indicate phenotypic P, (additive) genetic A, or environmental E)

P	phenotypic value of a trait
A	breeding value of a trait
E	environmental (residual) effect of a trait
$\rho_{\blacksquare x,y}$	correlation between traits x and y (population parameter)
$H_{x,y}$	coheritability between traits x and y (population parameter)
$E_{x,y}$	coenvironmentability between traits x and y (population parameter)
$r_{\blacksquare x,y}$	sample correlation between trait x and trait y
h_x^2	narrow-sense heritability of trait x (sample estimator)
e_x^2	environmentability of trait x $(1 - h_x^2)$ (sample estimator)
$h_{x,y}$	coheritability of trait x and trait y (sample estimator)
$e_{x,y}$	coenvironmentability of trait x and trait y (broad-sense) (sample estimator)
$\varepsilon_{x,y}$	coenvironmentability of trait x and trait y (narrow-sense) (sample estimator)
ϵ	error term of regression model
$C_{\blacksquare x,y}$	covariance between trait x and trait y (population parameter)
$s_{\blacksquare x,y}$	covariance between trait x and trait y (sample estimator)
$V_{\blacksquare x}$	variance of trait x (population parameter)
$s_{\blacksquare x}^2$, $\sigma_{\blacksquare x}^2$	sample variance of trait x
$\boldsymbol{x}$, $\boldsymbol{y}$	character, trait, phenotype

1 Characteristics of the population

1.1 The base population

Consider a population consisting of a large number of individuals that have a known genetic structure. The phenotype of the individuals can be specified by a number of observable, measurable, variable phenotypic traits or characters, which are subject to genetic and environmental influences. The population is therefore assumed to be an infinite, multivariate population.

1.2 Population parameters

The traits exhibit phenotypic variability. There is a fraction of the trait's phenotypic variability that can be attributed to all genetic contributions (additive, dominant, epistatic, maternal, paternal effects), and is measured by the population-level broad sense heritability. In addition, the additive component of the genetic variance is due to the average effects (additive effects) of the alleles. Since each parent transmits a single allele per locus to each offspring, the phenotypic resemblance among relatives is subject to the average effect of the single alleles. In this context, the additive genetic fraction of the phenotypic variance of the trait is the population-level narrow-sense-heritability (h^2).

The strength of a linear association between two phenotypic characters measured in the individuals of the population can be quantified by the phenotypic correlation between traits x and y ($\rho_{P_{x,y}}$). The phenotypic correlation between two traits in the population is modelled as the sum of the underlying population-level coheritability (H_{xy}) and coenvironmentability (E_{xy}) coefficients.

From a bivariate normal distribution with standard deviations $\sigma_x = \sqrt{V_{P_x}}$, $\sigma_y = \sqrt{V_{P_y}}$, and the correlation coefficient $\rho_{P_{x,y}}$, which can be expressed as

$$\rho_{P_{x,y}} \equiv \frac{C_{P_{x,y}}}{\sqrt{V_{P_x} \cdot V_{P_y}}} = \frac{C_{A_{x,y}}}{\sqrt{V_{P_x} \cdot V_{P_y}}} + \frac{C_{E_{x,y}}}{\sqrt{V_{P_x} \cdot V_{P_y}}}$$

Which is the sum of the population-level coheritability $H_{x,y}$,

$$H_{xy} = \frac{C_{A_{x,y}}}{\sqrt{V_{P_x} \cdot V_{P_y}}}$$

And population-level coenvironmentability $E_{x,y}$

$$E_{x,y} = \frac{C_{E\,x,y}}{\sqrt{V_{P_x} \cdot V_{P_y}}}$$

We further assume that some of these traits, say a pair of x and y, are under genetic control of alleles (in multiple loci) that affect (influence) both of them in varying (direct positive, negative, synergistic, antagonistic) degrees, causing a stable population-level genetic correlation between the traits x and y ($\rho_{A_{x,y}}$).

$$\rho_A \equiv \frac{C_{A_{x,y}}}{\sqrt{V_{A_x} \cdot V_{A_y}}}$$

Here we are cognizant that the sign of the phenotypic and genetic correlation may not necessarily be the same as the sign of the genetic correlation. The population-level environmental correlation($\rho_{E_{x,y}}$) is

$$\rho_E \equiv \frac{C_{E_{x,y}}}{\sqrt{V_{E_x} \cdot V_{E_{x,y}}}}$$

Phenotypic correlation, coheritability and coenvironmentability are population-based and population-dependent parameters.

2 Characteristics of the sample

Population parameters can only be calculated from the omniscient set of all observations of a population. However, estimator equations are used to estimate population parameters based on a collection of observations measured from a finite set of individuals drawn without observational bias from the whole population.

We draw a random sample of n individuals from a population. Phenotypic characters are measured on these sampled individuals. Looking at two characters at the time, say x and y, we consider a random bivariate sample (x_i, y_i), $i = 1, \ldots, n$ taken from a continuous bivariate population, whose joint distribution is denoted as a bivariate normal $f_{X,Y}(x, y)$, and the marginal distribution of the traits are $X \sim N(\mu_X, \sigma_X^2)$ and $Y \sim N(\mu_Y, \sigma_Y^2)$.

The purpose of this section is to briefly decompose the phenotypic statistics into its observational components of variance, namely the additive genetic, environmental and genetic x environment interaction terms.

2.1 The phenotypic value

The phenotype is constituted by characteristics (e.g., characters, features, traits) observed in an organism. It is considered to be the realization of influences exerted by genotypic (G) and environmental (E) factors. The phenotypic value P is a random variable obtained by measuring an individual's metric character, and can be represented as the sum of the genotypic value G, and all environmental values E

$$P = G + E$$

The genotypic value can be further subdivided into a sum of random variable, namely additive genetic component (or the breeding value) A; and a non-additive (NA) component made of dominance deviations D (interaction of alleles in a locus), and epistatic effects I (interaction between alleles of different loci).

$$P = \quad A \ + \ D \ + \ (AA + AD + DA + DD + AAA + \cdots) \ + \ \left(E_g + E_s\right) \ + \ (A \cdot E)$$

general   specific

$$P = \quad A \ + \ D \ + \qquad\qquad I \qquad\qquad + \qquad \epsilon$$

dominance genetic   epistatic interactions

$$P = \quad A \ + \qquad\qquad\qquad NA \qquad\qquad\qquad + \qquad \epsilon$$

non-additive genetic

$$P = \qquad\qquad\qquad\qquad G \qquad\qquad\qquad\qquad + \qquad \epsilon$$

genetic   environmental

$$P = \quad A \ + \qquad\qquad\qquad E$$

additive genetic   environmental and non-additive genetic

Note: In regard to the classical partitioning of the genetic variance (V_G) of quantitative traits in terms of the additive (V_A), dominance (V_D), and interlocus epistatic interactions (V_I), sometimes, erroneously, gives an appearance that a relationship exist with the homonymous mode of gene action (i.e. additive gene action, dominant gene action, or epistatic gene action). This classical $V_G = V_A + V_D + V_I$ decomposition and the modes of gene action of genes do not possess a oneto-one relationship to each other, and the partition cannot be used to support any specific underlying genetic architecture (Huang and Mackay 2016).

2-1a   The phenotypic value

$$P = A + E$$

2-1b   The phenotypic mean

$$E(P_x) = \bar{P}_x = \frac{\sum_{i=1}^{n} P_{x_i}}{n}$$

2-1c   Decomposition of the phenotypic mean

$$E(P_x) = \bar{P}_x = E(A_x + E_x) = \frac{\sum_{i=1}^{n}(A_{x\,i} + E_{x\,i})}{n} = \frac{\sum_{i=1}^{n} A_{x\,i}}{n} + \frac{\sum_{i=1}^{n} E_{x\,i}}{n} = \bar{A}_x + \bar{E}_x$$

2.2 The sample phenotypic variance

The sample phenotypic variance of a specified trait x is $s^2_{P_x}$, which becomes an estimator of the population parameter V_{P_x}. The variance is defined as the expected value of the square of deviations from the mean.

$$V_{P_x} = Var(P_x) = [\, E(P_x - E(P_x)\,)\,]^2 = E\left(P^2_x\right) - [\, E(P_x)\,]^2$$

It is generally biased due to the finite sample count and when the population mean is unknown (which for this reason it is estimated by the sample mean). This introduces an underestimation bias. The Bessel's correction is used here by placing in the denominator $(n-1)$ rathern than n. The sample phenotypic variance

$$s^2_{P_x} = \frac{1}{n-1} \sum_{i=1}^{n} \left(P_{x_i} - \bar{P}_x\right)^2$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} \left(P^2_{x_i} - 2\bar{P}_x P_{x_i} + \bar{P}_x^{\,2}\right)$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} P^2_{x_i} - 2\frac{1}{n-1} \bar{P}_x \sum_{i=1}^{n} P_{x_i} + \frac{n}{n-1} \bar{P}^2_x$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} P^2_{x_i} - 2\frac{n}{n-1} \bar{P}_x \frac{\sum_{i=1}^{n} P_{x_i}}{n} + \frac{n}{n-1} \bar{P}^2_x$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} P^2_{x_i} - 2\frac{n}{n-1} \bar{P}_x^{\,2} + \frac{n}{n-1} \bar{P}^2_x$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} P^2_{x_i} - \frac{n}{n-1} \bar{P}_x^{\,2}$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} (A_x + E_x)^2 - \frac{n}{n-1} \left(\bar{A}_x + \bar{E}_x\right)^2$$

$$s^2_{P_x} = \frac{1}{n-1} \sum_{i=1}^{n} A^2_{x_i} + \frac{2\sum_{i=1}^{n} A_{x_i} E_{x_i}}{n-1} + \frac{1}{n-1} \sum_{i=1}^{n} E^2_{x_i} - \frac{n}{n-1} \left(\bar{A}_x^{\,2} + 2A_x E_x + \bar{E}_x^{\,2}\right)$$

After some rearrangement

$$s^2_{P_x} = \left[\frac{1}{n-1} \sum_{i=1}^{n} A^2_{x_i} - \frac{n\bar{A}^2_x}{(n-1)}\right] + \left[\frac{1}{n-1} \sum_{i=1}^{n} E^2_{x_i} - \frac{n\,\bar{E}^2_x}{(n-1)}\right] + \left[\frac{2\sum_{i=1}^{n} A_{x_i} E_{x_i}}{n-1} - \frac{2\,n\,\bar{A}_x\bar{E}_x}{(n-1)}\right]$$

The sample phenotypic variance, therefore, is partitioned as follows:

2-2   The sample phenotypic variance

$$s_{P_x}^2 = \frac{1}{n-1}\left[\sum_{i=1}^{n} \bar{A}_x^2 - n\,\bar{A}_x^2\right] + \frac{1}{n-1}\left[\sum_{i=1}^{n} \bar{E}_x^2 - n\,\bar{E}_x^2\right] + \frac{2}{n-1}\left[\sum_{i=1}^{n} A_{x_i}E_{x_i} - n\bar{A}_x\,\bar{E}_x\right]$$

$$s_{P_x}^2 = \qquad s_{A_x}^2 \qquad + \qquad s_{E_x}^2 \qquad + \qquad 2\,s_{AE_x}^2$$

sample additive genetic variance   sample environmental variance   sample variance of the interaction
= sample variance of breeding values   between breeding values and
                                                                       environmental values

2.3 The sample phenotypic covariance

The sample phenotypic covariance between the phenotypic value of trait x and the phenotypic value of trait y, $S_{P_{x,y}}$, is the estimator of the population parameter, $C_{P_{x,y}}$. The covariance is a measure of joint variability of two random variables, which are the phenotypic values for trait x, P_x and trait y, P_y. The covariance is defined as the expected product of the deviations of the phenotypic values from their corresponding expected values.

$$C_{P_{x,y}} = Cov(P_x, P_y) = E[P_x - E(P_x)][P_y - E(P_y)] = [E(P_x P_y) - E(P_x)E(P_y)]$$

A sample of size n is drawn from a population of the random variable pair (P_x, P_y) such each observation (P_{x_i}, P_{y_i}) for $i = 1, \dots, n$, is drawn with equal probability n^{-1}, and employing the Bessel's correction, sample phenotypic covariance is:

$$S_{P_{x,y}} = \frac{1}{n-1} \sum_{i=1}^{n} (P_{x_i} - \bar{P}_x)(P_{y_i} - \bar{P}_y)$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} (P_{x_i} P_{y_i} - P_{x_i} \bar{P}_y - \bar{P}_x P_{y_i} + \bar{P}_x \bar{P}_y)$$

$$= \frac{1}{n-1} \sum_{i=1}^{n} (P_{x_i} P_{y_i} - P_{x_i} \bar{P}_y - \bar{P}_x P_{y_i} + \bar{P}_x \bar{P}_y)$$

$$= \frac{1}{n-1} \left[\sum_{i=1}^{n} P_{x_i} P_{y_i} - \sum_{i=1}^{n} P_{x_i} \bar{P}_y - \sum_{i=1}^{n} \bar{P}_x P_{y_i} + \sum_{i=1}^{n} \bar{P}_x \bar{P}_y \right]$$

$$= \frac{1}{n-1} \left[\sum_{i=1}^{n} P_{x_i} P_{y_i} - \frac{n}{n} \sum_{i=1}^{n} P_{x_i} \bar{P}_y - \frac{n}{n} \sum_{i=1}^{n} \bar{P}_x P_{y_i} + n \bar{P}_x \bar{P}_y \right]$$

$$= \frac{1}{n-1} \left[\sum_{i=1}^{n} P_{x_i} P_{y_i} - n \bar{P}_x \bar{P}_y - n \bar{P}_x \bar{P}_y + n \bar{P}_x \bar{P}_y \right]$$

2-3 The sample phenotypic covariance

$$S_{P_{x,y}} = \frac{1}{n-1} \left[\sum_{i=1}^{n} P_{x_i} P_{y_i} - n \bar{P}_x \bar{P}_y \right]$$

2.4 Decomposition of the sample phenotypic covariance

The sample phenotypic covariance $C_{P_{xy}}$ between traits x and y can be thought to be the sum of an additive genetic covariance $C_{A_{xy}}$, an environmental, residual covariance term, $C_{E_{xy}}$, and interaction terms $C_{A_x E_y}$ and $C_{A_y E_x}$. Thus, $C_{P_{xy}} = C_{A_{xy}} + C_{E_{xy}}$. The genetic covariance $C_{A_{xy}}$ of two traits is a component of the sample phenotypic covariance that represents the joint measure of genetic association between two traits.

A quantitative genetic model of the value P of trait is assumed to be the sum of an additive genetic value A and an environmental, residual value E, thus $P = A + E$.

$$s_{P_{x,y}} = \frac{1}{n-1} \left[\sum_{i=1}^{n} P_{x_i} P_{y_i} - n\bar{P}_x \bar{P}_y \right]$$

Replacing the corresponding $P = A + E$ for each trait, we obtain

$$s_{P_{x,y}} = \frac{1}{n-1} \left[\sum_{i=1}^{n} (A_{x_i} + E_{x_i})(A_{y_i} + E_{y_i}) - n \frac{(\bar{A}_x + \bar{E}_x)}{n} \frac{(\bar{A}_y + \bar{E}_y)}{n} \right]$$

$$= \frac{1}{n-1} \left[\sum_{i=1}^{n} (A_{x_i} A_{y_i} + A_{x_i} E_{y_i} + A_{y_i} E_{x_i} + E_{x_i} E_{y_i}) - \frac{(\bar{A}_x + \bar{E}_x)(\bar{A}_y + \bar{E}_y)}{n} \right]$$

$$= \frac{1}{n-1} \left[\sum_{i=1}^{n} A_{x_i} A_{y_i} + \sum_{i=1}^{n} E_{x_i} E_{y_i} + \left(\sum_{i=1}^{n} A_{x_i} E_{y_i} + \sum_{i=1}^{n} A_{y_i} E_{x_i} \right) - n\bar{A}_{x_i} \bar{A}_{y_i} - n\bar{A}_x \bar{E}_y - n\bar{A}_y \bar{E}_x - n\bar{E}_x \bar{E}_y \right]$$

$$s_{P_{x,y}} = \frac{1}{n-1} \left[\sum_{i=1}^{n} (A_{x_i} A_{y_i} - n\bar{A}_x \bar{A}_y) + \sum_{i=1}^{n} (E_{x_i} E_{y_i} - n\bar{E}_x \bar{E}_y) \right.$$
$$\left. + \left(\sum_{i=1}^{n} (A_{x_i} E_{y_i} - n\bar{A}_x \bar{E}_y) + \sum_{i=1}^{n} (A_{y_i} E_{x_i} - n\bar{A}_y \bar{E}_x) \right) \right]$$

2-4   Decomposition of the sample phenotypic covariance between traits x and y.

$$\frac{1}{n-1}\left[\sum_{i=1}^{n} P_{x_i}P_{y_i} - n\bar{P}_x\bar{P}_y\right]$$

$s_{P_{xy}}$ phenotypic covariance

$$= \frac{1}{n-1}\sum_{i=1}^{n}\left(A_{x_i}A_{y_i} - n\bar{A}_x\bar{A}_y\right)$$

$s_{A_{xy}}$ sample genetic covariance between the breeding values of traits x and y

$\left.\phantom{\begin{matrix}a\\a\\a\end{matrix}}\right\}$ $s_{A_{xy}}$ additive genetic covariance

$$+ \frac{1}{n-1}\sum_{i=1}^{n}\left(E_{x_i}E_{y_i} - n\bar{E}_x\bar{E}_y\right)$$

$s_{\epsilon_{xy}}$ sample covariance between environmental deviations of traits x and y

$$+ \frac{1}{n-1}\sum_{i=1}^{n}\left(A_{x_i}E_{y_i} - n\bar{A}_x\bar{E}_y\right)$$

$s_{A_xE_y}$ sample covariance of the GxE interaction of breeding values of trait x and the environmental deviations of trait y

$\left.\phantom{\begin{matrix}a\\a\\a\\a\\a\end{matrix}}\right\}$ $s_{E_{xy}}$ environmental covariance

$$+ \frac{1}{n-1}\sum_{i=1}^{n}\left(A_{y_i}E_{x_i} - n\bar{A}_y\bar{E}_x\right)$$

$s_{A_yE_x}$ sample covariance of the GxE interaction of breeding values of trait y and the environmental deviations of trait x

2.5 The sample phenotypic correlation

The sample phenotypic correlation between two traits x and , $r_{P_{x,y}}$, is the estimator of the population parameter $\rho_{x,y}$ also referred as the Pearson product-moment correlation coefficient, or Pearson's correlation coefficient, or simply "the correlation coefficient". It is obtained by dividing the covariance of the two variables by the product of their standard deviations.

The population correlation coefficient $\rho_{P_{x,y}}$ between two random variables, namely trait x and trait y with expected values $E(P_x)$ and $E(P_x)$ and variances V_{P_x} and V_{P_y} is defined as

$$\rho_{P_{x,y}} = Corr(P_x, P_y) = \frac{C_{P_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}} = \frac{E[P_x - E(P_x)][P_y - E(P_y)]}{\sqrt{V_{P_x} V_{P_y}}}$$

for $-1 < \rho_{P_{x,y}} < 1$

If $\rho_{P_{x,y}} = \pm 1$, then the phenotypic characters P_x and P_y are linearly related.

If the phenotypic characters P_x and P_y are linearly related, then $\rho_{P_{x,y}} = \pm 1$.

Suppose $(P_x, P_y), (P_{x_i}, P_{y_i}), i = 1, ..., n$ constitute a sample of n independent and identically distributed (i.i.d) random vectors drawn from a bivariate normal distribution of phenotypic values of trait x (P_x) and trait y (P_y) whose population-level phenotypic correlation parameter is $\rho_{P_{x,y}}$. The trait means are $\bar{P}_x$ and $\bar{P}_y$, variances $s_{P_x}^2$ and $s_{P_y}^2$. The sample phenotypic correlation $r_{P_{x,y}}$ of traits x and y is defined as the sample phenotypic covariance $s_{P_{x,y}}$ divided by the product of their standard deviations $s_{P_x} s_{P_y} = \sqrt{s_{P_x}^2 \, s_{P_y}^2}$.

2-5   The sample phenotypic correlation

$$r_{P_{x,y}} = \frac{s_{P_{x,y}}}{\sqrt{s_{P_x}^2 s_{P_y}^2}} = \frac{\frac{1}{n-1}\left[\sum_{i=1}^{n} P_{x_i} P_{y_i} - n\bar{P}_x \bar{P}_y\right]}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n} P_{x_i} - \bar{P}_x\right]^2} \sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n} P_{y_i} - \bar{P}_y\right]^2}}$$

See section 3.2.1 for a path analytical treatment of the phenotypic correlation.

A discussion about the Fisher's and Pearson's formulations, and properties associated to them is elaborated by Plata (2006).

2.6 Decomposition of the sample phenotypic correlation

The sample phenotypic correlation can be decomposed in an analogous as the sample phenotypic covariance.

$$r_{P_{x,y}} = \frac{\frac{1}{n-1}\sum_{i=1}^{n}(A_{x_i}A_{y_i} - n\bar{A}_x\bar{A}_y) + \frac{1}{n-1}\sum_{i=1}^{n}(E_{x_i}E_{y_i} - n\bar{E}_x\bar{E}_y) + \frac{1}{n-1}\sum_{i=1}^{n}\left(A_{x_i}E_{y_i} - n\bar{A}_x\bar{E}_y\right) + \frac{1}{n-1}\sum_{i=1}^{n}\left(A_{y_i}E_{x_i} - n\bar{A}_y\bar{E}_x\right)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i} - \bar{P}_x\right]^2}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i} - \bar{P}_y\right]^2}}$$

2-6   Components of the sample phenotypic correlation

$$r_{P_{x,y}} =$$

Sample phenotypic correlation

Sample coheritability

$$\frac{\frac{1}{n-1}\sum_{i=1}^{n}(A_{x_i}A_{y_i} - n\bar{A}_x\bar{A}_y)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i}{}^2 - \bar{P}_x^2\right]}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i}{}^2 - \bar{P}_y^2\right]}}$$

$$h_{x,y} = \begin{cases} \dfrac{s_{A_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_x}^2}} \\ \sqrt{h_y^2 h_x^2}\, r_{A_{x,y}} \end{cases}$$

Sample (narrow-sense) coenvironmentability

$$+ \frac{\frac{1}{n-1}\sum_{i=1}^{n}(E_{x_i}E_{y_i} - n\bar{E}_x\bar{E}_y)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i}{}^2 - \bar{P}_x^2\right]}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i}{}^2 - \bar{P}_y^2\right]}}$$

$$\varepsilon_{x,y} = \begin{cases} \dfrac{s_{E_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_x}^2}} \\ \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E_{x,y}} \end{cases}$$

genotype x environment interaction component

$$+ \frac{\frac{1}{n-1}\sum_{i=1}^{n}\left(A_{x_i}E_{y_i} - n\bar{A}_x\bar{E}_y\right)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i}{}^2 - \bar{P}_x^2\right]}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i}{}^2 - \bar{P}_y^2\right]}}$$

$$a_x e_y = \begin{cases} \dfrac{s_{A_x E_y}}{\sqrt{s_{P_x}^2 \, s_{P_x}^2}} \\ \sqrt{h_x^2(1-h_y^2)}\, r_{A_x E_y} \end{cases}$$

genotype x environment interaction component

$$+ \frac{\frac{1}{n-1}\sum_{i=1}^{n}\left(A_{y_i}E_{x_i} - n\bar{A}_y\bar{E}_x\right)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i}{}^2 - \bar{P}_x^2\right]}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i}{}^2 - \bar{P}_y^2\right]}}$$

$$a_y e_x = \begin{cases} \dfrac{s_{A_y E_x}}{\sqrt{s_{P_x}^2 \, s_{P_x}^2}} \\ \sqrt{(1-h_x^2)h_y^2}\, r_{A_y E_x} \end{cases}$$

e_{xy} coenvironmentability (broad-sense)

2.7 The sample coheritability

The sample coheritability $h_{x,y}$ between two traits x and y is the genetic component of the sample phenotypic correlation $r_{P_{x,y}}$, and is an estimator of the population coheritability ($H_{x,y}$) which is defined as the ratio of the additive genetic covariance between the characters x and y divided by the geometric mean of the phenotypic variances of the traits.

The population coheritability is defined as

$$H_{x,y} = \frac{C_{A_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}}$$

The sample coheritability is defined as the sample genetic covariance divided by the geometric mean of the sample phenotypic variances.

2-7   sample coheritability

$$h_{x,y} = \frac{S_{A_{x,y}}}{\sqrt{S_{P_x}^2 \, S_{P_y}^2}} = \frac{\frac{1}{n-1} \left[\sum_{i=1}^{n} Ax_i Ay_i - \frac{\sum_{i=1}^{n} Ax_i \cdot \sum_{i=1}^{n} Ay_i}{n} \right]}{\sqrt{\frac{1}{n-1} \left[\sum_{i=1}^{n} P_{x_i} - \bar{P}_x \right]^2} \sqrt{\frac{1}{n-1} \left[\sum_{i=1}^{n} P_{y_i} - \bar{P}_y \right]^2}}$$

For $-1 < h_{x,y} < 1$

The following statements provide a notion on the meaning of the sample coheritability.

● The coheritability is the fraction of the phenotypic correlation of two traits that can be attributed to additive genetic effects.

● The coheritability is the proportion of the total phenotypic variability of two traits that is due to joint/common/shared genetic causes.

● The coheritability is the relative contribution of shared genetics in determining the phenotypic association of two traits.

● The coheritability measures the extent to which resemblance among relatives in regard to two traits in comparison to unrelated individuals of the same species, is due to common heredity.

2.8 The sample coenvironmentability

The sample coenvironmentability $e_{x,y}$ between traits x and y is the residual, environmental component of the sample phenotypic correlation $r_{P_{x,y}}$, and is an estimator of the population coheritability ($E_{x,y}$).

The population coenvironmentability is defined as

$$E_{x,y} = \frac{C_{E_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}}$$

It is generally assumed that the genetic and environmental interaction effects between the breeding values of one trait and the environmental effects of another are negligible. These effects, if not explicitly formulated, will be added with the environmental covariance. Therefore, we can partition the numerator into a genetic covariance and a residual environmental covariance component, as follows:

The narrow-sense coenvironmentability is a measure of the shared effects of environmental deviations acting upon both traits.

$$\varepsilon_{x,y} = \sqrt{(1 - h_x^2)(1 - h_y^2)} \; r_{E_{X,y}}$$

2-8a   The sample narrow-sense sample coenvironmentability

$$\varepsilon_{x,y} = \frac{s_{E_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_x}^2}} = \frac{\frac{1}{n-1}\sum_{i=1}^{n}(E_{x_i}E_{y_i} - n\bar{E}_x\bar{E}_y)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n} P_{x_i} - \bar{P}_x\right]^2}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n} P_{y_i} - \bar{P}_y\right]^2}}$$

The broad-sense coenvironmentability is the combined effect of the narrow-sense coenvironmentability plus the interaction effects of the breeding values of a trait with the environmental effect of the other. Broad-sense coenvironmentability measures the degree to which the joint phenotypic variability of two traits is determined by all sources of variation excluding the additive genetic variation.

$$e_{x,y} = \sqrt{(1 - h_x^2)(1 - h_y^2)}\, r_{E_{X,y}} + \sqrt{h_x^2(1 - h_y^2)}\, r_{A_x E_y} + \sqrt{(1 - h_x^2)h_y^2}\, r_{A_y E_x}$$

2-8b   The sample broad-sense sample coenvironmentability

$$e_{x,y} =$$

$$\frac{\frac{1}{n-1}\sum_{i=1}^{n}(E_{x_i}E_{y_i} - n\bar{E}_x\bar{E}_y)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i} - \bar{P}_x\right]^2}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i} - \bar{P}_y\right]^2}}$$

sample broad-sense coenvironmentability $e_{x,y}$

sample coenvironmentability (narrow-sense)

$$\varepsilon_{x,y} = \sqrt{(1 - h_x^2)(1 - h_y^2)}\, r_{E_{X,y}}$$

$$+\; \frac{\frac{1}{n-1}\sum_{i=1}^{n}\left(A_{x_i}E_{y_i} - n\bar{A}_x\bar{E}_y\right)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i} - \bar{P}_x\right]^2}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i} - \bar{P}_y\right]^2}}$$

genotype x environment interaction component $A_x E_y$

$$a_x e_y = \sqrt{h_x^2(1 - h_y^2)}\, r_{A_x E_y}$$

$$+\; \frac{\frac{1}{n-1}\sum_{i=1}^{n}\left(A_{y_i}E_{x_i} - n\bar{A}_y\bar{E}_x\right)}{\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{x_i} - \bar{P}_x\right]^2}\sqrt{\frac{1}{n-1}\left[\sum_{i=1}^{n}P_{y_i} - \bar{P}_y\right]^2}}$$

genotype x environment interaction component $A_y E_x$

$$a_y e_x = \sqrt{(1 - h_x^2)h_y^2}\, r_{A_y E_x}$$

The broad-sense coenvironmentability included not only (narrow-sense) coenvironmentability, but in addition the interaction terms between genetic effects of one-trait and the environmental effects of the other. They are often assumed as being non-existent or negligible. Yet, statistically these components, if different than zero, may add "noise" to the estimators. In that case, it is expected that the interaction would inflate the (co-)environmental component. This addition of interaction effects on the coenvironmentability would cause increase in its magnitude and possibly surpassing the magnitude of the coheritability. Partitions (See section 6.2) where this may occur are S_{+3} and S_{-3}. Thus though environmental effects affect all phenotypic correlations, they have a preponderant influence over the coheritability in these particular partitions.

3 Equivalent formulae of the sample coheritability

3.1 Expressions of the sample coheritability

The value of an individual's phenotype (P) is determined by additive genetic (A) and environmental (E) effects, such that P = A + E. This simple decomposition holds also at the population level for variances (s^2), and covariances (C) between characters x and y. We can therefore apply this decomposition to a bivariate dataset of measurements of two characters from a number of individuals sampled from a population and calculate an additive genetic covariance ($s_{A_{x,y}}$). All the rest constitutes the environmental covariance ($s_{E_{x,y}}$) which includes environmental effects together with non-additive genetic variation,

$$s_{P_{x,y}} = s_{A_{x,y}} + s_{E_{x,y}}$$

To standardize, both sides are divided by the square root of the product of phenotypic variances of each character, and using observational variance components symbols, we obtain

$$\frac{s_{P_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}} = \frac{s_{A_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}} + \frac{s_{E_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}}$$

Expression I

The ratio of the sample genetic covariance and the bivariate phenotypic variability (i.e., geometric mean of the sample phenotypic variances)

$$h_{xy} = \frac{s_{A_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}}$$

for $s_{P_x}^2 > 0$, $s_{P_y}^2 > 0$

Rearranging Expression I by multiplying and diving by the geometric mean of the additive genetic variances we obtain:

$$h_{xy} = \frac{\sqrt{s_{A_x}^2 \, s_{A_y}^2}}{\sqrt{s_{A_x}^2 \, s_{A_y}^2}} \frac{s_{A_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}} = \sqrt{h_x^2 \, h_y^2} \; r_{A_{xy}}$$

for $s_{P_x}^2 > 0 \, , s_{P_y}^2 > 0$

Multiplying the numerator and denominator of Expression I by the phenotypic covariance , we obtain:

$$h_{xy} = \frac{s_{A_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}} = \frac{s_{P_{x,y}}}{s_{P_{x,y}}} \frac{s_{A_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}} = \frac{s_{A_{x,y}}}{s_{P_{x,y}}} \frac{s_{P_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}}$$

$$h_{xy} = \frac{s_{A_{x,y}}}{s_{P_{x,y}}} \, r_{P_{x,y}}$$

where $s_{P_{x,y}} \neq 0$.

Notice that only under extreme and rare circumstance when the phenotypic correlation $r_{P_{x,y}} = 1$ will the ratio of genetic and phenotypic covariance become a valid expression of the coheritability, $h_{xy} = \frac{s_{A_{x,y}}}{s_{P_{x,y}}}$, otherwise its range is from $-\infty$ to $+\infty$. (a version of this formulation is presented by Yamada 1968).

Expressions IV and V involve the use of a regression parameter

---

Expression IV

In the model $P_y = \beta_o + \beta_{P_y P_x} P_x + \epsilon +, \beta_{P_x P_y}$,

$\beta_{P_y P_x}$ represents the regression coefficient of independent phenotypic value P_x on dependent phenotypic value P_y,

$$\beta_{P_y P_x} = \frac{s_{P_{x,y}}}{s_{P_x}^2}$$

which can be related to the phenotypic correlation using the following relationship

$$r_{P_{x,y}} = \beta_{P_y P_x} \frac{\sqrt{s_{P_x}^2}}{\sqrt{s_{P_y}^2}}$$

Then, replacing this form of the phenotypic correlation in Expression III, the coheritability is

$$h_{x,y} = \frac{s_{A_{x,y}}}{s_{P_{x,y}}} \beta_{P_y P_x} \frac{\sqrt{s_{P_x}^2}}{\sqrt{s_{P_y}^2}}$$

Expression V

In the regression model $P_x = \beta_o + \beta_{P_y P_x} P_y + \epsilon$,

$\beta_{P_x P_y}$ represents the regression coefficient of independent phenotypic value P_y on dependent phenotypic value P_x, then

$$r_{P_{x,y}} = \beta_{P_x P_y} \frac{\sqrt{s_{P_y}^2}}{\sqrt{s_{P_x}^2}}$$

Then, replacing this form of the phenotypic correlation in expression III, the coheritability is

$$h_{x,y} = \frac{s_{A_{x,y}}}{s_{P_{x,y}}} \beta_{P_x P_y} \frac{\sqrt{s_{P_y}^2}}{\sqrt{s_{P_x}^2}}$$

$$h_{x,y} = \begin{cases} \dfrac{s_{A_{x,y}}}{\sqrt{s_{P_x}^2 \, s_{P_y}^2}} & s_{P_x}^2 \neq 0 \,,\; s_{P_y}^2 \neq 0 \\[2em] \sqrt{h_y^2 h_x^2} \; r_{A_{x,y}} & \\[2em] \dfrac{s_{A_{x,y}}}{s_{P_{x,y}}} \, r_{P_{x,y}} & C_{P_{x,y}} \neq 0 \\[2em] \dfrac{s_{A_{x,y}}}{s_{P_{x,y}}} \, \beta_{P_y P_x} \dfrac{\sqrt{s_{P_x}^2}}{\sqrt{s_{P_y}^2}} & s_{P_{x,y}} \neq 0,\, s_{P_y}^2 \neq 0 \\[2em] \dfrac{s_{A_{x,y}}}{s_{P_{x,y}}} \, \beta_{P_x P_y} \dfrac{\sqrt{s_{P_y}^2}}{\sqrt{s_{P_x}^2}} & s_{P_x}^2 \neq 0,\, s_{P_{x,y}} \neq 0 \end{cases}$$

These expressions reduce to the heritability if the traits are the same $x = y$.

Notice that in all forms, a coheritability value equal to zero implies that the genetic covariance is zero. The additive genetic variances, present in the denominator of the genetic correlation, cannot become zero since it would leave it undefined. Thus, the heritabilities cannot assume the value of zero. This shows that the coheritability estimator may, depending on the numbers involved, sometimes display numerical instability.

At this point the reader may wonder why we bother to spell out several mathematically equivalent formulations in a variety of variables and equations. The reasons for this are that (1) within a quantitative theoretical framework, it shows relationships among a variety of variables, thus providing conceptual insight among them. (2) The different expressions entail different implicit assumptions about what entities are related to each other. Third, some forms are more easily calculated than others, thus creates expressions that function more conceptually and others more operationally.

3.2 Path Analysis

Path analysis is a mathematical method that attempts to model the relationship among correlated variables. The path analysis begins with a path diagram that considers two types of variables. Endogenous variables such as the phenotypic trait (P) are measurable and observed. They are represented enclosed in squares. Exogenous variables which genetic (A) , as well as the environmental (E) variables, cannot be directly observed or measured, and are enclosed in circles.

The path diagram involves arrows, either singled-headed or double-headed. A single-headed arrow indicates simply statistical predictability of a latent variable to the observed variable, with no commitment made about causality. In this sense $(A_x) \rightarrow \boxed{P_x}$ denotes that the individual differences in exogenous variable A may influence endogenous variable P, even when all other variables that predict P are taken into account. Double-headed arrows indicate a correlation between exogenous variables, e.g. $(A_x) \leftrightarrow (A_y)$ However, a double-headed arrow can never be used between endogenous variables.

Path coefficients quantify the magnitude of a direct prediction. For example, the term $\sqrt{h_x^2}$ on the single-headed arrow between (A_x) and $\boxed{P_x}$ in figure 3.2.1 is a path coefficient that quantifies the additive genetic influences exerted by genotype A_x on the phenotypic trait P_x. In figure , the additive genetic correlation measure the strength of a linear association between breeding values of trait x and trait y, thus $(A_x) \leftrightarrow (A_y)$ possess a quantifiable $r_{A_{xy}}$. The model provides no assumptions as to the source of the association.

3.2.1 The phenotypic correlation

The phenotypic value of a trait is influenced by the (additive) genetic factors and the residual, environmental factors. The phenotypic correlation between traits x and y, therefore, is the sum of the coheritability path and the (broad-sense) coenvironmentability path (cf. Sections 2.7 and 2.8)
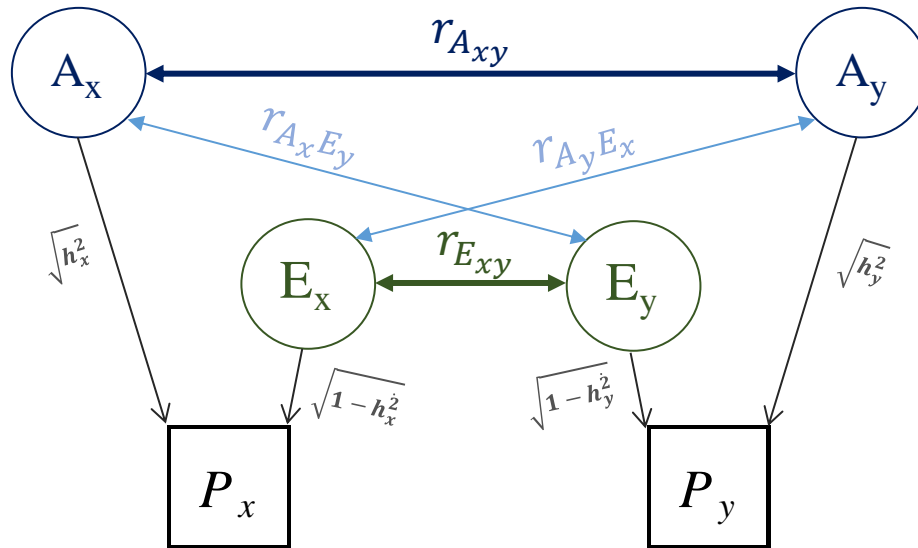
Figure 3.2.1. Path diagram relating two exogenous variables, namely, the phenotypic traits (P_x, P_y) to their corresponding additive genetic effects (A_x, A_y), and environmental influences (E_x, E_y), respectively. The path coefficient associated to a single headed arrow connecting a genotype A and its phenotypic trait P is equal to the square root of heritability, $\sqrt{h^2}$. Double headed arrows represent correlation coefficients. For the sake of completeness, genotype by environment covariance is considered.

Therefore, the phenotypic correlation becomes:

> 3-2-1 Decomposition of the sample phenotypic correlation
>
> $$r_{P_{x,y}} = \sqrt{h_x^2 h_y^2}\, r_{A_{x,y}} + \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E_{x,y}} + \sqrt{h_x^2(1-h_y^2)}\, r_{A_x E_y} + \sqrt{(1-h_x^2)h_y^2}\, r_{A_y E_x}$$
>
> $$r_{P_{x,y}} = \qquad h_{x,y} \qquad + \qquad \varepsilon_{x,y} \qquad + \qquad a_x e_y \qquad + \qquad a_y e_x$$

The last line invokes equation [2-6].

3.2.2 Type B coheritability of one trait expressed in different environments

In field trials, breeders are interested in measuring the intensity of the interaction of the environment and the genotype. The correlation between the breeding values of a trait measured in two distinct localities can be considered as two distinct traits (Falconer 1952), whose genetic correlation is denoted as Type B-genetic genetic correlation ($r_{B\,x1,x2}$) (coined by Burdon 1977).

In this sense, environment can represent a locality (site 1, site2,…), sex (male, female), generation (parental, progeny). The same rationale applies if considering distinct ages or ontogenic stages (juvenile, adult), intrinsic conditions (normal, affected), etc.

An important consideration is not only to have $r_{B\,x1,x2}$, but also the phenotypic correlation of the phenotypic values of both characters expressed in the environments. This would allow to estimate the Type B coenvironmentability.
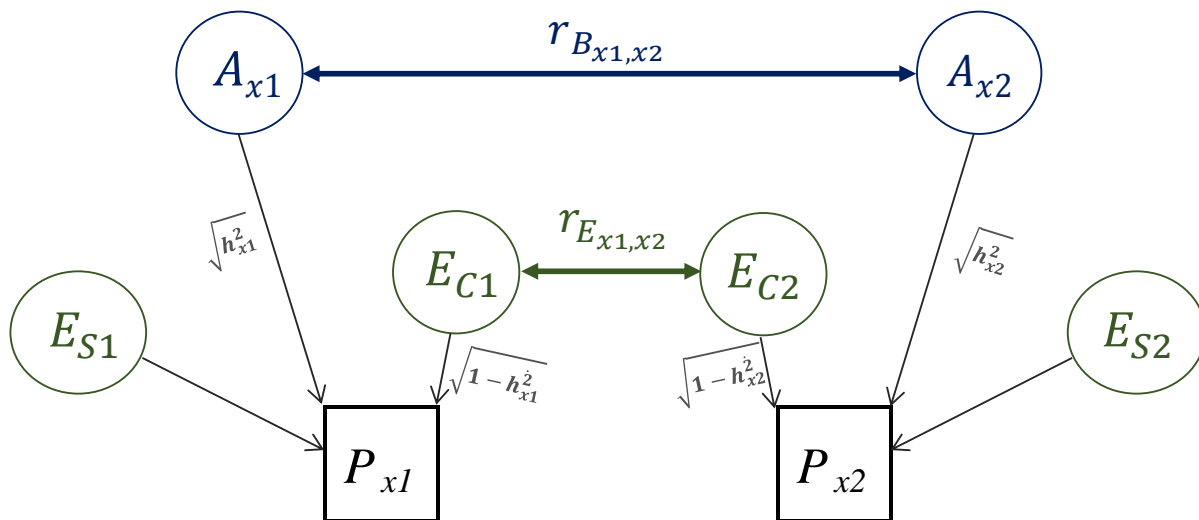
Figure 3.2.2. Type B genetic correlation between the breeding values of a trait measured in localities 1 and 2. A_p is denotes by the genetic component determined in environment p ($p = 1,2$), E_c is the common environment, E_s the specific environment. [Adapted from Falconer (1952)].

3-2-2 Type B coheritability of the same trait x in two environments (named 1 and 2)

$$h_{B_{x1,x2}} = \sqrt{h_{x1}^2 h_{x2}^2}\; r_{B_{x1,x2}}$$

3.2.3 Multiple regression

The graph below represents a path diagram expressing a multiple linear regression equation with one outcome variable, $r_{P_{x,y}}$, and two predictors, namely the coheritability $h_{x,y}$ and the coenvironmentability $e_{x,y}$. The model is

$$r_{P_{x,y}} = \boldsymbol{\beta_o} + \boldsymbol{\beta_1} \cdot h_{x,y} + \boldsymbol{\beta_2} \cdot e_{x,y} + 1\epsilon$$

where ϵ is a residual term with a mean of zero. There are four single-headed arrows pointing into the phenotypic correlation $r_{P_{x,y}}$, whose path coefficients are $\boldsymbol{\beta_o}, \boldsymbol{\beta_1}, \boldsymbol{\beta_2}$, and **1** corresponding to the four summands on the right hand side of regression equation. In a general linear model, the intercept $\boldsymbol{\beta_o}$ is estimated using a column of ones. For this reason, a constant is denoted by a triangle that maps onto that column of ones.
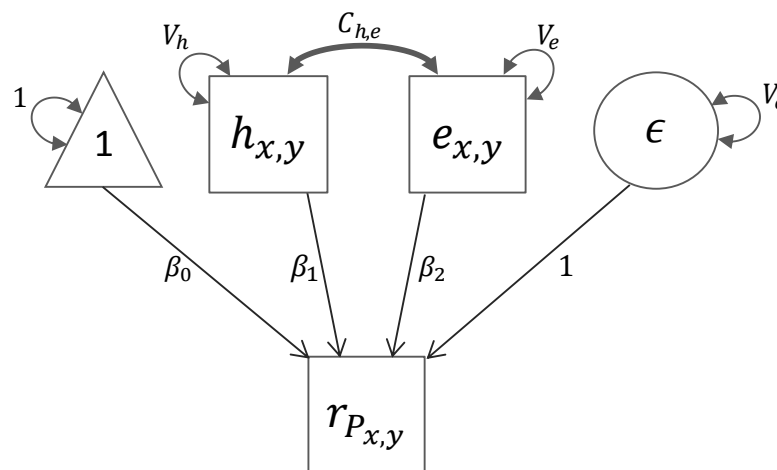
Figure 3.2.3 Path diagram of a multiple regression where the phenotypic correlation is the dependent variable. The coheritability and coenvironmentability are the independent predictor variables.

For simplicity of presentation in Figure 3.2.3, the two predictor variables $h_{x,y}$ and $e_{x,y}$ have means of zero. If $h_{x,y}$ and $e_{x,y}$ had nonzero then single-headed arrows would be drawn from the triangle to $h_{x,y}$ and from the triangle to $e_{x,y}$. There are double-headed variance arrows for each of the variables $h_{x,y}$, $e_{x,y}$, and ϵ on the right hand side of the equation, representing the variance of the predictor variables, V_h , V_e and residual variance V_ϵ respectively. The constant has, by convention, a nonzero variance term fixed at the value 1.0. While this double-headed arrow may seem counterintuitive since it is not formally a variance term, it is required in order to provide consistency to the path tracing rules described below. In addition, there is a double-headed arrow between $h_{x,y}$ and $e_{x,y}$ that specifies the potential covariance, $C_{h_{x,y} \cdot e_{x,y}}$ between the predictor variables.

3.3 Sampling variance approximation

The Delta method involves a first order approximation of a Taylor series expansion of the function and then taking the expectation of according to Taylor's Theorem (see Appendix 6).

3.3.1 Sampling variance of the phenotypic correlation

The sampling variance of the phenotypic correlation in terms of its components coheritability and coenvironmentability can be defined as:

$$Var\left(r_{P_{x,y}}\right) = Var(h_{x,y} + e_{x,y}) = Var(h_{x,y}) + Var(e_{x,y}) + 2Cov(h_{x,y}, e_{x,y})$$

The last term can be calculated as:

$$Cov(h_{x,y}, e_{x,y}) = \frac{1}{2}\left[Var\left(r_{P_{x,y}}\right) - Var(h_{x,y}) - Var(e_{x,y})\right].$$

The sample phenotypic correlation is defined in equation [2-5]

3-3-1   Sampling variance of the phenotypic correlation $r_{P_{x,y}}$

$$Var\left(r_{P_{x,y}}\right) = \frac{1}{4}r_{P_{x,y}}^2 \left[4\frac{Var(s_{P_{x,y}})}{s_{P_{x,y}}} + \frac{Var(s_{P_x}^2)}{s_{P_x}^2} + \frac{Var(s_{P_y}^2)}{s_{P_y}^2} \right.$$
$$\left. - 4\frac{Cov\left(s_{P_{x,y}}, s_{P_x}^2\right)}{s_{P_{x,y}}s_{P_x}^2} - 4\frac{Cov\left(s_{P_{x,y}}, s_{P_y}^2\right)}{s_{P_{x,y}}s_{P_y}^2} + 2\frac{Cov(s_{P_x}^2, s_{P_y}^2)}{s_{P_x}^2 s_{P_y}^2} \right]$$

For details, see Appendix 6.

3.3.2 Sampling variance and standard error of the coheritability estimator

Based on Robertson's (1959) approximation of the variance of the genetic correlation, it is possible to derive an approximation to the sampling variance of the coheritability as a function of the genetic correlation, the sampling variance of the heritabilities, as follows

$$Var\left(r_{A_{x,y}}\right) \approx \left(1 - r_{A_{x,y}}^2\right)^2 \frac{\sqrt{Var(h_x^2) \cdot Var(h_y^2)}}{2\, h_x^2 h_y^2}$$

$$h_x^2 h_y^2 Var\left(r_{A_{x,y}}\right) \approx (1 - r_{A_{x,y}}^2)^2 \frac{\sqrt{Var(h_x^2) \cdot Var(h_y^2)}}{2}$$

the right-hand side of the equation becomes $\quad h_x^2 h_y^2 \, Var\left(r_{A_{x,y}}\right) = Var\left(\sqrt{h_x^2 h_y^2}\, r_{A_{x,y}}\right) = Var(h_{x,y})$.

Therefore,

> **3-3-2a** Sampling variance of the coheritability estimator $h_{x,y}$ (as an extension of the Robertson's approximation of the sampling variance of the genetic correlation)
>
> $$Var\left(h_{x,y}\right) \approx \left(1 - r_{A_{x,y}}^2\right)^2 \frac{\sqrt{Var(h_x^2) \cdot Var(h_y^2)}}{2} = \left(1 - r_{A_{x,y}}^2\right)^2 \frac{SE(h_x^2) \cdot SE(h_y^2)}{2}$$

> **3-3-2b** Standard error (SE) of the coheritability estimator $h_{x,y}$ (as an extension of the Robertson's approximation of the sampling variance of the genetic correlation)
>
> $$SE(h_{x,y}) = \sqrt{Var\left(h_{x,y}\right)} = (1 - r_{A_{x,y}}^2)\sqrt{\frac{SE(h_x^2) \cdot SE(h_y^2)}{2}}$$

Another way to approximate the sampling variance of the coheritability is to use the Delta method

> **3-3-2c** Sampling variance of the coheritability estimator $h_{x,y}$ (Delta Method, see Appendix 6)
>
> $$Var\left(h_{x,y}\right) \approx \frac{1}{4}\left(h_{x,y}\right)^2 \left[\frac{Var[h_x^2]}{(h_x^2)^2} + \frac{Var[h_y^2]}{\left(h_y^2\right)^2} + \frac{4\, Var\left[r_{A_{x,y}}\right]}{r_{A_{x,y}}^2} \right.$$
> $$\left. + \frac{2\, Cov[h_x^2, h_y^2]}{h_x^2\, h_y^2} + \frac{4\, Cov\left[h_x^2,\, r_{A_{x,y}}\right]}{h_x^2\, r_{A_{x,y}}} + \frac{4\, Cov\left[h_y^2,\, r_{A_{x,y}}\right]}{h_y^2\, r_{A_{x,y}}} \right]$$

3.3.3 Sampling variance of the coenvironmentability estimator

3-3-3 Sampling variance of the coenvironmentability estimator $e_{x,y}$ (Delta Method)

$$
Var\left(e_{x,y}\right) \approx
$$

$$
\frac{1}{4}\left(e_{x,y}\right)^2 \left[\frac{Var\left[h_x^2\right]}{\left(1 - h_x^2\right)^2} + \frac{Var\left[h_y^2\right]}{\left(1 - h_y^2\right)^2} + 4\frac{Var\left(r_{E_{x,y}}\right)}{\left(r_{E_{x,y}}\right)^2} \right.
$$

$$
\left. + 2\frac{Cov\left[h_x^2, h_y^2\right]}{\left(1 - h_x^2\right)\left(1 - h_y^2\right)} - 4\frac{Cov\left[h_x^2, r_{E_{x,y}}\right]}{\left(1 - h_x^2\right) r_{E_{x,y}}} - 4\frac{Cov\left[h_y^2, r_{E_{x,y}}\right]}{\left(1 - h_y^2\right) r_{E_{x,y}}} \right]
$$

For details, see Appendix 6.

3.3.4 Sampling variance of the heritability estimator

> **3-3-4** Sampling variance of the heritability estimator $h^2 = \frac{V_A}{V_P}$ (Delta Method)
>
> $$Var\,(h^2) \approx (h^2)^2 \left[\frac{Var\,[V_A]}{(V_A)^2} + \frac{Var\,[V_P]}{(V_P)^2} + 2\frac{Cov\,[V_A, V_P]}{V_A\,V_P} \right]$$

For details, see Appendix 6.

3.3.5 Sampling variance and standard error of the genetic correlation estimator

The relationships presented in this section correspond to the formulae of Robertson (1959). For extensive review on the topic of the sampling variance of the genetic correlation, see Visscher (1998) and Koots and Gibson (1996).

3-3-5a Sampling variance of the genetic correlation estimator (from Robertson 1959 approximation)

$$Var\left(r_{A_{x,y}}\right) \approx \left(1 - r_{A_{x,y}}^2\right)^2 \frac{\sqrt{Var(h_x^2) \cdot Var(h_y^2)}}{2\,h_x^2 h_y^2} = \left(1 - r_{A_{x,y}}^2\right)^2 \frac{SE(h_x^2) \cdot SE(h_y^2)}{2\,h_x^2 h_y^2}$$

3-3-5b Standard error of the genetic correlation estimator (from Robertson 1959 aproximation)

$$SE(r_{A_{x,y}}) = \sqrt{Var\left(r_{A_{x,y}}\right)} \approx \sqrt{\left(1 - r_{A_{x,y}}^2\right)^2 \frac{SE(h_x^2) \cdot SE(h_y^2)}{2\,h_x^2 h_y^2}} = \left(1 - r_{A_{x,y}}^2\right) \sqrt{\frac{SE(h_x^2) \cdot SE(h_y^2)}{2\,h_x^2 h_y^2}}$$

4 Distribution of the sample correlation coefficient

4.1 Derivation of the distribution of the sample correlation coefficient

This section succinctly elaborates on the distribution of the sample phenotypic correlation in the case when the correlation parameter ρ is zero, and nonzero.

4.1.1 Distribution of r when ρ is zero

When $\rho = 0$, the three variates r, s_x^2 and s_y^2 are a completely independent set, since s_x^2 and s_y^2 are functions of separate sets of independent variates and are therefore mutually independent. Further details can be found elsewhere (Fisher 1928, Kym 1968, Chance 1986).

4-1-1   **Distribution of the sample correlation coefficient when $\rho = 0$**

$$f_r(r|\rho = 0, n) = \frac{\Gamma\left(\dfrac{n-1}{2}\right)}{\pi^{\frac{1}{2}}\,\Gamma\left(\dfrac{n-2}{2}\right)}\,(1-r)^{\frac{\eta-4}{2}}\,dr \qquad\qquad -1 \le r \le +1$$

4.1.2 Distribution of r when ρ is nonzero

The exact density function of the sample correlation coefficient r was originally obtained by Fisher (1915, 1928), following a geometric argument For ease of exposition, I present an exegesis of the derivation of the distribution the work by Hotelling (1950) (whose equation numbers are kept in this section for easy reference) .For purposes of this explanation we will use $\eta = (n-1)$, where n is the sample size.

The sample variances follow a chi-square distribution

Equation 10   Distribution of the sample variances

sample variance $\qquad\qquad$ chi-square distribution of the sample variance

$$s_x^2 = \frac{\sum(x_i - \bar{x})^2}{\eta} \quad , \qquad\qquad \frac{\eta s_x^2}{\sigma_x^2} \sim \chi_\eta^2 \qquad\qquad f_{S_x}\left(\frac{\eta s_x^2}{2}\right) = \frac{\left(\frac{\eta s_x^2}{2}\right)^{\frac{\eta}{2}-1} e^{-\frac{\eta s_x^2}{2}}}{\Gamma\left(\frac{\eta}{2}\right)} d\left(\frac{\eta s_x^2}{2}\right)$$

$$s_y^2 = \frac{\sum(y_i - \bar{y})^2}{\eta} \quad , \qquad\qquad \frac{\eta s_y^2}{\sigma_y^2} \sim \chi_\eta^2 \qquad\qquad f_{S_y}\left(\frac{\eta s_y^2}{2}\right) = \frac{\left(\frac{\eta s_y^2}{2}\right)^{\frac{\eta}{2}-1} e^{-\frac{\eta s_y^2}{2}}}{\Gamma\left(\frac{\eta}{2}\right)} d\left(\frac{\eta s_y^2}{2}\right)$$

Multiplying together the independent probability density functions of the correlation coefficient (when $\rho = 0$), the sample variance for trait x, and the sample variance for trait y.

$$\overbrace{f_r(r|\rho = 0, \eta)}^{\text{Equation 2}} \cdot \overbrace{f_{S_x}\left(\frac{\eta s_x^2}{2}\right)}^{\text{Equation 10}} \cdot f_{S_y}\left(\frac{\eta s_y^2}{2}\right)$$

$$g(r, s_x, s_y | \rho = 0)\, dr\, ds_x\, ds_y = \left[\frac{\Gamma\left(\frac{\eta}{2}\right)}{\pi^{\frac{1}{2}}\Gamma\left(\frac{\eta-1}{2}\right)}(1-r^2)^{\frac{\eta-3}{2}}dr\right]\left[\frac{\left(\frac{\eta s_x^2}{2}\right)^{\frac{\eta}{2}-1} e^{-\frac{\eta s_x^2}{2}}}{\Gamma\left(\frac{\eta}{2}\right)} d\left(\frac{\eta s_x^2}{2}\right)\right]\left[\frac{\left(\frac{\eta s_y^2}{2}\right)^{\frac{\eta}{2}-1} e^{-\frac{\eta s_y^2}{2}}}{\Gamma\left(\frac{\eta}{2}\right)} d\left(\frac{\eta s_y^2}{2}\right)\right]$$

$$= \frac{1}{\pi^{\frac{1}{2}}\Gamma\left(\frac{\eta-1}{2}\right)\Gamma\left(\frac{\eta}{2}\right)}(1-r^2)^{\frac{\eta-3}{2}}dr \cdot \frac{\eta^{\frac{\eta-2}{2}}s_x^{2\left(\frac{\eta-2}{2}\right)}e^{-\frac{\eta s_x^2}{2}}}{2^{\frac{\eta-2}{2}}}\left(\frac{2\eta s_x}{2}ds_x\right)\frac{\eta^{\frac{\eta-2}{2}}s_y^{2\left(\frac{\eta-2}{2}\right)}e^{-\frac{\eta s_y^2}{2}}}{2^{\frac{\eta-2}{2}}}\left(\frac{2\eta s_y}{2}ds_y\right)$$

$$= \frac{(1-r^2)^{\frac{\eta-3}{2}}dr}{\pi^{\frac{1}{2}}\Gamma\left(\frac{\eta-1}{2}\right)\Gamma\left(\frac{\eta}{2}\right)} \cdot \frac{\eta^{\frac{\eta-2}{2}+\frac{\eta-2}{2}+1+1}s_x^{\eta-2+1}s_y^{\eta-2+1}e^{-\frac{\eta}{2}(s_x^2+s_x^2)}}{2^{\frac{\eta-2}{2}+\frac{\eta-2}{2}}}ds_x\, ds_y$$

After some rearrangement, we obtain:

Equation 11 **The joint distribution of r , s_x , s_y**

$$g(r, s_x, s_y | \rho = 0) \, dr \, ds_x \, ds_y = \frac{\eta^{\eta} \ (1-r^2)^{\frac{\eta-3}{2}}}{\pi^{\frac{1}{2}} \ 2^{\eta-2} \ \Gamma\left(\frac{\eta-1}{2}\right) \Gamma\left(\frac{\eta}{2}\right)} \cdot e^{-\frac{\eta}{2}(s_x^2 + s_x^2)} (s_x s_y)^{\eta-1} \, ds_x \, ds_y \, dr$$

$$= \frac{(1-r^2)^{\frac{\eta-3}{2}} \, dr}{\pi^{\frac{1}{2}} \Gamma\left(\frac{\eta-1}{2}\right) \Gamma\left(\frac{\eta}{2}\right)} \cdot \frac{\eta^{\eta} \ e^{-\frac{\eta}{2}(s_x^2 + s_x^2)} (s_x s_y)^{\eta-1}}{2^{\eta-2}} \, ds_x \, ds_y \, dr$$

Equation 12 Proof that the denominator $\pi^{\frac{1}{2}} \Gamma\left(\frac{\eta-1}{2}\right) \Gamma\left(\frac{\eta}{2}\right) 2^{\eta-2} = \pi(\eta - 2)!$

Let $(\eta - 1) = m$

$\qquad \eta = m + 1$

Then $\qquad \pi^{\frac{1}{2}} \Gamma\left(\frac{m}{2}\right) \Gamma\left(\frac{m+1}{2}\right) 2^{m-1}$

The product of the gamma functions

$$\Gamma\left(\frac{m}{2}\right) \Gamma\left(\frac{m+1}{2}\right) = \frac{\pi^{\frac{1}{2}} \Gamma(m)}{2^{m-1}}$$

$$\pi^{\frac{1}{2}} \frac{\pi^{\frac{1}{2}} \Gamma(m)}{2^{m-1}} 2^{m-1} = \pi^{\frac{1}{2}} \pi^{\frac{1}{2}} \Gamma(m) = \pi(m - 1)! = \pi (\eta - 2)!$$

Consider two random variables $X \sim Normal(0,1)$ and $Y \sim Normal(0,1)$

We assume that each (x, y) datum has a bivariate normal probability density

$$f_{X,Y}(x,y) = \frac{1}{2\pi(1-\rho^2)^{\frac{1}{2}}} \ e^{\left\{-\frac{1}{2(1-\rho^2)} (x^2 - 2\rho xy + y^2)\right\}} dx \, dy$$

Multiplying the independent probability density functions assumed for each bivariate datum, it yields the joint distribution of the 2η observations which is written with the help of equations 10 and 11.

$$\varphi(r, s_x, s_y, \rho) = \prod_{i=1}^{\eta} f_{XY_i}(x,y) = \prod_{i=1}^{\eta} \frac{\eta}{2\pi^{\eta}(1-\rho^2)^{\frac{1}{2}\eta}} e^{\left\{ -\frac{1}{2(1-\rho^2)} (x_i^2 - 2\rho x_i y_i + y_i^2) \right\}} dx_i dy_i$$

$$= \frac{1}{2\pi^{\eta}(1-\rho^2)^{\frac{1}{2}\eta}} e^{-\frac{\eta}{2(1-\rho^2)} \left(\sum x_i^2 - 2\rho \sum x_i y_i + \sum y_i^2 \right)} dx_i dy_i$$

Since we know that $\bar{x} = \bar{y} = 0$, the following relationships can be use to replace terms of $\sum x_i^2$, $\sum x_i \, y_i$, and $\sum y_i^2$.

$$s_x^2 = \frac{\sum(x_i - \bar{x})^2}{\eta} \qquad \rightarrow \quad \sum(x_i - \bar{x})^2 = \eta s_x^2 \qquad\qquad \rightarrow \sum x_i^2 = \eta s_x^2$$

$$r = \frac{\sum(x_i - \bar{x})(y_i - \bar{y})}{\eta \, s_y \, s_x} \rightarrow \quad \sum(x_i - \bar{x})(y_i - \bar{y}) = \eta \, s_y \, s_x \, r \qquad \rightarrow \sum x_i \, y_i = \eta \, s_y \, s_x \, r$$

$$s_y^2 = \frac{\sum(y_i - \bar{y})^2}{\eta} \qquad \rightarrow \quad \sum(y_i - \bar{y})^2 = \eta s_y^2 \qquad\qquad \rightarrow \sum y_i^2 = \eta s_y^2$$

We obtain

Equation 14

$$\varphi(r, s_x, s_y, \rho) dx_1 dy_1 \, dx_2 dy_2 \ldots dx_{\eta} dy_{\eta} = \prod_{i=1}^{\eta} f_{XY_i}(x,y)$$

which becomes

Equation 15   **Joint distribution of** r, s_x, s_y, ρ

$$\varphi(r, s_x, s_y, \rho) = \prod_{i=1}^{n} f_{XY_i}(x,y) = = \frac{1}{2\pi^{\eta}(1-\rho^2)^{\frac{\eta}{2}}} e^{-\frac{\eta}{2(1-\rho^2)} \left(s_x^2 - 2\rho r s_x s_y + s_y^2 \right)} dx_1 dy_1 \ldots dx_n dy_n$$

When ρ varies, the joint probability elements of r, s_x, s_y varies in proportion to the density of equation 15.

The derivation of the joint probability distribution of r, s_x, s_y, ρ for $\rho = 0$

$$f(r, s_x, s_y) = \frac{[\,Equation\ 15\,]}{[\,Equation\ 15\ when\ \rho = 0\,]} [\,equation\ 11\,]$$

$$= \frac{\varphi(r, s_x, s_y, \rho) dx_1 dy_1 \ldots dx_n dy_n}{\varphi(r, s_x, s_y, 0) dx_1 dy_1 \ldots dx_n dy_n} g(r, s_x, s_y)\, ds_x\, ds_y\, dr$$

$$= \frac{\dfrac{1}{2\pi^\eta (1-\rho^2)^{\frac{\eta}{2}}} e^{-\frac{\eta}{2(1-\rho^2)}(s_x^2 - 2\rho r s_x s_y + s_y^2)}}{\dfrac{1}{2\pi^\eta} e^{-\frac{\eta}{2}(s_x^2 + s_y^2)}} \cdot \frac{(1-r^2)^{\frac{\eta-3}{2}}}{\pi^{\frac{1}{2}} \Gamma\left(\dfrac{\eta-1}{2}\right) \Gamma\left(\dfrac{\eta}{2}\right)} \cdot \frac{\eta^\eta e^{-\frac{\eta}{2}(s_x^2 + s_y^2)}(s_x s_y)^{\eta-1}}{2^{\eta-2}} ds_x\, ds_y dr$$

Equation 16 **The joint probability distribution of** r, s_x, s_y, ρ **for** $\rho = 0$

$$f(r, s_x, s_y) = \frac{\eta^\eta}{\pi\,(\eta-2)!} (1-\rho^2)^{-\frac{\eta}{2}} (1-r^2)^{\frac{\eta-3}{2}} e^{\left\{-\frac{\eta}{2(1-\rho^2)}(s_x^2 - 2\rho r s_x s_y + s_y^2)\right\}} (s_x s_y)^{\eta-1}\, ds_x\, ds_y\, dr$$

The distribution of r is found by integrating (16) with respect to s_x and s_y from 0 to positive infinity. For this purpose the following transformation is useful.

Put

$$s_x = \alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta}$$

$$s_y = \alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta}$$

Note that $s_x s_y = \alpha$

The Jacobian is

$$J = \frac{\delta(s_x, s_y)}{\delta(\alpha, \beta)} = \begin{bmatrix} \dfrac{\delta s_x}{\delta \alpha} & \dfrac{\delta s_x}{\delta \beta} \\ \dfrac{\delta s_y}{\delta \alpha} & \dfrac{\delta s_y}{\delta \beta} \end{bmatrix} = \begin{bmatrix} \dfrac{\delta}{\delta \alpha}\left(\alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta}\right) & \dfrac{\delta}{\delta \beta}\left(\alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta}\right) \\ \dfrac{\delta}{\delta \alpha}\left(\alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta}\right) & \dfrac{\delta}{\delta \beta}\left(\alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta}\right) \end{bmatrix}$$

$$= \begin{bmatrix} \dfrac{1}{2}\alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta} & -\dfrac{1}{2}\alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta} \\ \dfrac{1}{2}\alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta} & \dfrac{1}{2}\alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta} \end{bmatrix}$$

Now working in the exponential part of equation 16

$$f(s_x, s_y, r) = \frac{\eta^\eta}{\pi \, (\eta-2)!}(1 - \rho^2)^{-\frac{\eta}{2}} (1 - r^2)^{\frac{\eta-3}{2}} \; e^{\left\{-\frac{\eta}{2(1-\rho^2)}\left(s_x^2 - 2\rho r s_x s_y + s_y^2\right)\right\}}(s_x s_y)^{\eta-1} ds_x \, ds_y \, dr$$

$$\left\{-\frac{\eta}{2(1-\rho^2)}\left(s_x^2 - 2\rho r s_x s_y + s_y^2\right)\right\}$$

$$= \left\{-\frac{\eta}{2(1-\rho^2)}\left(\left(\alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta}\right)^2 - 2\rho r \left(\alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta}\right)\left(\alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta}\right) + \left(\alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta}\right)^2\right)\right\}$$

$$= -\frac{\eta}{2(1-\rho^2)}\left(\alpha e^{-\beta} - 2\,\rho r \alpha + \alpha e^\beta\right)$$

$$= -\frac{\eta\,\alpha}{(1-\rho^2)}\left(\frac{e^{-\beta} + e^\beta}{2} - \frac{2\,\rho r}{2}\right)$$

$$= -\frac{\eta\,\alpha}{(1-\rho^2)}\left(\cosh\beta - \rho r\right)$$

Working on the differentials $ds_x \, ds_y$ of equation 16.

$$f(s_x, s_y, r) = \frac{\eta^\eta}{\pi \, (\eta-2)!}(1 - \rho^2)^{-\frac{\eta}{2}} (1 - r^2)^{\frac{\eta-3}{2}} \; e^{\left\{-\frac{\eta}{2(1-\rho^2)}\left(s_x^2 - 2\rho r s_x s_y + s_y^2\right)\right\}} \left(s_x s_y\right)^{\eta-1} ds_x \, ds_y \, dr$$

We note that

$$\frac{\delta\,(s_x s_y)}{\delta\,s_x} = \frac{\delta\,\alpha}{\delta\,s_x} = s_y \qquad \rightarrow \qquad d\alpha = ds_x \cdot s_y$$

and

$$\frac{s_x}{s_y} = \frac{\alpha^{\frac{1}{2}} e^{\frac{1}{2}\beta}}{\alpha^{\frac{1}{2}} e^{-\frac{1}{2}\beta}} = e^\beta \qquad \rightarrow \qquad ln\left(\frac{s_x}{s_y}\right) = ln\left(e^\beta\right) = \beta$$

$$\frac{d\,\beta}{d\,s_y} = \frac{d\left(\ln\frac{s_x}{s_y}\right)}{d\,s_y} = \frac{1}{s_y} \qquad \rightarrow \qquad d\beta = \frac{1}{s_y} ds_y$$

Therefore, the product

$$da \, d\beta = ds_x \cdot s_y \frac{1}{s_y} ds_y = ds_x \, ds_y$$

We mark the factors involving s_x and s_y in Equation 16 and express them in terms of α and β.

$$e^{\left\{-\frac{\eta}{2(1-\rho^2)}(s_x^2 - 2\rho r s_x s_y + s_y^2)\right\}}(s_x s_y)^{\eta-1} ds_x \, ds_y = \left|\frac{1}{2}\right| \alpha^{\eta-1} e^{-\eta \frac{\alpha}{1-\rho^2}[\cosh\beta - \rho r]} da \, d\beta$$

Integration with respect to α (with integration limits $0 < \alpha < +\infty$)

$$\frac{1}{2}\int_0^{+\infty} e^{-\eta \frac{\alpha}{1-\rho^2}[\cosh\beta - \rho r]} \alpha^{\eta-1} da \, d\beta$$

$$\alpha = a$$

$$(1 - \rho^2) = y$$

$$\cosh\beta - \rho r = x$$

$$\frac{1}{2}\int_0^{\infty} e^{-\eta \frac{a}{y} x} a^{\eta-1} da \, d\beta$$

Steps to integrate with respect to a (Equation 16b)

$$\frac{1}{2}\int_0^\infty e^{-\eta\frac{a}{y}x}\ a^{\eta-1}\ da\ d\beta$$

① substitute

$$u = \frac{a}{y}\ \rightarrow\ a = uy\qquad and \qquad \frac{\delta a}{\delta u} = \frac{\delta(uy)}{\delta u} = y\ \rightarrow\ \delta a = y\ \delta u$$

Use $$a^{\eta-1} = y^{\eta-1}u^{\eta-1}$$

$$u = \frac{a}{y}$$

$$\frac{1}{2}\int_0^\infty y^{\eta-1}\ u^{\eta-1}e^{-\eta\ ux}\ y\ du\ d\beta$$

$$\frac{1}{2}y^\eta\int_0^\infty u^{\eta-1}e^{-\eta\ xu}\ du\ d\beta$$

② substitute in $\frac{1}{2}y^\eta\int_0^\infty u^{\eta-1}e^{-\eta\ ux}\ du\ d\beta$

$$b = \eta - 1 \qquad\rightarrow\qquad b + 1 = \eta$$
$$m = x(b+1) \qquad\rightarrow\qquad m = x\eta$$

$$\frac{1}{2}y^\eta\int_0^\infty u^b e^{-mu}\ du\ d\beta = \frac{1}{2}y^\eta\frac{\Gamma(b+1)}{m^{b+1}}\ d\beta$$

Undoing of variable substitution above

③ Undo substitution

$$\frac{1}{2}y^\eta\frac{\Gamma(b+1)}{m^{b+1}}\ d\beta \quad\rightarrow\quad \frac{1}{2}y^\eta\frac{\Gamma(\eta)}{x^\eta\ \eta^\eta}\ d\beta = \frac{1}{2}(1-\rho^2)^\eta\ \frac{\Gamma(\eta)}{\eta^\eta}\ \frac{1}{(cosh\beta - \rho r)^2}\ d\beta$$

④ Undo variable change. Finally we obtain

$$\frac{1}{2}\int_0^\infty e^{-\eta\frac{a}{y}x}\ a^{\eta-1}\ da\ d\beta = \frac{1}{2}\frac{(1-\rho^2)^\eta\ \Gamma(\eta)}{\eta^\eta}\ \frac{1}{(\cosh\beta - \rho r)^\eta}\ d\beta$$

$$= \frac{1}{2}\Gamma(\eta)\left(\frac{1-\rho^2}{\eta}\right)^\eta\ \frac{1}{(\cosh\beta - \rho r)^\eta}\ d\beta$$

Now we can reformulate the integrant as follows

$$\frac{1}{2} \int_0^\infty e^{-\frac{\eta\alpha}{1-\rho^2} [\cosh\beta - \rho r]} \alpha^{\eta-1} d\alpha \, d\beta$$

Finally, integrating with respect to α,

$$\frac{1}{2} \int_{\alpha=0}^{\alpha \to +\infty} \alpha^{\eta-1} e^{-\frac{\eta\alpha}{1-\rho^2} [\cosh\beta - \rho r]} d\alpha \, d\beta \;=\; \frac{1}{2} (\eta-1)! \left(\frac{1-\rho^2}{\eta}\right)^\eta \frac{1}{(\cosh\beta - \rho r)^\eta} d\beta$$

Equation 16c

Integration with respect to β (integration limits $-\infty < \beta < +\infty$), but since we work from 0 to $+\infty$, we multiply by 2.

$$\frac{1}{2} (\eta-1)! \left(\frac{1-\rho^2}{\eta}\right)^\eta 2 \int_0^{+\infty} \frac{1}{(\cosh\beta - \rho r)^\eta} d\beta$$

Up to now, we have arrived to the following expression

$$f(r,\rho) = \frac{\eta^\eta}{\pi (\eta-2)!} (1-\rho^2)^{-\frac{\eta}{2}} (1-r^2)^{\frac{1}{2}(\eta-3)} (\eta-1)! \left(\frac{1-\rho^2}{\eta}\right)^\eta \left[\int_0^\infty \frac{1}{(\cosh\beta - \rho r)^\eta} d\beta\right] dr$$

After some simplification and rearrangement, the general distribution of r is

$$f_n(r,\rho)dr = \frac{\eta-1}{\pi} (1-\rho^2)^{\frac{\eta}{2}} (1-r^2)^{\frac{1}{2}(\eta-3)} \left[\int_0^\infty \frac{1}{(\cosh\beta - \rho r)^\eta} d\beta\right] dr$$

Introducing the notation

Equation 17

$$I_n(\rho r) = \int_0^\infty \frac{1}{(\cosh\beta - \rho r)^\eta} d\beta \qquad\qquad |p| < 1$$

We replace the integral for equation 17

$$f_\eta(r,\rho)dr = \frac{\eta-1}{\pi}(1-\rho^2)^{\frac{\eta}{2}}\ (1-r^2)^{\frac{1}{2}(\eta-3)}I_n(\rho r)dr$$

The difficulties with the form presented lies in the integral factor, which will be denoted as $I_n(\rho r)$.
We can re-express

Equation 18

$$f_\eta(r,\rho)dr = \frac{\eta-1}{\pi}(1-\rho^2)^{\frac{1}{2}\eta}\ (1-r^2)^{\frac{1}{2}(\eta-3)}I_n(\rho r)dr$$

Introducing the notation $p = \rho r$

$$I_\eta(p) = \int_0^\infty \frac{1}{(\cosh\beta - p)^n}\,d\beta$$

A fundamental improvement is the use of the following substitution:

Equation 21

$$\cosh\beta = \frac{1-pz}{1-z}$$

Therefore

$$\cosh\beta - p = \left(\frac{1-pz}{1-z} - p\right) = \frac{1-p}{1-z}$$

$$\beta = arcosh\left(\frac{1-pz}{1-z}\right)$$

Taking the derivative of β with respect to z,

$$\frac{d\beta}{dz} = \frac{1-p}{(z-1)^2 \sqrt{\frac{(1-pz)^2}{(1-z)^2} - 1}}$$

$$= \frac{1-p}{(z-1)^2 \sqrt{\frac{1-pz}{1-z} - 1}\sqrt{\frac{1-pz}{1-z} + 1}}$$

$$= \frac{1-p}{(z-1)^2 \sqrt{\frac{z(1-p)}{1-z}}\sqrt{\frac{2-z-pz}{1-z}}}$$

$$= \frac{(1-p)(1-z)}{(z-1)^2 \sqrt{z}\sqrt{1-p}\sqrt{2-z-pz}}$$

Finally, we note that the term $(z-1)^2 = (1-z)^2$ and after simplification

$$d\beta = \frac{(1-p)^{\frac{1}{2}}}{(1-z)\sqrt{z}\sqrt{2-z-pz}} dz$$

Thus

$$I_\eta(p) = \int_0^\infty \frac{1}{(\cosh\beta - p)^\eta} d\beta = \int_0^\infty \frac{(1-z)^\eta}{(1-p)^\eta} \frac{(1-p)}{(1-z)\sqrt{z}\sqrt{2-z-pz}} dz$$

After some simplification and rearrangement we obtain

$$I_\eta(p) = \int_0^\infty (1-p)^{-\eta+\frac{1}{2}} z^{-\frac{1}{2}} (1-z)^{\eta-1} \frac{1}{\sqrt{2-z-pz}} dz$$

Multiplying the integrand by $\frac{\sqrt{2}}{\sqrt{2}}$

$$I_\eta(p) = \int_0^\infty (1-p)^{-\eta+\frac{1}{2}} z^{-\frac{1}{2}} (1-z)^{\eta-1} \frac{1}{\sqrt{2-z-pz}} \frac{\sqrt{2}}{\sqrt{2}} dz$$

Equation 22

$$I_\eta(p) = \frac{1}{\sqrt{2}}\,(1-p)^{-\eta+\frac{1}{2}} \int_0^\infty z^{-\frac{1}{2}}\,(1-z)^{\eta-1}\left(1-\frac{(1+p)}{2}z\right)^{-\frac{1}{2}} dz$$

This integral has the kernel of a hypergeometric integral

$$_2F_1(a_1,a_2\,;\,b_1;x) = \frac{\Gamma(b_1)}{\Gamma(a_2)\Gamma(b_1-a_2)} \int_0^1 z^{a_2}(1-z)^{b_1-a_2}(1-kz)^{-a_1} dz$$

$$\frac{\Gamma(a_2)\Gamma(b_1-a_2)}{\Gamma(b_1)}\cdot {_2F_1}(a_1,a_2\,;\,b_1;x) = \int_0^1 z^{a_2}(1-z)^{b_1-a_2}(1-kz)^{-a_1} dz$$

where $\quad a_1 = \frac{1}{2}, \qquad a_2 = \frac{1}{2}, \qquad b_1 = \eta+\frac{1}{2}, \qquad k = \frac{1+p}{2}$

Replacing this variables in equation we obtain

$$I_n(p) = \frac{1}{\sqrt{2}}\,(1-p)^{-\eta+\frac{1}{2}} \int_0^\infty z^{-\frac{1}{2}}\,(1-z)^{\eta-1}\left(1-\frac{(1+p)}{2}z\right)^{-\frac{1}{2}} dz$$

$$I_n(p) = \frac{1}{\sqrt{2}}\,(1-p)^{-\eta+\frac{1}{2}}\,\frac{\Gamma\left(\frac{1}{2}\right)\Gamma(\eta)}{\Gamma(\eta+\frac{1}{2})}\cdot {_2F_1}\left(\frac{1}{2},\frac{1}{2}\,;\,\eta+\frac{1}{2};\frac{1+p}{2}\right)$$

Since $\Gamma\left(\frac{1}{2}\right) = \pi^{\frac{1}{2}}$

$$I_n(p) = \frac{1}{\sqrt{2}}\,(1-p)^{-\eta+\frac{1}{2}}\,\frac{\pi^{\frac{1}{2}}\,\Gamma(\eta)}{\Gamma(\eta+\frac{1}{2})}\cdot {_2F_1}\left(\frac{1}{2},\frac{1}{2}\,;\,\eta+\frac{1}{2};\frac{1+p}{2}\right)$$

Equation 24

$$I_n(p) = \frac{\pi^{\frac{1}{2}}\,\Gamma(\eta)}{\sqrt{2}\,\Gamma(\eta+\frac{1}{2})}\,(1-p)^{-\eta+\frac{1}{2}}\;{_2F_1}\left(\frac{1}{2},\frac{1}{2}\,;\,\eta+\frac{1}{2};\frac{1+p}{2}\right)$$

Replacing $p = \rho r$, we obtain

$$I_\eta(\rho r) = \frac{\pi^{\frac{1}{2}} \Gamma(\eta)}{\sqrt{2}\, \Gamma(\eta + \frac{1}{2})} (1 - \rho r)^{-\eta + \frac{1}{2}} \; {}_2F_1\left(\frac{1}{2}, \frac{1}{2} \; ; \; \eta + \frac{1}{2}; \; \frac{1 + \rho r}{2}\right)$$

$$f_\eta(r|\rho, \eta)dr = \frac{\eta - 1}{\pi} (1 - \rho^2)^{\frac{\eta}{2}} \; (1 - r^2)^{\frac{1}{2}(\eta - 3)} I_\eta(\rho r) dr$$

Replacing this $I_\eta(\rho r)$ term in Equation 18, we obtain

Equation 25

$$f_\eta(r|\rho, \eta) = \frac{\eta - 1}{\pi} (1 - \rho^2)^{\frac{\eta}{2}} \; (1 - r^2)^{\frac{1}{2}(\eta - 3)} \frac{\pi^{\frac{1}{2}} \Gamma(\eta)}{\sqrt{2}\, \Gamma(\eta + \frac{1}{2})} (1 - \rho r)^{-\eta + \frac{1}{2}} \; {}_2F_1\left(\frac{1}{2}, \frac{1}{2} \; ; \; \eta + \frac{1}{2}; \; \frac{1 + \rho r}{2}\right)$$

which converges for $-1 < \rho r < +1$.

Finally, we exchange $\eta = n - 1$, and obtain the sampling distribution of the correlation coefficient in terms of the sample size n.

Probability density function of the distribution of the sample correlation coefficient in terms of ρ, n

$$\boldsymbol{f_r(r|\rho, n)} = \frac{n-2}{\sqrt{2\pi}} \frac{\Gamma(n-1)}{\Gamma(n-\frac{1}{2})} (1 - \rho^2)^{\frac{n-1}{2}} (1 - r^2)^{\frac{n-4}{2}} (1 - \rho r)^{-n+\frac{3}{2}} \cdot {}_2F_1\left(\frac{1}{2}, \frac{1}{2}; n - \frac{1}{2}; \frac{1+\rho r}{2}\right)$$

The hypergeometric function is expanded in Appendix 5. By using the first three terms one can obtain a very good approximation of the probability density function of r.

$$\boldsymbol{f_r(r|\rho, n)} \approx \frac{n-2}{\sqrt{2\pi}} \frac{\Gamma(n-1)}{\Gamma\left(n-\frac{1}{2}\right)} (1 - \rho^2)^{\frac{n-1}{2}} (1 - r^2)^{\frac{n-4}{2}} (1 - \rho r)^{-n+\frac{3}{2}} \left[1 + \frac{1}{4} \frac{(1 - \rho r)}{(2n-1)} + \frac{9}{32} \frac{(1 + \rho r)^2}{(2n-1)(2n+1)} + \cdots\right]$$

4.2 Comments on the distribution of r

4.2.1 General comments

The shape of the sample correlation coefficient when $\rho = 0$ is symmetric and/or when the sample size is very large. The distribution has a zero skew value indicating that the left and right hand sides of the distribution are roughly equally balanced around the mean.

However, the shape of the sampling distribution of the correlation coefficient is asymmetric when it differs from $\rho = 0$. This means that the tail on one side is longer or fatter than the other side. The reason for this asymmetry of the probability distribution is that the correlation coefficient cannot take values less than -1 or greater than +1. The skew of the distribution is more noticeable when the sample size is small ($n < 25$).

When $\rho < 0$ the distribution is positively skewed.

When $r > 0$, the distribution is negatively skewed.
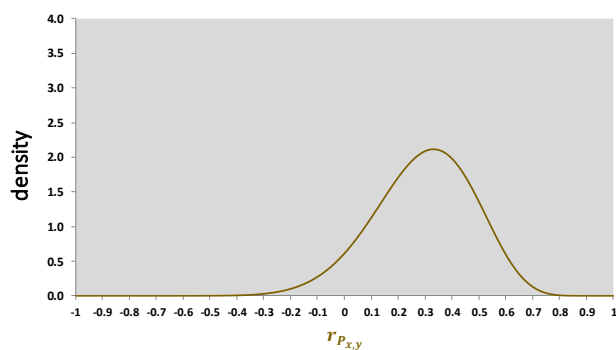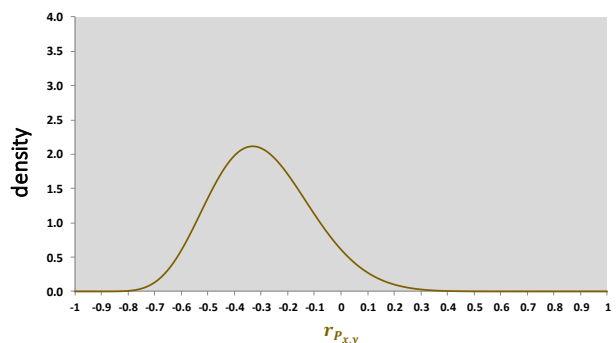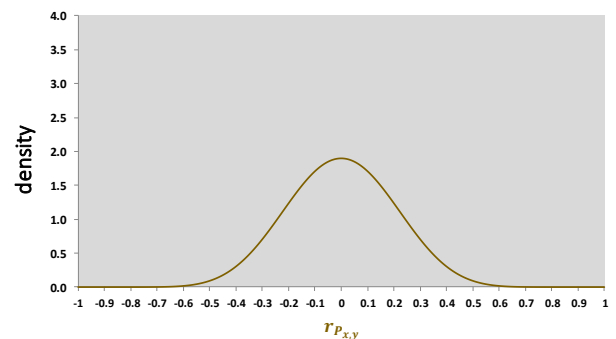
As the sample size n increases
the skew is less pronounced,
the distribution becomes narrower
(variance decreases),
and density (y axis) reaches larger values

$n = \quad 25$

density

$r_{P_{x,y}}$

$n = \quad 50$

density

$r_{P_{x,y}}$

$n = \quad 75$

density

$r_{P_{x,y}}$

$n = \quad 100$

density

$r_{P_{x,y}}$
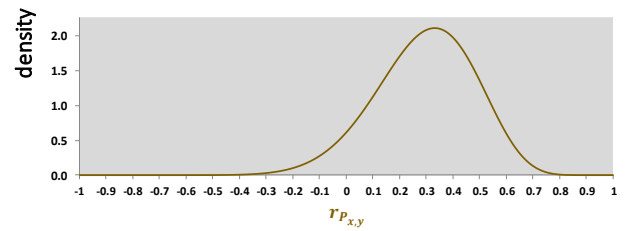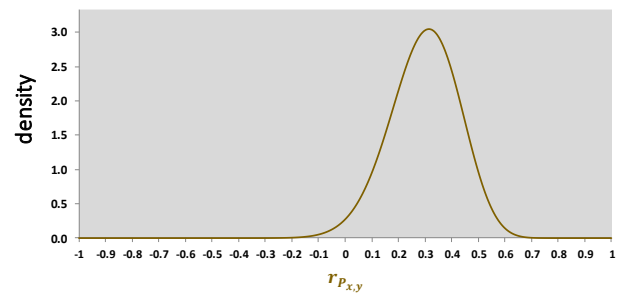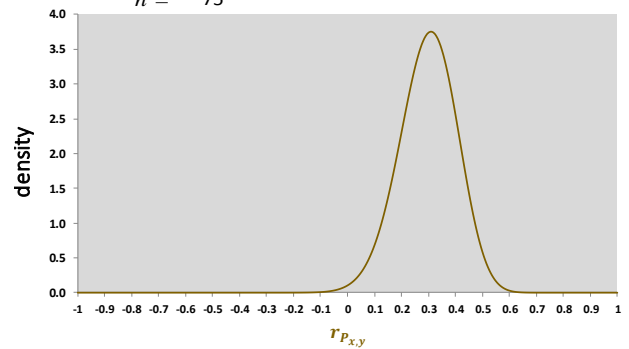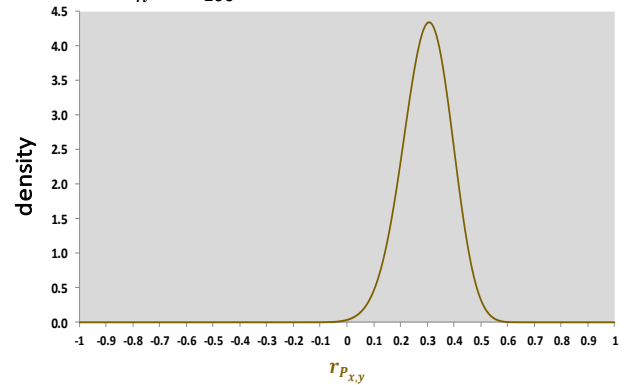
As ρ approaches $+1$ or -1, the sampling variance decreases, so that when ρ is either at $+1$ or -1, all sample values equal the parameter and the sampling variance is zero.
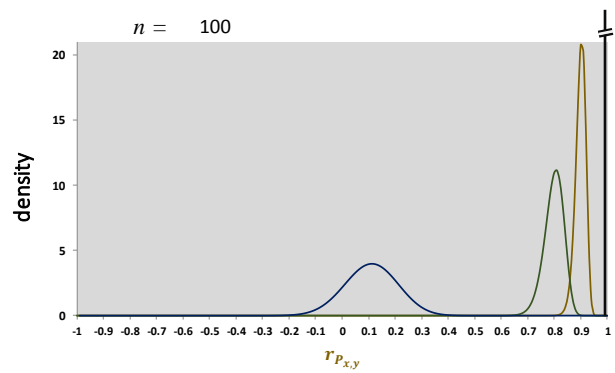
Note that as $|\rho|$ approaches 1, the sampling variance approaches zero.

The shape of the sampling distribution depends on the sample size n. The shape becomes increasingly normal with large values of n, and becomes increasingly skewed with increasing $|\rho|$.

4.2.2 Comments on the distribution of r when the correlation coefficient parameter ρ is zero

Independence implies zero correlation, but not the converse.

If the population phenotypic correlation is zero, then two possible cases exist:

    (a) both the population coheritability $H_{x,y}$ and the population coenvironmentability $E_{x,y}$ are zero,

        or

    (b) both the population coheritability $H_{x,y}$ and the population coenvironmentability $E_{x,y}$ are nonzero, have the same magnitude, but differ in sign.

In the latter case, one must be mindful that a zero phenotypic correlation does not necessarily indicate that the coheritability and coenvironmentability are zero. From a statistical point of view, their values may be significantly different than zero, yet possess a different sign.

Examples of distribution of $r_{P_{x,y}}$, $h_{x,y}$, and $e_{x,y}$ when the parameter values of the population-level coheritability and coenvironmentability sum up to zero.
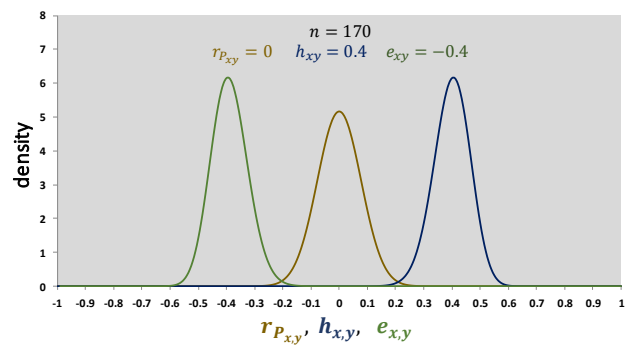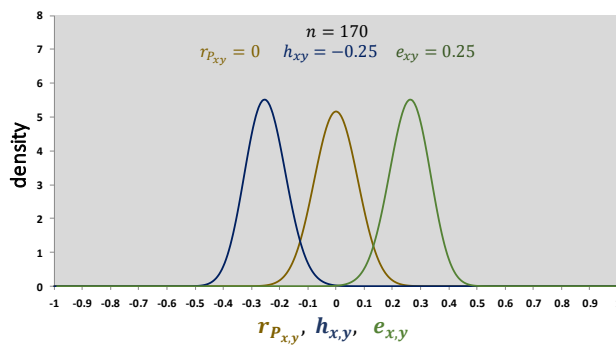
4.2.3 Comments on the distribution of r when the correlation coefficient parameter ρ is nonzero

The closed-form representation of the probability density function of the sample correlation coefficient r is dependent on the population correlation coefficient ρ and the sample size n (see section 4.1.2). Figure 4.2.3-1 presents a hypothetical but realistic case of data plotted on the 2DHER-field where the phenotypic correlation is $r_{P_{x,y}} = -0.5$, the coheritability $h_{x,y} = -0.35$, and the coenvironmentability $e_{x,y} = -0.15$. Further examples are presented in Figure 4.2.3-2 where, for ease of comparison, the density curves are overlaid in the same graph.
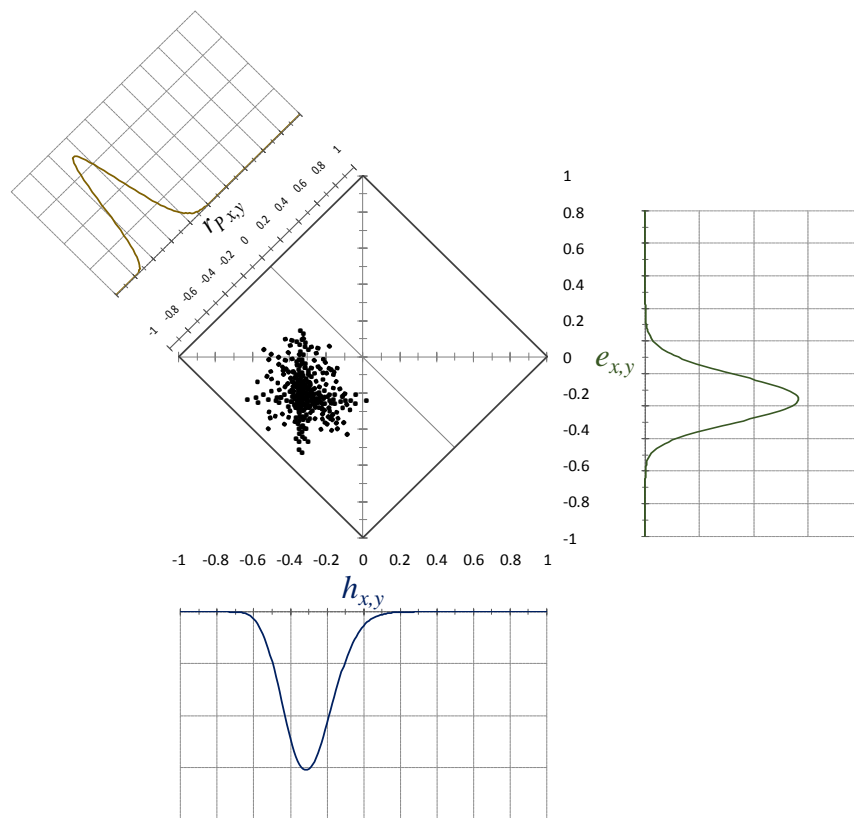
Figure 4.2.3-1 Sampling distribution of phenotypic correlation, coheritability, and coenvironmnetability. Data is plotted on the 2DHER-field showing the phenotypic correlation between two traits obtained from $n = 150$ samples drawn from a population with $\rho_{P_{x,y}}$ =-0.51, decomposed into its coheritability, coenvironmentability components
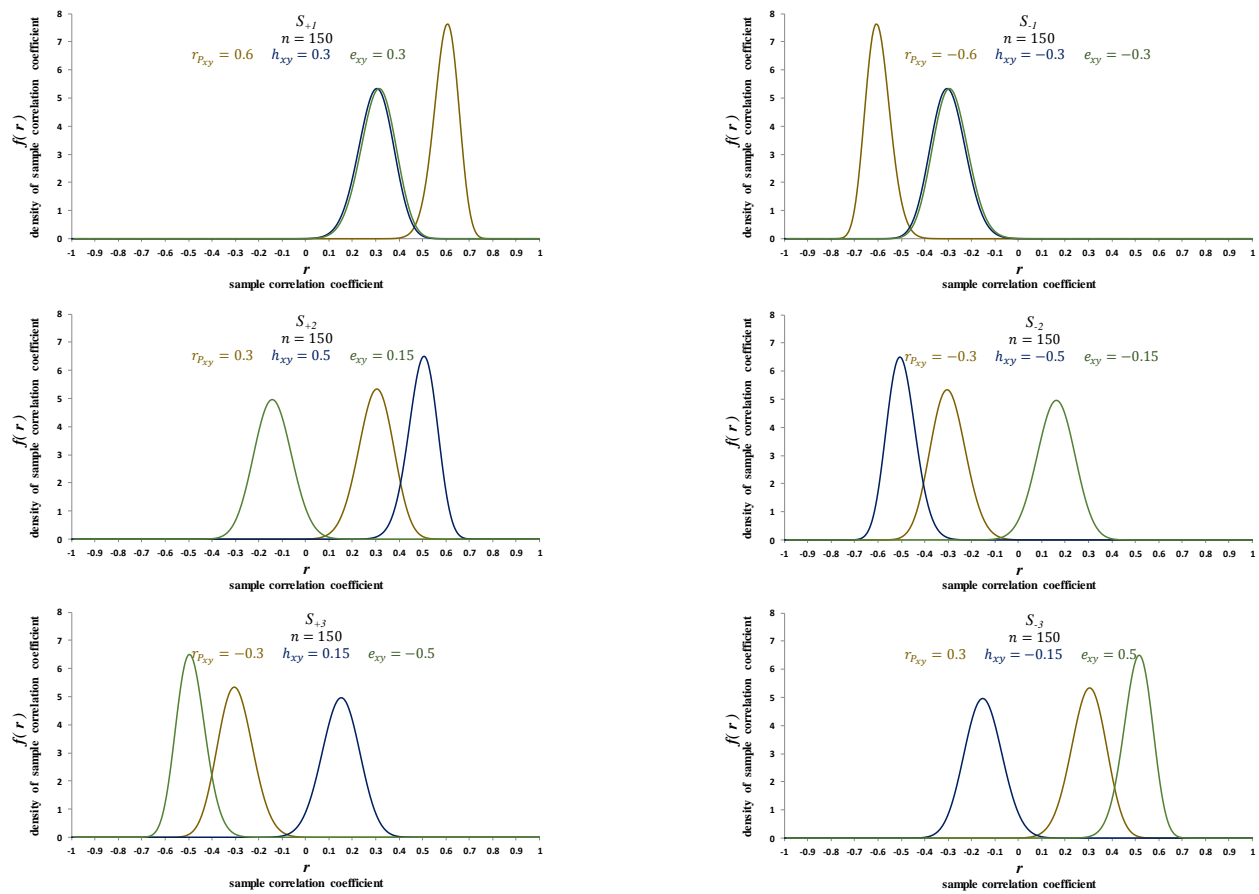
Figure 4.2.3-2 Example of distributions of the phenotypic correlation, coheritability and coenvironmentability. Density curves are overlaid to facilitate comparison.

Pham-Gia and Choulakian (2014) proposed an original expression for the density of the correlation matrix, with sample variances as parameters for the case of the multivariate normal population with non-identity population correlation.

4.3 Moments of the sample correlation coefficient distribution

Hotelling (1953, page 212) presents the moments of the sample correlation coefficient r around its mean. Rady et al. (2005) introduced a method to easily determine the moments of r around its mean, which are the same as those found by Gosh (1966). Romero-Padilla (2016) presents the moments of r around the origin using hypergeometric functions.

Mean sample correlation

4-3a Mean of the sample correlation coefficient around its mean

$$E(r) = \bar{r} = \rho\left\{1 - \frac{1}{2(n-1)}(1-\rho^2) - \frac{3}{8(n-1)^2}(1-\rho^2)(1+3\rho^2)\right\}$$

4-3b Variance of the sample correlation coefficient

$$Var(r) = \sigma_r^2 = \frac{(1-\rho^2)^2}{n-1}\left\{1 + \frac{5.5\,\rho^2}{n-1} + \frac{-24\rho^2 + 75\rho^4}{2(n-1)^2} +. . .\right\}$$

4-3c Skewness of the sample correlation coefficient

$$skewness = \frac{6\rho}{\sqrt{n-1}}\;1 + \frac{-30 + 77\rho^2}{12\,(n-1)} +. . .$$

4-3c Kurtosis of the sample correlation coefficient

$$kurtosis = \frac{6(12\rho^2 - 1)}{\sqrt{n-1}} +. . .$$

4.4 The Fisher r-to-Z transform of the correlation coefficient

The Pearson product moment correlation coefficient r based on n independent units of observation has an asymptotic normal distribution. However, its distribution can be highly skewed at small-to-moderate sample sizes, and its sampling variance varies as a function of the population correlation coefficient ρ. Noting these limitations, Fisher (1921) proposed using the inverse hyperbolic tangent function Z_r as a normalizing and variance-stabilizing transformation:

4-4a Fisher r-to-Z transformation of Z_r

$$Z_r = atanh(r) = \frac{1}{2} \ln\left(\frac{1+r}{1-r}\right)$$

note the equivalent ways to denote the inverse hyperbolic tangent:

$$atanh(r) = artanh(r) = arctanh(r) = tanh^{-1}(r)$$

For the transformed z, the approximate variance $\sigma_{Z_r}^2 = 1/(n-3)$ is independent of the correlation. Fouladi and Steiger (2008) provide a thorough discussion on the consequence of the use of this transformation and its implications in inferential statistics.
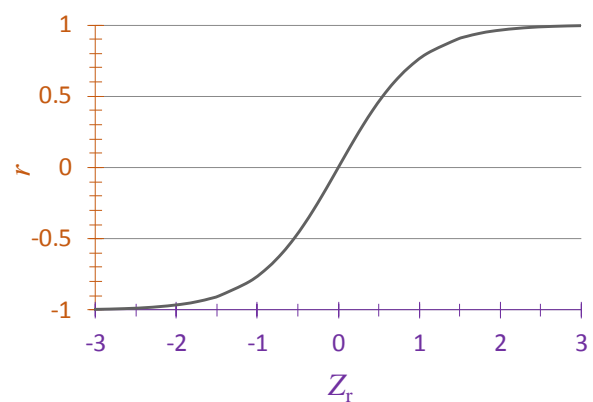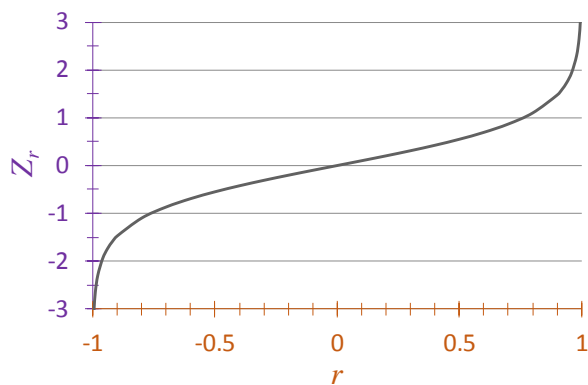
4-4b   Mean of the Fisher transform of Z_r

$$\bar{Z}_r = E\left(Z_r - Z_\rho\right)$$

$$= \frac{\rho}{2(n-1)} + \frac{5\rho + \rho^3}{8(n-1)^2} + \frac{11\rho + 2\rho^3 + 3\rho^5}{16(n-1)^3} + \frac{83\rho + 13\rho^3 - 27\rho^5 + 75\rho^7}{128(n-1)^4} + O(n^{-5})$$

4-4c   Variance of the Fisher transform of Z_r

$$\sigma^2_{Z_r - Z_\rho} = E(Z_r - Z_\rho - \bar{r})^2$$

$$= \frac{1}{n-1} + \frac{8 - \rho^2}{4(n-1)^2} + \frac{88 - 9\rho^2 - 9\rho^4}{24(n-1)^3} + \frac{384 - 19\rho^2 + 2\rho^4 - 75\rho^6}{64(n-1)^4} + O(n^{-5})$$

Figure 4.4. Distribution of the sample correlation coefficient r (orange line), and its corresponding Fisher transform Z_r (purple line).
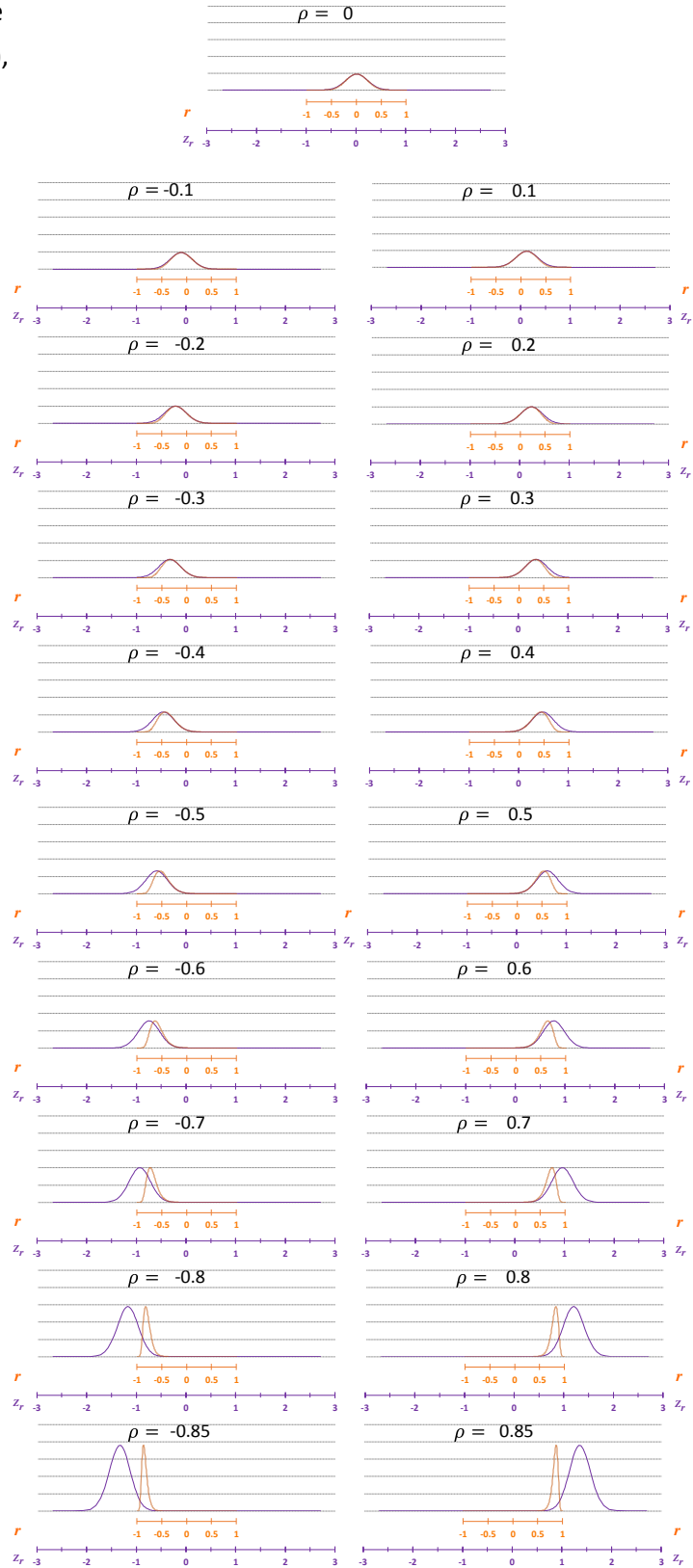
5 Inferential statistics

Statistical inference is often conducted through significance testing and confidence interval construction. Although closely related, significance testing focuses on a single *a priori* hypothesis, usually a null value (e.g. $\rho = 0$). In contrast, a confidence interval can avoid such problems by providing a range of plausible parameter values. The confidence interval reveals both the magnitude and the precision of the estimated effect, whereas the p-value obtained from significance testing confounds these two aspects of the data (Lee 2016).

5.1 Statistical justification

In this section I apply well-established statistical tools for the analysis of correlations and extend them to the analysis of the coheritability coefficient. The heritabilities are treated here as scalars, which may be considered a potential caveat of the method.

The distribution of a random variable multiplied by a scalar creates a scale family distribution, with well-known statistical properties. Thus, the coheritability h_{xy} has a distribution similar to the one of $r_{A_{x,y}}$, but rescaled by $\sqrt{h_x^2 \, h_y^2}$.

(1) It has been demonstrated that at limiting cases (Section 7.4) the phenotypic correlation can equate either the coheritability (if both heritabilities are unity) or the coenvironmentability (if at least one heritability is zero). This fact indicates that the same inferential statistical tools to test correlations can also be used to test the coheritability and the coenvironmentability.

(2) The coheritability is composed of additive genetic correlation multiplied by the factor $\sqrt{h_x^2 \, h_y^2}$ which is the geometric mean of the heritabilities. Although, the heritabilities are random variables, here they are going to be regarded as constants (i.e. scalars). Thus, the coheritability coefficient $h_{xy} = \sqrt{h_x^2 \, h_y^2} \, r_{A_{x,y}}$ can be thought of as the weighed genetic correlation, with a distribution that is a scale family of the original correlation distribution.

The $\sqrt{h_x^2 \, h_x^2}$ factor is expressed as a strictly positive decimal numeral bound by the interval (0 , +1]. This causes the values of $h_{x,y}$ to compare to $r_{A_{x,y}}$ as follows:

Multiplying $\sqrt{h_x^2 \, h_x^2}$ to the genetic correlation $r_{A_{x,y}}$ will cause (a) the modulus (i.e. absolute value) of the product to decrease, but still maintaining the same sign.

  (a) if $-1 \leq r_{A_{x,y}} < 0$ then the value of the coheritability would oscillate in the range
  $r_{A_{x,y}} \leq h_{x,y} < 0$, because multiplying a decimal numeral to a negative $r_{A_{x,y}}$ will cause its

magnitude to move towards zero, making $h_{x,y}$ comparatively higher than $r_{A_{x,y}}$, yet keeping its sign.

(b) If $0 < r_{A_{xy}} \leq 1$ then $0 < h_{xy} \leq r_{A_{xy}}$, because multiplying a positive decimal numeral to a strictly positive $r_{A_{xy}}$ will cause its magnitude to move towards zero thus decreasing it, and maintain its sign.

(3) The form of the $r_{A_{xy}}$ sampling distribution does not change with the factoring $\sqrt{h_x^2 h_y^2}$. It simply becomes a scale family distribution of $r_{A_{xy}}$.

(4) The r-to-Z Fisher transformed of the phenotypic correlation cannot be decomposed into a coheritability term and a coenvironmentability term. However, a naïve and heuristic approach could be assumed in which the proportion of the coheritability or coenvironmentability with respect to the phenotypic correlation in the r-space does not change with the transformation to the Z-space.

5.2 Hypothesis testing when null hypothesis sets the parameters to a zero value

Although the fundamental results and associated use of the sample correlation are described in most introductory textbooks of statistics. The rationale used for the testing of the correlation coefficients (phenotypic, genetic, environmental) $\rho = 0$, is extended, in a heuristic way, to the hypothesis test of the coheritability $H_{x,y} = 0$, and the coenvironmentability $E_{x,y} = 0$. Here I used the term parameter to refer to $\theta = \{\rho_{P_{x,y}}, \rho_{A_{x,y}}, \rho_{E_{x,y}}, H_{x,y}, E_{x,y}\}$.

The sample correlation coefficient r is a point estimator of ρ. The distribution of r when $\rho = 0$ is presented in Section 4.1.1. To test whether or not a linear relationship exists between two traits x and y, a following test statistic is used

$$t_{\alpha,(n-2)} = \frac{r}{\sqrt{\dfrac{1-r^2}{n-2}}}$$

Which can also be rearranged as

$$r = \frac{t_{\alpha,(n-2)}}{\sqrt{n-2+t^2}}$$

(see Samiuddin 1970 for an exact test statistic).

Which is the basis of the critical value method, used in this work.

$$r_{critical} = \frac{t_{\alpha,(n-2)\,critical}}{\sqrt{n-2+t^2}}$$

There is extensive criticism in the literature of testing of parameters hypothesized to be equal to zero (Beaulieu-Prévost 2006, Lee 2016). Simply reporting that a correlation is significant at a given α level just because the p-value for the test $Ho: \rho = 0$ is less than α is generally not sufficient (Looney 2008). The argument that $Ho: \rho = 0$ is the appropriate null hypothesis to test and that using sample sizes that actually yield a desirable level of power (say 80%) for the test can result in confidence intervals that are so wide that they provide very little useful information about the magnitude of the population correlation coefficient.

A better approach is to test null values other than $\rho_o = 0$ (Section 5.3), and then determine the sample size (Section 5.6) so as to achieve a certain level of precision of the estimate of ρ as measured by the width of the resulting confidence interval.

Hypothesis test of population phenotypic correlation

Column 1

hypotheses

$H_o: \rho_{P_{x,y}} = 0$

$H_1: \rho_{P_{x,y}} < 0$

significance level

$\alpha = 0.05$

critical value

$r_{P_{crit}} = \dfrac{t_{crit}}{\sqrt{n - 2 + t_{crit}^2}} = -0.1646$

$n = 101 \quad \alpha = 0.05$

$t_{crit} = -t_{\alpha, n-2} = -1.6604$

test statistic

$r_{P_{x,y}} = 0.45$

test criteria

$if \begin{cases} r_{P_{x,y}} \leq r_{P_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $\quad r_{P_{x,y}} < r_{P_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05 \quad$ significance level

Column 2

hypotheses

$H_o: \rho_{P_{x,y}} = 0$

$H_1: \rho_{P_{x,y}} \neq 0$

significance level

$\alpha = 0.05$

critical value

$r_{P_{crit}} = \dfrac{t_{crit}}{\sqrt{n - 2 + t_{crit}^2}} = \pm 0.1956$

$n = 101 \quad \alpha = 0.05$

$|t_{crit}| \rightarrow \pm t_{1-\frac{\alpha}{2}, n-2} = \pm 1.9842$

test statistic

$r_{P_{x,y}} = 0.45$

test criteria

$if \begin{cases} |r_{P_{x,y}}| \geq r_{P_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $\quad |r_{P_{x,y}}| > r_{P_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05 \quad$ significance level

Column 3

hypotheses

$H_o: \rho_{P_{x,y}} = 0$

$H_1: \rho_{P_{x,y}} > 0$

significance level

$\alpha = 0.05$

critical value

$r_{P_{crit}} = \dfrac{t_{crit}}{\sqrt{n - 2 + t_{crit}^2}} = 0.1646$

$n = 101 \quad \alpha = 0.05$

$t_{crit} = t_{\alpha, n-2} = 1.6604$

test statistic

$r_{P_{x,y}} = 0.45$

test criteria

$if \begin{cases} r_{P_{x,y}} \geq r_{P_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $\quad r_{P_{x,y}} < r_{P_{crit}}$

The test does not rejects the H_o at an
$\alpha = 0.05 \quad$ significance level

Hypothesis test of population genetic correlation

Column 1

hypotheses

$H_o: \rho_{A_{x,y}} = 0$

$H_1: \rho_{A_{x,y}} < 0$

significance level

$\alpha = 0.05$

critical value

$r_{A_{crit}} = \dfrac{t_{crit}}{\sqrt{n-2+t_{crit}^2}} = -0.1646$

$n = 101 \quad \alpha = 0.05$

$t_{crit} = -t_{\alpha,n-2} = -1.6604$

test statistic

$r_{A_{x,y}} = -0.8165$

test criteria

$if \begin{cases} r_{A_{x,y}} \leq r_{A_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

-0.8165   -0.1646

-1   0   0 1
r

test conclusion

Because $\quad r_{A_{x,y}} < r_{A_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05 \quad$ significance level

Column 2

hypotheses

$H_o: \rho_{A_{x,y}} = 0$

$H_1: \rho_{A_{x,y}} \neq 0$

significance level

$\alpha = 0.05$

critical value

$r_{A_{crit}} = \dfrac{t_{crit}}{\sqrt{n-2+t_{crit}^2}} = \pm 0.1956$

$n = 101 \quad \alpha = 0.05$

$|t_{crit}| \to \pm t_{1-\frac{\alpha}{2},n-2} = \pm 1.9842$

test statistic

$r_{A_{x,y}} = -0.8165$

test criteria

$if \begin{cases} |r_{A_{x,y}}| \geq r_{A_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

-0.8165   -0.1956   0.1956

-1   0   0 0 0 1
r

test conclusion

Because $\quad |r_{A_{x,y}}| > r_{A_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05 \quad$ significance level

Column 3

hypotheses

$H_o: \rho_{A_{x,y}} = 0$

$H_1: \rho_{A_{x,y}} > 0$

significance level

$\alpha = 0.05$

critical value

$r_{A_{crit}} = \dfrac{t_{crit}}{\sqrt{n-2+t_{crit}^2}} = 0.1646$

$n = 101 \quad \alpha = 0.05$

$t_{crit} = t_{\alpha,n-2} = 1.6604$

test statistic

$r_{A_{x,y}} = -0.8165$

test criteria

$if \begin{cases} r_{A_{x,y}} \geq r_{A_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

-0.8165   0.1646

-1   0   0 1 0
r

test conclusion

Because $\quad r_{A_{x,y}} < r_{A_{crit}}$

The test does not rejects the H_o at an
$\alpha = 0.05 \quad$ significance level

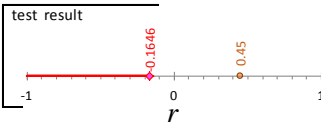## Hypothesis test of population environmental correlation

Column 1

hypotheses

$H_o: \rho_{E_{x,y}} = 0$

$H_1: \rho_{E_{x,y}} < 0$

significance level

$\alpha = 0.05$

critical value

$r_{E_{crit}} = \dfrac{t_{crit}}{\sqrt{n - 2 + t_{crit}^2}} = -0.1646$

$n = 101 \qquad \alpha = 0.05$

$t_{crit} = -t_{\alpha, n-2} = -1.6604$

test statistic

$r_{E_{x,y}} = 0.8686$

test criteria

$if \begin{cases} r_{E_{x,y}} \leq r_{E_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $\quad r_{E_{x,y}} < r_{E_{crit}}$

The test does not reject the H_o at an
$\alpha = 0.05 \qquad$ significance level

Column 2

hypotheses

$H_o: \rho_{E_{x,y}} = 0$

$H_1: \rho_{E_{x,y}} \neq 0$

significance level

$\alpha = 0.05$

critical value

$r_{E_{crit}} = \dfrac{t_{crit}}{\sqrt{n - 2 + t_{crit}^2}} = \pm 0.1956$

$n = 101 \qquad \alpha = 0.05$

$|t_{crit}| \to \pm t_{1-\frac{\alpha}{2}, n-2} = \pm 1.9842$

test statistic

$r_{E_{x,y}} = 0.8686$

test criteria

$if \begin{cases} |r_{E_{x,y}}| \geq r_{E_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $\quad |r_{E_{x,y}}| > r_{E_{crit}}$

The test rejects the H_o at an
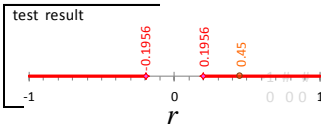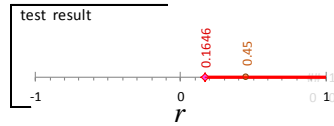$\alpha = 0.05 \qquad$ significance level

Column 3

hypotheses

$H_o: \rho_{E_{x,y}} = 0$

$H_1: \rho_{E_{x,y}} > 0$

significance level

$\alpha = 0.05$

critical value

$r_{E_{crit}} = \dfrac{t_{crit}}{\sqrt{n - 2 + t_{crit}^2}} = 0.1646$

$n = 101 \qquad \alpha = 0.05$

$t_{crit} = t_{\alpha, n-2} = 1.6604$

test statistic

$r_{E_{x,y}} = 0.8686$

test criteria

$if \begin{cases} r_{E_{x,y}} \geq r_{E_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $\quad r_{E_{x,y}} > r_{E_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05 \qquad$ significance level

Hypothesis test of population coheritability

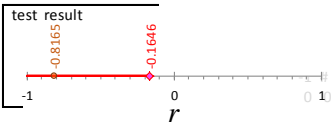### Column 1

hypotheses

$$H_o: H_{x,y} = 0$$

$$H_1: H_{x,y} < 0$$

significance level

$$\alpha = 0.05$$

critical value

$$h_{x,y_{crit}} = \sqrt{h_x^2\, h_y^2}\; r_{A_{x,y_{crit}}} = \frac{\sqrt{h_x^2\, h_y^2}\; t_{crit}}{\sqrt{n-2+t_{crit}^2}} = -0.0403$$

$$n = 101 \qquad \alpha = 0.05$$

$$t_{crit} = \pm t_{\alpha,n-2} = -1.6604$$

test statistic

$$h_{x,y} = -0.2$$

test criteria

$$if \begin{cases} h_{x,y} \leq h_{x,y_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$$

test result

$$h_{x,y}$$

test conclusion

Because $\quad h_{x,y} < h_{x,y_{crit}}$

The test rejects the H$_o$ at an
$\alpha = 0.05 \qquad$ significance level

Column 2

hypotheses

$$H_o: H_{x,y} = 0$$

$$H_1: H_{x,y} \neq 0$$

significance level

$$\alpha = 0.05$$

critical value

$$h_{x,y_{crit}} = \sqrt{h_x^2\, h_y^2}\; r_{A_{x,y_{crit}}} = \frac{\sqrt{h_x^2\, h_y^2}\; t_{crit}}{\sqrt{n-2+t_{crit}^2}} = \pm 0.0479$$

$$n = 101 \qquad \alpha = 0.05$$

$$|t_{crit}| \rightarrow \pm t_{1-\frac{\alpha}{2},n-2} = \pm \quad 1.9842$$

test statistic

$$h_{x,y} = -0.2$$

test criteria

$$if \begin{cases} |h_{x,y}| \geq h_{x,y_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$$

test result

$$h_{x,y}$$

test conclusion

Because $\quad |h_{x,y}| > h_{x,y_{crit}}$

The test rejects the H$_o$ at an
$\alpha = 0.05 \qquad$ significance level

Column 3

hypotheses

$$H_o: H_{x,y} = 0$$

$$H_1: H_{x,y} > 0$$

significance level

$$\alpha = 0.05$$

critical value

$$h_{x,y_{crit}} = \sqrt{h_x^2\, h_y^2}\; r_{A_{x,y_{crit}}} = \frac{\sqrt{h_x^2\, h_y^2}\; t_{crit}}{\sqrt{n-2+t_{crit}^2}} = 0.0403$$

$$n = 101 \qquad \alpha = 0.05$$

$$t_{crit} = t_{\alpha,n-2} = 1.6604$$

test statistic

$$h_{x,y} = -0.2$$

test criteria

$$if \begin{cases} h_{x,y} \geq h_{x,y_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$$

test result

$$h_{x,y}$$

test conclusion

Because $\quad h_{x,y} < h_{x,y_{crit}}$

The test does not rejects the H$_o$ at an
$\alpha = 0.05 \qquad$ significance level

Hypothesis test of population coenvironmentability

hypotheses

$H_o: E_{x,y} = 0$

$H_1: E_{x,y} < 0$

significance level

$\alpha = 0.05$

critical value

$e_{x,y_{crit}} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E_{xy_{crit}}} = \dfrac{\sqrt{(1-h_x^2)(1-h_y^2)}\, t_{crit}}{\sqrt{n-2+t_{crit}^2}}$

$= -0.1232$

$n = 101 \quad \alpha = 0.05$
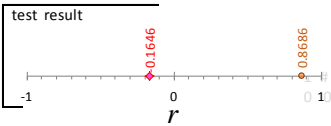
$t_{crit} = -t_{\alpha,n-2} = -1.6604$

test statistic

$e_{x,y} = 0.65$

test criteria

$if \begin{cases} e_{x,y} \le e_{x,y_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $r_{E_{x,y}} < r_{E_{crit}}$

The test does not reject the H_o at an
$\alpha = 0.05$ significance level

---

hypotheses

$H_o: E_{x,y} = 0$

$H_1: E_{x,y} \ne 0$

significance level

$\alpha = 0.05$

critical value

$e_{x,y_{crit}} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E_{xy_{crit}}} = \dfrac{\sqrt{(1-h_x^2)(1-h_y^2)}\, t_{crit}}{\sqrt{n-2+t_{crit}^2}}$

$= \pm 0.1464$

$n = 101 \quad \alpha = 0.05$
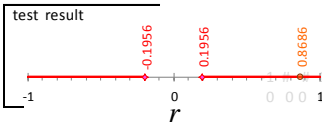
$|t_{crit}| \to \pm t_{1-\frac{\alpha}{2},n-2} = \pm 1.9842$

test statistic

$e_{x,y} = 0.65$

test criteria

$if \begin{cases} |e_{x,y}| \ge e_{x,y_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $|r_{E_{x,y}}| > r_{E_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05$ significance level

---

hypotheses

$H_o: E_{x,y} = 0$

$H_1: E_{x,y} > 0$

significance level

$\alpha = 0.05$

critical value

$e_{x,y_{crit}} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E_{xy_{crit}}} = \dfrac{\sqrt{(1-h_x^2)(1-h_y^2)}\, t_{crit}}{\sqrt{n-2+t_{crit}^2}}$

$= 0.1232$

$n = 101 \quad \alpha = 0.05$
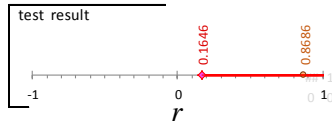
$t_{crit} = t_{\alpha,n-2} = 1.6604$

test statistic

$e_{x,y} = 0.65$

test criteria

$if \begin{cases} e_{x,y} \ge e_{x,y_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $r_{E_{x,y}} > r_{E_{crit}}$
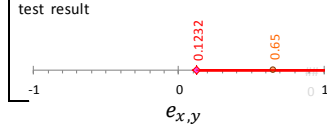
The test rejects the H_o at an
$\alpha = 0.05$ significance level

5.3 Hypothesis testing for a parameter equal to a nonzero value

To test the significance of point estimators of the population parameters $\theta = \{\rho_{P_{x,y}}, \rho_{A_{x,y}}, \rho_{E_{x,y}}, H_{x,y}, E_{x,y}\}$, the hypothesized values used in H_o must satisfy the following relationship:

$$\rho_{P_{x,y}} = \underbrace{\sqrt{h_x^2\, h_y^2}\ \rho_{A_{x,y}}}_{H_{x,y}} + \underbrace{\sqrt{(1 - h_x^2)(1 - h_y^2)}\ \rho_{E_{x,y}}}_{E_{x,y}}$$

Since the sampling distribution of the Pearson's r is not normally distributed, a common practice is to use the Fisher's r-to-Z transformation (Section 4.4).

Hypothesis test of population phenotypic correlation

Column 1

hypotheses
$H_o: \rho_{P_{x,y}} = 0.6$

$H_1: \rho_{P_{x,y}} < 0.6$

significance level
$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_P} = \frac{1}{2} ln\left[\frac{1+(0.45)}{1-(0.45)}\right] = 0.4847$

$Z_{\rho_P} = \frac{1}{2} ln\left[\frac{1+(0.6)}{1-(0.6)}\right] = 0.6931$

$\sigma_{Z_{r_P}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value
$z_{crit} = z_\alpha = -1.645$

test statistic

$z = \frac{z_{r_P} - z_{\rho_P}}{\sigma_{Z_{r_P}}} = \frac{(0.4847)-(0.69315)}{0.1010} = -2.06$

test criteria

$if \begin{cases} z \leq z_{P_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

r

test conclusion

Because $z < z_{P_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05$ significance level

Column 2

hypotheses
$H_o: \rho_{P_{x,y}} = 0.6$

$H_1: \rho_{P_{x,y}} \neq 0.6$

significance level
$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_P} = \frac{1}{2} ln\left[\frac{1+(0.45)}{1-(0.45)}\right] = 0.4847$

$Z_{\rho_P} = \frac{1}{2} ln\left[\frac{1+(0.6)}{1-(0.6)}\right] = 0.6931$

$\sigma_{Z_{r_P}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value
$z_{crit} = \pm z_{1-\frac{\alpha}{2}} = \pm 1.96$

test statistic

$z = \frac{z_{r_P} - z_{\rho_P}}{\sigma_{Z_{r_P}}} = \frac{(0.4847)-(0.69315)}{0.1010} = -2.06$

test criteria

$if \begin{cases} |z| \geq z_{P_{crit}} & \text{then reject the } H_o \\ |z| < z_{crit} & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

r

test conclusion

Because $z < -z_{P_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05$ significance level

Column 3

hypotheses
$H_o: \rho_{P_{x,y}} = 0.6$

$H_1: \rho_{P_{x,y}} > 0.6$

significance level
$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_P} = \frac{1}{2} ln\left[\frac{1+(0.45)}{1-(0.45)}\right] = 0.4847$

$Z_{\rho_P} = \frac{1}{2} ln\left[\frac{1+(0.6)}{1-(0.6)}\right] = 0.6931$

$\sigma_{Z_{r_P}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value
$z_{P_{crit}} = z_{1-\frac{\alpha}{2}} = 1.645$

test statistic

$z = \frac{z_{r_P} - z_{\rho_P}}{\sigma_{Z_{r_P}}} = \frac{(0.4847)-(0.69315)}{0.1010} = -2.06$

test criteria

$if \begin{cases} z \geq z_{P_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

r
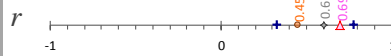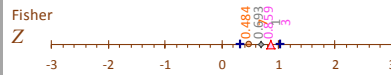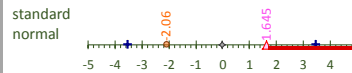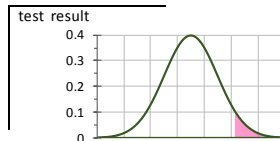
test conclusion

Because $z < z_{P_{crit}}$

The test does not reject the H_o at an
$\alpha = 0.05$ significance level

Hypothesis test of population genetic correlation

Column 1

hypotheses

$H_o: \rho_{A_{x,y}} = -0.7071$

$H_1: \rho_{A_{x,y}} < -0.7071$

significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_A} = \frac{1}{2} ln \left[\frac{1 + (-0.8165)}{1 - (-0.8165)} \right]$ -1.1462

$Z_{\rho_A} = \frac{1}{2} ln \left[\frac{1 + (-0.7071)}{1 - (-0.7071)} \right]$ -0.8814

$\sigma_{Z_{r_A}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value

$z_{A_{crit}} = z_{\alpha} = -1.645$

test statistic

$z = \frac{z_{r_A} - z_{\rho_A}}{\sigma_{Z_{r_A}}} = \frac{(-1.1462) - (-0.8814)}{0.1010} = -2.62$

test criteria

$if \begin{cases} z \leq z_{A_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

r

test conclusion

Because $\quad Z < z_{A_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05$ significance level

Column 2

hypotheses

$H_o: \rho_{A_{x,y}} = -0.7071$

$H_1: \rho_{A_{x,y}} \neq -0.7071$

significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_A} = \frac{1}{2} ln \left[\frac{1 + (-0.8165)}{1 - (-0.8165)} \right]$ -1.1462

$Z_{\rho_A} = \frac{1}{2} ln \left[\frac{1 + (-0.7071)}{1 - (-0.7071)} \right]$ -0.8814

$\sigma_{Z_{r_A}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value

$z_{A_{crit}} = \pm z_{1 - \frac{\alpha}{2}} = \pm 1.96$

test statistic

$z = \frac{z_{r_A} - z_{\rho_A}}{\sigma_{Z_{r_A}}} = \frac{(-1.1462) - (-0.8814)}{0.1010} = -2.62$

test criteria

$if \begin{cases} |z| \geq z_{A_{crit}} & \text{then reject the } H_o \\ |z| < z_{crit} & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

r

test conclusion

Because $\quad z < -z_{A_{crit}}$

The test rejects the H_o at an
$\alpha = 0.05$ significance level

Column 3

hypotheses

$H_o: \rho_{A_{x,y}} = -0.7071$

$H_1: \rho_{A_{x,y}} > -0.7071$

significance level

$\alpha = 0.05$
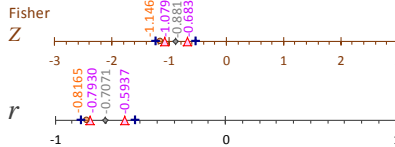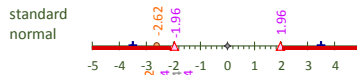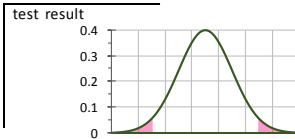
Fisher r-to-Z transformation

$Z_{r_A} = \frac{1}{2} ln \left[\frac{1 + (-0.8165)}{1 - (-0.8165)} \right]$ -1.1462

$Z_{\rho_A} = \frac{1}{2} ln \left[\frac{1 + (-0.7071)}{1 - (-0.7071)} \right]$ -0.8814

$\sigma_{Z_{r_A}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value

$z_{A_{crit}} = z_{1 - \frac{\alpha}{2}} = 1.645$

test statistic

$z = \frac{z_{r_A} - z_{\rho_A}}{\sigma_{Z_{r_A}}} = \frac{(-1.1462) - (-0.8814)}{0.1010} = -2.62$

test criteria

$if \begin{cases} z \geq z_{A_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

r

test conclusion

Because $\quad Z < z_{A_{crit}}$

The test does not reject the H_o at an
$\alpha = 0.05$ significance level

Column 1

hypotheses

$H_o: \rho_{A_{x,y}} = 0.8250$

$H_1: \rho_{A_{x,y}} < 0.8250$

significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

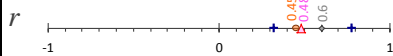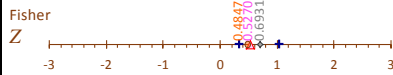$Z_{r_E} = \frac{1}{2} ln\left[\frac{1+(0.8686)}{1-(0.8686)}\right] = 1.3273$

$Z_{\rho_E} = \frac{1}{2} ln\left[\frac{1+(0.8250)}{1-(0.8250)}\right] = 1.1721$

$\sigma_{Z_{r_E}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value

$z_{crit} = z_\alpha = -1.645$

test statistic

$z = \frac{z_{r_E} - z_{\rho_E}}{\sigma_{Z_{r_E}}} = \frac{(-1.1462) - (-0.8814)}{0.1010} = 1.54$

test criteria

$if \begin{cases} z \leq z_{E_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $z > z_{r_E\ crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Column 2

hypotheses

$H_o: \rho_{A_{x,y}} = 0.8250$

$H_1: \rho_{A_{x,y}} \neq 0.8250$

significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

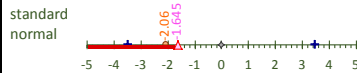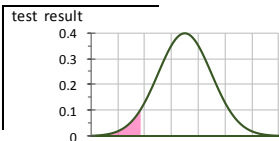$Z_{r_E} = \frac{1}{2} ln\left[\frac{1+(0.8686)}{1-(0.8686)}\right] = 1.3273$

$Z_{\rho_E} = \frac{1}{2} ln\left[\frac{1+(0.8250)}{1-(0.8250)}\right] = 1.1721$

$\sigma_{Z_{r_E}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value

$z_{crit} = \pm z_{1-\frac{\alpha}{2}} = \pm 1.96$

test statistic

$z = \frac{z_{r_E} - z_{\rho_E}}{\sigma_{Z_{r_E}}} = \frac{(-1.1462) - (-0.8814)}{0.1010} = 1.54$

test criteria

$if \begin{cases} |z| \geq z_{E_{crit}} & \text{then reject the } H_o \\ |z| < z_{crit} & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $-z_{r_E\ crit} < z < +z_{r_E\ crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Column 3

hypotheses

$H_o: \rho_{A_{x,y}} = 0.8250$

$H_1: \rho_{A_{x,y}} > 0.8250$

significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_E} = \frac{1}{2} ln\left[\frac{1+(0.8686)}{1-(0.8686)}\right] = 1.3273$
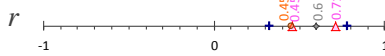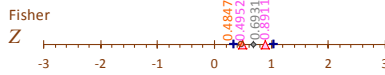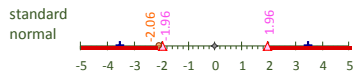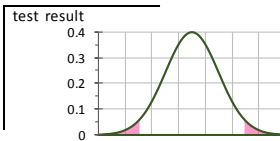
$Z_{\rho_E} = \frac{1}{2} ln\left[\frac{1+(0.8250)}{1-(0.8250)}\right] = 1.1721$

$\sigma_{Z_{r_E}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value

$z_{crit} = z_{1-\frac{\alpha}{2}} = 1.645$

test statistic

$z = \frac{z_{r_E} - z_{\rho_E}}{\sigma_{Z_{r_E}}} = \frac{(1.3273) - (1.17214)}{0.1010} = 1.54$

test criteria

$if \begin{cases} z \geq z_{E_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

test conclusion

Because $z > z_{r_E\ crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Hypothesis test of population environmental correlation

Column 1

hypotheses $H_o: \rho_{A_{x,y}} = 0.8250$

$H_1: \rho_{A_{x,y}} < 0.8250$

significance level $\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_E} = \frac{1}{2} ln\left[\frac{1 + (0.8686)}{1 - (0.8686)}\right] = 1.3273$

$Z_{\rho_E} = \frac{1}{2} ln\left[\frac{1 + (0.8250)}{1 - (0.8250)}\right] = 1.1721$

$\sigma_{Z_{r_E}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value $z_{crit} = z_\alpha = -1.645$

test statistic

$z = \frac{z_{r_E} - z_{\rho_E}}{\sigma_{Z_{r_E}}} = \frac{(-1.1462) - (-0.8814)}{0.1010} = 1.54$

test criteria

$if \begin{cases} z \leq z_{E_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

-5 -4 -3 -2 -1 0 1 2 3 4 5
−1.645 1.54

Fisher Z

-3 -2 -1 0 1 2 3
1.006 1.1721 1.3273

r

-1 0 1
0.7641 0.8250 0.8686

test conclusion

Because $z > z_{r_E crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Column 2

hypotheses $H_o: \rho_{A_{x,y}} = 0.8250$

$H_1: \rho_{A_{x,y}} \neq 0.8250$

significance level $\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_E} = \frac{1}{2} ln\left[\frac{1 + (0.8686)}{1 - (0.8686)}\right] = 1.3273$

$Z_{\rho_E} = \frac{1}{2} ln\left[\frac{1 + (0.8250)}{1 - (0.8250)}\right] = 1.1721$

$\sigma_{Z_{r_E}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value $z_{crit} = \pm z_{1-\frac{\alpha}{2}} = \pm 1.96$

test statistic

$z = \frac{z_{r_E} - z_{\rho_E}}{\sigma_{Z_{r_E}}} = \frac{(-1.1462) - (-0.8814)}{0.1010} = 1.54$

test criteria

$if \begin{cases} |z| \geq z_{E_{crit}} & \text{then reject the } H_o \\ |z| < z_{crit} & \text{do not reject } H_o \end{cases}$

test result

standard normal

-5 -4 -3 -2 -1 0 1 2 3 4 5
−1.96 1.54 1.96

Fisher Z

-3 -2 -1 0 1 2 3
0.9742 1.3273 1.1721 1.3701

r

-1 0 1
0.7505 0.8250 0.8686 0.8787

test conclusion

Because $-z_{r_E crit} < z < +z_{r_E crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Column 3

hypotheses $H_o: \rho_{A_{x,y}} = 0.8250$

$H_1: \rho_{A_{x,y}} > 0.8250$

significance level $\alpha = 0.05$

Fisher r-to-Z transformation

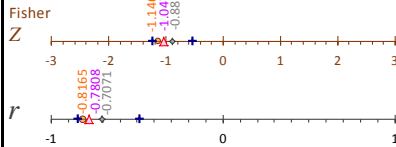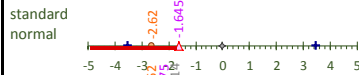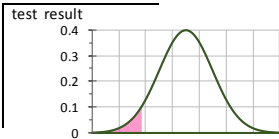$Z_{r_E} = \frac{1}{2} ln\left[\frac{1 + (0.8686)}{1 - (0.8686)}\right] = 1.3273$

$Z_{\rho_E} = \frac{1}{2} ln\left[\frac{1 + (0.8250)}{1 - (0.8250)}\right] = 1.1721$

$\sigma_{Z_{r_E}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$

critical value $z_{crit} = z_{1-\frac{\alpha}{2}} = 1.645$

test statistic

$z = \frac{z_{r_E} - z_{\rho_E}}{\sigma_{Z_{r_E}}} = \frac{(1.3273) - (1.17214)}{0.1010} = 1.54$

test criteria

$if \begin{cases} z \geq z_{E_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

-5 -4 -3 -2 -1 0 1 2 3 4 5
1.54 1.645

Fisher Z

-3 -2 -1 0 1 2 3
1.1721 1.1721 1.3383

r

-1 0 1
0.8250 0.8686 0.8713

test conclusion

Because $z > z_{r_E crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Hypothesis test of population coenvironmentability

Column 1

hypotheses $H_o: E_{x,y} = 0.7$

$H_1: E_{x,y} < 0.7$

significance level $\alpha = 0.05$

Fisher r-to-Z transformation

$$\widehat{Z_{e_{x,y}}} = Z_{r_P} - \widehat{Z_{h_{x,y}}} = (0.4847) - (0.2154) = 0.7001$$

$$Z_{E_{x,y}} = \frac{1}{2} ln\left[\frac{1 + (0.7)}{1 - (0.7)}\right] = 0.8673$$

$$\sigma_{\widehat{Z_{e_{x,y}}}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$$

critical value $z_{e\;crit} = z_\alpha = -1.645$

test statistic

$$z = \frac{\widehat{Z_{e_{x,y}}} - Z_{E_{x,y}}}{\sigma_{\widehat{Z_{e_{x,y}}}}} = \frac{(0.7001) - (0.8673)}{0.1010} = -1.65$$

test criteria

$if \begin{cases} z \leq z_{e\;crit} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

$e_{x,y}$

test conclusion

Because $z > z_{e\;crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Column 2
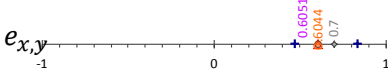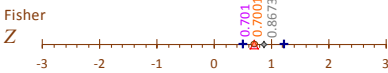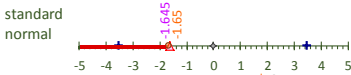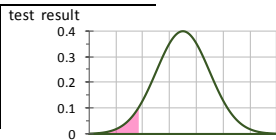
hypotheses $H_o: E_{x,y} = 0.7$

$H_1: E_{x,y} \neq 0.7$

significance level $\alpha = 0.05$

Fisher r-to-Z transformation

$$\widehat{Z_{e_{x,y}}} = Z_{r_P} - \widehat{Z_{h_{x,y}}} = (0.4847) - (0.2154) = 0.7001$$

$$Z_{E_{x,y}} = \frac{1}{2} ln\left[\frac{1 + (0.7)}{1 - (0.7)}\right] = 0.8673$$

$$\sigma_{\widehat{Z_{e_{x,y}}}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$$

critical value $z_{e\;crit} = \pm z_{1-\frac{\alpha}{2}} = \pm 1.96$

test statistic

$$z = \frac{\widehat{Z_{e_{x,y}}} - Z_{E_{x,y}}}{\sigma_{\widehat{Z_{e_{x,y}}}}} = \frac{(0.7001) - (0.8673)}{0.1010} = -1.65$$

test criteria

$if \begin{cases} |z| \geq z_{e_{crit}} & \text{then reject the } H_o \\ |z| < z_{h_{crit}} & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

$e_{x,y}$
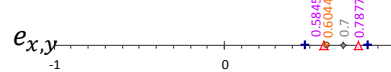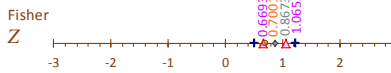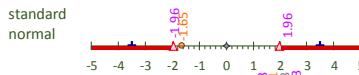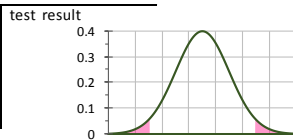
test conclusion

Because $-z_{e\;crit} < z < +z_{e\;crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

Column 3

hypotheses $H_o: E_{x,y} = 0.7$

$H_1: E_{x,y} > 0.7$

significance level $\alpha = 0.05$

Fisher r-to-Z transformation

$$\widehat{Z_{e_{x,y}}} = Z_{r_P} - \widehat{Z_{h_{x,y}}} = (0.4847) - (0.2154) = 0.7001$$

$$Z_{H_{x,y}} = \frac{1}{2} ln\left[\frac{1 + (0.7)}{1 - (0.7)}\right] = 0.8673$$

$$\sigma_{\widehat{Z_{e_{x,y}}}} \approx \sqrt{\frac{1}{n-3}} = 0.1010$$

critical value $z_{e\;crit} = z_{1-\frac{\alpha}{2}} = 1.645$

test statistic

$$z = \frac{\widehat{Z_{e_{x,y}}} - Z_{E_{x,y}}}{\sigma_{\widehat{Z_{e_{x,y}}}}} = \frac{(0.7001) - (0.8673)}{0.1010} = -1.65$$

test criteria

$if \begin{cases} z \geq z_{e_{crit}} & \text{then reject the } H_o \\ otherwise & \text{do not reject } H_o \end{cases}$

test result

standard normal

Fisher Z

$e_{x,y}$
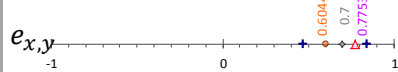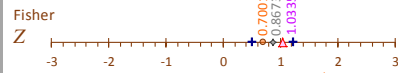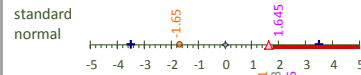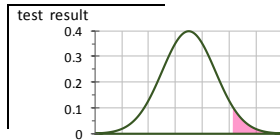
test conclusion

Because $z > z_{e\;crit}$

The test does not reject the H_o at an $\alpha = 0.05$ significance level

5.4 Power of the hypothesis test

Power (sensitivity) is defined as the chance of appropriately rejecting the H_0 if the data are drawn from the alternative hypothesis H_1. It is calculated from the area of H_1 in the points set under the Ho distribution as the critical values.

Here the classical approach for determining the power of the test is presented for the case where the null hypothesis states that the parameter is has a nonzero value.

The method to calculate the power of the test for the coheritability is based on the Fisher's Z transformation. Since there is no way to analytically determine the Z transform of the heritability and coenvironmentability given the value of the phenotypic correlation, the approach taken here was to determine the proportion of the coheritability in reference to the phenotypic correlation (i.e. $\frac{h_{x,y}}{r_{P_{x,y}}}$). The assumption is that the proportion is retained even when the phenotypic correlation has been transformed to Z_{r_P} (which is a very demanding assumption). Multiplying the calculated proportion times the Z_{r_P} will yield a product " $Z_{h_{x,y}}$ " which is assumed to be the coheritability in the Z-space.

This method is certainly not robust enough, and rather indicates that further work is needed in this topic.

Hypothesis test of population phenotypic correlation

Column 1

Hypotheses

$H_0: \rho_P = -0.5$

$H_1: \rho_P < -0.5$

This is a single left-tailed test

Significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_P} = \ln\left[\dfrac{1+(\quad -0.3183\quad)}{1-(\quad -0.3183\quad)}\right] = -0.330$

$Z_{\rho_P} = \ln\left[\dfrac{1+(\quad -0.5\quad)}{1-(\quad -0.5\quad)}\right] = -0.549$

Standard deviation $\quad \sigma_{Zr_P} = 0.101$

Critical Value

$P(z < z_{CRIT}) = \alpha = 0.05 \qquad z_{CRIT} = -1.645$

Test Statistic

$z = \dfrac{Z_{r_P} - Z_{\rho_P}}{\sigma_{Zr_P}} = \dfrac{(\ -0.330\ ) - (\ -0.549\ )}{0.101} = 2.173$

Test Criterion

if $\begin{cases} z \le z_{crit} & \text{then reject the } H_0 \\ z > z_{crit} & \text{do not reject } H_0 \end{cases}$

Test Result

Standard normal score z $\quad$ -1.645 $\quad$ 0 $\quad$ 2.173

Fisher $\mathbb{Z}$ $\quad$ -0.715 $\quad$ -0.549 $\quad$ -0.330

Sample Correlation coefficient $\mathbf{r}$ $\quad$ **-0.614** $\quad$ **-0.50** $\quad$ **-0.318**

Test Conclusion

Because $\quad z > z_{CRIT}$

The test does not reject the H_0 at an $\alpha = 0.05$ significance level

Column 2

Hypotheses

$H_0: \rho_P = -0.5$

$H_1: \rho_P \ne -0.5$

Significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_P} = \ln\left[\dfrac{1+(\quad -0.3183\quad)}{1-(\quad -0.3183\quad)}\right] \quad -0.330$

$Z_{\rho_P} = \ln\left[\dfrac{1+(\quad -0.5\quad)}{1-(\quad -0.5\quad)}\right] \quad -0.549$

Standard deviation $\quad \sigma_{Zr_P} \ 0.101$

Critical Value

$P(|z| > z_{CRIT}) = \alpha = 0.05 \qquad z_{CRIT} = \pm 1.96$

Test Statistic

$z = \dfrac{Z_{r_P} - Z_{\rho_P}}{\sigma_{Zr_P}} = \dfrac{(\ -0.330\ ) - (\ -0.549\ )}{0.101} = 2.173$

Test Criterion

if $\begin{cases} |z| \ge z_{crit} & \text{then reject the } H_0 \\ |z| < z_{crit} & \text{do not reject } H_0 \end{cases}$

Test Result

Standard normal score z $\quad$ -1.96 $\quad$ 0 $\quad$ 1.96 $\quad$ 2.173

Fisher $\mathbb{Z}$ $\quad$ -0.747 $\quad$ -0.549 $\quad$ -0.351 $\quad$ -0.33

Sample Correlation correlation $\mathbf{r}$ $\quad$ **-0.614** $\quad$ **-0.50** $\quad$ **-0.338** $\quad$ **-0.318**

Test Conclusion

Because $\quad z > z_{CRIT}$

The test rejects the H_0 at an $\alpha = 0.05$ significance level

Column 3

Hypotheses

$H_0: \rho_P = -0.5$

$H_1: \rho_P > -0.5$

Significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{r_P} = \ln\left[\dfrac{1+(\quad -0.3183\quad)}{1-(\quad -0.3183\quad)}\right] = -0.330$

$Z_{\rho_P} = \ln\left[\dfrac{1+(\quad -0.5\quad)}{1-(\quad -0.5\quad)}\right] = -0.549$

Standard deviation $\quad \sigma_{Zr_P} = 0.101$

Critical Value

$P(z < z_{CRIT}) = \alpha = 0.05 \qquad z_{CRIT} = 1.645$

Test Statistic

$z = \dfrac{Z_{r_P} - Z_{\rho_P}}{\sigma_{Zr_P}} = \dfrac{(\ -0.330\ ) - (\ -0.549\ )}{0.101} = 2.173$

Test Criterion

if $\begin{cases} z \ge z_{crit} & \text{then reject the } H_0 \\ z < z_{crit} & \text{do not reject } H_0 \end{cases}$

Test Result

Standard normal score z $\quad$ 0 $\quad$ 1.645 $\quad$ 2.173

Fisher $\mathbb{Z}$ $\quad$ -0.549 $\quad$ -0.383 $\quad$ -0.330

Sample Correlation coefficient $\mathbf{r}$ $\quad$ **-0.50** $\quad$ **-0.365** $\quad$ **-0.318**

Test Conclusion

Because $\quad z > z_{CRIT}$

The test rejects the H_0 at an $\alpha = 0.05$ significance level

---

Power $1 - \beta$

$r_{P_{x,y}}$

Power $1 - \beta$

$r_{P_{x,y}}$

Power $1 - \beta$

$r_{P_{x,y}}$

Hypothesis test of population genetic correlation

Column 1
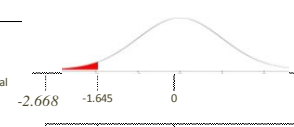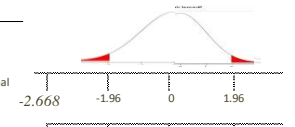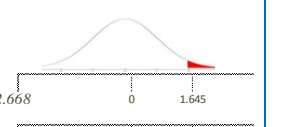
Hypotheses

$$H_0: \rho_A = 0.6$$

$$H_1: \rho_A < 0.6$$

This is a single left-tailed test

Significance level

$$\alpha = 0.05$$

Fisher r-to-Z transformation

$$Z_{r_A} = \ln\left[\frac{1+(0.4)}{1-(0.4)}\right] = 0.424$$

$$Z_{\rho_A} = \ln\left[\frac{1+(0.6)}{1-(0.6)}\right] = 0.693$$

Standard deviation $\sigma_{Zr_P} = 0.101$

Critical Value

$$P(z < z_{CRIT}) = \alpha = 0.05 \qquad z_{CRIT} = -1.645$$

Test Statistic

$$z = \frac{Z_{r_A} - Z_{\rho_A}}{\sigma_{Zr_A}} = \frac{(-0.330)-(-0.549)}{0.101} = -2.668$$

Test Criterion

if
- $z \leq z_{crit}$ then reject the H_0
- $z > z_{crit}$ do not reject H_0

Test Result

Standard normal score z : -2.668, -1.645, 0

Fisher Z : 0.424, 0.527, 0.693

Sample Correlation coefficient r : **0.4**, **0.483**, **0.60**

Test Conclusion

Because $z < z_{CRIT}$
The test reject the H_0 at an
$\alpha = 0.05$ significance level

Column 2

Hypotheses

$$H_0: \rho_A = 0.6$$

$$H_1: \rho_A \neq 0.6$$

Significance level

$$\alpha = 0.05$$

Fisher r-to-Z transformation

$$Z_{r_A} = \ln\left[\frac{1+(0.4)}{1-(0.4)}\right] \quad 0.424$$

$$Z_{\rho_A} = \ln\left[\frac{1+(0.6)}{1-(0.6)}\right] \quad 0.693$$

Standard deviation σ_{Zr_P} 0.101

Critical Value

$$P(|z| > z_{CRIT}) = \alpha = 0.05 \qquad z_{CRIT} = \pm 1.96$$

Test Statistic

$$z = \frac{Z_{r_A} - Z_{\rho_A}}{\sigma_{Zr_A}} = \frac{(-0.330)-(-0.549)}{0.101} = -2.668$$

Test Criterion

if
- $|z| \geq z_{crit}$ then reject the H_0
- $|z| < z_{crit}$ do not reject H_0

Test Result

Standard normal score z : -2.668, -1.96, 0, 1.96

Fisher Z : 0.424, 0.495, 0.693, 0.891

Sample Correlation correlation r : **0.4**, **0.458**, **0.60**, **0.712**

Test Conclusion

Because $z < z_{CRIT}$
The test rejects the H_0 at an
$\alpha = 0.05$ significance level

Column 3

Hypotheses

$$H_0: \rho_A = 0.6$$

$$H_1: \rho_A > 0.6$$

Significance level

$$\alpha = 0.05$$

Fisher r-to-Z transformation

$$Z_{r_A} = \ln\left[\frac{1+(0.4)}{1-(0.4)}\right] = 0.424$$

$$Z_{\rho_A} = \ln\left[\frac{1+(0.6)}{1-(0.6)}\right] = 0.693$$

Standard deviation $\sigma_{Zr_P} = 0.101$

Critical Value

$$P(z < z_{CRIT}) = \alpha = 0.05 \qquad z_{CRIT} = 1.645$$

Test Statistic

$$z = \frac{Z_{r_A} - Z_{\rho_A}}{\sigma_{Zr_A}} = \frac{(-0.330)-(-0.549)}{0.101} = -2.668$$

Test Criterion

if
- $z \geq z_{crit}$ then reject the H_0
- $z < z_{crit}$ do not reject H_0

Test Result

Standard normal score z : -2.668, 0, 1.645

Fisher Z : 0.424, 0.693, 0.859

Sample Correlation coefficient r : **0.4**, **0.60**, **0.696**

Test Conclusion

Because $z < z_{CRIT}$
The test does not reject the H_0 at an
$\alpha = 0.05$ significance level

Power $1 - \beta$

$r_{A_{x,y}}$

Power $1 - \beta$

$r_{A_{x,y}}$

Power $1 - \beta$

$r_{A_{x,y}}$

Hypothesis test of population coheritability

Column 1

Hypotheses

$H_0 : H_{xy} = 0.25$

$H_1 : H_{xy} < 0.25$

This is a single left-tailed test

Significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{hxy} = \dfrac{hxy}{rP}\,\text{arctanh}(rP) = 0.160$

$Z_{Hxy} = ln\left[\dfrac{1+(\ \ 0.25\ \ )}{1-(\ \ 0.25\ \ )}\right] = 0.255$

Standard deviation $\sigma_{ZhXJ} = 0.101$

Critical Value

$P(z < z_{CRIT}) = \alpha = 0.05$ $z_{CRIT} = -1.645$

Test Statistic

$z = \dfrac{Z_{hxy} - Z_{Hxy}}{\sigma_{Zhxy}} = \dfrac{(\ 0.160\ ) - (\ 0.255\ )}{0.101} = -0.940$

Test Criterion

$if \begin{cases} z \le z_{crit} & \text{then reject the } H_0 \\ z > z_{crit} & \text{do not reject } H_0 \end{cases}$

Test Result

Standard normal score z

-1.645 -0.940 0

Fisher $\mathbb{Z}$ 0.089 0.16 0.255

Sample Correlation coefficient Γ 0.089 0.159 0.25

Test Conclusion

Because $z < z_{CRIT}$
The test reject the H_0 at an
$\alpha = 0.05$ significance level

Column 2

Hypotheses

$H_0 : H_{xy} = 0.25$

$H_1 : H_{xy} \neq 0.25$

Significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{hxy} = \dfrac{hxy}{rP}\,\text{arctanh}(rP) = 0.160$

$Z_{Hxy} = ln\left[\dfrac{1+(\ \ 0.25\ \ )}{1-(\ \ 0.25\ \ )}\right] = 0.255$

Standard deviation σ_{hxy} 0.101

Critical Value

$P(|z| > z_{CRIT}) = \alpha = 0.05$ $z_{CRIT} = \pm 1.96$

Test Statistic

$z = \dfrac{Z_{rp} - Z_{\rho P}}{\sigma_{Zrp}} = \dfrac{(\ 0.160\ ) - (\ 0.255\ )}{0.101} = -0.940$

Test Criterion

$if \begin{cases} |z| \ge z_{crit} & \text{then reject the } H_0 \\ |z| < z_{crit} & \text{do not reject } H_0 \end{cases}$

Test Result

Standard normal score z

-1.96 -0.940 0 1.96

Fisher $\mathbb{Z}$ 0.057 0.16 0.255 0.453

Sample Correlation correlation Γ 0.057 0.159 0.25 0.425

Test Conclusion

Because $z < z_{CRIT}$
The test rejects the H_0 at an
$\alpha = 0.05$ significance level

Column 3

Hypotheses

$H_0 : H_{xy} = 0.25$

$H_1 : H_{xy} > 0.25$

Significance level

$\alpha = 0.05$

Fisher r-to-Z transformation

$Z_{hxy} = \dfrac{hxy}{rP}\,\text{arctanh}(rP) = 0.160$

$Z_{Hxy} = ln\left[\dfrac{1+(\ \ 0.25\ \ )}{1-(\ \ 0.25\ \ )}\right] = 0.255$

Standard deviation $\sigma_{hxy} = 0.101$

Critical Value

$P(z < z_{CRIT}) = \alpha = 0.05$ $z_{CRIT} = 1.645$

Test Statistic

$z = \dfrac{Z_{rp} - Z_{\rho P}}{\sigma_{Zrp}} = \dfrac{(\ 0.160\ ) - (\ 0.255\ )}{0.101} = -0.940$

Test Criterion

$if \begin{cases} z \ge z_{crit} & \text{then reject the } H_0 \\ z < z_{crit} & \text{do not reject } H_0 \end{cases}$

Test Result

Standard normal score z

-0.940 0 1.645

Fisher $\mathbb{Z}$ 0.16 0.255 0.422

Sample Correlation coefficient Γ 0.159 0.25 0.398

Test Conclusion

Because $z < z_{CRIT}$
The test does not reject the H_0 at an
$\alpha = 0.05$ significance level

Power $1 - \beta$

Power $1 - \beta$

Power $1 - \beta$

5.5 Confidence interval of $r_{P_{xy}}$, h_{xy} and e_{xy}

The confidence interval for a single correlation ($\rho_\blacksquare$: phenotypic ρ_P , genetic ρ_A, environmental ρ_E) is often obtained using Fisher's r to Z transformation because the sampling distribution of r displays a positive (for $r < 0$) and negative ($r > 0$) skew. To do this, one first forms confidence limits for $Z_{\rho_\blacksquare} = \operatorname{atanh}(r) = \frac{1}{2}\ln\left[\frac{1+\rho_\blacksquare}{1-\rho_\blacksquare}\right]$ (Section 4.4) and then back transform the resultant limits $r = \tanh(Z_r) = \frac{e^{2Z_r}-1}{e^{2Z_r}+1}$ to obtain a confidence interval for $\rho_\blacksquare$.

The Z_r is the Fisher transform of ρ, whose confidence interval are calculated as follows:

the lower bound $Z_L = Z_r - z_{1-\frac{\alpha}{2}}\sqrt{\sigma_{Z_r}^2}$, and

the upper bound $Z_U = Z_r + z_{1-\frac{\alpha}{2}}\sqrt{\sigma_{Z_r}^2}$

Where α is the significance level, $z_{1-\frac{\alpha}{2}}$ is the $1-\frac{\alpha}{2}$ quantile of the standard normal distribution

$$z_{1-\frac{\alpha}{2}} = \begin{cases} 1.645 & for\ \alpha = 90\%\ CI \\ 1.96 & for\ \ \alpha = 95\%\ CI \\ 2.57 & for\ \alpha = 99\%\ CI \end{cases}$$

and $\sigma_{Z_r}^2 = \frac{1}{n-3}$ is the (approximate) variance of the Z_r distribution, which depends only in the sample size n.

It is assumed that the variance of the Fisher transform can be adequately approximated by this value. Fouladi and Steiger (2008) show that although a better approximation to the variance of the Fisher transform $(n-3)^{-1}$ can be obtained, the use of these values or even exact value for the variance of the Fisher transform does not directly translate into statistics with improved size or coverage probabilities with respect to tests or confidence intervals on single correlations.

A worked example follows accompanied by Figure 5.5-1. Another example, in a more succinct presentation is given and represented graphically in Figure 5.5-2.

STEP 0. Data

	EXAMPLE
The following be parameter estimators must be obtained from the sample	Let the following data obtained from a quantitative genetics experiment

Sample size $\quad n = \quad 100$

Phenotypic correlation of traits x and y $\quad r_{P_{x,y}} \quad 0.34$

Additive genetic correlation of traits x and y $\quad r_{A_{x,y}} = \quad -0.4131$

Environmental correlation of traits x and y $\quad r_{E_{x,y}} = \quad 0.8451$

Narrow-sense heritability of trait x $\quad h_x^2 = \quad 0.5 \qquad h_{x,y} = -0.16$

Narrow-sense heritability of trait y $\quad h_y^2 = \quad 0.3 \qquad e_{x,y} = 0.50$

STEP 1. Fisher r-to-Z transformation

Perform the Fisher r-to-Z transformation of the phenotypic $r_{P_{x,y}}$ and genetic $r_{A_{x,y}}$ correlations.

Phenotypic
$$Z_{r_P} = 0.5\, ln\left(\frac{1 + r_{P_{x,y}}}{1 - r_{P_{x,y}}}\right)$$

Genetic
$$Z_{r_A} = 0.5\, ln\left(\frac{1 + r_{A_{x,y}}}{1 - r_{A_{x,y}}}\right)$$

Phenotypic
$$Z_{r_P} = 0.5\, ln\left(\frac{1 + 0.34}{1 - 0.34}\right) = 0.3541$$

Genetic
$$Z_{r_A} = 0.5\, ln\left(\frac{1 + (-0.4131)}{1 - (-0.4131)}\right) = -0.4393$$

STEP 2. Determination of upper and lower bounds for a given α level

for a two-tailed confidence interval the the standard normal z score is given for a fiven significance level α.

$$\underbrace{\left[Z_r - \left(z_{1-\frac{\alpha}{2}}\right)\sqrt{\frac{1}{N-3}} \right]}_{\substack{Z_{r\_L} \\ lower\ bound}} < Z_r < \underbrace{\left[Z_r - \left(z_{1-\frac{\alpha}{2}}\right)\sqrt{\frac{1}{N-3}} \right]}_{\substack{Z_{r\_U} \\ upper\ bound}}$$

$$z_{1-\frac{\alpha}{2}} = \begin{cases} 1.960 & for\ \alpha = 0.05,\ z_{1-\frac{0.95}{2}} \\ \quad\vdots \\ 2.576 & for\ \alpha = 0.01,\ z_{1-\frac{0.99}{2}} \end{cases}$$

for a two-tailed 95% confidence interval we obtained the following bounds:

Phenotypic
$$0.3541 - 1.96\sqrt{\frac{1}{100-3}} < Z_{r_P} < 0.3541 + 1.96\sqrt{\frac{1}{100-3}}$$

$$\underbrace{0.1551}_{Z_{r_{P\_L}}} < Z_{r_P} < \underbrace{0.5531}_{Z_{r_{P\_U}}}$$

Genetic
$$-0.4393 - 1.96\sqrt{\frac{1}{100-3}} < Z_{r_A} < -0.4393 + 1.96\sqrt{\frac{1}{100-3}}$$

$$\underbrace{-0.6384}_{Z_{r_{A\_L}}} < Z_{r_A} < \underbrace{-0.2403}_{Z_{r_{A\_U}}}$$

Use the following relationship to transform Z_r back into correlations in r

$$\underbrace{\frac{e^{2\,Z_{r\_P\_L}}-1}{e^{2\,Z_{r\_L}}+1}}_{r_{\blacksquare\_L}} < \rho < \underbrace{\frac{e^{2\,Z_{r\_U}}-1}{e^{2\,Z_{r\_U}}+1}}_{r_{\blacksquare\_U}}$$

Phenotypic

$$\frac{e^{2\,(0.1551)}-1}{e^{2\,(0.1551)}+1} < \rho_P < \frac{e^{2\,(0.5531)}-1}{e^{2\,(0.5531)}+1}$$

$$\underbrace{0.1539}_{r_{P\_L}} < \rho_P < \underbrace{0.5028}_{r_{P\_U}}$$

Genetic

$$\frac{e^{2\,(-0.6384)}-1}{e^{2\,(-0.6384)}+1} < \rho_A < \frac{e^{2\,(-0.2403)}-1}{e^{2\,(-0.2403)}+1}$$

$$\underbrace{-0.5638}_{r_{A\_L}} < \rho_A < \underbrace{-0.2358}_{r_{A\_U}}$$

Multiply the confidence interval of the genetic correlation by the product of the square root of the heritabilities

$$\underbrace{\sqrt{h_x^2 \cdot h_y^2}\, r_{A\_L}}_{h_{x,y\_L}} < \underbrace{\sqrt{h_x^2 \cdot h_y^2}\, \rho_A}_{H_{x,y}} < \underbrace{\sqrt{h_x^2 \cdot h_y^2}\, r_{A\_U}}_{h_{x,y\_U}}$$

$$\sqrt{0.5 x 0.3}\,(-0.5638) < \sqrt{h_x^2 \cdot h_y^2}\, \rho_A < \sqrt{0.5 x 0.3}\,(-0.2358)$$

$$\underbrace{-0.2183}_{h_{x,y\_L}} < H_{x,y} < \underbrace{-0.0913}_{h_{x,y\_U}}$$

The lower bound r_{E_L} equals the lower bound of phenotypic correlation minus the lower bound of the coheritability.

The upper bound r_{E_U} equals the upper bound of the phenotypic correlation minus the upper bound of the coheritability.

$$\underbrace{\left(r_{P_L} - h_{x,y\_L}\right)}_{r_{E_L}} < E_{x,y} < \underbrace{\left(r_{P_U} - h_{x,y\_U}\right)}_{r_{E_U}}$$

$$0.1539 - (-0.2138) < E_{x,y} < 0.5028 - (-0.0913)$$

$$0.4059 < E_{x,y} < 0.5941$$

To summarize, the confidence interval for the parameters (sample size n=100) are

$$\underbrace{0.1539}_{r_{P\_L}} < \rho_P < \underbrace{0.5028}_{r_{P\_U}}$$

$$\underbrace{-0.2183}_{h_{x,y\_L}} < H_{x,y} < \underbrace{-0.0913}_{h_{x,y\_U}}$$

$$0.4059 < E_{x,y} < 0.5941$$
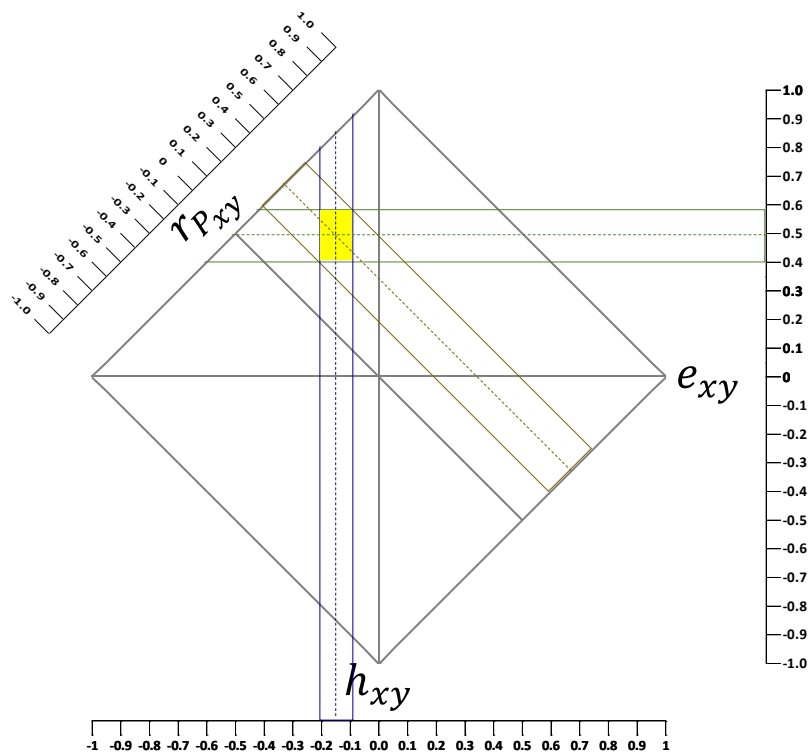
Figure 5.5-1 Confidence intervals of the phenotypic correlation, coheritability and coenvironmentability (yellow rectangle) .

$n = 628$ $h_x^2 = 0.3$ $h_y^2 = 0.4$		Fisher's r-to-Z transformation $Z_{r_\bullet} = 0.5 \ln\left(\frac{1+r_{\bullet x,y}}{1-r_{\bullet x,y}}\right)$	Confidence Interval of Z_r $\left[Z_r - (z_{1-\frac{\theta}{2}})\sqrt{\frac{1}{N-3}}\right] < Z_r < \left[Z_r - (z_{1-\frac{\theta}{2}})\sqrt{\frac{1}{N-3}}\right]$	back transformation from Z_r to r $\frac{e^{2\,Z_{r_{P,L}}}-1}{e^{2\,Z_{r,L}}+1}_{r_{\bullet,L}} < \rho < \frac{e^{2\,Z_{r,U}}-1}{e^{2\,Z_{r,U}}+1}_{r_{\bullet,U}}$	confidence interval coheritability $\frac{\sqrt{h_x^2\,h_y^2}\,r_{A,L}}{h_{x,y\_L}} < \sqrt{h_x^2\,h_y^2}\,\rho_A < \frac{\sqrt{h_x^2\,h_y^2}\,r_{A,U}}{h_{x,y\_U}}$	confidence interval coenvironmentability $\frac{(r_{P_L} - h_{x,y,L})}{r_{e_L}} < E_{x,y} < \frac{(r_{P_U} - h_{x,y,U})}{r_{e_U}}$
$r_{P_{x,y}}$	0.24	0.549	$0.549 - 1.96\sqrt{\frac{1}{628-3}} < Z_{r_p} < 0.549 + 1.96\sqrt{\frac{1}{628-3}}$ $\underset{Z_{r_{P\_L}}}{\underline{0.4706}} < Z_{r_p} < \underset{Z_{r_{P\_U}}}{\underline{0.6274}}$	$\frac{e^{2(0.4706)}-1}{e^{2(0.4706)}+1} < \rho_P < \frac{e^{2(0.6274)}-1}{e^{2(0.6274)}+1}$ $\underset{r_{P\_L}}{\mathbf{0.165}} < \rho_P < \underset{r_{P\_U}}{\mathbf{0.312}}$		
$r_{A_{x,y}}$	-0.58	-0.662	$-0.662 - 1.96\sqrt{\frac{1}{628-3}} < Z_{r_A} < -0.662 + 1.96\sqrt{\frac{1}{628-3}}$ $\underset{Z_{r_{A\_L}}}{\underline{-0.7404}} < Z_{r_A} < \underset{Z_{r_{A\_U}}}{\underline{-0.5836}}$	$\frac{e^{2(-0.7404)}-1}{e^{2(-0.7404)}+1} < \rho_A < \frac{e^{2(-0.5836)}-1}{e^{2(-0.5836)}+1}$ $\underset{r_{A\_L}}{\underline{-0.629}} < \rho_A < \underset{r_{A\_U}}{\underline{-0.526}}$		
$h_{x,y} = \sqrt{h_x^2\,h_y^2}\,r_{A_{x,y}}$	-0.2				$\sqrt{0.3 \times 0.4}(-0.629) < \sqrt{h_x^2\,h_y^2}\,\rho_A < \sqrt{0.3 \times 0.4}(-0.526)$ $\underset{h_{x,y\_L}}{\mathbf{-0.218}} < H_{x,y} < \underset{h_{x,y\_U}}{\mathbf{-0.182}}$	
$e_{x,y} = r_{P_{x,y}} - h_{x,y}$	0.348					$0.165 - (-0.218) < E_{x,y} < 0.312 - (-0.182)$ $\mathbf{0.383} < E_{x,y} < \mathbf{0.494}$

5.6 Sample size

An important aspect in planning a study that will require inference on the phenotypic correlation and its components is the determination of the appropriate sample size n in order to maximize the probability of credible results. Sometimes, the sample size is determined by practical issues regarding resources, time, and money. In this case the number of individuals to be measure is known, yet it is nevertheless important to determine the inferential extent the data can provide when used for hypothesis testing. A usual procedure of choosing n aims to achieve sufficient power of the test and level of significance to determine whether a parameter is zero ($Ho: \theta = 0$). The following formula can be used to that effect:

$$
n = \left(\frac{z_{1-\frac{\alpha}{2}} + z_{1-\beta}}{\frac{1}{2} ln \left[\frac{1+\theta}{1-\theta} \right]} \right)^2 + 3
$$

where $z_{1-\frac{\alpha}{2}}$ and $z_{1-\beta}$ are the standard normal z scores corresponding to the $1 - \frac{\alpha}{2}$ and $1 - \beta$ quantiles of the standard normal distribution (e.g. for $\alpha = 0.05$, $z_{1-\frac{\alpha}{2}} = 1.96$; $\beta = 0.2$, $z_{1-\beta} = 0.842$), and the denominator within the brackets is the Fisher's transformation of θ (where θ is the parameter to be assessed, e.g., $r_{P_{x,y}}$, $r_{A_{x,y}}$, $h_{x,y}$)

A better procedure for the determination of the optimum sample size for the study of joint inheritance of two traits uses confidence intervals. This procedure aims to find a sample size that guarantees confidence intervals with a given width to detect a given effect size. Here we intend to specify a null hypothesis in which the parameter is equal to a nonzero value. The attention, therefore, is on confidence level estimation of the population parameter instead of the test of a parameter hypothesized null value. The following equation can be used to determine the sample size required to obtain a 95% CI for the parameter θ with a desired width (Moinester and Gottfried 2014).

$$n = \frac{3.84\,(1 - \theta^2)^2}{w^2} + 6\theta^2 + 1$$

And the corresponding equation for the half-width of the confidence interval is

$$w = 1.96\,\frac{(1 - \theta^2)}{\sqrt{n - 1 - 6\theta^2}}$$

where θ is the effect size, that is the value of the parameter of interest, e.g., $r_{P_{x,y}}$, $r_{A_{x,y}}$, $h_{x,y}$; and w is half-width of the desired confidence interval. If the sample size is already fixed, one can calculate the corresponding half-width w for a given expected effect size θ.

Effect size θ is the expected value of the parameter that one suspects or guesses.

Figure 5.6. (A) Sample size required to obtain a desired 95% confidence interval half-width for different values of the correlations, or coheritability) according to the formula of Moinester and Gottfried (2014). (B) Sample size required to test a null hypothesis that the parameter is zero with a significance level $\alpha = 0.05$, and power $1 - \beta = 0.8$.

A

half-width w

$|\theta|$	0.03	0.035	0.04	0.05	0.07	0.1
0.05	4255	3127	2394	1533	782	384
0.10	4192	3080	2358	1510	771	378
0.15	4086	3003	2299	1472	751	369
0.20	3942	2896	2218	1420	725	356
0.25	3759	2762	2115	1354	692	340
0.30	3542	2603	1993	1276	652	320
0.35	3294	2420	1854	1187	606	298
0.40	3019	2218	1699	1088	556	273
0.45	2721	2000	1532	981	502	247
0.50	2408	1769	1355	868	444	219
0.55	2083	1531	1173	752	385	190
0.60	1754	1290	988	634	325	161
0.65	1429	1051	806	517	265	132
0.70	1116	821	629	404	208	104
0.75	823	606	465	299	155	78
0.80	559	412	317	204	107	55
0.85	335	247	191	124	66	35
0.90	160	119	93	61	34	20
0.95	47	36	29	21	14	10

effect size $|\theta|$

B

$|\theta|$	$\alpha = 0.05$ $\beta = 0.20$
0.05	3138
0.10	783
0.15	347
0.20	194
0.25	123
0.30	85
0.35	62
0.40	47
0.45	36
0.50	29
0.55	24
0.60	19
0.65	16
0.70	13
0.75	11
0.80	10
0.85	8
0.90	7
0.95	5

test statistic $|\theta|$

Since in absolute value the coheritability is generally smaller than the genetic correlation, it has implications on lowering the effect size, and it is expected that the sample size for testing the coheritability will generally be larger than that for the genetic correlation. For example, if a test is to be carried out having a test statistic $r_{A_{x,y}} = 0.6$ and set the probability to reject a true null hypothesis to $\alpha = 0.05$ (Type I error), and a probability for failing to reject a false null hypothesis to $\beta = 0.2$ (Type II error) then the sample size required to determine whether a genetic correlation differs from zero would be $n = 19$. In contrast, given the same genetic correlation and $h_x^2 = 0.28$, $h_y^2 = 0.405$, the coheritability becomes $h_{x,y} = (\sqrt{0.28 \cdot 0.405} \cdot 0.6) = 0.202$, and the sample size would be $n = 190$ to establish a 80% power of the hypothesis test.

A more meaningful approach, however, is to determine a sample size that guarantees a narrow confidence interval for the coheritability. For instance, using the data from Figure 5.5.2, if the genetic correlation is expected to be $r_{A_{x,y}} = -0.58$ (this is the effect size), and would like to measure it within a confidence interval $[-0.62, -0.54]$, which is -0.58 ± 0.04, then using the equation of Moinester and Gottfried refereed above,

$$n = \frac{3.84\,(1 - (0.58)^2)^2}{(0.04)^2} + 6\,(0.58)^2 + 1 = \mathbf{1596}$$

If the coheritability is expected to be $h_{x,y} = -0.2$, and also would like to measure around a $\pm w = \pm 0.04$, that is $[-0.24, -0.16]$, then

$$n = \frac{3.84\,(1 - (0.2)^2)^2}{(0.04)^2} + 6\,(0.2)^2 + 1 = \mathbf{2305}$$

which results in a larger sample size for the coheritability because its effect size (0.2) is smaller than the one for the genetic correlation (0.58).

On the other hand, if we have already a fixed number of individuals to measure, say a sample of size $n = 981$ and would like to know what is the confidence level that can be obtained if the coheritability is $h_{x,y} = -0.2$. Again, we use the equation from Moinester and Gottfried,

$$w = 1.96 \frac{(1 - (0.2)^2)}{\sqrt{981 - 1 - 6(0.2)^2}} = 0.06$$

Therefore, with a fixed sample size $n = 981$, the coheritability $h_{x,y} = -0.2$ would be calculated within a confidence interval $[(-0.2 - 0.06), (-0.2 + 0.06)] = [-0.26, -0.14]$. Note that the interval is a little broader because of the reduced sample size.

6 Visualizing the $h_{xy} \cdot e_{xy} \cdot r_{P_{xy}}$-relationship

6.1 The three-dimensional $h_{x,y} \cdot e_{x,y} \cdot r_{P_{x,y}}$-plane (3DHER-plane)

The relationship $r_{P_{x,y}} = (h_{x,y} + e_{x,y})$ allow us to infer the domains of the phenotypic correlation, coheritability and coenvironmentability, as follows

$$-1 \leq r_{P_{x,y}} \leq 1$$

$$-1 \leq h_{x,y} \leq 1$$

$$-1 \leq e_{x,y} \leq 1$$
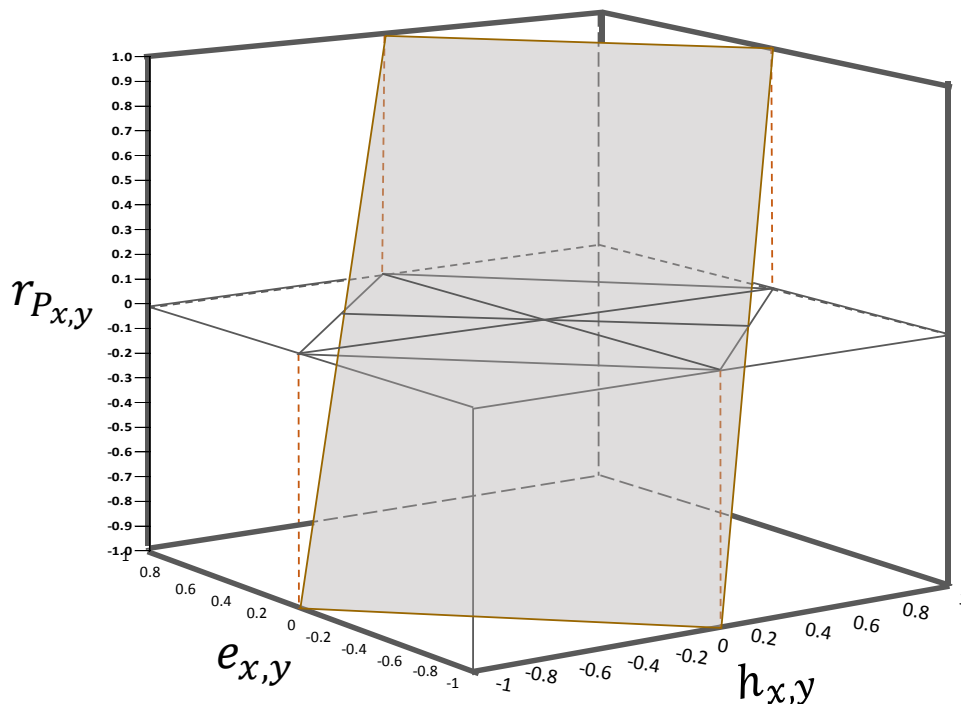
Figure 6.1 3DHER-plane

If each variable (coheritability, coenvironmentability, phenotypic correlation) are assigned to an ordered triplet of axis lines, which are numerical, intersect at the origin, are pair-wise perpendicular, and all have a single unit of length, it is possible to uniquely specify, in this Cartesian system, the values of a single point by signed distances from the origin, i.e. three numbers in a chosen order $\left(h_{x,y}, e_{x,y}, r_{P_{x,y}} \right)$. This

is illustrated in Figure 6.1 and is called the three-dimensional coheritability-coenvironmentability-phenotypic correlation plane, 3DHER-plane.

The data align on a plane (i.e. it has zero volume) due to the interdependencies established by the intrinsic linear dependency of the axes, namely, $r_{P_{x,y}} = (h_{x,y} + e_{x,y})$ (see Section 6.4).

6.2 The two-dimensional $h_{xy} \cdot e_{xy} \cdot r_{P_{xy}}$ -field (2DHER-field)

The orthogonal projection of the 3D $h_{x,y} \cdot e_{x,y} \cdot r_{P_{x,y}}$ –plane on the surface defined by h_{xy} x $e_{xy}| r_{P_{xy}} = 0$, results in the two-dimensional $h_{x,y} \cdot e_{x,y} \cdot r_{P_{x,y}}$ –field. This field is circumscribed by the relationship $|h_{x,y}| + |e_{x,y}| = 1$, which in a more explicit way, is demarcated by the lines $h_{x,y} + e_{x,y} = 1$, $h_{x,y} + e_{x,y} = -1$, $h_{x,y} - e_{x,y} = 1$, and $h_{x,y} - e_{x,y} = -1$ (Figure 6.2)

The field $h_{xy} \blacksquare e_{xy} \blacksquare r_P$ can be partitioned according to the sign of the phenotypic correlation, coheritability and coenvironmentability. Note here that the coheritability sign is conferred by the additive genetic correlation. The sign of the cohenvironmentability is given by the environmental correlation. By tracing the lines $r_{P_{xy}} = 0$, $h_{xy} = 0$, and $e_{xy} = 0$, sectors are demarcated within the field forming isosceles triangles. These partitions are characterized by (1) a particular sign combination among components, (2) the range of values the components can have, and (3) and the relationship between the sign of the phenotypic correlation and the coheritability and coenvironmentability.

The partitions are denoted by the letter S followed by a subscripted numeral having the sign of the coheritability of that sector. For instance, partitions S_{+1} , S_{+2} , S_{+3} have a positive coheritability, and therefore a positive genetic correlation. The sign of the phenotypic correlation does not follow necessarily the sign of the coheritability or genetic correlation.

The subscripts with the same numeral but with opposite signs indicate sectors that are reciprocal to each other. For example, partition S_{+3} has $h_{xy} > 0$, and $e_{xy} < 0$, while partition S_{-3} has $h_{xy} < 0$, and $e_{xy} > 0$. In both S_{+3} and S_{-3} the phenotypic correlation $r_{P_{xy}}$ has the sign of e_{xy} , indicating the preponderant effect of the coenvironmentability over the coheritability component. Notice that it implies that $r_{P_{xy}}$ and $r_{A_{xy}}$ have opposite sign.

Partitions S_{+1} and S_{-1} are reciprocal sectors where the coheritability and coenvironmentability have the same sign, and contribute to the magnitude of the phenotypic correlation in the same direction (sign). Both h_{xy} and e_{xy} act in the same direction (same sign).

Partitions S_{+2} and S_{-2} are reciprocal sectors characterized by the preponderant effect of the coheritability on the phenotypic correlation, at the expense of the coenvironmentability. This is clearly seen by $r_{P_{xy}}$ having the same sign as the coheritability (and $r_{A_{xy}}$). Both h_{xy} and e_{xy} display an antagonistic relationship, they act in opposite directions (different signs). This may also suggest the reduced effect of the GxE interaction.

Partitions S_{+3} and S_{-3} are reciprocal sectors characterized by the phenotypic correlation and the coheritability having opposite signs, and the coenvironmentability having a preponderant effect on the magnitude and sign of the phenotypic correlation. Both h_{xy} and e_{xy} display an antagonistic

relationship, they act in opposite directions (different signs). This may be an indicator that a probable GxE interaction may be present.
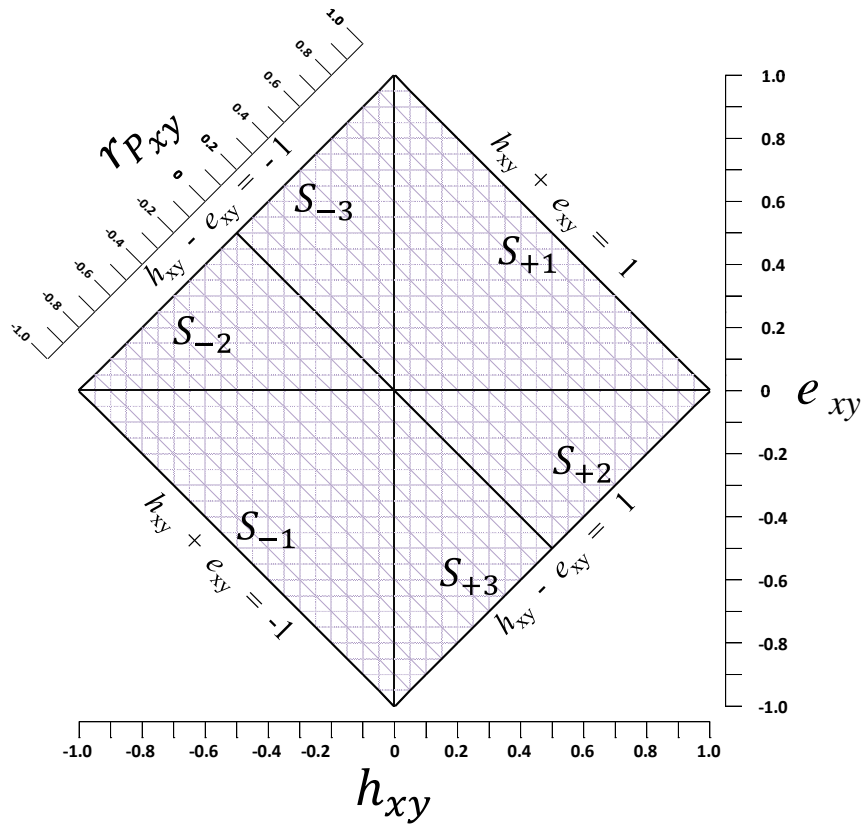
$r_{P_{xy}}$	h_{xy}	e_{xy}	
[-1 , 0)	[-1 , 0)	[-1 , 0)	S_{-1}
[-1 , 0)	[-1 , 0)	(0 , 0.5]	S_{-2}
(0 , 1]	[-0.5 , 0)	(0 , 1]	S_{-3}

	$r_{P_{xy}}$	h_{xy}	e_{xy}
S_{+1}	(0 , 1]	(0 , 1]	(0 , 1]
S_{+2}	(0 , 1]	(0 , 1]	[-0.5 , 0)
S_{+3}	[-1 , 0)	(0 , 0.5]	[-1 , 0)

Figure 6.2 (A) The two-dimensional coheritability-coenvironmentability-phenotypic correlation-field (2DHER). This field is demarcated by the relationship $\left|h_{x,y}\right| + \left|e_{x,y}\right| = 1$. Lines at zero for each variable define partitions, labeled by an S followed by the sign of the coheritability and an indicator numeral. (B) Range of values for the variables for each partition.

6.3 The $h_{xy} \cdot e_{xy} \cdot r_{P_{xy}}$-plane in a three-dimensional spherical space

The coheritability, coenvironmentability and the phenotypic correlation, being three numerical coordinates that define a point in a 3-dimensional Cartesian system, could easily be represented into a spherical coordinate system where the position of a point in space is specified by spherical coordinates (r, θ, φ), (symbols as often used in mathematics)(Figure 6.3-1).

> r, the radius (radial coordinate, $r \geq 0$) defined as the Euclidean distance from the origin O to the point P.

> θ, the azimuthal angle (azimuth coordinate, $0 < \theta < 2\pi$) is the signed angle measured from the azimuth reference direction (positive x-axis) to the orthogonal projection of the line segment OP on the reference plane (x-y plane). The azimuth coordinate corresponds to the coheritability.

> φ, the polar angle (zenith angle coordinate, $0 < \varphi < \pi$) is the angle between the zenith direction (z-axis) to the line segment OP that connects the origin O to the point P. The zenith coordinate corresponds to the phenotypic correlation.

$$h_{xy} = r \, \sin\varphi \, \cos\theta$$
$$e_{xy} = r \, \sin\varphi \, \sin\theta$$
$$r_{P_{xy}} = r \, \cos\varphi$$
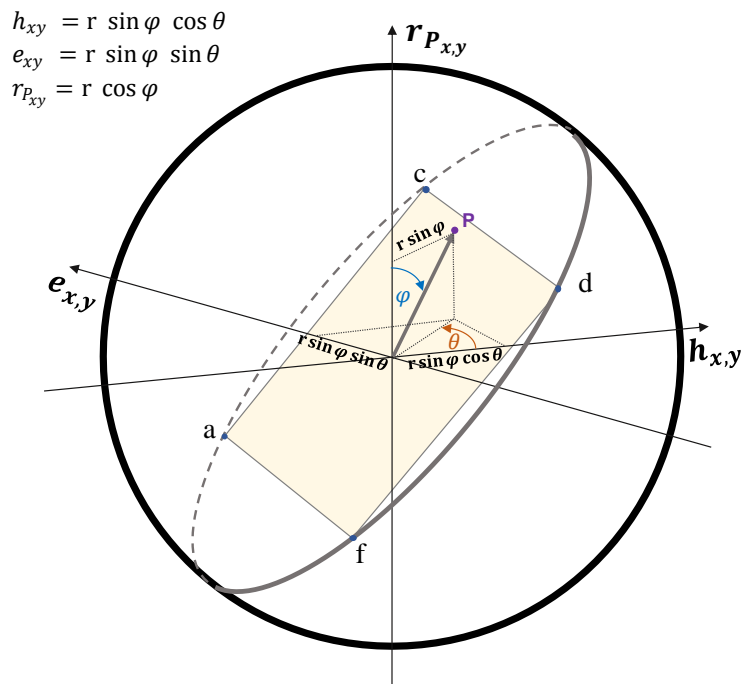
Figure 6.3-1 The spherical coordinate system corresponding to the variables coheritability, coenvironmentability and phenotypic correlation. The point can be uniquely specified by (r, θ, φ). The plane is inclined $35.26438968°$ in reference to the $r_{P_{x,y}} . e_{x,y}$-plane and rotated $45°$. The radius of the sphere is equal to $\sqrt{2}$.
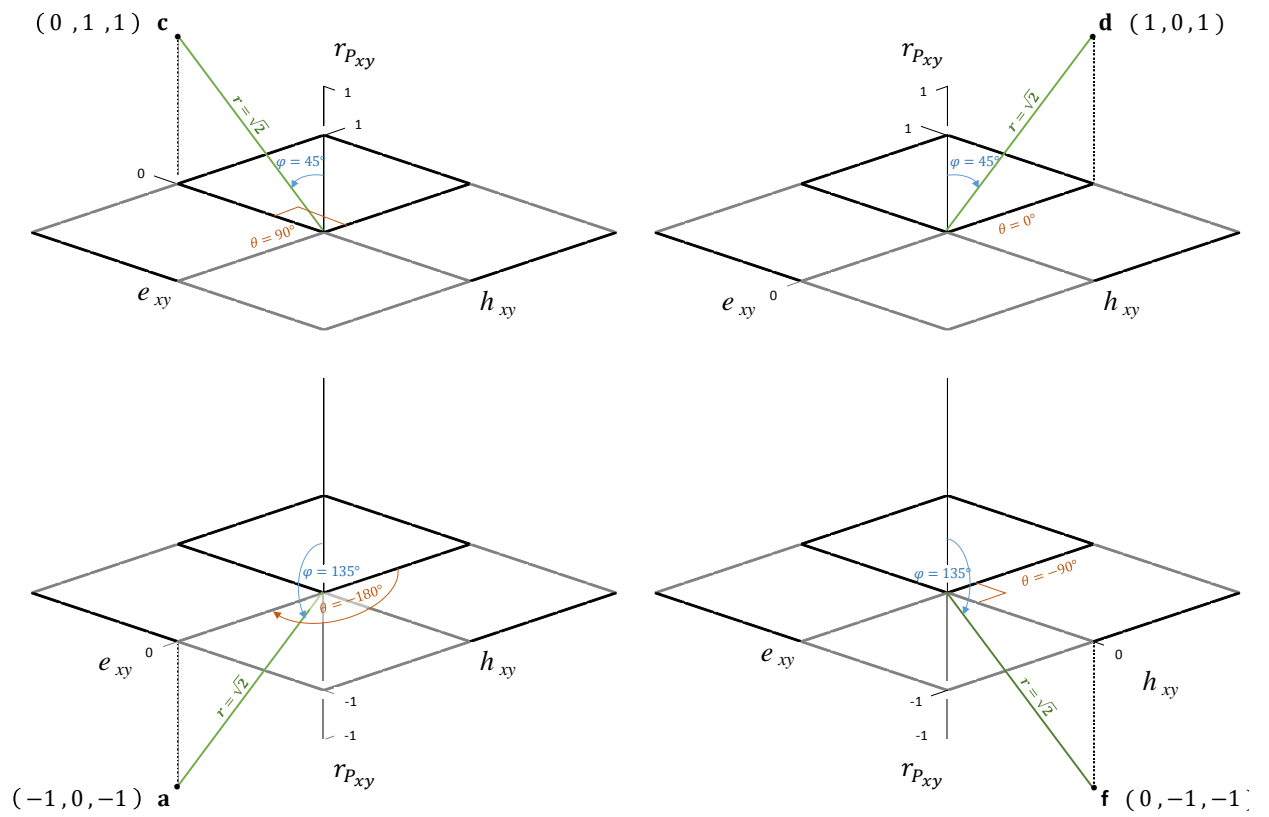
		Cartesian coordinates			Spherical coordiantes									
		h_{xy}	e_{xy}	r_p	azimuth Θ	polar φ	radius r	sinΘ	cosΘ	sinφ	cosφ	$h_{x,y}$ ρ sin φ cos Θ	$e_{x,y}$ ρ sin φ sin Θ	$r_{Px,y}$ ρ cos φ
point	a	0	1	1	90	45	$\sqrt{2}$	1	0	$\frac{\sqrt{2}}{2}$	$\frac{\sqrt{2}}{2}$	0	1	1
	b	1	0	1	0	45	$\sqrt{2}$	0	1	$\frac{\sqrt{2}}{2}$	$\frac{\sqrt{2}}{2}$	1	0	1
	c	0	-1	-1	-90	135	$\sqrt{2}$	-1	0	$\frac{\sqrt{2}}{2}$	$-\frac{\sqrt{2}}{2}$	0	-1	-1
	d	-1	0	-1	180	135	$\sqrt{2}$	0	-1	$\frac{\sqrt{2}}{2}$	$-\frac{\sqrt{2}}{2}$	-1	0	-1

Figure 6.3-2 Examples of determination of specified positions in the spherical coordinate system corresponding to the coheritability, coenvironmentability and phenotypic correlation.

The spherical coordinates (r, θ, φ) are related to the Cartesian coordinates $(h_{xy}, e_{xy}, r_{P_{xy}})$ by the formulae

$$r = \sqrt{h_{xy}^2 + e_{xy}^2 + r_{P_{xy}}^2}, \qquad\qquad r \in [0, \sqrt{2}]$$

$$\theta = \arctan\left(\frac{e_{xy}}{h_{xy}}\right), \qquad\qquad \theta \in \begin{cases} [0, 2\pi) \\ [0°, 360°) \end{cases}$$

$$\varphi = \arccos\left(\frac{r_{P_{xy}}}{r}\right), \qquad\qquad \varphi \in \begin{cases} [0, \pi) \\ [0°, 180°) \end{cases}$$

The Cartesian coordinates are related to the spherical coordinates as follows

$$h_{xy} = x = r \sin\varphi \cos\theta$$

$$e_{xy} = y = r \sin\varphi \sin\theta$$

$$r_{P_{xy}} = z = r \cos\varphi$$

The following relationship must be satisfied

$$\overbrace{r\cos(\varphi)}^{r_{Px,y}} = \overbrace{\sin(\varphi)\cos\theta}^{h_{x,y}} + \overbrace{\sin(\varphi)\sin(\theta)}^{e_{x,y}}$$

Relationship between the azimuthal θ and polar φ angles (Figure 6.3-3) is derived as follow

$$r_{Px,y} = h_{x,y} + e_{x,y}$$

$$r\cos\varphi = r\sin\varphi \cos\theta + r\sin\varphi \sin\theta$$

$$\cos\varphi = \sin\varphi [\sin\theta + \cos\theta]$$

$$\frac{\cos\varphi}{\sin\varphi} = \sin\theta + \cos\theta$$

$$\left(\frac{1}{\tan\varphi}\right)^2 = (\sin\theta + \cos\theta)^2 = (\sin^2\theta + \cos^2\theta + 2\sin\theta \cos\theta) = 1 + 2\sin\theta \cos\theta$$

$$\frac{1}{\varphi} = \sqrt{1 + 2\sin\theta \ \cos\theta} = \sqrt{1 + \sin(2\theta)}$$

$$\tan\varphi = \frac{1}{\sqrt{1 + \sin(2\theta)}}$$

Finally we obtain

$$\varphi = arctan\left[\frac{1}{\sqrt{1 + \sin(2\theta)}}\right]$$
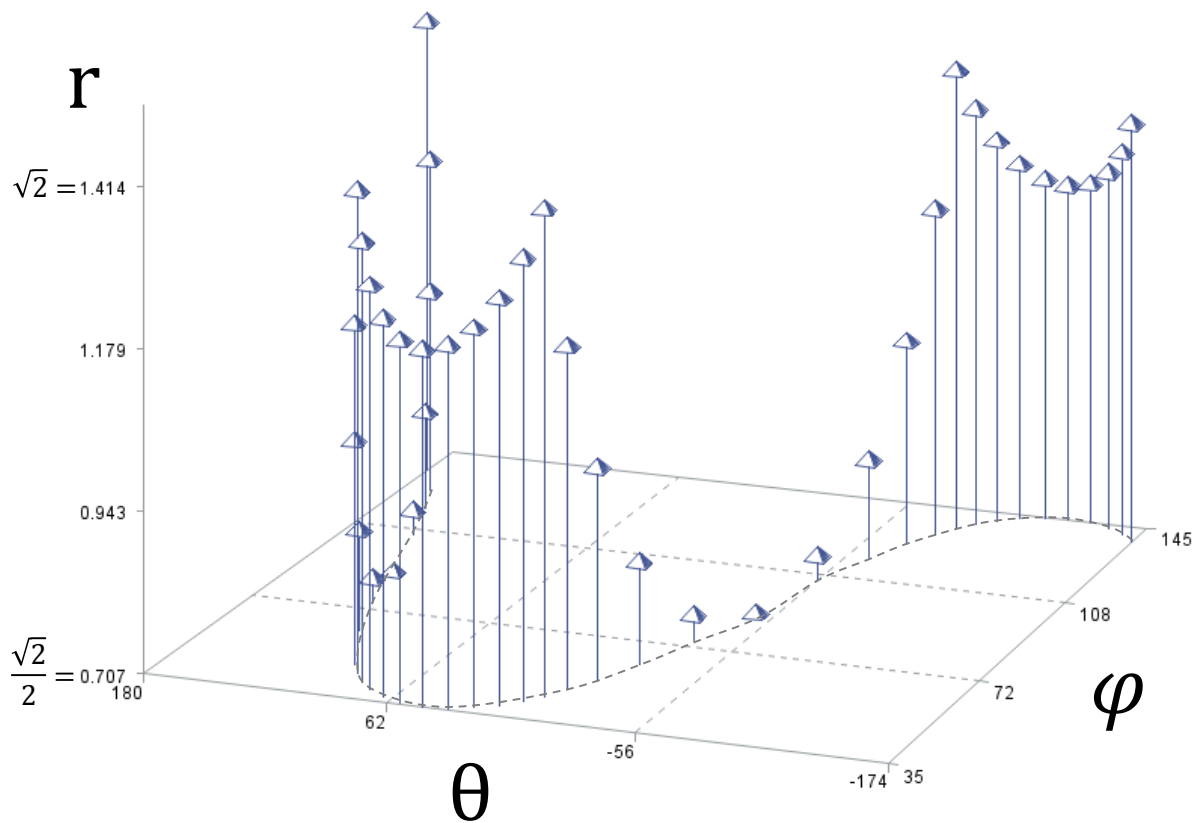
Figure 6.3-3 Relationship between the radius r, the azimuthal angle θ, and the polar angle φ.

6.4 The determinant of the $h_{xy} \cdot e_{xy} \cdot r_{P_{xy}}$-plane

The equation $r_{P_{xy}} = h_{xy} + e_{xy}$ establishes a *linear* dependency between the variables that constraints their values. Therefore, a 3x3 matrix in which a column corresponds to a single datum, of the form $\begin{vmatrix} h_{xy} \\ e_{xy} \\ r_{P_{xy}} \end{vmatrix}$ will have a determinant equal to zero, which means that all the data is "squeezed" to a flat plane of zero volume.

Using three of the points a, c, d, f which touch an imaginary sphere of radius $\sqrt{2}$
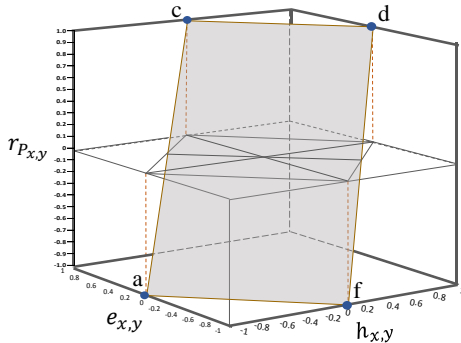
$$a = \begin{vmatrix} -1 \\ 0 \\ -1 \end{vmatrix}, \quad c = \begin{vmatrix} 0 \\ 1 \\ 1 \end{vmatrix}, \quad d = \begin{vmatrix} 1 \\ 0 \\ 1 \end{vmatrix}, \quad f = \begin{vmatrix} 0 \\ -1 \\ -1 \end{vmatrix}$$

In Cartesian Coordinates

$$det\,[\,\mathbf{a\,c\,d}\,] = \quad det\,[\,\mathbf{a\,c\,f}\,] = \quad det\,[\,\mathbf{a\,d\,f}\,] = \quad det\,[\mathbf{c\,d\,f}\,]$$

$$det \begin{vmatrix} -1 & 0 & 1 \\ 0 & 1 & 0 \\ -1 & 1 & 1 \end{vmatrix} = det \begin{vmatrix} -1 & 0 & 0 \\ 0 & 1 & -1 \\ -1 & 1 & -1 \end{vmatrix} = det \begin{vmatrix} -1 & 1 & 0 \\ 0 & 0 & -1 \\ -1 & 1 & -1 \end{vmatrix} = det \begin{vmatrix} 0 & 1 & 0 \\ 1 & 0 & -1 \\ 1 & 1 & -1 \end{vmatrix} = 0$$

Using the values in of Figure 6.3-2 above, one can find the determinant for three points, say points c, d, f, the determinant has the following format:

$$det \begin{vmatrix} (r\,\sin\varphi\,\cos\theta)_c & (r\,\sin\varphi\,\cos\theta)_d & (r\,\sin\varphi\,\cos\theta)_f \\ (r\,\sin\varphi\,\sin\theta)_c & (r\,\sin\varphi\,\sin\theta)_d & (r\,\sin\varphi\,\sin\theta)_f \\ (\quad r\cos\varphi\quad)_c & (\quad r\cos\varphi\quad)_d & (\quad r\cos\varphi\quad)_f \end{vmatrix} = 0$$

7 Set of values and limiting cases

7.1 The range of values of the coheritability for a given value of the coenvironmentability

Given the interdependencies, it is possible to relate the range of values of the coheritability based on a given value of the coenvironmentability, as follows:

$$-(1-|e_{x,y}|) < h_{x,y} < (1-|e_{x,y}|) \qquad\qquad -1 < e_{x,y} \leq 1$$

which can be written more explicitly as

$$-(1-e_{x,y}) < h_{x,y} < (1-e_{x,y}) \qquad\qquad 0 < e_{x,y} \leq 1$$

$$-1 < h_{x,y} < 1 \qquad\qquad e_{x,y} = 0$$

$$-(1+e_{x,y}) < h_{x,y} < (1+e_{x,y}) \qquad\qquad -1 \leq e_{x,y} < 0$$

To illustrate: for $e_{x,y} = 0.8$ $-(1-0.8) < h_{x,y} < (1-0.8)$ $\rightarrow$ $-0.2 < h_{x,y} < 0.2$

$e_{x,y} = 0$ $-1 < h_{x,y} < 1$ $\rightarrow$ $-1 < h_{x,y} < 1$

$e_{x,y} = 0.8$ $-(1+(-0.35)) < h_{x,y} < (1+(-0.35))$ $\rightarrow$ $-0.65 < h_{x,y} < 0.65$
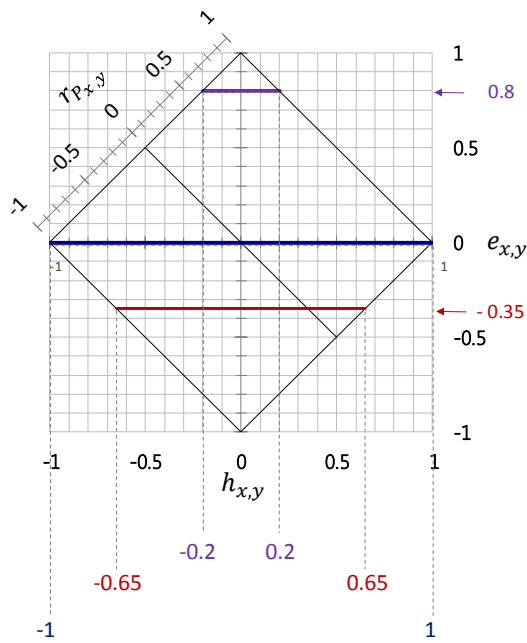
7.2 The set of values of coheritability and coenvironmentability for a given phenotypic correlation

Provided a value of phenotypic correlation, what is the range values allowed for its coheritability and coenvironmentability components? The problem can be expressed as follows:

$$r_{P_{x,y}} \rightarrow (h_{x,y}, e_{x,y} | r_{P_{x,y}})$$

(a) The set of (h_{xy}, e_{xy}) values valid for a given $r_{P_{x,y}}$, is a collection of bivariate data whose boundaries are:

$$\left(-0.5(1 - r_{P_{x,y}}), \ 0.5(1 + r_{P_{x,y}}) \right) < \left(h_{x,y}, e_{x,y} | r_{P_{x,y}} \right) < \left(0.5(1 + r_{P_{x,y}}), \ -0.5(1 - 0.5\, r_{P_{x,y}}) \right)$$

and (b) the elements of the datum sum up to the phenotypic correlation

$$h_{x,y} + e_{x,y} = r_{P_{xy}}$$

and, (c) where the linear equation relating the coenvironmentability as a function of the coheritability is

$$e_{x,y} = r_{P_{xy}} - h_{x,y}$$

a line whose intercept is the value of the phenotypic correlation, and the slope of the coheritability factor is -1.

For example, if the phenotypic correlation $r_{P_{xy}} = -0.35$, then the $(h_{x,y}, e_{x,y})$ values follow:

(a) The $(h_{x,y}, e_{x,y})$ must be within the boundaries

$$(-0.675, 0.325) \leq (h_{x,y}, e_{x,y} | r_{P_{x,y}} = -0.35) \leq (0.325, -0.675)$$

(b) The elements of the datum must necessarily sum up to the phenotypic correlation

$$h_{x,y} + e_{x,y} = -0.35$$

using the boundaries as an example:

$$-0.675 + 0.325 = -0.35, \text{ and } 0.325 - 0.675 = -0.35$$

(c) and the linear relationship is that relates the coenvironmentability and coheritability is
$$e_{x,y} = -0.35 - h_{x,y}, \qquad (-0.675 < h_{x,y} < 0.325)$$

This line allows to determine the coenvironmentability value for any value of coheritability within the set boundaries. Figure 7.2 illustrates this example.
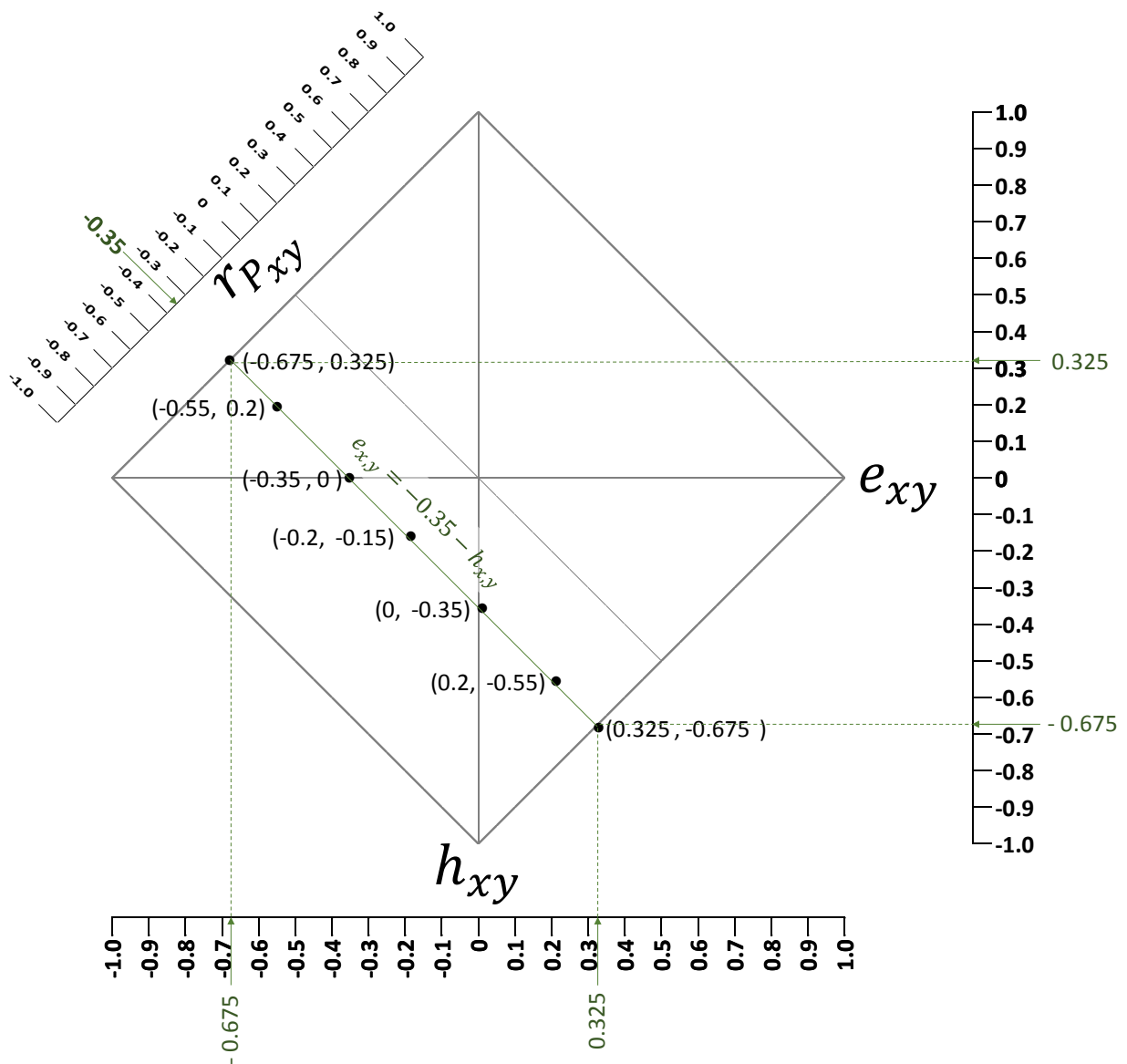
Figure 7.2. Example of some of the possible values of the bivariate datum (coheritability, coenvironmentability) for the given phenotypic correlation of -0.35, presented in the 2DHER-field. Notice that the boundaries of coheritability and coenvironmentability are the numerically the same yet antiparallel. Note that the elements constituting each datum sum up to the phenotypic correlation. The line equation has as intercept the value of the phenotypic correlation, and a slope of -1.

7.3 The set of possible values of heritabilities, and correlations (genetic, environmental) for a given (coheritability, coenvironmentability) datum.

Provided a value of a (coheritability, coenvironmentability) datum, what are the possible values of the heritabilities of the traits and the genetic and the environmental correlations? In other words, knowing a datum involving coheritability,coenvironmentability corresponding to a phenotypic correlation $(h_{x,y}, e_{x,y} \mid r_{P_{x,y}})$ what would be the collection of possible values of the heritability of trait x and of trait y, the genetic correlation, and the environmental correlation, $(h_x^2, h_y^2, r_{A_{x,y}}, r_{E_{x,y}})$? The problem can be expressed as follows:

$$(h_{x,y}, e_{x,y} \mid r_{P_{x,y}}) \rightarrow \left\{ h_x^2, h_y^2, r_{A_{x,y}}, r_{E_{x,y}} \right\}$$

In principle, the values of the phenotypic, genetic and environmental correlations are independent and random variables. A high phenotypic correlation does not imply a comparable value of the genetic correlation. A high genetic correlation between two traits, do not necessarily indicates that the heritabilities of the traits are high also. Traits that have high heritabilities may display a weak genetic correlation, and visceversa. In this sense the heritabilities and genetic correlations are independent. In addition, the effect of the heritabilities may result in changes in the rank of the genetic correlation compared to the rank observed in the coheritabilities.

However, as explained in the previous section, by imposing a constraint (i.e. fixing the value of a variable) such as equating the phenotypic correlation to a specific value would affect the set of bivariate coheritability-coenvironmentability combinations.

To address the problem of finding heritabilities and correlations, here I use an empirical, graphical method where the set of values $r_{A_{x,y}}$, $r_{E_{x,y}}$ are plotted against $\sqrt{h_x^2 h_y^2}$. The algorithm to can be sumnmarized as follows:

(1) list a set of heritabilities combinations, ranked by the value of their geometric mean $\sqrt{h_x^2 h_y^2}$.

$\sqrt{h_x^2 h_y^2}$	0.1	0.14142	0.17321	0.2	0.22361	0.24495	0.26458	0.28284	0.3	0.31623	0.34641	0.37417	0.3873	0.4	0.42426	0.44721	0.45826	0.4899	0.5	0.51962	0.52915	0.54772	0.56569	0.59161	0.6	0.63246	0.64807	0.69282	0.7	0.73485	0.79373	0.8	0.84853	0.9
h_x^2	0.1	0.2	0.3	0.2	0.5	0.3	0.7	0.4	0.9	0.5	0.4	0.7	0.5	0.4	0.9	0.5	0.7	0.6	0.5	0.9	0.7	0.6	0.8	0.7	0.9	0.8	0.7	0.8	0.7	0.9	0.9	0.8	0.9	0.9
h_y^2	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.2	0.1	0.2	0.3	0.2	0.3	0.4	0.2	0.4	0.3	0.4	0.5	0.3	0.4	0.5	0.4	0.5	0.4	0.5	0.6	0.6	0.7	0.6	0.7	0.8	0.8	0.9
$\sqrt{(1-h_x^2)(1-h_y^2)}$	0.9	0.8485	0.7937	0.8	0.6708	0.7483	0.5196	0.6928	0.3	0.6325	0.6481	0.4899	0.5916	0.6	0.2828	0.5477	0.4583	0.4899	0.5	0.2646	0.4243	0.4472	0.3464	0.3873	0.2449	0.3162	0.3464	0.2828	0.3	0.2	0.1732	0.2	0.1414	0.1

in this case, the values are within the interval [0.1 , 0.9] in order to avoid numerical instability.

(2) Second, set the boundaries of the heritabilities. In which the magnitude of the correlation becomes 1. This is determined using the following relationship:

$$h_x^2 = h_y^2 = \sqrt{h_x^2 h_y^2} = |h_{x,y}|$$, it results in $r_{A_{x,y}} = \frac{|h_{x,y}|}{h_{x,y}}$, with value either -1 or +1

and

$$h_x^2 = h_y^2 = \sqrt{h_x^2 h_y^2} = 1 - |e_{x,y}|$$, it results in $r_{E_{x,y}} = \frac{|e_{x,y}|}{e_{x,y}}$, with value either -1 or +1

To summarize, when both heritabilities are either $|h_{x,y}|$ or $(1 - |e_{x,y}|)$, it establish the boundaries of the heritability values. Note that even within this interval the correlations may be greater than +1 or less than -1.

(3) The correlations that are within the heritability boundaries and contained in [-1 , +1] are the possible valid values to be selected.

Figure 7.3 Example of values of heritabilities and correlations (genetic, environmental) for given values of coheritability and coenvironmentability $(h_{x,y}, e_{x,y})\, r_{P_{x,y}}$. (A) Values of genetic (blue) and environmental (orange) correlations as a function of the square root of the product of heritabilities. These graphs are dependent on (B) the list of combinations of heritabilities of the traits ranked by their geometric mean.

$\sqrt{h_x^2 h_y^2}$	0.1	0.14142	0.17321	0.2	0.22361	0.24495	0.26458	0.28284	0.3	0.31623	0.34641	0.37417	0.3873	0.4	0.42426	0.44721	0.45826	0.4899	0.5	0.51962	0.52915	0.54772	0.56569	0.59161	0.6	0.63246	0.64807	0.69282	0.7	0.73485	0.79373	0.8	0.84853	0.9
h_x^2	0.1	0.2	0.3	0.2	0.5	0.3	0.7	0.4	0.9	0.5	0.4	0.7	0.5	0.4	0.9	0.5	0.7	0.6	0.5	0.9	0.7	0.6	0.8	0.7	0.9	0.8	0.7	0.8	0.7	0.9	0.9	0.8	0.9	0.9
h_y^2	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.2	0.1	0.2	0.3	0.2	0.3	0.4	0.2	0.4	0.3	0.4	0.5	0.3	0.4	0.5	0.4	0.5	0.4	0.5	0.6	0.6	0.7	0.6	0.7	0.8	0.8	0.9
$\sqrt{(1-h_x^2)(1-h_y^2)}$	0.9	0.8485	0.7997	0.8	0.6708	0.7483	0.5196	0.6928	0.3	0.6325	0.6481	0.4899	0.5916	0.6	0.2828	0.5477	0.4583	0.4899	0.5	0.2646	0.4243	0.4472	0.3464	0.3873	0.2449	0.3162	0.3464	0.2828	0.3	0.2	0.1732	0.2	0.1414	0.1

7.4 The relationship of the heritabilities to yield a given geometric mean

In the previous section, the algorithm requires to list an ordered set of geometric means of pair of heritabilities. The major caveat of such a method is that there is not a 1-to-1 relationship between a geometric mean and a pair of heritabilities. In fact, a given geometric mean can be obtained by a number of alternative pairs.

For instance, following example consists of heritability pairs whose product is 0.18, and its geometric mean is 0.424264.

$$\sqrt{h_x^2 \cdot h_y^2} \qquad \sqrt{(1 - h_x^2)(1 - h_y^2)}$$

$\sqrt{h_x^2 \cdot h_y^2}$	$\sqrt{(1 - h_x^2)(1 - h_y^2)}$
$\sqrt{1 \cdot 0.18}$	0
$\sqrt{0.9 \cdot 0.2}$	0.28284
$\sqrt{0.8 \cdot 0.225}$	0.39370
$\sqrt{0.75 \cdot 0.24}$	0.43589
$\sqrt{0.6 \cdot 0.3}$	0.52915
$\sqrt{0.5 \cdot 0.36}$	0.56568
$\sqrt{0.4 \cdot 0.45}$	0.57445
$\sqrt{0.18 \cdot 0.18}$	0.82

0.424264

7.5 Limiting cases

Limiting cases provide insight into the nature of the coheritability and coenvironmentability in relation to the phenotypic correlation. For instance, if one of the heritabilities approaches 1, results in vanishing coenvironmentability, and $r_{P_{x,y}} = h_{xy}$. If conversely one of the heritabilities approaches zero, it causes the coheritability to vanish, leading to $r_{P_{x,y}} = e_{xy}$. Clearly this shows that at extreme values of the heritability, the phenotypic correlation can become either the coheritability or coenvironmentability. Therefore the statistical inferences designed to test $r_{P_{x,y}}$ can be used for h_{xy} and e_{xy} as well.

Note that

if $r_{A_{x,y}} < 0$, the multiplying by $\sqrt{h_x^2 h_y^2}$, will result in coheritability with larger value than $r_{A_{x,y}}$.

If $r_{A_{x,y}} > 0$ then the product of $\sqrt{h_x^2 h_y^2}$ and $r_{A_{x,y}}$ results in a coheritability value smaller than $r_{A_{x,y}}$.

In both cases, the coheritability will move in a direction towards zero.

Additionally, if $h_x^2 + h_y^2 = 1$, then $\sqrt{h_x^2 h_y^2} = \sqrt{(1 - h_x^2)(1 - h_x^2)}$.

The phenotypic correlation would be zero if the coheritability and coenvironmentability are of the same magnitude but of different sign. Another case exists when both the coheritability and coenvironmentability are zero; this would happen if one of the heritabilities is unity and the other zero, or if both genetic and environmental correlations is zero.

The sample correlation coefficient, as well as the coheritability estimator, depending on the sample size involved, can display numerical instability, especially at the proximity± 1. Both the sample correlation and the coheritability are not sufficiently robust, so its values can be misleading if outliers are present. Cognizant of this fact, we can make some deductions in this regard:

(A) A heritability equal to zero can only occur if the additive genetic variance (in the numerator) is zero. Under this condition, however, such zero genetic variance enters into the formula of the genetic correlation and causes it to be mathematically undefined (i.e. division by zero). Therefore, zero heritability cannot coexist with non null genetic correlation.

(B) A similar rationale can also be applied to the environmental correlation. A heritability equal to 1 implies that the additive genetic variance and the phenotypic variance are the same, and that the environmental variance is zero. Since the zero environmental variance is part of the denominator of the environmental correlation, it will cause to become undefined. Therefore, a heritability equal to 1 and a non null environmental correlation cannot exist.

Table 7.5 presents the algebraic formula for coheritability, coenvironmentability and phenotypic correlations, as affected by the heritabilities and the correlations.

Table 7.5 Special Cases

	$0 < h_x^2 < 1$ and $0 < h_y^2 < 1$	$h_x^2 = 0.5$ and $h_y^2 = 0.5$	$h_x^2 = h_y^2$	$h_x^2 + h_y^2 = 1$
$-1 < r_{A,x,y} < 1$ $-1 < r_{E,x,y} < 1$	**[1]** $r_{P_{x,y}} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y} + \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$	**[10]** $r_{P_{x,y}} = 0.5\left[r_{A,x,y} + r_{E,x,y}\right]$ $h_{x,y} = 0.5\, r_{A,x,y}$ $e_{x,y} = 0.5\, r_{E,x,y}$	**[19]** $r_{P_{x,y}} = h_x^2\left(r_{A,x,y} + r_{E,x,y}\right) + r_{E,x,y}$ $h_{x,y} = h_x^2\, r_{A,x,y}$ $e_{x,y} = (1-h_x^2)\, r_{E,x,y}$	**[28]** $r_{P_{x,y}} = \sqrt{h_x^2(1-h_x^2)}\left[r_{A,x,y} + r_{E,x,y}\right]$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $e_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{E,x,y}$
$-1 < r_{A,x,y} < 1$ $r_{E,x,y} = 0$	**[2]** $r_{P_{x,y}} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $e_{x,y} = 0$	**[11]** $r_{P_{x,y}} = 0.5\, r_{A,x,y}$ $h_{x,y} = 0.5\, r_{A,x,y}$ $e_{x,y} = 0$	**[20]** $r_{P_{x,y}} = h_x^2\, r_{A,x,y}$ $h_{x,y} = h_x^2\, r_{A,x,y}$ $e_{x,y} = 0$	**[29]** $r_{P_{x,y}} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $e_{x,y} = 0$
$r_{A,x,y} = 0$ $-1 < r_{E,x,y} < 1$	**[3]** $r_{P_{x,y}} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$ $h_{x,y} = 0$ $e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$	**[12]** $r_{P_{x,y}} = 0.5\, r_{E,x,y}$ $h_{x,y} = 0$ $e_{x,y} = 0.5\, r_{E,x,y}$	**[21]** $r_{P_{x,y}} = r_{A,x,y} + (1-h_x^2)$ $h_{x,y} = 0$ $e_{x,y} = (1-h_x^2)\, r_{E,x,y}$	**[30]** $r_{P_{x,y}} = \sqrt{h_x^2(1-h_x^2)}\, r_{E,x,y}$ $h_{x,y} = 0$ $e_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{E,x,y}$
$-1 < r_{A,x,y} < 1$ $r_{E,x,y} = 1$	**[4]** $r_{P_{x,y}} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y} + \sqrt{(1-h_x^2)(1-h_y^2)}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}$	**[13]** $r_{P_{x,y}} = 0.5\left[r_{A,x,y} + 1\right]$ $h_{x,y} = 0.5\, r_{A,x,y}$ $e_{x,y} = 0.5$	**[22]** $r_{P_{x,y}} = h_x^2\, r_{A,x,y} + (1-h_x^2)$ $h_{x,y} = h_x^2\, r_{A,x,y}$ $e_{x,y} = (1-h_x^2)$	**[31]** $r_{P_{x,y}} = \sqrt{h_x^2(1-h_x^2)}\left[r_{A,x,y}+1\right]$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $e_{x,y} = \sqrt{h_x^2(1-h_x^2)}$
$r_{A,x,y} = 1$ $-1 < r_{E,x,y} < 1$	**[5]** $r_{P_{x,y}} = \sqrt{h_x^2 h_y^2} + \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}$ $e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$	**[14]** $r_{P_{x,y}} = 0.5\left[1 + r_{E,x,y}\right]$ $h_{x,y} = 0.5$ $e_{x,y} = 0.5$	**[23]** $r_{P_{x,y}} = h_x^2 + (1-h_x^2)\, r_{E,x,y}$ $h_{x,y} = h_x^2$ $e_{x,y} = (1-h_x^2)\, r_{E,x,y}$	**[53]** $r_{P_{x,y}} = \sqrt{h_x^2(1-h_x^2)}\left[r_{E,x,y}+1\right]$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{E,x,y}$ $e_{x,y} =$
$r_{A,x,y} = r_{E,x,y}$	**[6]** $r_{P_{x,y}} = \left[\sqrt{h_x^2 h_y^2} + \sqrt{(1-h_x^2)(1-h_y^2)}\right] r_{A,x,y}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{A,x,y}$	**[15]** $r_{P_{x,y}} = r_{A,x,y} = r_{E,x,y}$ $h_{x,y} = 0.5\, r_{A,x,y}$ $e_{x,y} = 0.5\, r_{E,x,y}$	**[24]** $r_{P_{x,y}} = 1$ $h_{x,y} = h_x^2\, r_{A,x,y}$ $e_{x,y} = (1-h_x^2)\, r_{E,x,y}$	**[32]** $r_{P_{x,y}} = 2\sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}$ $e_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$
$r_{A,x,y} = -r_{E,x,y}$	**[7]** $r_{P_{x,y}} = \left[\sqrt{h_x^2 h_y^2} - \sqrt{(1-h_x^2)(1-h_y^2)}\right] r_{A,x,y}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $e_{x,y} = -\sqrt{(1-h_x^2)(1-h_y^2)}\, r_{A,x,y}$	**[16]** $r_{P_{x,y}} = 0$ $h_{x,y} = 0.5\, r_{A,x,y}$ $e_{x,y} = -0.5\, r_{A,x,y}$	**[25]** $r_{P_{x,y}} = -1 + 2\, h_x^2\, r_{A,x,y}$ $h_{x,y} = h_x^2\, r_{A,x,y}$ $e_{x,y} = -(1-h_x^2)\, r_{A,x,y}$	**[33]** $r_{P_{x,y}} = 0$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $e_{x,y} = -(1-h_x^2)\, r_{A,x,y}$
$r_{A,x,y} + r_{E,x,y} = 1$	**[8]** $r_{P_{x,y}} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y} + \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E,x,y}$	**[17]** $r_{P_{x,y}} = 0.5$ $h_{x,y} = 0.5\, r_{A,x,y}$ $e_{x,y} = 0.5\,(1-r_{A,x,y})$	**[26]** $r_{P_{x,y}} = 1 + 2\, h_x^2\, r_{A,x,y} - h_x^2 - r_{A,x,y}$ $h_{x,y} = h_x^2\, r_{A,x,y}$ $e_{x,y} = (1-h_x^2)(1 - r_{A,x,y})$	**[34]** $r_{P_{x,y}} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$ $e_{x,y} = -\sqrt{h_x^2(1-h_x^2)}\, r_{A,x,y}$
$r_{A,x,y} + r_{E,x,y} = 1$	**[9]** $r_{P_{x,y}} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y} + \sqrt{(1-h_x^2)(1-h_y^2)}$ $h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A,x,y}$ $e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}$	**[18]** $r_{P_{x,y}} = 1$ $h_{x,y} = 0.5$ $e_{x,y} = 0.5$	**[27]** $r_{P_{x,y}} = 1$ $h_{x,y} = h_x^2$ $e_{x,y} = (1-h_x^2)$	**[35]** $r_{P_{x,y}} = 2\sqrt{h_x^2(1-h_x^2)}$ $h_{x,y} = \sqrt{h_x^2(1-h_x^2)}$ $e_{x,y} = \sqrt{h_x^2(1-h_x^2)}$

Finally, the value that of the phenotypic correlation "approaches" as the covariance input "approaches" zero, shows that at the limit the phenotypic correlation can become one of its components, the coheritability or the coenvironmentability.

$$\lim_{C_{E_{x,y}} \to 0} \left(r_{P_{x,y}} \right) = \lim_{C_{E_{x,y}} \to 0} \left(\frac{C_{P_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}} \right) = \lim_{C_{E_{x,y}} \to 0} \left(\frac{C_{A_{x,y}} + C_{E_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}} \right) = h_{x,y}$$

and

$$\lim_{C_{A_{x,y}} \to 0} \left(r_{P_{x,y}} \right) = \lim_{C_{A_{x,y}} \to 0} \left(\frac{C_{P_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}} \right) = \lim_{C_{A_{x,y}} \to 0} \left(\frac{C_{A_{x,y}} + C_{E_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}} \right) = e_{x,y}$$

7.6 The assumption that $r_{P_{x,y}} = r_{A_{x,y}}$

To assume that the phenotypic correlation is a suitable proxy for the genetic correlation. At the extreme case when $r_{P_{x,y}} = r_{A_{x,y}}$, some implications can be deduced:

(A) The phenotypic variance of each trait is entirely composed of additive genetic variance and null environmental variance.
(B) This implies that the heritability of each trait is unity.
(C) The environmental correlation becomes undefined because its denominator would include zero.
(D) Thus,

$$r_{P_{x,y}} = \sqrt{h_x^2 \, h_y^2} \; r_{A_{x,y}} + \sqrt{(1 - h_x^2)(1 - h_y^2)} \; r_{E_{x,y}}$$

$$r_{P_{x,y}} = \sqrt{1 \cdot 1} \; r_{A_{x,y}} = r_{A_{x,y}}$$

These are problematic assumptions, especially if applied in studies in the wild, and even in field tests of plant and animal breeding, where the environmental effects are generally strong and of importance.

7.7 Disparity between the phenotypic and genetic correlations

Disparity D denotes the absolute difference of the phenotypic and genetic correlations (Willis et al. 1991).

$$D = |r_{P_{x,y}} - r_{A_{x,y}}|$$

This is a measure to assess the closeness of the values of the phenotypic and genetic correlations to one another.

The disparity index D is equivalent to the following relationship,

$$\left| \underbrace{\sqrt{h_x^2 \, h_y^2} \, r_{A_{x,y}} + \sqrt{(1 - h_x^2)(1 - h_y^2)} \, r_{E_{x,y}}}_{r_{P_{x,y}}} - r_{A_{x,y}} \right|$$

which reduces to

$$D = \left| \left(\sqrt{h_x^2 \, h_y^2} - 1 \right) r_{A_{x,y}} + \sqrt{(1 - h_x^2)(1 - h_y^2)} \, r_{E_{x,y}} \right|$$

7.7.1 The domain of the Disparity Index

To properly address issues regarding the domain of the Disparity Index, it is useful to review the relationship maintained by the heritabilities and correlations, as presentred in table 7.7.1.

If $r_{P_{x,y}} = 1$, it means that either the coheritability or the coenvironmentability equals 1. Let's analyze each case.

Case 1: If $r_{P_{x,y}} = 1$, and $h_{x,y} = 1$ ($e_{x,y} = 0$). If the coheritability equals 1 then the only combination of values allowed is that all $h_x^2 = 1, h_y^2 = 1$, $r_{A_{x,y}} = 1$ (causing the coenvironmentability to become zero, note if the heritabilities are 1, then $\sqrt{(1 - h_x^2)(1 - h_y^2)} = 0$). The disparity is $D = |1 - 1| = 0$.

Case 2: If $r_{P_{x,y}} = 1,\ and\ h_{x,y} = 0\ (\ e_{x,y} = 1\ )$. In the case that the coheritability is zero, it is useful to analyze it by decomposing it into its constituents.

$$h_{x,y} = \sqrt{h_x^2\, h_y^2} \cdot r_{A_{x,y}} \qquad \text{for } 0 < h_{\blacksquare}^2 < 1, -1 < r_{A_{x,y}} < 1$$

$$= \frac{\sigma_{A_x}\,\sigma_{A_y}}{\sigma_{P_x}\,\sigma_{P_y}} \cdot \frac{\sigma_{A_{x,y}}}{\sigma_{A_x}\sigma_{A_y}} \qquad \text{for } \sigma_{A_x} > 0,\ \sigma_{A_x} > 0,\ \sigma_{P_x} > 0,\ \sigma_{P_y} > 0$$

One notices that the numerator of the square root of the product of the heritabilities is also the denominator of the genetic correlation. If a heritability equals zero, it means that the genetic variance (the numerator) is zero, is also part of the denominator of the genetic correlation (see Section 7.5) Additional cases are presented in Table 7.7.1 .

An intuitive way to express this finding is presented below.

$$D = |r_{P_{x,y}} - r_{A_{x,y}}|$$

$$\left|r_{P_{x,y}} - r_{A_{x,y}}\right| < 1$$

$$-1 < r_{P_{x,y}} - r_{A_{x,y}} \le 1$$

$$-1 + r_{A_{x,y}} < r_{P_{x,y}} < 1 + r_{A_{x,y}}$$

Note at this point that if $r_{A_{x,y}} = 0$, then $-1 < r_{P_{x,y}} < 1$

Let's analyze each bound separately.

When $r_{P_{x,y}} > 0$, the upper bound, $r_{P_{x,y}} < 1 + r_{A_{x,y}}$ cannot exceed unity, therefore to satisfy this condition $r_{A_{x,y}}$ must have negative values.

When $r_{P_{x,y}} < 0$, the lower bound, $r_{P_{x,y}} > -1 + r_{A_{x,y}}$, cannot be lower than -1, therefore $r_{A_{x,y}}$ should have positive values.

To summarize, the bounds the bounds of the Disparity Index is $-1 < D < 1$, or more explicitly

$$D = \begin{cases} r_{P_{x,y}} - r_{A_{x,y}} < 1 & for\ r_{A_{x,y}} < 0,\ r_{P_{x,y}} > 0 \\ r_{P_{x,y}} & for\ r_{A_{x,y}} = 0 \\ r_{P_{x,y}} - r_{A_{x,y}} > -1 & for\ r_{A_{x,y}} > 0, r_{P_{x,y}} < 0 \end{cases}$$

$r_{P_{x,y}}$	$\sqrt{h_x^2}$	$\sqrt{h_y^2}$	$r_{A_{x,y}}$	$\sqrt{(1-h_x^2)}$	$\sqrt{(1-h_y^2)}$	$r_{E_{x,y}}$	$D=\lvert r_{P_{x,y}}-r_{A_{x,y}}\rvert$
		$h_{x,y}$			$e_{x,y}$		
1	$\sqrt{1}$	$\sqrt{1}$	1	$\sqrt{1-1}$	$\sqrt{1-1}$	$r_{E_{x,y}}$	0 = |1 - 1|
		$h_{x,y}=1$			$e_{x,y}=0$		
1	$\sqrt{1}$	$\sqrt{1}$	$r_{A_{x,y}}$	$\sqrt{1-1}$	$\sqrt{1-1}$	$r_{E_{x,y}}$	$\lvert 1-r_{A_{x,y}}\rvert$
		$h_{x,y}=r_{A_{x,y}}$			$e_{x,y}=0$		
1	$\sqrt{0.5}$	$\sqrt{0.5}$	1	$\sqrt{1-0.5}$	$\sqrt{1-0.5}$	1	0 = |1 - 1|
		$h_{x,y}=0.5$			$e_{x,y}=0.5$		
-1	$\sqrt{1}$	$\sqrt{1}$	-1	$\sqrt{1-1}$	$\sqrt{1-1}$	$r_{E_{x,y}}$	0 = |-1 - (-1)|
		$h_{x,y}=-1$			$e_{x,y}=0$		
-1	$\sqrt{0.5}$	$\sqrt{0.5}$	-1	$\sqrt{1-0.5}$	$\sqrt{1-0.5}$	-1	0 = |-1 -(- 1)|
		$h_{x,y}=-0.5$			$e_{x,y}=-0.5$		
0	$\sqrt{1}$	$\sqrt{h_y^2}$	0	$\sqrt{1-1}$	$\sqrt{1-h_y^2}$	$r_{E_{x,y}}$	0 = |0 - 0|
		$h_{x,y}=0$			$e_{x,y}=0$		
0	$\sqrt{h_x^2}$	$\sqrt{h_y^2}$	0	$\sqrt{(1-h_y^2)}$	$\sqrt{1-h_y^2}$	0	0 = |0 - 0|
		$h_{x,y}=0$			$e_{x,y}=0$		
0	$\sqrt{0.5}$	$\sqrt{0.5}$	1	$\sqrt{1-0.5}$	$\sqrt{1-0.5}$	-1	1 = |0 - 1|
		$h_{x,y}=0.5$			$e_{x,y}=-0.5$		
0	$\sqrt{0.5}$	$\sqrt{0.5}$	-1	$\sqrt{1-0.5}$	$\sqrt{1-0.5}$	1	1 = |0 - (-1)|
		$h_{x,y}=-0.5$			$e_{x,y}=0.5$		
0	$\sqrt{0.5}$	$\sqrt{0.5}$	$r_{A_{x,y}}$	$\sqrt{1-0.5}$	$\sqrt{1-0.5}$	$r_{E_{x,y}}=-r_{A_{x,y}}$	$\lvert r_{A_{x,y}}\rvert=\lvert 0-r_{A_{x,y}}\rvert$
		$h_{x,y}=0.5\,r_{A_{x,y}}$			$e_{x,y}=-0.5\,r_{A_{x,y}}$		

$r_{P_{x,y}}$	$\sqrt{h_x^2}$	$\sqrt{h_y^2}$	$r_{A_{x,y}}$	$\sqrt{(1-h_x^2)}$	$\sqrt{(1-h_y^2)}$	$r_{E_{x,y}}$	D
1	$\sqrt{0}$	$\sqrt{0}$	$r_{A_{x,y}}$	$\sqrt{1-0}$	$\sqrt{1-0}$	1	$\lvert 1-r_{A_{x,y}}\rvert$
		$h_{x,y}=0$			$e_{x,y}=1$		
-1	$\sqrt{0}$	$\sqrt{0}$	$r_{A_{x,y}}$	$\sqrt{1-0}$	$\sqrt{1-0}$	-1	$\lvert -1-r_{A_{x,y}}\rvert$
		$h_{x,y}=0$			$e_{x,y}=-1$		
1	$\sqrt{0}$	$\sqrt{0}$	-1	$\sqrt{1-0}$	$\sqrt{1-0}$	1	2 = | 1 - (-1) |
		$h_{x,y}=0$			$e_{x,y}=1$		
-1	$\sqrt{0}$	$\sqrt{0}$	1	$\sqrt{1-0}$	$\sqrt{1-0}$	-1	2 = | -1 - 1 |
		$h_{x,y}=0$			$e_{x,y}=-1$		

Table 7.7.1 Disparity index measures under varying values of phenotypic and genetic correlations. Note the last four rows, which show incongruence relationship between the genetic and the environmental correlations, produce invalid disparity indices.
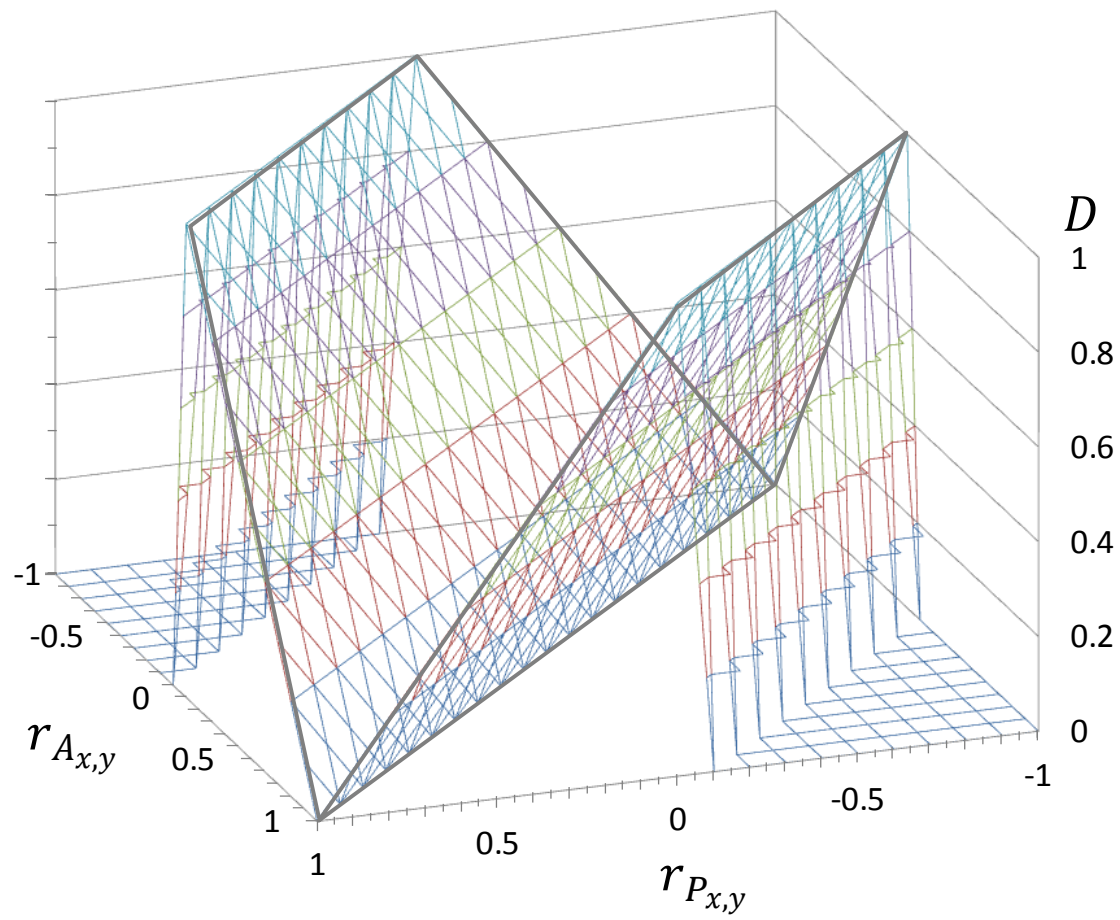
Figure 7.7.1 Surface graph depicting the Disparity Index D as a function of the phenotypic correlation $r_{P_{x,y}}$ and the genetic correlation $r_{A_{x,y}}$.

7.7.2 Distribution of the Disparity Index

The distribution of D can be modelled as the absolute difference of two uniform variables, which results in the triangular distribution. Our purpose now is to find the cumulative density function (CDF) and the probability density function (PDF) of D.

Let P and A be random variables distributed identically and independently as standard uniform, such that

$$P \sim U(0,1), \quad f_P(p) = 1, \quad 0 < p < 1,$$

$$A \sim U(0,1), \quad f_A(a) = 1, \quad 0 < a < 1,$$

Define the new variable $D = |P - A|$.

The subset within the unit square that is between the two lines represents the area where the event $\{|P - A| \le d\}$ for $0 \le d \le 1$ occurs. The area of the unit square is 1. The dimension of the subset (a hexagon) is obtained by subtracting the area of the two triangles, each encompassing $\frac{(1-d)^2}{2}$.
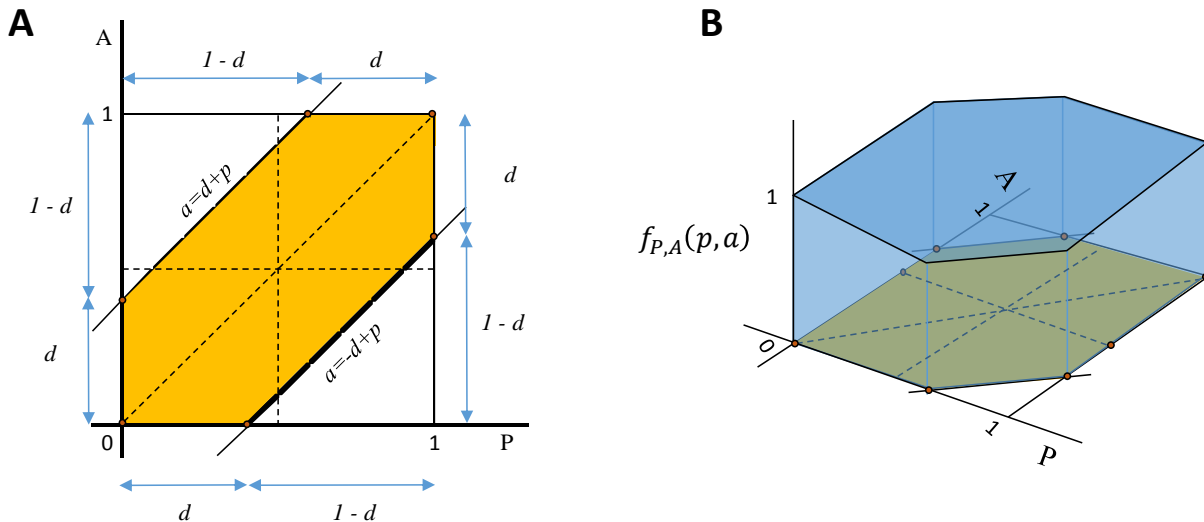
Figure 7.7.2-1 Event $\{|P - A| \le d\}$. (A) Area representing the occurrence of the event. (B) Volume representing the probability of the event.

Within this region, the probability is the volume within the two lines (yellow region in Figure 7.7.2-1A). The overall volume is a cube with dimension 1x1x1=1 is obtained by multiplying by 1 since that is the uniform pdf in each point (P, A) (Figure 7.7.2-2).

The cumulative density function of D

Is obtained by determining the probability of D taking values less than d

$$F_D(d) = Pr\{D \leq d\} = Pr\{\{||P - A|\}| \leq d\}$$

$$= 1 - 2\frac{(1-d)^2}{2} = 2d - d^2$$

$$= d(2 - d) \qquad \text{for } 0 \leq d \leq 1$$

$$F_D(d) = \begin{cases} 0 & d < 1 \\ d(2 - d) & 0 \leq d \leq 1 \\ 0 & d > 1 \end{cases}$$

$F_D(d)$
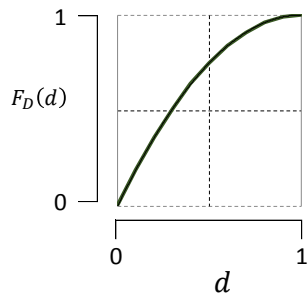
The probability density function of D

Is obtained by differentiating the cumulative function F_D with respect to d.

$$f_D(d) = \begin{cases} 0 & d < 0 \\ \dfrac{\mathrm{d}(F_D)}{\mathrm{d}d} = 2 - 2d & 0 \leq d \leq 1 \\ 0 & d > 1 \end{cases}$$

$f_D(d)$
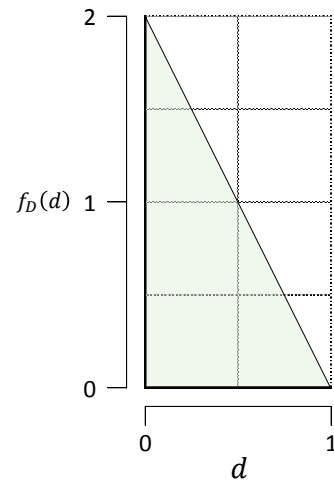
7.7.3 A simulation model to generate disparity data

The disparity between the phenotypic and genetic correlation, as we have seen, can only obtain values between zero and one (Section 7.7.1).

To generate simulated data of the disparity index, a model can be devised as the distribution of a simple difference of two standard uniform random variables. Here a convolution method is employed.

Let X_1 and X_2 be random variables distributed identically and independently as standard uniform, such that

$$X_1 \sim U(0,1), \quad f_{X_1}(x_1) = 1, \quad 0 < x_1 < 1$$

$$X_2 \sim U(0,1), \quad f_{X_2}(x_2) = 1, \quad 0 < x_2 < 1$$

The joint density of (X_1, X_2) is

$$f_{X_1, X_2}(x_1, x_2) = f_{X_1}(x_1) \cdot f_{X_2}(x_2) = \begin{cases} 1 & for\ 0 \leq x_1 \leq 1\ ,\ 0 \leq x_2 \leq 1 \\ 0 & elsewhere \end{cases}$$

Let's define $= X_1 - X_2$, such that the value of $x_1 = z + x_2$

$$0 \leq x_1 \leq 1$$

$$0 \leq z + x_2 \leq 1$$

$$-x_2 \leq\ z\ \leq 1 - x_2$$

which can be replaced in the joint density pdf, as follows.

$$f_{X_1, X_2}(x_1, x_2) = f_{X_1, X_2}(z + x_2, x_2) = \begin{cases} 1 & for\ 0 \leq x_2 \leq 1\ ,\ z \geq -x_2\ ,\ z + x_2 \leq 1 \\ 0 & elsewhere \end{cases}$$
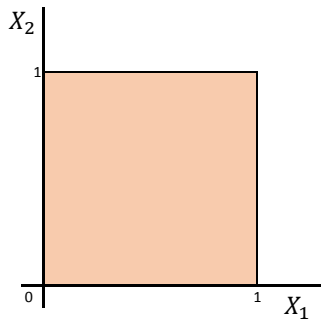
X_1	X_2
0	0
0	1
1	0
1	1
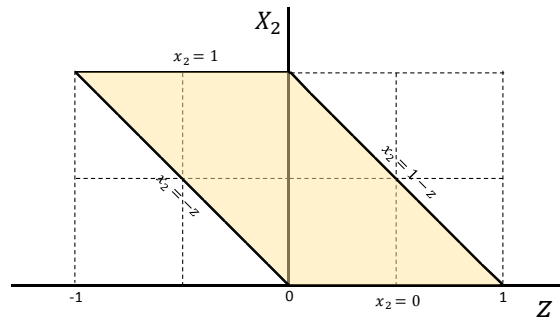
Z $X_1 - X_2$	X_2
0	0
-1	1
1	0
0	1

The tables above help corroborate that this is a 1-to-1 transformation.

The probability density function of z is obtained by solving the convolution integrals

$$f_Z(z) = \int_{-\infty}^{+\infty} f_{X_1,X_2}(z + x_2 , x_2) \, dx_2 = \int_{-\infty}^{+\infty} f_{X_1}(z + x_2) \cdot f_{X_2}(x_2) \, dx_2 = \int_{-\infty}^{+\infty} f_{X_1}(z + x_2) \, dx_2$$

$$f_Z(z) = \begin{cases} 0 & z < -1 \\ \int_{-z}^{1} 1 \, dx_2 = [1 - (-z)] = 1 + z & -1 \leq z < 0 \\ 1 & z = 0 \\ \int_{0}^{1-z} 1 \, dx_2 = [1 - z - 0] = 1 - z & 0 < z \leq 1 \\ 0 & z > 0 \end{cases}$$

And the cumulative density function of z is

$$F_Z(z) = Pr\{Z \leq z\} = Pr\{X_1 - X_2 \leq z\}$$

$$F_Z(z) = \begin{cases} 0 & z < -1 \\ \int_{x_1=0}^{z} \int_{x_2=x_1-z}^{1} 1 \, dx_2 \, dx_1 = \dfrac{z^2}{2} + z + \dfrac{1}{2} & -1 \leq z < 0 \\ 0.5 & z = 0 \\ 1 - \int_{x_1=z}^{1} \int_{x_2=0}^{x_1-z} 1 \, dx_2 \, dx_1 = -\dfrac{z^2}{2} + z + \dfrac{1}{2} & 0 < z \leq 1 \\ 0 & z > 0 \end{cases}$$

The cumulative density function of z	The probability density function of z
$$F_Z(z) = \begin{cases} 0 & z < -1 \\ \dfrac{z^2}{2} + z + \dfrac{1}{2} & -1 \leq z < 0 \\ 0.5 & z = 0 \\ -\dfrac{z^2}{2} + z + \dfrac{1}{2} & 0 < z \leq 1 \\ 0 & z > 0 \end{cases}$$	$$f_Z(z) = \begin{cases} 0 & z < -1 \\ 1 + z & -1 \leq z < 0 \\ 1 & z = 0 \\ 1 - z & 0 < z \leq 1 \\ 0 & z > 0 \end{cases}$$
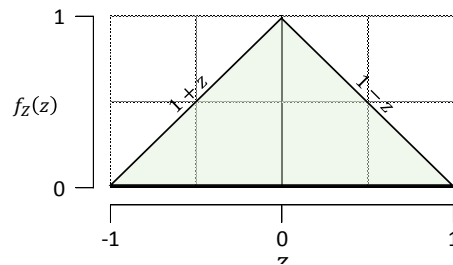
7.7.4 The ratio of the genetic correlation over the phenotypic correlation

The ratio k between the genetic correlation and the phenotypic correlation can be deduced if the phenotypic correlation and the disparity index are known. This ratio is another parameter that reveal the degree of difference between the genetic and phenotypic correlations.

Figure 7.7.4 illustrates how the ratio behave as a function of the phenotypic correlation and the disparity index.

(A) When the genetic and phenotypic correlation have the same sign, the ratio oscillates between zero and is 1 (or 100%). The latter is equivalent that $r_{A_x} = r_{P_x}$, and its line correspond to the base of the triangle.

(B) When the genetic and phenotypic correlation have different sign, the ratio goes from zero to extreme values (< -900%). A ratio equal to -200% indicates that the henetic correlation value is the double of the phenotypic correlation, $|r_{A_x}| = 2|r_{P_x}|$, the sign indicating the genetic correlation has a different sign than the phenotypic correlation.

(C) When $r_{A_x} = 0$, then the disparity is $D = r_{P_x}$ and the ratio is zero (**0 %**).

(D) For a given disparity value there are different ratios that can be associated to it , dependning on the value of r_{P_x} .

(E) For a given value of r_{P_x} , there is a continuum of ratios that depend upon the D value.

(F) As the phenotypic correlation approaches zero, irrespective of the disparity value, the ratio assumes extreme values, showing a marked difference between r_{A_x} and r_{P_x}.
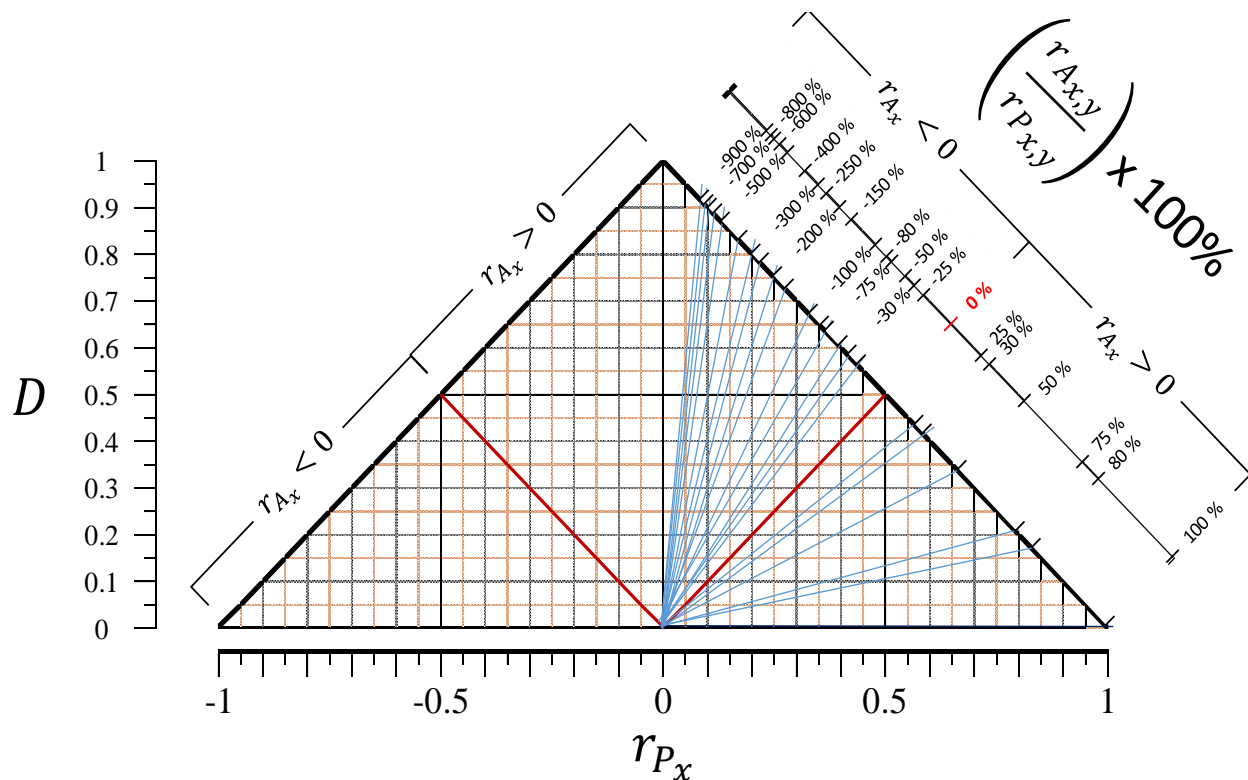
Figure 7.7.4-1 Ratio of the genetic correlation over the phenotypic correlation as a function of the disparity index and the phenotypic correlation. Only one size is labeled. A mirror image of the lines apply at the left side of the triangle where the $r_{P_x} < 0$. The sign associated to the percentage indicates that r_{A_x} has a different sign than the phenotypic correlation. At the right side ($r_{P_x} > 0$), negative sign percentages indicate that the r_{A_x} is negative. At the left side ($r_{P_x} < 0$), negative sign indicates that r_{A_x} is positive.

Table 7.7.4-1

Values of the ratio k, and parameters of the line that starts at the origin and reaches the side of the triangle at the point (r_{P_k} , D_k) having a slope m.
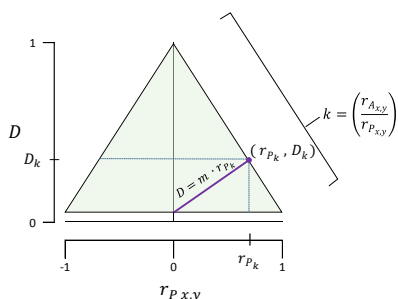
$k = \left(\dfrac{r_{A_{x,y}}}{r_{P_{x,y}}}\right)$	m	$r_{P_{x,y\,k}}$	D_k	$k \cdot$
-10	11	0.083	0.917	-1
-9	10	0.091	0.909	-9
-8	9	0.100	0.900	-8
-7	8	0.111	0.889	
-6	7	0.125	0.875	-6
-5	6	0.143	0.857	-5
-4	5	0.167	0.833	
-3	4	0.200	0.800	-3
-2.5	3.5	0.222	0.778	
-2	3	0.250	0.750	-2
-1.5	2.5	0.286	0.714	
-1	2	0.333	0.667	1
-0.8	1.8	0.357	0.643	
-0.75	1.75	0.364	0.636	
-0.5	1.5	0.400	0.600	
-0.3	1.3	0.435	0.565	
-0.25	1.25	0.444	0.556	
0	**1**	**0.500**	**0.500**	
0.25	0.75	0.571	0.429	
0.3	0.7	0.588	0.412	
0.5	0.5	0.667	0.333	
0.75	0.25	0.800	0.200	

See below for a description of the algorithm used to create Figure 7.7.4-1.
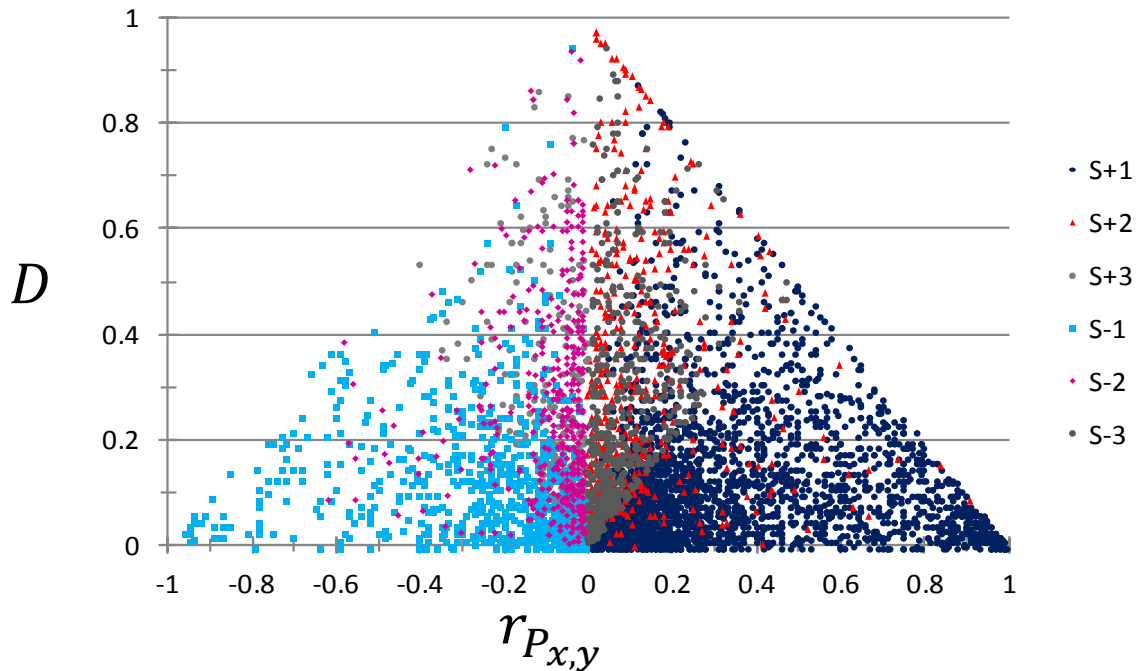
Figure 7.7.4-2 Disparity data derived from genetic and phenotypic correlations collected from an extensive literature review ($n = 6280$). A first impression points out to the fact that in the majority of the cases, the value of the genotypic correlation differ quite significantly from the value of the phenotypic correlation.

Algorithm to derive the line corresponding to a given ratio k of the genetic correlation over the phenotypic correlation

.1 Select a given value of the ratio $k = \left(\frac{r_{A_{x,y}}}{r_{P_{x,y}}}\right)$. If the phenotypic correlation has the same sign as the genetic correlation, then the maximum k is 1. If the phenotypic correlation and the genetic correlation differ in sign, then k can be from zero to 10 (above 10 is possible, but the value of r_P will be extremely small). For example, choosing a value of 5 means that r_A is 5 times larger than , or that r_A is 500% the value of r_P.

.2 Determine the slope of the line $m = 1 - k$.

.3 Determine the phenotypic correlation value $r_{P_k} = \frac{1}{1+|m|}$. (If working with the negative phenotypic correlation, multiply by -1.

.4 Determine the disparity index D_k .

.5 Trace the line from the origin to the point $\left(r_{P_k},\ D_k \right)$. The line covers all the combinations of $\left(r_{P_{x,y}},\ D \right)$ that have a ratio equal to k.

8 Selection

The term $\sqrt{h_x^2\, h_y^2}\; r_{A_{x,y}}$ is a measure of coinheritance of a pair of phenotypic traits that is due to shared genetics. This expression has named *coheritability* by Nei (1960), and further studied by others (Searle 1961, Falconer 1960). It is in the last edition of *Principles of Quantitative Genetics* by Falconer and Mackay (1996) in which the term coheritability was reintroduced.   The name is derived from the context of correlated response to selection. The formula for the expected response R_X of a progeny in terms of phenotypic gain in trait x due to selection of parents based on the same trait is

$$ R_x = i\,(\,h_x^2\,)\,\sigma_{P_X} \qquad\qquad [\,8-1\,] $$

where i is the intensity of selection, and σ_{P_x} is the phenotypic standard deviation of trait x. In an analogous way, the expected response of correlated trait x when parental selection is based one trait y is:

$$ R_{X|Y} = i\,\left(\sqrt{h_x^2 h_y^2}\; r_{A_{x,y}}\right)\sigma_{P_X} \qquad\qquad [\,8-2\,] $$

The term in brakets is the coheritability, which functions in an analogous manner as the heritability in equation [8-1].

Yet despite its implicit use, very little attention has been paid to understand the statistical and mathematical properties of coheritability. There is a persistent confusion in the scientific literature of what this term means or how should be calculated. Denoted as *coheritability* some reports present expressions that do not possess any consistent theoretical background, such as the mere ratio of additive genetic to phenotypic covariances $\frac{C_A}{C_P}$ (de Reggi 1972, Janssens 1979). The simple ratio

$\frac{C_A}{C_P} = \frac{\sqrt{V_{Ax}V_{Ay}}\, r_A}{\sqrt{V_{Px}V_{Py}}\, r_P} = \frac{\sqrt{h_x^2\, h_y^2}\; r_{Axy}}{r_P} = \frac{h_{x,y}}{r_P} \neq h_{xy}$, clearly is not a recognizable coheritability form (its bounds go from zero to infinity).

Most quantitative phenotypes are polygenic, and for these traits, selection is likely to act on many preexisting genetic variants of small effect. Detecting so called polygenic selection is challenging because selection acts on multiple loci simultaneously.

For the sake of completeness and to introduce symbols denoting estimators to be used later, this section starts with a brief explanation of the theory of mass selection and correlated response.

8.1 Realized heritability

The mass selection method aims in choosing a subset of individuals from a original population to breed and generate the progeny (or offspring) generation. Individuals are ordered my their phenotypic value. Individuals whose phenotypic value are above a pre-specified value (i.e., truncation point), generally at an extreme of the distribution, are selected. Therefore, individuals are selected solely strictly by their rank judge by their phenotypic values.

Based on the assumption that the distribution of phenotypic values of the population follows a normal distribution $N(\bar{P}_o, \sigma_P^2)$, the observed mean phenotypic value of the original distribution ($\bar{P}_o$), and the mean phenotypic value of the subset of individuals chosen ($\bar{P}_s$) differ in the amount called the selection differential

$$S = (\bar{P}_s - \bar{P}_o).$$

S depends on the percentage k of individuals of the original population selected as parents, and the phenotypic standard deviation of the original population. The expected mean value of the selected individuals above the truncation point t $(t > 0)$ is

$$E(x_s) = E(P \mid P > t) = \frac{h}{k}$$

and the variance of the selected individuals is

$$Var(P_s) = Var(P \mid P > t) = 1 - \frac{h}{k}\left(\frac{h}{k} - t\right)$$

where h is the height (i.e. ordinate) of the standard normal curve at point t.

parental generation

s_P^2

h k

t

$\bar{P}_o$ $\bar{P}_S$

S

progeny generation

$\bar{P}_1$

R

-3.5 -3.0 -2.5 -2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
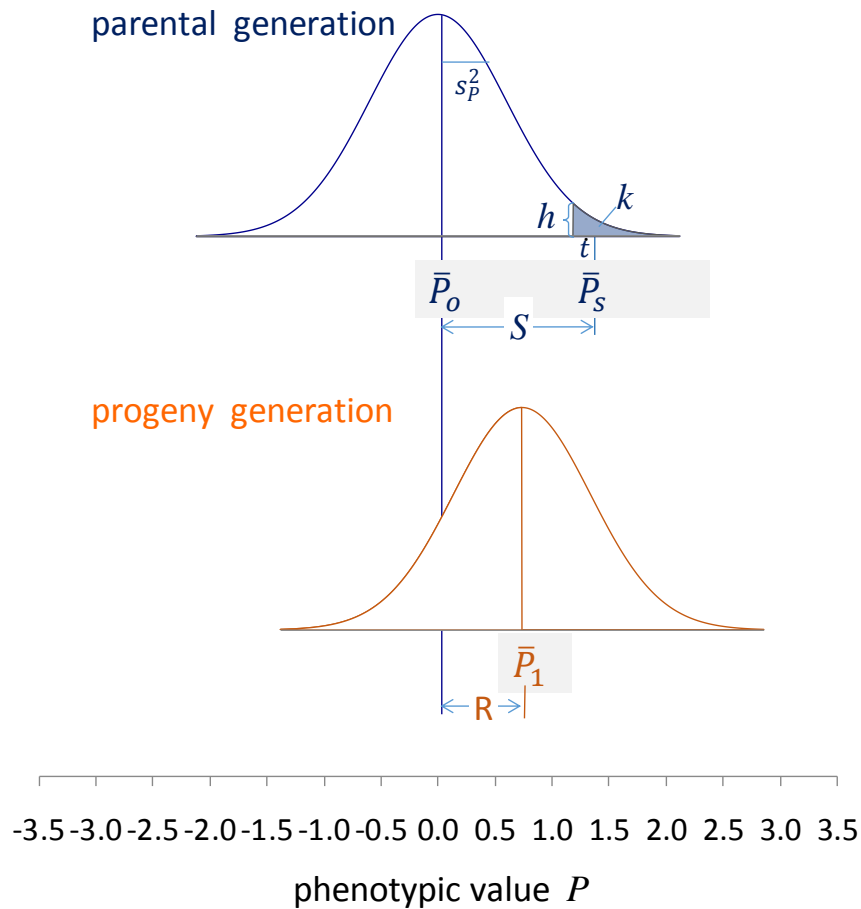
phenotypic value P

The expected response (R) to mass selection for a desired trait is

$$R = h^2 S$$

When the progeny has been obtained and its mean phenotypic value $(\bar{P}_1)$ determined, the realized response to selection is calculated as

$$R_{realized} = \bar{P}_1 - \bar{P}_o$$

Given than the both the selection differential S and the realized response $R_{realized}$ are known, it is then possible to determine the realized heritability of the trait as follows:

$$h^2_{realized} = \frac{R_{realized}}{S}$$

In practice, the cumulative response is plotted against the cumulated selection differential (Falconer and MacKay 1996, page 197ss), a a simple regression line is fitted. The slope of this line (b) is a function of the realized heritability, such that $b = v \cdot h_r^2$. The coefficient $v = 1$ if the trait is measured in all

individuals irrespective of their sex. If the measurements are obtained from either male or female, then $v = 0.5$, and the realized heritability in this case is obtained by doubling the slope.

8.2 Realized coheritability

Using the correlated response of trait y when selection was directed to trait x, a similar rationale can be used to determined the realized bivariate measures of genetic relationship.

By performing mass selection on an original population, based on the phenotypic value of trait x, using a specified selection differential S_x, both a direct response to selection for trait x (R_x) as well as a correlated response in trait y $(CR_{X|Y})$ are obtained.

(A) If one round of selection has been performed, then the realized coheritability is the ratio of the correlated response on the selection differential,

$$h_{x,y\ realized} = \frac{CR_{X|Y}}{S_x}$$

If several rounds of selection have been done, then one can plot cumulative correlated response of trait y on the cumulative selection differential of trait x, an a liner regression model fitted. The slope parameter b (which can be positive or negative) becomes a function of the coheritability, such that:

$$h_{x,y\ realized} = \begin{cases} b & \text{if analyses employ measurements of all individuals irrespective of sex} \\ 2b & \text{if analyses employ measurements of either male or female individuals} \end{cases}$$

(B) In the case of double selection experiments, in which one group of individuals is directly selected for the primary trait x yielding R_x, and trait y is assessed as a secondary (correlated) trait as $CR_{X|Y}$, and another group is directly selected for y (R_x), and x becomes the secondary trait $CR_{Y|X}$. Both are plotted and the coheritabilities calculated as expounded above. It is expected that the two estimates should be numerically close, provided the theory of correlated response is adequate to describe the results, and no discernible asymmetry is found in the direct and correlated responses. The estimate of the realized coheritability is the geometric mean of the slope parameters of the regressions.

$$h_{x,y\ realized} = \begin{cases} \pm v \cdot \sqrt{\left|\frac{CR_{X|Y}}{|\ S_{C_Y}} \frac{CR_{Y|X}}{S_{C_X}\ |}\right|} & \text{for one single round of double selection} \\ \pm v \cdot \sqrt{b_{X|Y}\ b_{Y|X}} & \text{for several rounds of double selection} \end{cases}$$

where S_{C_X} and S_{C_Y} are the selection differentials used for direct selection of trait x and y respectively. The sign depends on the relationship observed in the plot of the data. Again, $v = 1$ when individuals are selected irrespective of sex, and $v = 0.5$ if measurements come from only one sex.

(C) It both the realized heritabilities and genetic correlations (see below) have been estimated, then

$$h_{x,y\ realized} = \sqrt{h^2_{x\ realized}\ h^2_{y\ realized}\ r_{A_{x,y\ realized}}}$$

All the formulas presented are subject to large experimental variation and must be taken to indicate tendency rather than magnitude.
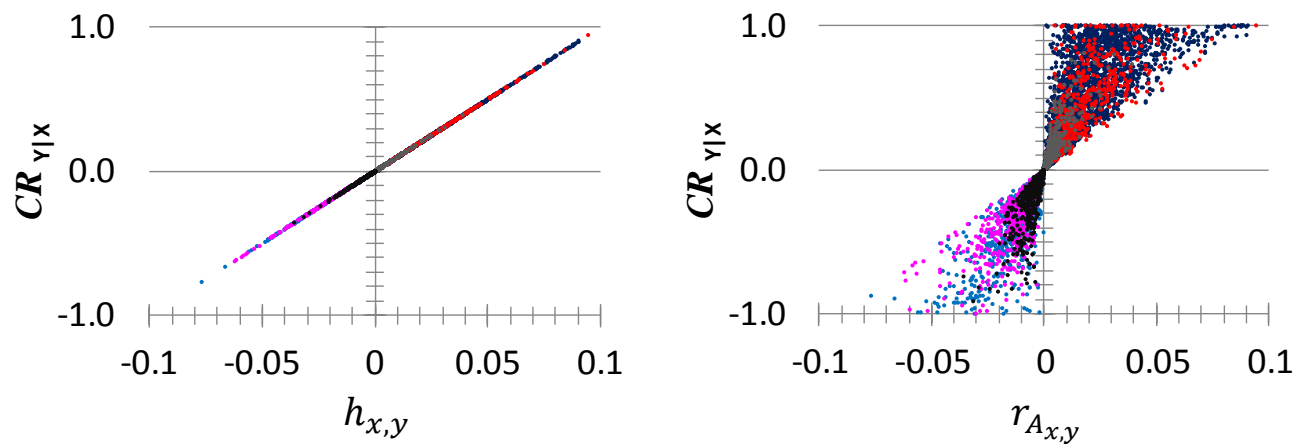
Figure 8.2 The coheritability and the genetic correlation in relation to their capability to predict the correlated response to selection. The intensity of selection was set to an intensity of selection $i = 0.1$ and the phenotypic variance of the correlated trait standardized to 1 ($n = 6288$).

8.3 Realized genetic correlation

The realized genetic correlation between two traits is,

$$
r_{A_{x,y}\ realized} =
\begin{cases}
\dfrac{CR_{Y|X}}{R_x} & \text{for single round of selection} \\[3ex]
\sqrt{\dfrac{CR_{X|Y}}{R_x}\ \dfrac{CR_{Y|X}}{R_y}} & \text{for double selection experiment}
\end{cases}
$$

Note that the value of the correlated response may be either positive or negative.

8.4 Relative efficiency of indirect selection with respect to direct selection

Observation of the response to selection of correlated traits may lead to consider that in certain circumstances it would be feasible to obtain more rapid and efficient advance of a desired character when applying selection for a secondary trait y which is correlated to x. This means that to improve character x, selection should be applied to another (secondary) character y and achieve progress through the correlated response of character x.

Indirect selection is advantageous under special conditions.

Let $R_x = i_x\, h_x^2\, \sigma_{P_x}$ be the direct response of the desired trait when selection is applied directly on character x.

Let $CR_{x|y} = i_y\, h_{xy}\, \sigma_{P_x}$ be the correlated response of character x resulting from selection applied to secondary character y.

The relative efficiency (RE) of selection is the value of indirect selection relative to that of direct selection, and could be expressed as the ratio of expected responses, as follows

$$RE = \frac{CR_{x|y}}{R_x} = \frac{i_y\, h_{x,y}\, \sigma_{P_x}}{i_x\, h_x^2\, \sigma_{P_x}} = \frac{i_Y\, h_{x,y}}{i_x\, h_x^2}$$

Lerner and Cruden (1948) defined as relative efficiency of indirect selection the expression $\frac{h_Y r_A}{h_X}$ which is equivalent to

$$RE = \frac{h_{x,y}}{h_X^2}$$

this equation allows to determine conditions of when indirect selection of x when selecting for y would be greater than the direct response to selection for x (see Figure 8.4),

$$i_Y\, h_{x,y} > i_x\, h_x^2$$

$$i_Y\, \sqrt{h_x^2\, h_y^2}\, r_{A_{xy}} > i_x\, h_x^2$$

$$i_Y\, \sqrt{h_y^2}\, r_{A_{xy}} > i_x\, \sqrt{h_x^2}$$

Inspection of this relationship shows that indirect selection would be greater if the heritability h_y^2 is greater than h_x^2, and the genetic correlation $r_{A_{xy}}$ is high. Cases like this would occur if trait x is difficult to measure with precision but y is not.

If the selection intensity is much greater for y than x would also result in a greater response of indirect selection. This would apply if y were measurable in both sexes by x measurable in only one sex.
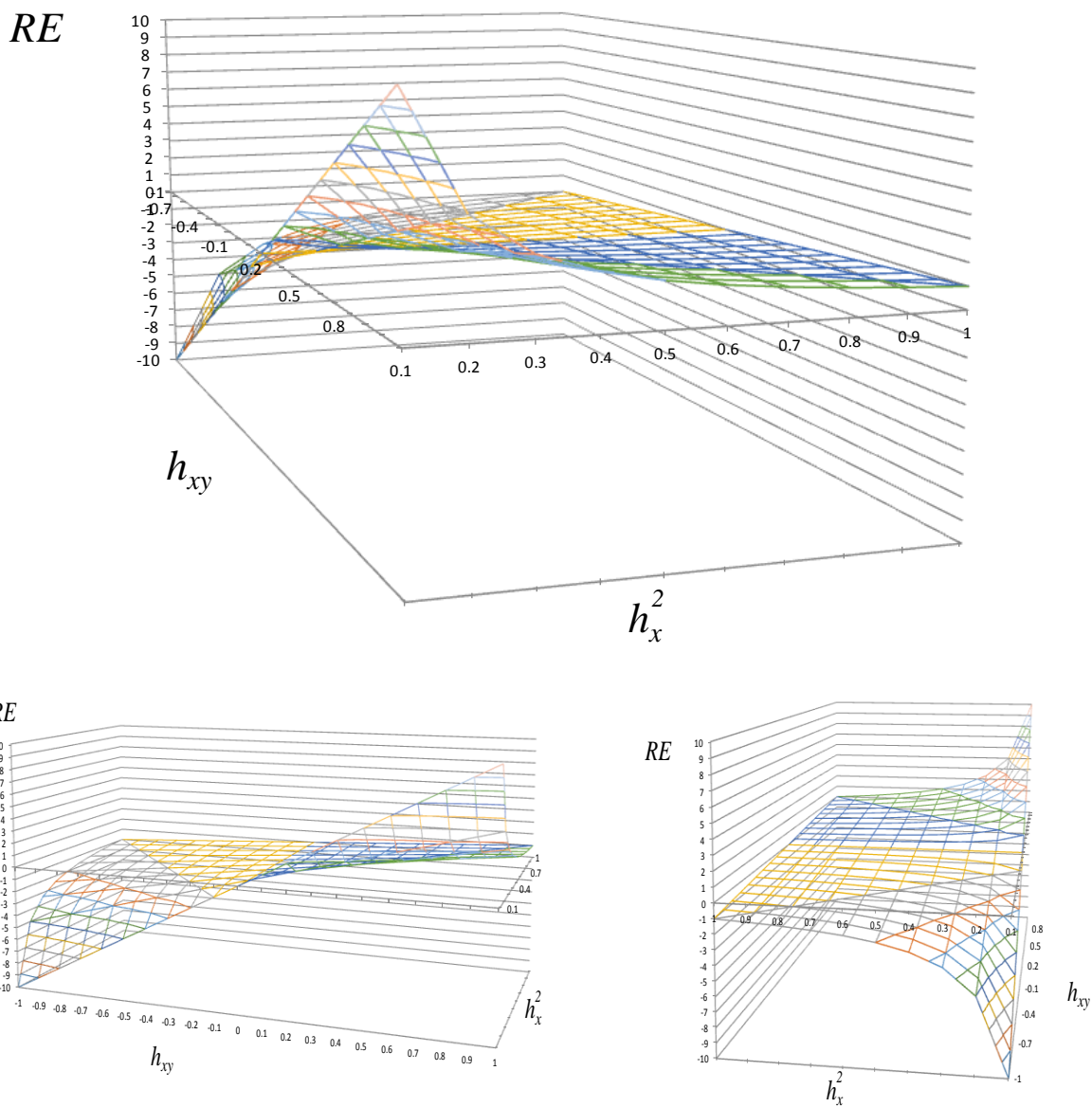
Figure 8.4 Different views of the relationship between relative efficiency of selection as a function of the coheritability of the traits and the heritability of the directly selected trait.

8.3 A measure of the intensity of GxE Interaction

8.3.1 Type B coheritability and the intensity of GxE interaction S

It is well recognized by breeders that if the rank order and relative magnitude of phenotypic expression are the same across locations, it does not matter in which environment the parental selection is conducted. However, if the rank changes, it might be best to select in the environment in which the organisms will ultimately be reared. Falconer (1952) proposed that the magnitude of genotype-by-environment interaction (GxE) be quantified by the cross-environment genetic correlations, in which the same characters measured in two environments is considered to be two different characters. Type B genetic correlation (using Burdon's 1977 naming) is defined as

$$r_{B_{x\,1,2}} = \frac{s_{x1,x2}}{\sqrt{s_{x1}^2\ s_{x2}^2}}$$

where $s_{x1,x2}$ refers to the genotypic covariance between the same trait x in environments 1 and 2. The terms s_{x1}^2 and s_{x2}^2 denotes the estimated genetic variance for the trait x in environments 1 and 2, respectively.

Nevertheless, the heritabilities displayed by the traits in the different environments are also important and informative, and they must be taken into account. Therefore, to have a better idea of the intensity of GxE, would be rather preferable to use the Type B coheritability of the trait, which is defined was defined in Section 3.2.2 as:

$$h_{B_{x\,1,2}} = \sqrt{h_{x1}^2\ h_{x2}^2}\ r_{B_{x\,1,2}}$$

$h_{Bx\,1,2}$ is the coheritability between trait x in environment 1 and 2, $h_{x\blacksquare}^2$ is the heritability of trait x in a given environment (1=env1, 2=env2), and $r_{B_{x\,1,2}}$ is the Type B-genetic correlation. The intensity of GxE is inversely related to the coheritability, $[GxE] \propto \frac{1}{h_{x1,x2}}$. When the intensity of GxE is high it means that the environment exert a larger influence on the phenotype manifested in their change of rank of the mean performance of the trait, and thus the coheritability is low. On the other hand, a high coheritability across sites shows that the genetic component is stable across environments. Cognizant that one cannot infer the underlying genetic architecture from an observed coheritability, because many different underlying causal pathways can generate the same pattern. Such patterns, however, might suggest causal hypotheses, yet caution must be exercised to make statements about causes of observed coheritabilities (Pigliucci 2005).

Here I present a measure of the intensity of the genotype-by-environment interaction, called S, based on the Type B coheritability of a trait exhibited by members of a genotype (i.e. family, clones, variety) in two distinct environments.

The measure S is defined as

$$S = \frac{1 - |h_{B_{x\,1,2}}|}{1 + |h_{B_{x\,1,2}}|} \qquad\qquad 0 < S < 1$$

Which can be plotted as a function of the absolute value of the Type coheritability $h_{B_{x\,1,2}}$.
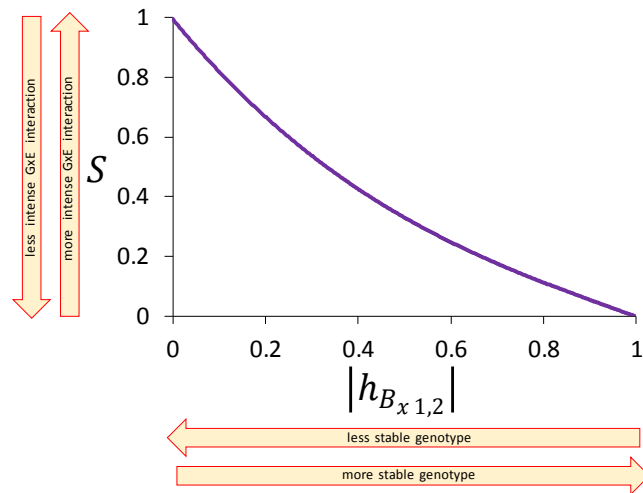
The graph illustrates the inverse relationship between intensity of genotype x environment interaction (S) and the coheritability of the same trait in two environments.

The low absolute value of the coheritability means that the breeding values of a trait displayed by a genotype in an environment are not linearly related to the breeding values of the same genotype in another environment, thus S would be high. High absolute value of the coheritability indicates that the genotype is stable across environments, and the intensity of S is reduced.

8.3.2 Relationship of coheritabilities across environments. Case for two traits.

How the coheritabilities across environments relate to the coheritabilities between traits within an environment?
In the case that two traits are of interest in both environments, the Type B coheritability across sites of each single trait and the coheritability between both traits within each environment can be related, as follows,

Let $h_{B_{x\,1,2}} = \sqrt{h_{x1}^2\, h_{x2}^2}\; r_{B_{x\,1,2}}$ and $h_{B_{y\,1,2}} = \sqrt{h_{y1}^2\, h_{y2}^2}\; r_{B_{y\,1,2}}$ be the Type B coheritability for trait x and y, respectively. Then its product is

$$h_{B_{x\,1,2}} \cdot h_{B_{y\,1,2}} = \sqrt{h_{x1}^2\, h_{x2}^2}\; r_{B_{x\,1,2}} \sqrt{h_{y1}^2\, h_{y2}^2}\; r_{B_{y\,1,2}} \qquad [\,8.3.2-1]$$

After some rearrangement

$$h_{B_{x\,1,2}} \cdot h_{B_{y\,1,2}} = \sqrt{h_{x1}^2\, h_{y1}^2}\; \sqrt{h_{x2}^2\, h_{y2}^2}\; r_{B_{x\,1,2}}\, r_{B_{y\,1,2}} \qquad [\,8.3.2-2]$$

the geometric means of the heritabilities $\sqrt{h_x^2\, h_y^2}$ can be replaced by $\dfrac{h_{x,y}}{r_{A_{x,y}}}$ employed now in equation 8.3.2-2], which yields,

$$h_{B_{x\,1,2}} \cdot h_{B_{y\,1,2}} = h_{x1,y1} h_{x2,y2} \frac{r_{B_{x\,1,2}}}{r_{A_{x1,y1}}} \frac{r_{B_{y\,1,2}}}{r_{A_{x2,y2}}} \qquad [\,8.3.2-2]$$

Therefore, the product of Type B coheritabilities of two traits is the product of the coheritabilities between the traits in each environment multiplied by the ratio of Type B correlation and the genetic correlation, for both tratits.

9 Comparing correlations and coheritabilities

9.1 Types of comparisons

Testing single statistics (correlations, coheritability) was the purview of Section 5. This section deals with comparing two values of correlations or coheritabilities. A proper comparison of correlations between two groups must also involve comparing the groups based on other measures such as the response variable. For details of a method aiming to do this, see Tabesh et al. 2010.

Analogous to the statistical treatment concerning the comparison of correlations (Didenhofen and Musch 2015,), we can use the same statistical tools to perform the comparison of coheritabilities. There are two cases that can be distinguished in the comparison. A test that of *independent coheritabilities* compares two values obtained from distinct individuals/samples. A test of *dependent coheritabilities* compares two values obtained from the same individuals/sample. It can be referred as either an *dependent, overlapping* test if it compares two coheritabilities with one trait in common, or *dependent, non-overlapping* test if it compares two coheritabilities involving different traits, none in common. Although different interpretation, these two cases of dependent testing are identical from a statistical perspective. An example may explain this better. If, in a forestry progeny trial, the coheritability between height growth and diameter is to be compared to the coheritability between height growth and wood volume, there is a common factor, namely, the variable height growth. This comparison is classified as *dependent* because it compares data obtained from the same group and *overlapping* because both coheritabilities have one factor in common. On the other hand, any of these will be compared to the coheritability between early and late wood density, then the comparison is classified as dependent and non-overlapping. In the case that the data comes from different groups or experiments, then it is classified as non-overlapping (see Example Box 9.1).

		Non-overlapping	Non-overlapping
Factor	Dependent	Two correlations or coheritabilities are calculated from the same sample without commom variables involved.	Two correlations or coheritabilities are calculated from the same sample with commom variables involved.
	Independent	Two correlations obtained from independent samples without common variable involved.	

Example Box 9.1

Dependent, overlapping

		Trait 2				
		H1	H3	H6	H9	H12
		1	2	3	4	5
Trait 1	H1 1	1	$h_{1,2}$	$h_{1,3}$	$h_{1,4}$	$h_{1,5}$
	H3 2		1	$h_{2,3}$	$h_{2,4}$	$h_{2,5}$
	H6 3			1	$h_{3,4}$	$h_{3,5}$
	H9 4				1	$h_{4,5}$
	H12 5					1

Problem: To determine whether the genetic control of a phenotype in a juvenile age is the same as the same phenotype in a mature age.

Question 1: At what age is the juvenile phenotype significantly correlated to the phenotype at the mature age?

Question 2: At what age is the juvenile phenotype a better predictor of the phenotype at the mature age?

Data collection: Measurements of the trait regularly taken from the same individuals during development.

Dependent, nonoverlapping

		Trait 2				
		D1	D3	D6	D9	D12
		6	7	8	9	10
Trait 1	H1 1	$h_{1,6}$	$h_{1,7}$	$h_{1,8}$	$h_{1,9}$	$h_{1,10}$
	H3 2		$h_{2,7}$	$h_{2,8}$	$h_{2,9}$	$h_{2,10}$
	H6 3			$h_{3,8}$	$h_{3,9}$	$h_{3,10}$
	H9 4				$h_{4,9}$	$h_{4,10}$
	H12 5					$h_{5,10}$

Problem: We look at whether the degree of genetic control of two traits remains the same or not at juvenile and mature stages.

Question 1: Is the correlation between two traits at juvenile and the mature age the same throughout development?

Question 2: Is the coheritability between two traits at a given age the same as in any other ages?

Data collection: Measurements of both traits regularly taken from the same individuals during development.

Non-dependent, nonoverlapping

		Generation		
		parental	progeny	
		D	H	D
		2	3	4
Generation (parental)	H 1	$h_{1,2}$	$h_{1,3}$	$h_{1,4}$
	D 2	1	$h_{2,3}$	$h_{2,4}$
(progeny)	H 3		1	$h_{3,4}$

Problem: We look at whether selection influences the degree of genetic control of two traits in two generations.

Question 1: What is the influence of selection on the genetic correlations between two traits?

Question 2: How selection influences the coinheritance of two traits?

Data collection: Measurements of both traits regularly taken from the same individuals at the same age in each generation.

To perform the statistical comparison of the magnitude of two coheritabilities, as well as the confidence interval for such comparison, the free software package *cocor* (Didenhofen and Munsch 2015, available online at http://comparingcorrelations.org) covers a broad range of tests including the comparisons of independent and dependent variables in overlapping or nonoverlapping cases. A thorough elaboration

on statistical comparison of correlations (which do also apply to coheritabilities) is provided by the useful appendix accompanying the article (https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0121945#sec010).

9.2 The nature of the coheritability in terms of traits, environment and state

Another aspect pertinent to comparisons is the conceptual nature of the variables (i.e. correlations, coheritabilities) involved in a single correlation of coheritability measure. Table 9 defines the traits, expands the concept of environment, and introduces the concept of state

Table 9 Conceptual considerations in bivariate measures of relationship such as correlations and coheritability

	Trait	Environment	State
Definition	measure of a phenotypic character, or an aggregate of characters,observed in members of a sample or population.	it refers to any external or extrinsic factor that modulates, modifies, or influence the genetic control of the traits.	it refers to any intrinsic biological condition, quality, or event that influence the genetic control of the traits.
Example	continuous, discrete, complex	**spatial**: physical environmental, site. **subject**: individual, cohort, family **generationa**l: parent, progeny **temporal**: circadian, year **treatment**: before, during, after test	**developmental stage**: juvenile, adult. **disease state**: unaffected, affected. **sex:** male, female **ethnic provenance, strain, biovar, clone**
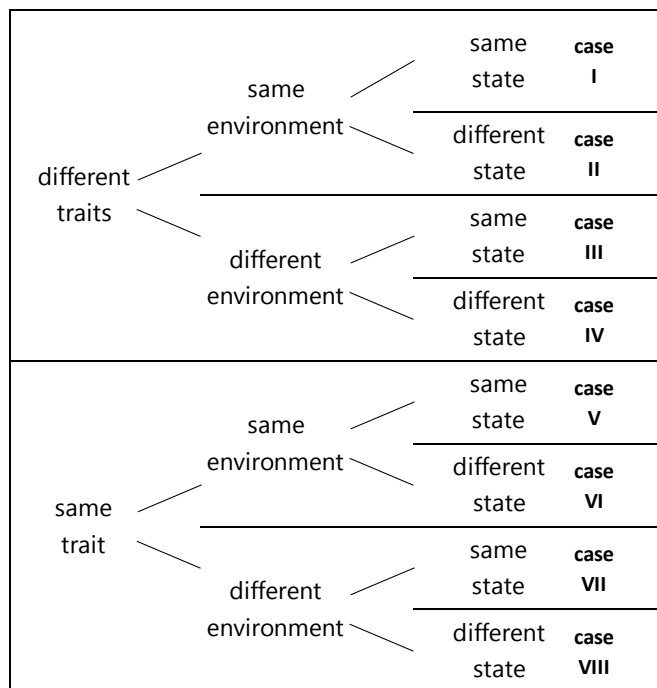
Case I   coheritability between two distinct traits, say insect resistance and the abundance of certain metabolite in the leaf (traits) in a localities with varying insect pest abundance (environment) and obtained in individual trees of certain age (state).

Case II   coheritability between the concentration of two pollutants (traits) in a contaminated site (environment), evaluated in pregnant mothers and the fetuses (state)

Case III   coheritability between two types of cholesterol evaluated before and after a diet change (environment) in the same individuals in a juvenile and a mature age (state).

Case IV   coheritability between the abundance of two hormones (traits) measured in individuals when awake and sleeping (environment), in males and females (state).

Case V coheritability between wood volume growth (trait) measured in trees planted in the same site (environment) measured at distinct ages (state).

Case VI coheritability between concentrations of a pollutant in the blood (trait) measured in specific homes (environments) and among individuals before and after some treatment (state).

Case VII coheritability between height growth (trait) measured in individuals growing in different sites (environment) and from different clones (state).

Case VIII coheritability between pest resistance (trait) in different plantation sites (environment) and among resistant and susceptible genotypes.

Examples for some cases are show below.

Case VIII

same trait, same environment, same state

	H_{age2}	H_{age3}	H_{age4}
H_{age1}	$h_{H_1 H_2}$	$h_{H_1 H_3}$	$h_{H_1 H_4}$
H_{age2}		$h_{H_2 H_3}$	$h_{H_2 H_4}$
H_{age3}			$h_{H_3 H_4}$

Measurement in the same individuals

$h_{H_1 H_2}$ $\qquad h_{H_3 H_4}$ dependent nonoverlapping

$h_{H_1 H_4}$ $\qquad h_{H_3 H_4}$ dependent overlapping

The H represents the trait, the numeral indicate the age in which the measurement was taken. The coheritability is represented by h and the symbols of the traits as subscripts.

Case VII

same trait, different environment, same state

Type B correlations coheritability

	H_{site2}	H_{site3}	H_{site4}
H_{site1}	$h_{H site_1 H_{site2}}$	$h_{H_{site1} H_{site3}}$	$h_{H_{site1} H_{site4}}$
H_{site2}		$h_{H_{site2} H_{site3}}$	$h_{H_{site2} H_{site4}}$
H_{site3}			$h_{H_{site3} H_{site4}}$

$h_{H_1 H_3}$ $\qquad h_{H_2 H_4}$ dependent nonoverlapping

$h_{H_1 H_4}$ $\qquad h_{H_1 H_3}$ dependent overlapping

if different organs in same individuals, dependent

different individuals yet belonging to the same family

The H represents the trait, the subscript indicate the locality at which the measurement was taken. The coheritability is represented by h and the symbols of the traits as subscripts.

Case VI

different traits, same environment, same state

	D	E	F
H	h_{HD}	h_{HE}	h_{HF}
J		h_{JE}	h_{JF}
K			h_{KF}

h_{HD} h_{KF} dependent nonoverlapping

h_{HF} h_{KF} dependent overlapping

The H, J, K, D, E, F represent the trai. The coheritability is represented by h and the symbols of the traits as subscripts.

Case II

different traits, same environment, different state

	D_j	D_m
H_j	$h_{(HD)_j}$	
H_m		$h_{(HD)_m}$

$h_{(HD)_j}$ $h_{(HD)_m}$ independent

different individuals

The H and D represent the traits, the subscript j refers to a juvenile state, m to the mature state. Also applicable is that j represents the parental generation, and m the progeny generation. The coheritability is represented by h and the symbols of the traits as subscripts.

Case III

different traits, different environment, same state

site 2

	D_{site1}	D_{site2}
H_{site1}	$h_{(HD)_{site1}}$	
H_{site2}		$h_{(HD)_{site2}}$

(site 1)

$h_{(HD)_1}$ $h_{(HD)_2}$ (in)dependent

The H and D represent the traits, the subscript refers to a environments where the measurements were taken. Also applicable is that j represents the parental generation, and m the progeny generation. The coheritability is represented by h and the symbols of the traits as subscripts.

10 Simulation of coheritability and coenvironmentability data

10.1 Derivation of joint probability density function of simulated h_{xy} and e_{xy}

Let $(X_1,\ X_2)$ be a bivariate random vector in which the X_1 and X_2 variables independently have a Uniform $\left(-\frac{1}{2}\ ,\ \frac{1}{2}\right)$ distribution. The joint distribution of X_1 and X_2 is

$$f_{X_1,X_2}(x_1,x_2) = f_{X_1}(x_1) \times f_{X_2}(x_2) = 1 \times 1 = 1\ , \quad \text{for } -1 < x_1 < 1 \text{ and } -1 < x_2 < 1.$$

Now consider a new bivariate random $(H,\ E)$ vector be defined by

$$H = g_1(X_1,X_2) = X_1 + X_2\ , \quad -1 \le H \le 1,$$

$$E = g_2(X_1,X_2) = X_1 - X_2\ , \quad -1 \le E \le 1$$

Our goal is to find the joint distribution of H and E expressed in terms of $f_{X_1,X_2}(x_1,x_2)$. The set

$$\mathcal{A} = \left\{(x_1,\ x_2): f_{X_1,X_2}(x_1,x_2) > 0\right\}, \text{ and}$$

$$\mathcal{B} = \{(h,e): h = g_1(x_1,x_2) = x_1 + x_2\ ;\ e = g_2(x_1,x_2) = x_1 - x_{2,}, \text{ for } (x_1,\ x_2) \in \mathcal{A}\ \ \}$$

Thus, the joint pdf $f_{H,E}(h,e)$ will be positive on the set $\mathcal{B}$.

Verification of the 1-to-1 transformation

Here we demonstrate that $h = g_1(x_1,x_2)$ and $e = g_2(x_1,x_2)$ define a one-to-one transformation of $\mathcal{A}$ onto $\mathcal{B}$. The transformation is onto because of the definition of $\mathcal{B}$. Thus, for each $(h,e) \in \mathcal{B}$ there is only one $(x_1,x_2) \in \mathcal{A}$ such that $(h,e) = (g_1(x_1,x_2), g_2(x_1,x_2))$. Therefore, we aim to express x_1 and x_2 in terms of h and e. Thus, we obtain the following inverse transformation:

$$x_1 = g_1^{-1}(h,e) = \frac{h+e}{2}$$

$$x_2 = g_2^{-1}(h,e) = \frac{h-e}{2}$$

X_2

X_1

h

e
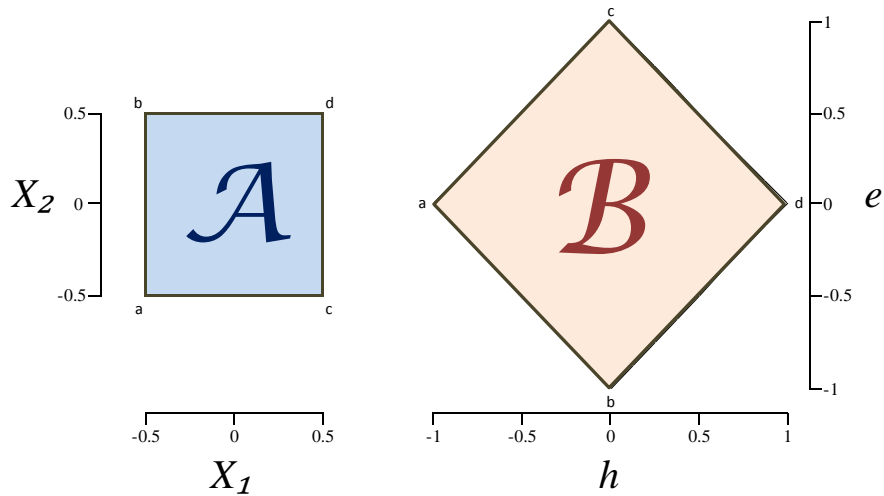
	X_1	X_2
a	-0.5	-0.5
b	-0.5	0.5
c	0.5	-0.5
d	0.5	0.5

	h $X_1 + X_2$	e $X_1 + X_2$
a	-1	0
b	0	-1
c	0	1
d	1	0

The tables below each graph show that the transformation is 1-to-1.

(5) Jacobian determinant of the transformation

$$J = \begin{vmatrix} \dfrac{\partial x_1}{\partial h} & \dfrac{\partial x_1}{\partial e} \\[2mm] \dfrac{\partial x_2}{\partial h} & \dfrac{\partial x_2}{\partial e} \end{vmatrix} = \begin{vmatrix} \dfrac{\partial}{\partial h}\left(\dfrac{h+e}{2}\right) & \dfrac{\partial}{\partial e}\left(\dfrac{h+e}{2}\right) \\[2mm] \dfrac{\partial}{\partial h}\left(\dfrac{h-e}{2}\right) & \dfrac{\partial}{\partial e}\left(\dfrac{h-e}{2}\right) \end{vmatrix} = \begin{vmatrix} \dfrac{1}{2} & \dfrac{1}{2} \\[2mm] \dfrac{1}{2} & -\dfrac{1}{2} \end{vmatrix} = -0.5$$

We observe that J is not identical to zero in $\mathcal{B}$. Then the joint pdf of (H, E) is zero outside the set $\mathcal{B}$, and on the set $\mathcal{B}$ is given by

$$f_{H,E}(h, e) = f_{X_1, X_2}(g_1^{-1}(h, e), g_2^{-1}(h, e)) \, | \, J \, |$$

$$= 1 | -0.5 |$$

$$f_{H,E}(h, e) = 0.5$$

Thus, $P\ [(H,E) \in \mathcal{B}] = P[(X_1, X_2) \in \mathcal{A}]$, and the probability distribution of (H, E) is completely determined by the probability distribution of (X_1, X_2).

Joint probability density function of the variables H and E.
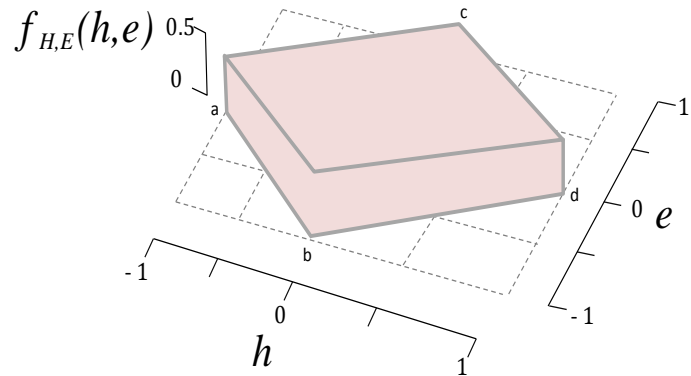
Results of generating simulated data using the model explained in this section.

The data $(n = 3000)$ obtained using a SAS program. Notice that the data allocates randomly throughout the 2DHER-field, all partitions have approximately similar content of data points.
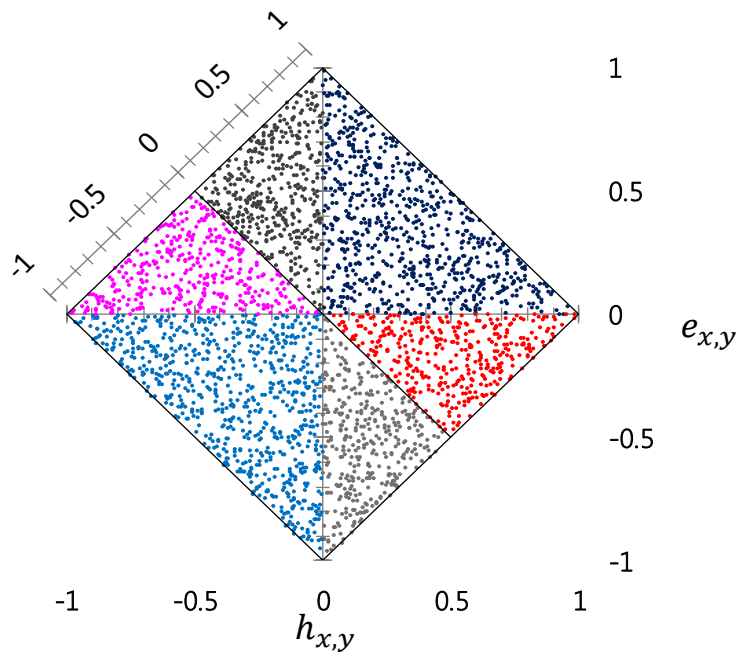
11 The Breeder's Equation

This section attempts to illustrate that role of the coheritability in the context of the multivariate form of the breeder's equation, particularly the $H = GP^{-1}$ component, includes terms of coheritability and correlations related in a complex manner, and would remain hidden were not derived explicitly. The equations for a 2x2 and a 3x3 matrices are presented here, this just to show the complex relationship when the covariance terms are not zero.

The breeder's equation measures within-generation response to selection. Predictions from the breeder's equation typically do not hold well in natural populations (Morrisey et al. 2010). Rollinson and Rowe (2015) discuss about the persistent directional selection on body size that is widely observed in wild populations, yet response to selection is generally not in the direction predicted by the breeder's equation. Stasis tends to dominate the temporal dynamic of traits in nature (Uyeda et al. 2010).

This lack of correspondence between expectation and observation may be due, in part, to an incomplete picture of all traits under selection (Pujol et al. 2018), or how the traits interact and correlate properly (Lande and Arnold 1983). Kruuk et al. (2008) acknowledge that the breeder's equation is too simplistic a representation to apply to studies of natural selection in heterogeneous environments. An alternative form of a breeder's equation is presented by Houchmandzadeh (2014).

The breeder's equation, in multivariate form, is given as: $\Delta z = GP^{-1}s$, where Δz is a vector of the change in trait means between generations, G is the genetic variance-covariance matrix, P^{-1} is the inverse of the phenotypic variance-covariance matrix, and s is the vector of selection differentials (or alternatively, $\Delta z = G\beta$ where β is a vector of selection gradients (Lande and Arnold 1983). Matrix formulations involving phenotypic and genetic correlations are important and must possess certain characteristics. Methods to generate realistic correlation matrices have been proposed for simulation studies (Hardin et al. 2013, Numpacharoen and Atsawarunruagkit 2012).

11.1 The 2x2 Breeder's equation matrix

Let G_{2x2} be the 2x2 (unstructured) genetic variance-covariance matrix

$$G_{2x2} = \begin{bmatrix} V_{A_1} & C_{A_{1.2}} \\ C_{A_{1.2}} & V_{A_2} \end{bmatrix}$$

And P_{2x2} the 2x2 (unstructured) phenotypic variance-covariance matrix P_{2x2}

$$P_{2x2} = \begin{bmatrix} V_{P_1} & C_{P_{1.2}} \\ C_{P_{1.2}} & V_{P_2} \end{bmatrix}$$

whose determinant is $det\ P_{2x2} = V_{P_1}V_{P_2} - C_{P_{1,2}}^2$ or

$$det\ P_{2x2} = V_{P_1}V_{P_2}(1 - r_{P_{1,2}}^2)$$

Inverse of P is

$$P_{2x2}^{-1} = \frac{1}{V_{P_1}V_{P_2}(1 - r_{P_{1,2}}^2)} \begin{bmatrix} V_{P_2} & -C_{P_{1.2}} \\ -C_{P_{1.2}} & V_{P_1} \end{bmatrix} = \frac{1}{(1 - r_{P_{1,2}}^2)} \begin{bmatrix} \dfrac{1}{V_{P_1}} & -\dfrac{r_{P_{1,2}}}{\sqrt{V_{P_1}V_{P_2}}} \\ -\dfrac{r_{P_{1,2}}}{\sqrt{V_{P_1}V_{P_2}}} & \dfrac{1}{V_{P_2}} \end{bmatrix}$$

Which we can use to derive the the 2x2 heritability-coheritability $H_{2x2} = GP^{-1}{}_{2x2}$

$$H_{2x2} = GP^{-1}{}_{2x2} = \frac{1}{\left(1 - r_{P_{1,2}}^2\right)} \begin{bmatrix} V_{A_1} & C_{A_{1.2}} \\ C_{A_{1.2}} & V_{A_2} \end{bmatrix} \begin{bmatrix} \dfrac{1}{V_{P_1}} & -\dfrac{r_{P_{1,2}}}{\sqrt{V_{P_1}V_{P_2}}} \\ -\dfrac{r_{P_{1,2}}}{\sqrt{V_{P_1}V_{P_2}}} & \dfrac{1}{V_{P_2}} \end{bmatrix}$$

$$= \frac{1}{(1 - r_{P_{1,2}}^2)} \begin{bmatrix} \dfrac{V_{A_1}}{V_{P_1}} - \dfrac{C_{A_{1,2}}}{\sqrt{V_{P_1} V_{P_2}}} r_{P_{1,2}} & \dfrac{C_{A_{1,2}}}{V_{P_2}} - \dfrac{V_{A_1}}{\sqrt{V_{P_1} V_{P_2}}} r_{P_{1,2}} \\ \dfrac{C_{A_{1,2}}}{V_{P_1}} - \dfrac{V_{A_2}}{\sqrt{V_{P_1} V_{P_2}}} r_{P_{1,2}} & \dfrac{V_{A_2}}{V_{P_2}} - \dfrac{C_{A_{1,2}}}{\sqrt{V_{P_1} V_{P_2}}} r_{P_{1,2}} \end{bmatrix}$$

Finally, the 2x2 heritability-coheritability matrix is

$$\mathbf{H_{2x2}} = \mathbf{GP^{-1}}_{2x2} = \frac{1}{\left(1 - r_{P_{1,2}}^2\right)} \begin{bmatrix} h_1^2 - h_{1,2}\, r_{P_{1,2}} & h_{1,2}\left(\sqrt{\dfrac{V_{P_1}}{V_{P_2}}} - \dfrac{r_{P_{1,2}}}{r_{A_{1,2}}} \sqrt{\dfrac{V_{A_1}}{V_{A_2}}} \right) \\ h_{1,2}\left(\sqrt{\dfrac{V_{P_2}}{V_{P_1}}} - \dfrac{r_{P_{1,2}}}{r_{A_{1,2}}} \sqrt{\dfrac{V_{A_2}}{V_{A_1}}} \right) & h_2^2 - h_{1,2}\, r_{P_{1,2}} \end{bmatrix}$$

Note that the diagonal elements consist of functions of heritability, coheritability, and phenotypic correlation. The off-diagonal elements involve the coheritabilities affected by raios of variances and covariances.

11.2 The 3x3 Breeder's equation matrix

Let G_{3x3} be the 3x3 (unstructured) genetic variance-covariance matrix

$$G_{3x3} = \begin{bmatrix} V_{A_1} & C_{A_{1.2}} & C_{A_{1.3}} \\ C_{A_{1.2}} & V_{A_2} & C_{A_{2.3}} \\ C_{A_{1.2}} & C_{A_{2.3}} & V_{A_3} \end{bmatrix}$$

And P_{3x3} the 3x3 (unstructured) phenotypic variance-covariance matrix

$$P_{3x3} = \begin{bmatrix} V_{P_1} & C_{P_{1.2}} & C_{P_{1.3}} \\ C_{P_{1.2}} & V_{P_2} & C_{P_{2.3}} \\ C_{P_{1.2}} & C_{P_{2.3}} & V_{P_3} \end{bmatrix}$$

whose determinant is

$$\det P_{3x3} = V_{P_1} V_{P_2} V_{P_3} + 2\, C_{P_{1.2}} C_{P_{1.3}} C_{P_{2.3}} - V_{P_1} C_{P_{2.3}} - V_{P_2} C_{P_{1.3}} - V_{P_3} C_{P_{1.2}}$$

Multiplying and dividing by $V_{P_1} V_{P_2} V_{P_3}$, it yields

$$\det P_{3x3} = V_{P_1} V_{P_2} V_{P_3} (1 + 2 r_{P_{1,2}} r_{P_{1,3}} r_{P_{2,3}} - r_{P_{1,2}}^2 r_{P_{1,3}}^2 r_{P_{2,3}}^2)$$

The inverse of the phenotypic variance-covariance matrix is

$$P_{3x3}^{-1} = \frac{1}{(1 + 2 r_{P_{1,2}} r_{P_{1,3}} r_{P_{2,3}} - r_{P_{1,2}}^2 r_{P_{1,3}}^2 r_{P_{2,3}}^2)} \begin{bmatrix} \frac{1}{V_{P_1}}(1 - r_{P_{2,3}}^2) & \frac{1}{\sqrt{V_{P_1}V_{P_2}}}(r_{P_{1,3}} r_{P_{2,3}} - r_{P_{1,2}}) & \frac{1}{\sqrt{V_{P_1}V_{P_3}}}(r_{P_{1,2}} r_{P_{2,3}} - r_{P_{1,3}}) \\ \frac{1}{\sqrt{V_{P_1}V_{P_2}}}(r_{P_{1,3}} r_{P_{2,3}} - r_{P_{1,2}}) & \frac{1}{V_{P_2}}(1 - r_{P_{1,3}}^2) & \frac{1}{\sqrt{V_{P_2}V_{P_3}}}(r_{P_{1,2}} r_{P_{1,3}} - r_{P_{2,3}}) \\ \frac{1}{\sqrt{V_{P_1}V_{P_3}}}(r_{P_{1,2}} r_{P_{2,3}} - r_{P_{1,3}}) & \frac{1}{\sqrt{V_{P_2}V_{P_3}}}(r_{P_{1,2}} r_{P_{1,3}} - r_{P_{2,3}}) & \frac{1}{V_{P_3}}(1 - r_{1,2}^2) \end{bmatrix}$$

Then $H_{3x3} = GP^{-1}{}_{3x3}$ is

$GP^{-1}{}_{3x3}$

$$= \frac{1}{\det P_{3x3}} \begin{bmatrix} V_{A_1} & C_{A_{1.2}} & C_{A_{1.3}} \\ C_{A_{1.2}} & V_{A_2} & C_{A_{2.3}} \\ C_{A_{1.2}} & C_{A_{2.3}} & V_{A_3} \end{bmatrix} \begin{bmatrix} \frac{1}{V_{P_1}}(1 - r_{P_{2,3}}^2) & \frac{1}{\sqrt{V_{P_1}V_{P_2}}}(r_{P_{1,3}} r_{P_{2,3}} - r_{P_{1,2}}) & \frac{1}{\sqrt{V_{P_1}V_{P_3}}}(r_{P_{1,2}} r_{P_{2,3}} - r_{P_{1,3}}) \\ \frac{1}{\sqrt{V_{P_1}V_{P_2}}}(r_{P_{1,3}} r_{P_{2,3}} - r_{P_{1,2}}) & \frac{1}{V_{P_2}}(1 - r_{P_{1,3}}^2) & \frac{1}{\sqrt{V_{P_2}V_{P_3}}}(r_{P_{1,2}} r_{P_{1,3}} - r_{P_{2,3}}) \\ \frac{1}{\sqrt{V_{P_1}V_{P_3}}}(r_{P_{1,2}} r_{P_{2,3}} - r_{P_{1,3}}) & \frac{1}{\sqrt{V_{P_2}V_{P_3}}}(r_{P_{1,2}} r_{P_{1,3}} - r_{P_{2,3}}) & \frac{1}{V_{P_3}}(1 - r_{1,2}^2) \end{bmatrix}$$

Then $\mathbf{H_{3x3}}$ results in

$$
GP^{-1}{}_{3x3} = \frac{1}{(1+2r_{P_{1,2}}r_{P_{1,3}}r_{P_{2,3}}-r^2_{P_{1,2}}r^2_{P_{1,3}}r^2_{P_{2,3}})}
\begin{bmatrix}
h_1^2\left(1-r_{P_{2,3}}^2\right)+h_{1,2}(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}})+h_{1,3}(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}}) & \frac{\sqrt{V_{P_1}}}{\sqrt{V_{P_2}}}\left[h_1^2(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}})+h_{1,2}\left(1-r_{P_{1,3}}^2\right)+h_{1,3}(r_{P_{1,2}}r_{P_{1,3}}-r_{P_{2,3}})\right] & \frac{\sqrt{V_{P_1}}}{\sqrt{V_{P_3}}}\left[h_1^2(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}})+h_{1,2}(r_{P_{1,2}}r_{P_{1,3}}-r_{P_{2,3}})+h_{1,3}\left(1-r_{P_{1,2}}^2\right)\right] \\[2mm]
\frac{\sqrt{V_{P_2}}}{\sqrt{V_{P_1}}}\left[h_{1,2}\left(1-r_{P_{2,3}}^2\right)+h_2^2(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}})+h_{2,3}(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}})\right] & h_{1,2}(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}})+h_2^2\left(1-r_{P_{1,3}}^2\right)+h_{2,3}(r_{P_{1,2}}r_{P_{1,3}}-r_{P_{2,3}}) & \frac{\sqrt{V_{P_2}}}{\sqrt{V_{P_3}}}\left[h_{1,2}(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}})+h_2^2(r_{P_{1,2}}r_{P_{1,3}}-r_{P_{2,3}})+h_{2,3}\left(1-r_{P_{1,2}}^2\right)\right] \\[2mm]
\frac{\sqrt{V_{P_3}}}{\sqrt{V_{P_1}}}\left[h_{1,3}\left(1-r_{P_{2,3}}^2\right)+h_{2,3}(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}})+h_3^2(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}})\right] & \frac{\sqrt{V_{P_3}}}{\sqrt{V_{P_2}}}\left[h_{1,3}(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}})+h_{1,2}\left(1-r_{P_{1,3}}^2\right)+h_3^2(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}})\right] & h_{1,3}(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}})+h_{2,3}(r_{P_{1,2}}r_{P_{1,3}}-r_{P_{2,3}})+h_3^2\left(1-r_{P_{1,2}}^2\right)
\end{bmatrix}
$$

To facilitate visualization, the $\mathbf{H_{3x3}}$ is presented below as a block matrix where the $\boldsymbol{GP^{-1}}_{3x3}$ has been partition in one row-group and three col-groups (column vectors), namely $\mathbf{H_{11}}$, $\mathbf{H_{12}}$, $\mathbf{H_{13}}$.

$$
\mathbf{H_{3x3}} = \boldsymbol{GP^{-1}}_{3x3} = \frac{1}{(1+2r_{P_{1,2}}r_{P_{1.3}}r_{P_{2,3}}-r^2_{P_{1,2}}r^2_{P_{1,3}}r^2_{P_{2,3}})}\left[\,\mathbf{H_{11}}\ \ \mathbf{H_{12}}\ \ \mathbf{H_{13}}\,\right]
$$

Where

$$
\boldsymbol{H_{11}} =
\begin{bmatrix}
h_1^2\left(1-r_{P_{2,3}}^2\right)+h_{1,2}\left(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}}\right)+h_{1,3}\left(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}}\right) \\[3mm]
\frac{\sqrt{V_{P_2}}}{\sqrt{V_{P_1}}}\left[h_{1,2}\left(1-r_{P_{2,3}}^2\right)+h_2^2\left(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}}\right)+h_{2,3}\left(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}}\right)\right] \\[3mm]
\frac{\sqrt{V_3}}{\sqrt{V_{P_1}}}\left[h_{1,3}\left(1-r_{P_{2,3}}^2\right)+h_{2,3}\left(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}}\right)+h_3^2\left(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{1,3}}\right)\right]
\end{bmatrix}
$$

$$
\boldsymbol{H_{12}} =
\begin{bmatrix}
\frac{\sqrt{V_{P_1}}}{\sqrt{V_{P_2}}}\left[h_1^2\left(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}}\right)+h_{1,2}\left(1-r_{P_{1,3}}^2\right)+h_{1,3}\left(r_{P_{1,2}}r_{P_{1,3}}-r_{P_{2,3}}\right)\right] \\[3mm]
h_{1,2}\left(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}}\right)+h_2^2\left(1-r_{P_{1,3}}^2\right)+h_{2,3}\left(r_{P_{1,2}}r_{P_{1,3}}-r_{P_{2,3}}\right) \\[3mm]
\frac{\sqrt{V_{P_3}}}{\sqrt{V_{P_2}}}\left[h_{1,3}\left(r_{P_{1,3}}r_{P_{2,3}}-r_{P_{1,2}}\right)+h_{1,2}\left(1-r_{P_{1,3}}^2\right)+h_3^2\left(r_{P_{1,2}}r_{P_{2,3}}-r_{P_{2,3}}\right)\right]
\end{bmatrix}
$$

$$H_{13} = \begin{bmatrix} \dfrac{\sqrt{V_{P_1}}}{\sqrt{V_{P_3}}} \left[h_1^2\left(r_{P_{1,2}}r_{P_{2,3}} - r_{P_{1,3}}\right) + h_{1,2}\left(r_{P_{1,2}}r_{P_{1,3}} - r_{P_{2,3}}\right) + h_{1,3}\left(1 - r_{P_{1,2}}^2\right) \right] \\[2ex] \dfrac{\sqrt{V_{P_2}}}{\sqrt{V_{P_3}}} \left[h_{1,2}\left(r_{P_{1,2}}r_{P_{2,3}} - r_{P_{1,3}}\right) + h_2^2\left(r_{P_{1,2}}r_{P_{1,3}} - r_{P_{2,3}}\right) + h_{2,3}\left(1 - r_{P_{1,2}}^2\right) \right] \\[2ex] h_{1,3}\left(r_{P_{1,2}}r_{P_{2,3}} - r_{P_{1,3}}\right) + h_{2,3}\left(r_{P_{1,2}}r_{P_{1,3}} - r_{P_{2,3}}\right) + h_3^2\left(1 - r_{P_{1,2}}^2\right) \end{bmatrix}$$

In the case that the phenotypic matrix P has zero off-diagonal elements (no covariances), it becomes a diagonal matrix whose elements are the phenotypic variances of the traits, and further consider that the phenotypic variances have been standardized to 1, then the heritability-coheritability $\mathbf{H}$ matrices become

$$\mathbf{H}_{2x2} = GP^{-1}{}_{2x2} = \begin{bmatrix} h_1^2 & h_{1,2} \\ h_{1,2} & h_2^2 \end{bmatrix}$$

and

$$\mathbf{H}_{3x3} = GP^{-1}{}_{3x3} = \begin{bmatrix} h_1^2 & h_{1,2} & h_{1,3} \\ h_{1,2} & h_2^2 & h_{2,3} \\ h_{1,3} & h_{2,3} & h_3^2 \end{bmatrix}$$

The null phenotypic covariance between the traits implies that the phenotypic correlations between the traits is zero. As we have seen, this fact does not preclude the coheritability to have statistically significant values, and be of importance. In addition, under the condition $r_{P_{x,y}} = 0$, then $h_{x,y} = -e_{x,y}$.

12 Supplementary Text

12.1 Alternative conceptual frameworks to assess quantitative joint inheritance

The notion that a phenotype is by nature a composite of an organism's observable characters that are manifested in morphological, developmental, biochemical, behavioral or physiological properties, leads to think that a phenotype is inherently a multivariate concept. This has prompted researchers to find ways to express a multivariate form of heritability (Carper 2008).

Based on Lande (1979) proposal of a multivariate generalization of the Breeder's equation $\Delta z = GP^{-1}s$ (where G and P are the additive genetic and (co)variance matrices, respectively; and s the selection differential), Klingenberg and Leamy (2001) interpreted the dominant eigenvalue of GP^{-1} as a multivariate heritability estimate. Myers et al. (2006) re-scaled the largest eigenvalue by the sum of the eigenvalues. These eigenvalue-based multivariate heritability measures have drawbacks mainly in the difficulty of estimating the standard errors of eigenvalues. In addition, as the number of traits increase, concomitantly increase the number of variance and covariance to be estimated, leading to an over parametrized model.

While imbalance is fairly easily accommodated in the multivariate setting, the inclusion of multiple traits greatly increases the number of variance and covariance components to be estimated, and consequently of computation time. The lack of reliable standard error estimates has led to the use of nonparametric resampling techniques in connection with multivariate analysis (Myers et al. 2006, Carper 2008).

Other forms have been proposed such as the ratio of the sum of the diagonal elements of G and P, h=tr $(G)/\mathrm{tr}(P)$ proposed by Klingender and Monteiro (2005). They recognize that the method ignores the covariation among traits, and the direction of the selection differential or the direction of variation in G and P. Basset and De Jong (2011) used an Evolutionary Algorithm to express multivariate heritability of M traits as a metric function of GP^{-1} namely, $h = m(GP^{-1}) = \sqrt[M]{\det(GP^{-1})}$. Guo et al. (2016) present two measures of coheritability between a pair traits using GWAs data in the framework of high dimensional linear models.

12.2 Is there a "missing" coheritability?

In the framework of genome-wide association studies, the problem of a "missing" coheritability is expected, and estimates of coheritability of a pair of traits using GWAS data must be taken cautiously, under the view that methodological and statistical artifacts have a higher risk of influencing such estimates.

Gianola et al. (2015) rightly stated accurate predictions of complex traits and estimation of genomic correlations can be obtained from multivariate quantitative genetic analysis based on markers. But such determinations (SNPS heritability, correlations) cannot be confused with heritabilities and genetic correlations because of the discrepancy and distinctiveness of the sources that bring forth the data. Certainly in single-trait analyses, imperfect marker-QTL linkage disequilibrium results in missing heritability. In a multivariate context the problem is compounded by missing correlations. Therefore, caution is recommended in making pronouncements on causality when dealing with SNP heritabilities and genomic correlations involving complex traits. Speculating about genetic correlations in the study of complex traits, using marker data must be considered conjectural.

12.3 Coheritability of threshold traits

This brief explanation of coheritability of threshold traits is based on Lee et al. (2011, 2012).

First, two models are presented that describe the phenotypic trait in its observed scale, and in an unobserved underlying liability scale.

OBSERVED SCALE	LIABILITY SCALE
$$x = u_x + e_x \qquad y = u_y + e_y$$ where The X and Y are the threshold traits defined as $$x = \begin{cases} 1 & \text{for individuals having the condition } x \\ \square & \square \\ 0 & \text{for individuals not having the condition } y \end{cases}$$ $$Var(x) = K_x(1 - K_x)$$ $$y = \begin{cases} 1 & \text{for individuals having the condition } x \\ \square & \square \\ 0 & \text{for individuals not having the condition } y \end{cases}$$ $u_\blacksquare$ is the random additive genetic effects from aggregate marker data $e_\blacksquare$ is the random residual $$Var(y) = K_y(1 - K_y)$$ K_x and K_y represent the prevalence of the condition in the population	$$l_x = g_x + e_{l\,x} \qquad\qquad l_y = g_y + e_{l\,y}$$ where $l_\blacksquare$ is the liability phenotype corresponding to trait $\blacksquare$. $l_\blacksquare \sim N(0,1)$, $g_\blacksquare$ is the random additive genetic effect on the liability scale, $g_\blacksquare \sim N(0, \sigma^2_{g_\blacksquare})$, $e_{l\,\blacksquare}$ is the random residual on the liability scale, $e_\blacksquare \sim N(0, \sigma^2_{e_\blacksquare})$,

A simple linear regression can be used as an approximate model of the relationship between the genetic value on the observed scale and the genetic value in the liability scale, for each trait

$$u_\blacksquare = c + b_\blacksquare g_\blacksquare$$

Where the regression parameter b is defined as the covariance of the dependent variable u divided by the variance of the independent variable g

$$b = \frac{Cov(u,g)}{\sigma_g^2} = z$$

Therefore,

$$u_\blacksquare = z_\blacksquare g_\blacksquare$$

The genetic covariance between the additive values of u_x, and u_y are related to the covariance to the additive values in the liability scale, as follows:

$$Cov(u_x, u_y) = Cov(z_x g_x, z_y g_y) = z_x z_y \, Cov(g_x, g_y)$$

We define the coheritability as the ratio of the genetic covariance divided by the square root of the product of the phenotypic variance of the traits.

Note that the $Cov(g_x, g_y) = h_{l_{x,y}}$ because the variance of the liability phenotype for each trait is unity.

Thus

$$Cov(u_x, u_y) = z_x z_y \, h_{l_{x,y}}$$

In the observed scale, the coheritability between threshold traits x and y,

$$h_{o_{x,y}} = \frac{\sigma_{u_x, u_y}}{\sqrt{K_x(1-K_x)\,K_y(1-K_y)}}$$

The relationship between the coheritability in the observed $(h_{o_{x,y}})$ and liability $(h_{l_{x,y}})$ scales is,

$$h_{o_{x,y}} = \frac{z_x\, z_y\, h_{l_{x,y}}}{\sqrt{K_x(1-K_x)\,K_y(1-K_y)}}$$

In the liability scale, the coheritability between traits x and y, is

$$h_{l_{x,y}} = \frac{h_{o_{x,y}}\sqrt{K_x(1-K_x)\,K_y(1-K_y)}}{z_x\, z_y}$$

12.4 Partitions of the additive genetic covariance

The additive genetic covariance between two traits x and y can be partitioned into a pleiotropic component and a linkage component (Gardner and Latta 2007):

$$C_{G_{x,y}} = 2 \underbrace{\sum_{i=1}^{n} p_i \, q_i \, a_{ix} \, a_{iy}}_{pleiotropic} + \; 2 \underbrace{\sum_{j=1}^{l_1} \sum_{k \neq j}^{l_2} a_{jx} \, a_{ky} \, D_{jk}}_{linkage \; disequilibrioum}$$

More explicitly, for the case of a two biallelic, pleiotropic loci that are in linkage disequilibrium, the genetic covariance on two traits (x, y) is

$$C_{G_{x,y}} = \underbrace{2 \, p_1 \, q_1 \, a_{1x} \, a_{1y} \; + \; 2 \, p_2 \, q_2 \, a_{2x} \, a_{2y}}_{pleiotropic} + \underbrace{2 \; a_{1x} \, a_{2y} \, D_{12} \; + \; 2 \; a_{1y} \, a_{2x} \, D_{12}}_{linkage \; disequilibrioum}$$

where p is the allele frequency of the ith locus, $q = 1 - p$, a_{1x} is the additive effect of the locus 1 on trait x, D_{12} is the measure of linkage disequilibrium (D_{jk} depends upon the recombination distance between loci).

Details regarding the pleiotropic component

Consider a single biallelic locus whose alleles A₁ and A₂ exert effects on two traits, namely trait x and trait y. Using Falconer and Mackay's notation, we associate an arbitrarily-assigned value to the genotypes formed by random association of the alleles, whose frequencies in the population are p for A₁, and q for A₂ The objective is to determine a measure of an individual based upon the particular allele combination present in the locus, and transmitted to the progeny. The average effect of an allele on a trait is such value, and depends on the genotypic values a and d. Table 12.4 shows the results of the derivation of the average effect of the alleles A₁ and A₂ on each of the traits x and y, expressed as the mean deviation (from the population mean) of individuals which received that allele from one parent, the other allele come from a random parent from the population.

Figures 12.4-1 and 12.4-2 display the average effect of alleles when the

Table 12.4 Average effect of alleles of a biallelic, pleotropic locus affecting traits x and y

Allele in population
A$_1$
p
A$_2$
q

			A$_1$ A$_1$ +a	A$_1$ A$_2$ d	A$_2$ A$_2$ -a	genotypic value	Mean genotypic value	Population genotypic (and phenotypic) mean to be deducted	Average effect of the allele on a trait
Trait x	A$_1$	A$_1$ A$_1$	p			$+a_x$	$pa_x + qd_x$	$-[\,a_x\,(p\text{-}q) + 2d_x\,pq\,]$	$q\alpha_x = q\,[a_x + d_x\,(q\text{-}p\,)]$
		A$_1$ A$_2$		q		d_x			
	A$_2$	A$_1$A$_2$	p			d_x	$-\,qa_x + pd_x$	$-[\,a_x\,(p\text{-}q) + 2d_x\,pq\,]$	$-p\alpha_x = -p\,[a_x + d_x\,(q\text{-}p\,)]$
		A$_2$ A$_2$			q	$-a_x$			
Trait y	A$_1$	A$_1$ A$_1$	p			$+a_y$	$pa_y + qd_y$	$-[\,a_y(p\text{-}q) + 2d_y\,pq\,]$	$q\alpha_y = q\,[a_y + d_y\,(q\text{-}p)]$
		A$_1$ A$_2$		q		d_y			
	A$_2$	A$_1$A$_2$	p			$-a_y$	$-\,qa_y + pd_y$	$-[\,a_y(p\text{-}q) + 2d_y\,pq\,]$	$-p\alpha_y = -p\,[a_y + d_y\,(q\text{-}p)]$
		A$_2$ A$_2$			q	d_y			

We can see that in these derivations $\alpha_x = [a_x + d_x(q - p)]$ and $\alpha_y = [a_y + d_y(q - p)]$ are the average effect on a trait due to allele substitution in that locus.

genotype		genotype frequency f_G	Breeding value Trait x B_x	Breeding value Trait y B_y
	A$_1$A$_1$	p^2	$2q\alpha_x$	$2q\alpha_y$
	A$_1$A$_2$	$2pq$	$(q\text{-}p)\alpha_x$	$(q\text{-}p)\alpha_y$
	A$_2$A$_2$	q^2	$-2q\alpha_x$	$-2q\alpha_y$

The genotypic covariance is obtained by summing up the product of the genotype frecuency f_G times the breeding values of trait B_x and B_y for each genotype, as follows:

$$C_{G_{x,y}} = \sum_{i \in S}\left(f_G B_x B_y\right)_i \qquad\qquad S = \{\,A_1A_1\,,\,A_1A_2\,,\,A_2A_2\,\}$$

Genotypic covariance of breeding values of trait x and trait y

$$C_{G_{x,y}} = p^2(2q\alpha_x)(2q\alpha_y) + 2qp(q-p)\alpha_x(q-p)\alpha_y + (-2p\alpha_x)(-2p\alpha_y)q^2$$

$$= 4p^2q^2\alpha_x\alpha_y + 2pq(q-p)^2\alpha_x\alpha_y + 4p^2q^2\alpha_x\alpha_y$$

$$= 2pq\alpha_x\alpha_y \left(2pq + (q-p)^2 + 2pq\right)$$

$$= 2pq\alpha_x\alpha_y(4pq + q^2 - 2pq + p^2)$$

$$= 2pq\alpha_x\alpha_y(p^2 + 2pq + q^2)$$

$$= 2pq\alpha_x\alpha_y$$

Therefore the genotypic covariance between two traits influenced by a single locus is a function of the average effect of gene substitution exerted on each trait and the frequency of the alleles in the population.

Genotypic covariance among traits x and y controlled by a biallelic locus (three equivalent expressions):

$$C_{G_{x,y}} = \begin{cases} 2pq\alpha_x\alpha_y \\ 2pq\left[a_x + d_x(q-p)\right]\left[a_y + d_y(q-p)\right] \\ 2pq\left[a_x a_y + \left(a_x d_y + a_y d_x\right)(q-p) + d_x d_y(q-p)^2\right] \end{cases}$$

Notice that if dealing with the same trait, then $x = y$, it results in the familiar expression of the genotypic variance of the trait

Genotypic variance of a trait controlled by an biallelic locus

$$V_G = \begin{cases} 2pq\alpha^2 \\ 2pq\left[a + d(q-p)\right]^2 \\ 2pq\left[a^2 + 2ad(q-p) + d^2(q-p)^2\right] \end{cases}$$

Derivation of the average effect expressions of Table 12.4

Average effect of allele A₁ on trait x

$\alpha_{1x} = pa_x + qd_x - [a_x(p-q) + 2d_x pq]$
$2d_y pq$]

$\quad = pa_x + a_x(p-q) - qd_x - 2pqd_x$

$\quad = a_x(p-p+q) - qd_x(1-2p)$

$\quad = qa_x + qd_x(q-p)$

$\quad = q[a_x + d_x(q-p)]$

$\quad = q\alpha_x$

Average effect of allele A₁ on trait y

$\alpha_{1y} = pa_y + qd_y - [a_y(p-q) +$
$2d_y pq$]

$\quad = pa_y + a_y(p-q) - qd_y - 2pqd_y$

$\quad = a_y(p-p+q) - qd_y(1-2p)$

$\quad = qa_y + qd_y(q-p)$

$\quad = q[a_y + d_y(q-p)]$

$\quad = q\alpha_y$

Average effect of allele A₂ on trait x

$\alpha_{2x} = -qa_x + pd_x - [a_x(p-q) + 2d_x pq]$
$2d_y pq$]

$\quad = -qa_x + pd_x - a_x(p-q) + 2d_x pq$
$2d_y pq$

$\quad = -qa_x(q+p-q) - pd_x(1-2p)$

$\quad = -pa_x - pd_x(p-q)$

$\quad = -p[a_x + d_x(q-p)]$

$\quad = -p\alpha_x$

Average effect of allele A₂ on trait y

$\alpha_{2y} = -qa_y + pd_y - [a_y(p-q) +$

$\quad = -qa_y + pd_y - a_y(p-q) +$

$\quad = -qa_y(q+p-q) - pd_y(1-2p)$

$\quad = -pa_y - pd_y(p-q)$

$\quad = -p[a_y + d_y(q-p)]$

$\quad = -p\alpha_y$
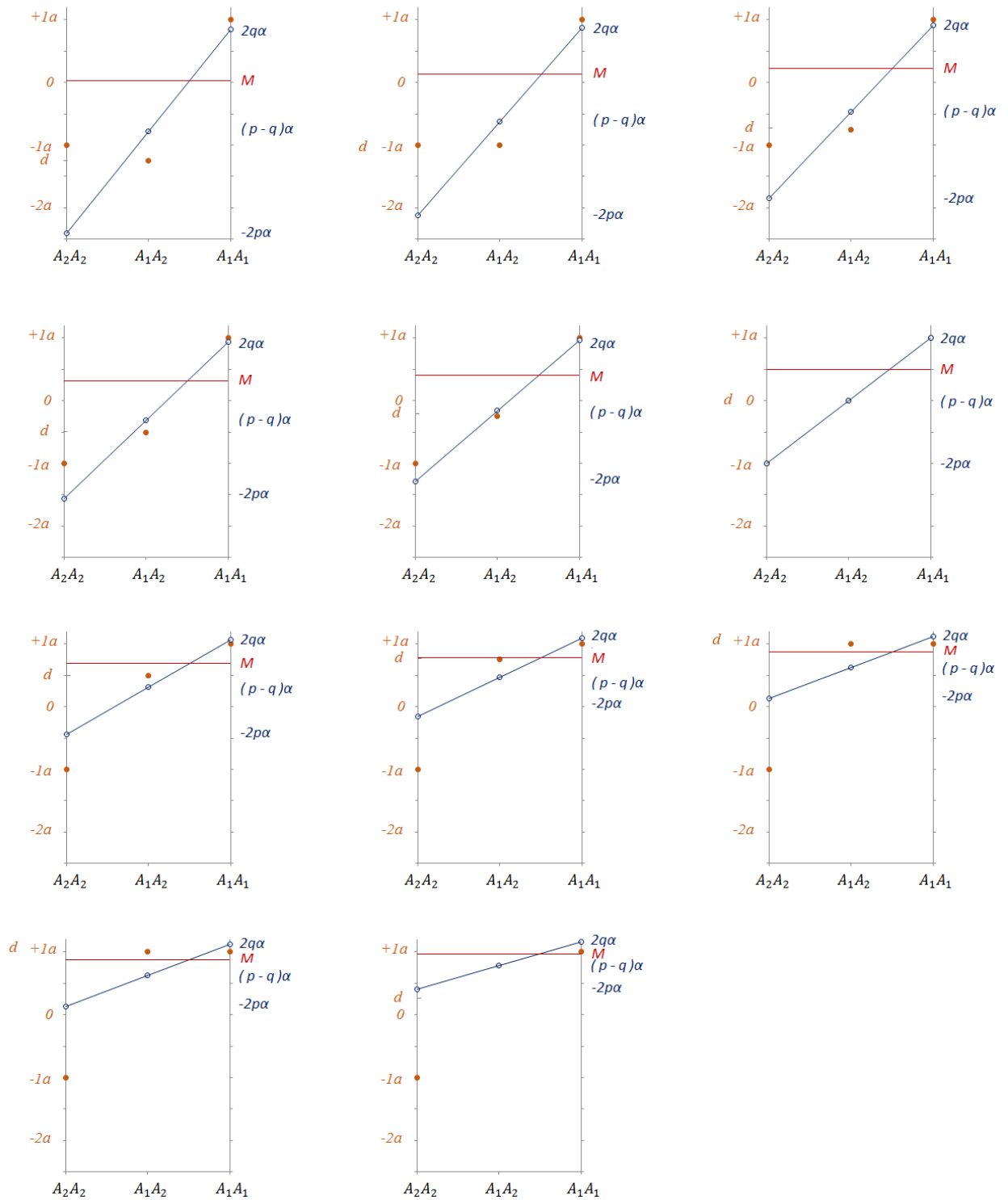
Figure 12.4-1 Average effect of a allele on a single trait, under varying values of d. The allele frequency of $p = 0.25$, $q = 0.75$
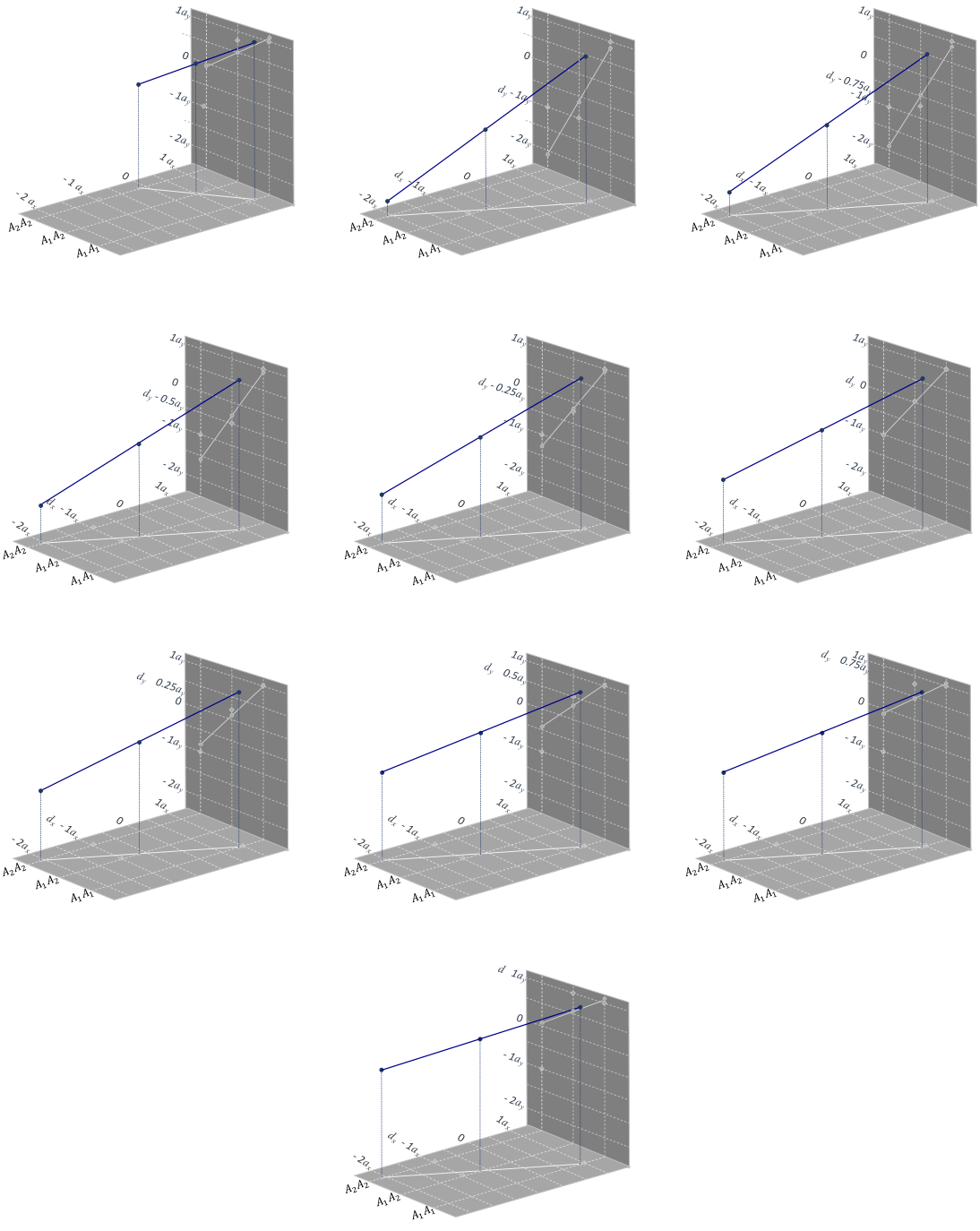
Figure 12.4-2 Average effect of two alleles of a locus on two traits. The horizontal plane is for trait x and has a fixed value of $d = -1.25a$, the vertical plane is the effect on trait y and has varying values of d. This is an extension to the Figure 12.4-1.

12.5 An epidemiological bivariate measure gene-trait relationship

Here I present an extension of the concept positive predictive value, as generally used in epidemiology. The experimental scheme is to screen-test individuals for a particular genetic variant(s) that affects at least two traits. The data is meristic in nature, it uses count data to perform calculations. I called this measure bivariate positive predictive value, and is defined as,

$$bPPV = \frac{\begin{array}{c} Number\ of\ individuals\ with\ genetic\ variant\ \ V \\ exhibiting\ traits\ \ x\ \ and\ \ y \end{array}}{Number\ of\ individuals\ with\ genetic\ variant\ \ V}$$

The denominator includes all individuals with genetic variant V that have both traits, and those having one of the traits, and those not presenting any of the traits. The bivariate positive predictive value of the genetic screening test is the probability of returning a positive result (i.e. the individual has a genetic variant in a locus of interest) correctly identifying those individuals possessing variant V that do show both traits under consideration (see Trevethan 2017).

To illustrate this concept with hypothetical, yet realistic, examples.

Total 1954

FP 144

TP 130

FN 23

TN 1531
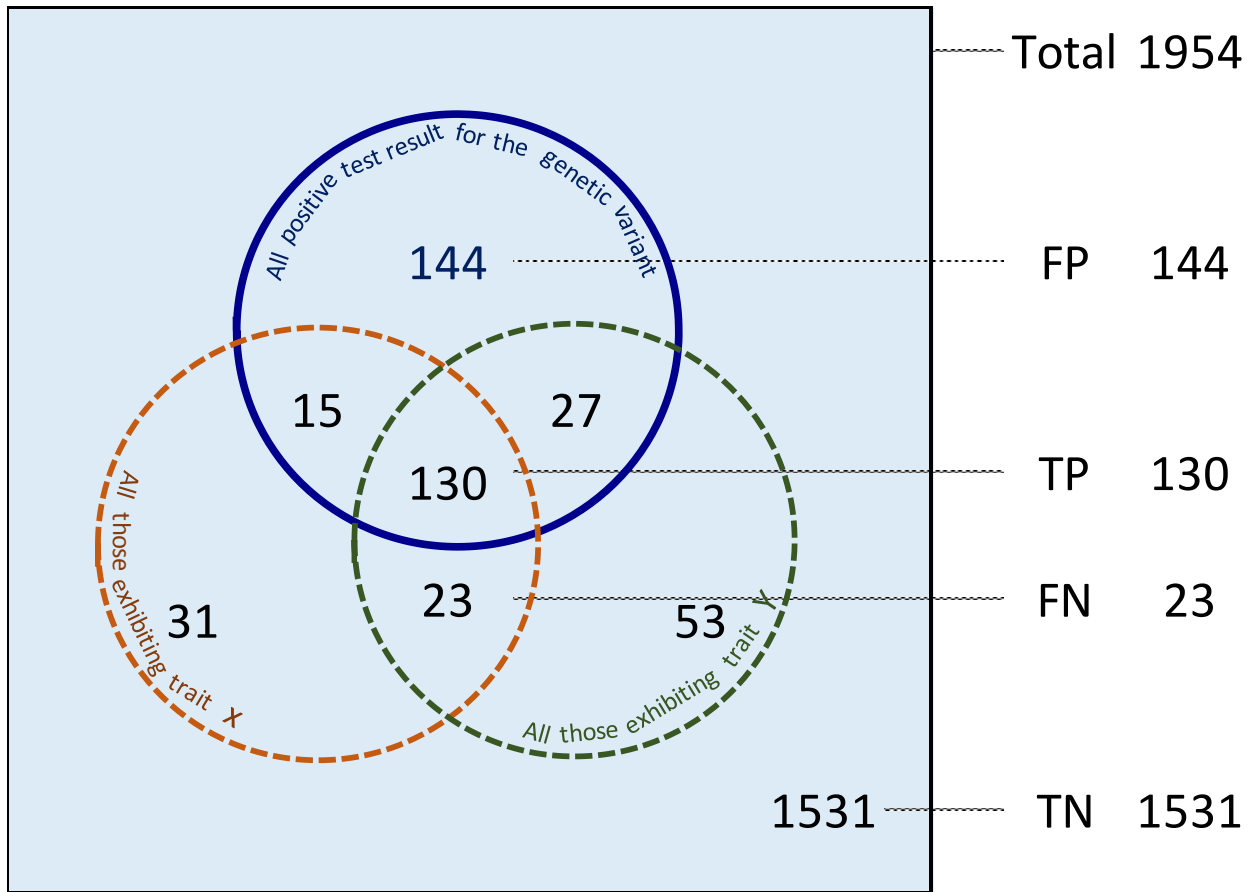
$$proportion\ of\ individuals\ exhibiting\ both\ traits = \frac{130 + 23}{1954} = 8\ \%$$

$$sensitivity = \frac{TP}{all\ those\ exhibiting\ both\ traits} = \frac{130}{130 + 23} = 85\ \%$$

$$specificity = \frac{TN}{all\ those\ not\ exhibiting\ both\ traits} = \frac{1531}{1531 + 31 + 15 + 144 + 27 + 53} = 85\ \%$$

$$\mathbf{bPPV} = \frac{TP}{all\ those\ with\ positive\ test\ result} = \frac{130}{130 + 15 + 27 + 144} = 41\ \%$$

Figure 12.5-1 Determination of the bivariate positive predictive value (bPPV) of a genetic screening test. (**FP**, False positive; **TP**, True Positive; **FN**, False Negative, **TN**, True Negative)
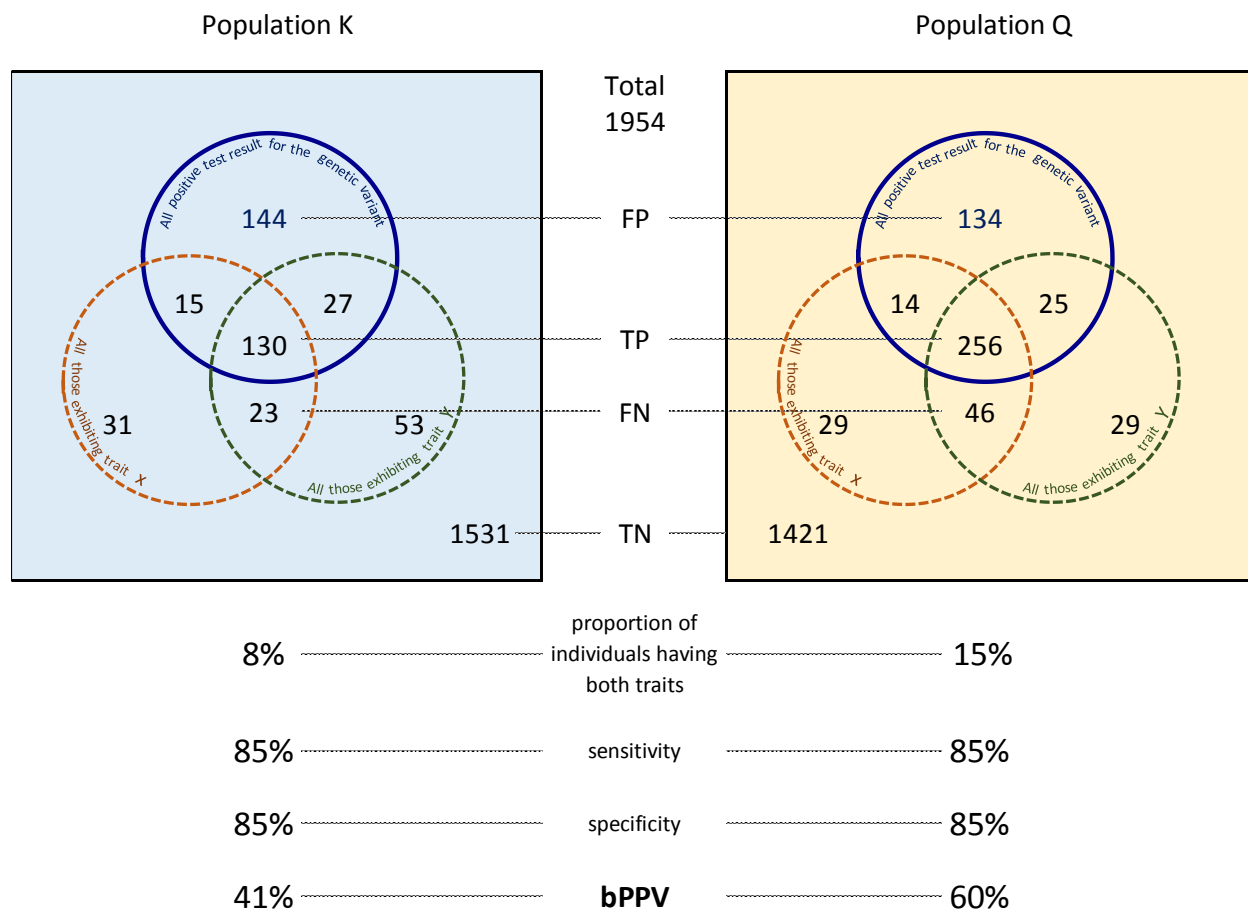
Figure 12.5-1 Venn diagrams of on the determination of the bivariate positive predictive value (bPPV) of a genetic screening test in two populations of size n=1954. Both populations have a sensitivity of 85% and a specificity of 85%. The bivariate positive predictive value in population K is 41% and in population K is 60%. One of the reason for this difference is that only 8% of individual display both traits, whereas in population Q is 15%. (**FP**, False positive; **TP**, True Positive; **FN**, False Negative, **TN**, True Negative)

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Appendix 1. Literature sources of data use in the study

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Appendix 2. Data Validation

Criteria for data validation

In order to ensure the quality of the data that are input, validation rules must be used beforehand analyses are carried out to check for fitness, accuracy, and consistency of the data. The validation logic included simple range and constraint validation (range of parameter estimates within their domains), structured validation (involves operations to check the data for consistency to mathematical relationships).

<u>Domain condition</u>

This range criteria establish that

heritabilities $\qquad h^2 \in [0, +1]$

correlations $\qquad r_{\blacksquare_{x,y}} \in [-1, +1]$

coheritability $\qquad h_{x,y} \in [-1, +1]$

coenvironmentability $\quad e_{x,y} \in [-1, +1]$

It, therefore, checks that the values of the parameter estimators are numerically within their domains.

<u>Boundary Condition</u>

The criterion states that

$$\left| h_{x,y} \right| + |e_{x,y}| \leq 1$$

It verifies that the calculated coheritabilities and coenvironmentabilities are located within the boundaries of the field due to their satisfying all the following conditions: $r_{P_{x,y}} = h_{x,y} + e_{x,y}$, and $-1 < r_{P_{x,y}} < 1$, and $-1 < h_{x,y} < 1$, and $-1 < e_{x,y} < 1$.

Disparity Condition

This structured validation criterion involves the disparity $D = \left| r_{P_{x,y}} - r_{A_{x,y}} \right|$ between the phenotypic and genetic correlations.

$$\left| r_{P_{x,y}} \right| + D \leq 1$$

This procedure checks that the phenotypic and genetic correlations maintain a congruent relationship as expressed in the equation $r_{P_{x,y}} = \sqrt{h_x^2 \, h_y^2} \; r_{A_{x,y}} + \sqrt{(1 - h_x^2)(1 - h_y^2)} \; r_{E_{x,y}}$.

Limit Check

The limit criteria are

$$\left| h_{x,y} \right| \leq \sqrt{h_x^2 \, h_y^2}$$

$$\left| e_{x,y} \right| \leq \sqrt{(1 - h_x^2)(1 - h_y^2)}$$

To check that the coheritability and coenvironmentability values are always below or equal to what would be expected were the genetic or environmental correlation be equal to 1, respectively. That is, $\left| h_{x,y} \right| \leq \sqrt{h_x^2 \, h_y^2}$ means that the factor $\sqrt{h_x^2 \, h_y^2}$ which takes values between zero and positive 1, is multiplied by another variable $\left| r_{A_{x,y}} \right|$ which also varies in the same range, the result necessarily will be a number smaller than the factor itself.

Flow chart of data management

$$r_{P_{x,y}} \quad r_{A_{x,y}} \quad r_{E_{x,y}} \quad h_x^2 \quad h_y^2$$

$$r_{P_{x,y}} \quad r_{A_{x,y}} \qquad h_x^2 \quad h_y^2$$

$$r_{A_{x,y}} \quad r_{E_{x,y}} \quad h_x^2 \quad h_y^2$$

Calculate $r_{E_{x,y}}$

$$r_{E_{x,y}} = \frac{r_{P_{x,y}} - \sqrt{h_x^2 \, h_y^2} \, r_{A_{x,y}}}{\sqrt{(1-h_x^2)(1-h_y^2)}}$$

Calculate $r_{P_{x,y}}$

$$r_{P_{x,y}} = \sqrt{h_x^2 \, h_y^2} \, r_{A_{x,y}} + \sqrt{(1-h_x^2)(1-h_y^2)} \, r_{E_{x,y}}$$

$$r_{P_{x,y}} \quad r_{A_{x,y}} \quad r_{E_{x,y}} \quad h_x^2 \quad h_y^2$$

Calculate $\quad h_{x,y} = \sqrt{h_x^2 \, h_y^2} \, r_{A_{x,y}}$

Calculate $\quad e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)} \, r_{E_{x,y}}$

$$r_{P_{x,y}} \quad r_{A_{x,y}} \quad r_{E_{x,y}} \quad h_x^2 \quad h_y^2 \quad h_{x,y} \quad e_{x,y}$$

Calculation $\quad D = |\, r_{A_{x,y}} - r_{A_{x,y}} \,|$

Determination of partitions $\quad S_\blacksquare$

$$r_{P_{x,y}} \quad r_{A_{x,y}} \quad r_{E_{x,y}} \quad h_x^2 \quad h_y^2 \quad h_{x,y} \quad e_{x,y} \quad D \quad S_\blacksquare$$

Violation of parameter domain

$$h_\blacksquare^2 > 1$$

$$r_{\blacksquare x,y} > 1 \; , \; r_{\blacksquare x,y} < -1$$

Violation of boundary condition

$$|h_{x,y}| + |e_{x,y}| > 1$$

Violation of disparity

$$|r_{P_{x,y}}| + D > 1$$

Violation of limit criteria

$$|h_{x,y}| < \sqrt{h_x^2 \, h_y^2}$$

$$|e_{x,y}| < \sqrt{(1-h_x^2)(1-h_y^2)}$$

$$r_{P_{x,y}} \quad r_{A_{x,y}} \quad r_{E_{x,y}} \quad h_x^2 \quad h_y^2 \quad h_{x,y} \quad e_{x,y} \quad D \quad S_\blacksquare$$

Appendix 3. Statistical Analyses

Part A. Basic Statistics

The UNIVARIATE Procedure
Variable: rP

Moments			
N	6286	Sum Weights	6286
Mean	0.15800175	Sum Observations	993.199
Std Deviation	0.30906791	Variance	0.09552297
Skewness	0.4063202	Kurtosis	0.94320413
Uncorrected SS	757.289053	Corrected SS	600.361873
Coeff Variation	195.610433	Std Error Mean	0.00389822

Basic Statistical Measures			
Location		**Variability**	
Mean	0.158002	Std Deviation	0.30907
Median	0.108000	Variance	0.09552
Mode	0.020000	Range	1.95200
		Interquartile Range	0.32000

Tests for Location: Mu0=0				
Test		**Statistic**	**p Value**	
Student's t	t	40.53173	Pr > |t|	<.0001
Sign	M	1385	Pr >= |M|	<.0001
Signed Rank	S	5559832	Pr >= |S|	<.0001

Extreme Observations			
Lowest		**Highest**	
Value	Obs	Value	Obs
-0.96	2240	0.990	2064
-0.95	4639	0.990	2067
-0.95	2408	0.990	2212
-0.95	1355	0.990	2511

The UNIVARIATE Procedure
Variable: rA

Moments			
N	6286	Sum Weights	6286
Mean	0.19502733	Sum Observations	1225.9418
Std Deviation	0.42936089	Variance	0.18435078
Skewness	-0.0800828	Kurtosis	-0.332983
Uncorrected SS	1397.7368	Corrected SS	1158.64464
Coeff Variation	220.154218	Std Error Mean	0.00541546

Basic Statistical Measures			
Location		Variability	
Mean	0.195027	Std Deviation	0.42936
Median	0.160500	Variance	0.18435
Mode	0.010000	Range	2.00000
		Interquartile Range	0.57000

Note: The mode displayed is the smallest of 2 modes with a count of 69.

Tests for Location: Mu0=0				
Test		Statistic	p Value	
Student's t	t	36.01307	Pr > |t|	<.0001
Sign	M	1184.5	Pr >= |M|	<.0001
Signed Rank	S	4744694	Pr >= |S|	<.0001

Extreme Observations			
Lowest		Highest	
Value	Obs	Value	Obs
-1	5222	1	4384
-1	2754	1	4398
-1	2753	1	5931
-1	2750	1	6008

Extreme Observations			
Lowest		Highest	
Value	Obs	Value	Obs
-1	2748	1	6121

The UNIVARIATE Procedure

Variable: rE			
Moments			
N	6286	Sum Weights	6286
Mean	0.14026039	Sum Observations	881.676821
Std Deviation	0.31501491	Variance	0.09923439
Skewness	0.31095032	Kurtosis	0.97735159
Uncorrected SS	747.352486	Corrected SS	623.68815
Coeff Variation	224.592918	Std Error Mean	0.00397323

Basic Statistical Measures			
Location		Variability	
Mean	0.140260	Std Deviation	0.31501
Median	0.091000	Variance	0.09923
Mode	0.060000	Range	2.00000
		Interquartile Range	0.32100

Tests for Location: Mu0=0				
Test		Statistic	p Value	
Student's t	t	35.30134	Pr > |t|	<.0001
Sign	M	1245	Pr >= |M|	<.0001
Signed Rank	S	4947997	Pr >= |S|	<.0001

Extreme Observations			
Lowest		Highest	
Value	Obs	Value	Obs

Extreme Observations

Lowest		Highest	
Value	Obs	Value	Obs
-1.000	2406	0.993	2402
-0.982	2408	0.993	2403
-0.981	6267	0.995	2212
-0.980	2419	1.000	1838
-0.971	6273	1.000	2445

The UNIVARIATE Procedure
Variable: hxy

Moments

N	6286	Sum Weights	6286
Mean	0.07545434	Sum Observations	474.306
Std Deviation	0.17795416	Variance	0.03166768
Skewness	0.72275883	Kurtosis	2.61925239
Uncorrected SS	234.819846	Corrected SS	199.031398
Coeff Variation	235.843502	Std Error Mean	0.00224451

Basic Statistical Measures

Location		Variability	
Mean	0.075454	Std Deviation	0.17795
Median	0.049000	Variance	0.03167
Mode	0.000000	Range	1.71200
		Interquartile Range	0.17100

Tests for Location: Mu0=0

Test		Statistic		p Value	
Student's t	t	33.61733	Pr > |t|	<.0001
Sign	M	1190.5	Pr >= |M|	<.0001
Signed Rank	S	4740642	Pr >= |S|	<.0001

Quantiles (Definition 5)

Level	Quantile

Quantiles (Definition 5)	
Level	Quantile
100% Max	0.945
90%	0.306
75% Q3	0.155
50% Median	0.049
25% Q1	-0.016
10%	-0.105
5%	-0.172
1%	-0.357
0% Min	-0.767

The UNIVARIATE Procedure
Variable: exy

Moments			
N	6286	Sum Weights	6286
Mean	0.0825867	Sum Observations	519.14
Std Deviation	0.19845122	Variance	0.03938289
Skewness	0.59411701	Kurtosis	2.2046199
Uncorrected SS	290.395492	Corrected SS	247.521432
Coeff Variation	240.294399	Std Error Mean	0.00250303

Basic Statistical Measures			
Location		Variability	
Mean	0.082587	Std Deviation	0.19845
Median	0.053000	Variance	0.03938
Mode	0.000000	Range	1.74000
		Interquartile Range	0.17900

Tests for Location: Mu0=0				
Test		Statistic	p Value	
Student's t	t	32.99465	Pr > |t|	<.0001
Sign	M	1237	Pr >= |M|	<.0001
Signed Rank	S	4838707	Pr >= |S|	<.0001

Quantiles (Definition 5)	
Level	**Quantile**
100% Max	0.876
99%	0.669
75% Q3	0.161
50% Median	0.053
25% Q1	-0.018
10%	-0.107
5%	-0.195
1%	-0.435
0% Min	-0.864

Part B. Multinomial Test

The FREQ Procedure

Statistics for Table of partition

**Chi-Square Test
for Specified Proportions**

Chi-Square	9.3370
DF	5
Pr > ChiSq	0.0964

Deviations of partition
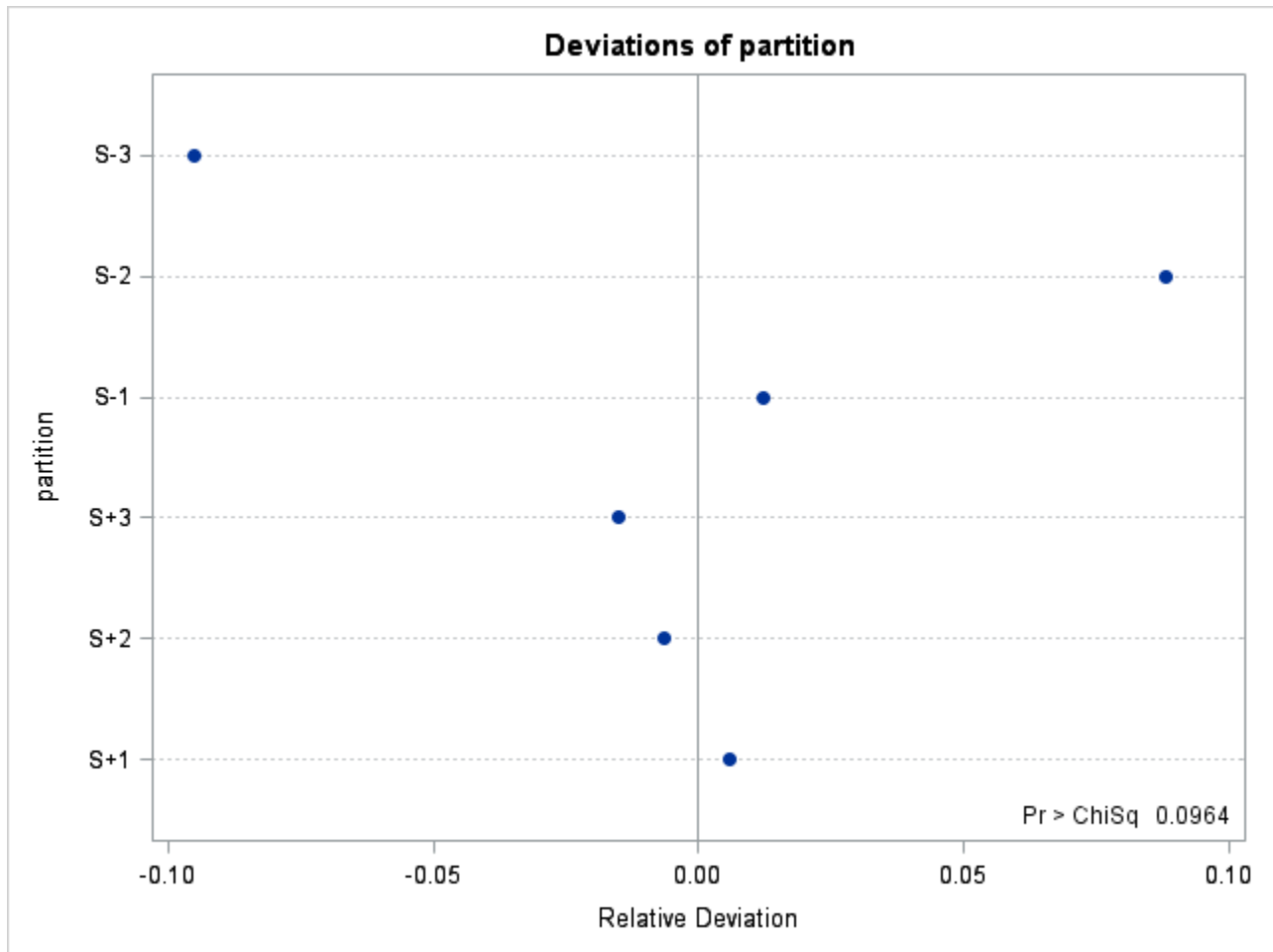
Part C. Model 1: Multiple Regression Analysis

rP=hxy exy -ALL

The REG Procedure
Model: MODEL1
Dependent Variable: rP

Number of Observations Read	6290
Number of Observations Used	6290

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	604.38562	302.19281	2.498E7	<.0001
Error	6287	0.07605	0.00001210		
Corrected Total	6289	604.46167			

Root MSE	0.00348	R-Square	0.9999
Dependent Mean	0.15790	Adj R-Sq	0.9999
Coeff Var	2.20262		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-0.00003174	0.00004923	-0.64	0.5191
hxy	1	1.00008	0.00026117	3829.29	<.0001
exy	1	0.99983	0.00023442	4265.11	<.0001

Collinearity Diagnostics

Number	Eigenvalue	Condition Index	Proportion of Variation		
			Intercept	hxy	exy
1	1.80892	1.00000	0.13712	0.14292	0.14240
2	0.63233	1.69137	0.86067	0.15532	0.21786

Collinearity Diagnostics					
			Proportion of Variation		
Number	**Eigenvalue**	**Condition Index**	**Intercept**	**hxy**	**exy**
3	0.55875	1.79929	0.00222	0.70176	0.63974

The REG Procedure
Model: MODEL1
Dependent Variable: rP
<mark>partition=S+1</mark>

Number of Observations Read	3311
Number of Observations Used	3311

Analysis of Variance					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Value**	**Pr > F**
Model	2	227.80716	113.90358	1.439E9	<.0001
Error	3308	0.00026185	7.915681E-8		
Corrected Total	3310	227.80742			

Root MSE	0.00028135	R-Square	1.0000
Dependent Mean	0.34818	Adj R-Sq	1.0000
Coeff Var	0.08081		

Parameter Estimates					
Variable	**DF**	**Parameter Estimate**	**Standard Error**	**t Value**	**Pr > |t|**
Intercept	1	0.00000626	0.00000814	0.77	0.4420
hxy	1	0.99997	0.00003262	30658.4	<.0001
exy	1	1.00002	0.00002787	35877.0	<.0001

The REG Procedure
Model: MODEL1
Dependent Variable: rP

Number of Observations Read	617
Number of Observations Used	617

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	9.75769	4.87885	6.839E7	<.0001
Error	614	0.00004380	7.133518E-8		
Corrected Total	616	9.75773			

Root MSE	0.00026709	R-Square	1.0000
Dependent Mean	0.11935	Adj R-Sq	1.0000
Coeff Var	0.22378		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.00000866	0.00001802	0.48	0.6310
hxy	1	1.00000	0.00008550	11695.6	<.0001
exy	1	0.99987	0.00020235	4941.33	<.0001

The REG Procedure

Model: MODEL1
Dependent Variable: rP

==partition=S+3==

Number of Observations Read	367
Number of Observations Used	367

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	2.51740	1.25870	2.451E7	<.0001
Error	364	0.00001869	5.135616E-8		
Corrected Total	366	2.51742			

Root MSE	0.00022662	R-Square	1.0000
Dependent Mean	-0.07991	Adj R-Sq	1.0000
Coeff Var	-0.28358		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-0.00004385	0.00001926	-2.28	0.0234
hxy	1	1.00029	0.00026374	3792.79	<.0001
exy	1	0.99986	0.00014283	7000.37	<.0001

The REG Procedure
Model: MODEL1
Dependent Variable: rP
<mark>partition=S-1</mark>

Number of Observations Read	880
Number of Observations Used	880

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	37.41069	18.70535	4.02E8	<.0001
Error	877	0.00004080	4.652576E-8		
Corrected Total	879	37.41073			

Root MSE	0.00021570	R-Square	1.0000
Dependent Mean	-0.24035	Adj R-Sq	1.0000
Coeff Var	-0.08974		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.00002168	0.00001123	1.93	0.0539
hxy	1	1.00011	0.00006963	14362.4	<.0001
exy	1	1.00002	0.00005087	19656.8	<.0001

The REG Procedure
Model: MODEL1
Dependent Variable: rP
<mark>partition=S-2</mark>

Number of Observations Read	473
Number of Observations Used	473

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	4.74065	2.37033	3.301E7	<.0001
Error	470	0.00003375	7.181444E-8		
Corrected Total	472	4.74069			

Root MSE	0.00026798	R-Square	1.0000
Dependent Mean	-0.08663	Adj R-Sq	1.0000
Coeff Var	-0.30934		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-0.00003170	0.00002128	-1.49	0.1370
hxy	1	1.00001	0.00012337	8105.59	<.0001
exy	1	1.00037	0.00025993	3848.65	<.0001

The REG Procedure
Model: MODEL1
Dependent Variable: rP

Number of Observations Read	562
Number of Observations Used	562

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	3.74976	1.87488	2.68E7	<.0001
Error	559	0.00003911	6.995705E-8		
Corrected Total	561	3.74980			

Root MSE	0.00026449	R-Square	1.0000
Dependent Mean	0.08616	Adj R-Sq	1.0000
Coeff Var	0.30697		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.00006554	0.00002007	3.26	0.0012
hxy	1	0.99986	0.00026281	3804.57	<.0001
exy	1	0.99957	0.00013691	7301.15	<.0001

Part D. Model 2: Multiple Regression Analysis

rP=rA rE - ALL

The REG Procedure
Model: MODEL1
Dependent Variable: rP

Number of Observations Read	6290
Number of Observations Used	6290

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	559.23457	279.61728	38869.5	<.0001
Error	6287	45.22710	0.00719		
Corrected Total	6289	604.46167			

Root MSE	0.08482	R-Square	0.9252
Dependent Mean	0.15790	Adj R-Sq	0.9252
Coeff Var	53.71456		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.00264	0.00121	2.19	0.0289
rA	1	0.39036	0.00285	137.05	<.0001
rE	1	0.56490	0.00388	145.62	<.0001

rP=rA rE -PARTITION

Number of Observations Read	3311
Number of Observations Used	3311

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	214.72230	107.36115	27141.6	<.0001
Error	3308	13.08512	0.00396		
Corrected Total	3310	227.80742			

Root MSE	0.06289	R-Square	0.9426
Dependent Mean	0.34818	Adj R-Sq	0.9425
Coeff Var	18.06363		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-0.01006	0.00194	-5.19	<.0001
rA	1	0.39393	0.00448	87.93	<.0001
rE	1	0.59921	0.00511	117.36	<.0001

rP=rA rE -PARTITION

The REG Procedure
Model: MODEL1
Dependent Variable: rP
partition=S+2

Number of Observations Read	617
Number of Observations Used	617

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	2.92511	1.46256	131.43	<.0001
Error	614	6.83262	0.01113		
Corrected Total	616	9.75773			

Root MSE	0.10549	R-Square	0.2998
Dependent Mean	0.11935	Adj R-Sq	0.2975
Coeff Var	88.38666		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.00804	0.00825	0.97	0.3302
rA	1	0.25936	0.01665	15.57	<.0001
rE	1	0.01197	0.02959	0.40	0.6859

rP=rA rE -PARTITION

The REG Procedure
Model: MODEL1
Dependent Variable: rP
partition=S+3

Number of Observations Read	367
Number of Observations Used	367

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	0.97356	0.48678	114.77	<.0001
Error	364	1.54386	0.00424		
Corrected Total	366	2.51742			

Root MSE	0.06513	R-Square	0.3867
Dependent Mean	-0.07991	Adj R-Sq	0.3834
Coeff Var	-81.49611		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-0.03867	0.00543	-7.12	<.0001
rA	1	0.11735	0.02188	5.36	<.0001
rE	1	0.30134	0.01989	15.15	<.0001

rP=rA rE -PARTITION

The REG Procedure
Model: MODEL1
Dependent Variable: rP
partition=S-1

Number of Observations Read	880
Number of Observations Used	880

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	33.38106	16.69053	3632.45	<.0001
Error	877	4.02967	0.00459		
Corrected Total	879	37.41073			

Root MSE	0.06779	R-Square	0.8923
Dependent Mean	-0.24035	Adj R-Sq	0.8920
Coeff Var	-28.20244		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-0.00809	0.00367	-2.20	0.0277
rA	1	0.36761	0.01029	35.73	<.0001
rE	1	0.60166	0.01215	49.54	<.0001

rP=rA rE -PARTITION

The REG Procedure
Model: MODEL1
Dependent Variable: rP
partition=S-2

Number of Observations Read	473
Number of Observations Used	473

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	1.11413	0.55706	72.20	<.0001
Error	470	3.62656	0.00772		
Corrected Total	472	4.74069			

Root MSE	0.08784	R-Square	0.2350
Dependent Mean	-0.08663	Adj R-Sq	0.2318
Coeff Var	-101.39814		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-0.00466	0.00796	-0.59	0.5582
rA	1	0.21788	0.01982	10.99	<.0001
rE	1	-0.03615	0.02960	-1.22	0.2226

The REG Procedure
Model: MODEL1
Dependent Variable: rP
partition=S-3

Number of Observations Read	562
Number of Observations Used	562

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	1.86161	0.93080	275.56	<.0001
Error	559	1.88820	0.00338		
Corrected Total	561	3.74980			

Root MSE	0.05812	R-Square	0.4965
Dependent Mean	0.08616	Adj R-Sq	0.4947
Coeff Var	67.45178		

Parameter Estimates					
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.02795	0.00447	6.25	<.0001
rA	1	0.09673	0.01367	7.08	<.0001
rE	1	0.35169	0.01511	23.28	<.0001

Part E. Simple regression of phenotypic correlation against a single factor

model rP=hxy ALL

The REG Procedure
Model: MODELx1
Dependent Variable: rP

Number of Observations Read	6290
Number of Observations Used	6290

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	384.34137	384.34137	10979.2	<.0001
Error	6288	220.12030	0.03501		
Corrected Total	6289	604.46167			

Root MSE	0.18710	R-Square	0.6358
Dependent Mean	0.15790	Adj R-Sq	0.6358
Coeff Var	118.49176		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.05364	0.00256	20.95	<.0001
hxy	1	1.38262	0.01320	104.78	<.0001

rP=exy -ALL

Number of Observations Read	6290
Number of Observations Used	6290

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	427.01299	427.01299	15131.5	<.0001
Error	6288	177.44868	0.02822		
Corrected Total	6289	604.46167			

Root MSE	0.16799	R-Square	0.7064
Dependent Mean	0.15790	Adj R-Sq	0.7064
Coeff Var	106.38845		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.04994	0.00229	21.78	<.0001
exy	1	1.30811	0.01063	123.01	<.0001

rP=rA -ALL

The REG Procedure
Model: MODEL1
Dependent Variable: rP

Number of Observations Read	6290
Number of Observations Used	6290

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	406.69694	406.69694	12931.1	<.0001
Error	6288	197.76473	0.03145		
Corrected Total	6289	604.46167			

Root MSE	0.17734	R-Square	0.6728
Dependent Mean	0.15790	Adj R-Sq	0.6728
Coeff Var	112.31365		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.04254	0.00246	17.32	<.0001
rA	1	0.59191	0.00521	113.71	<.0001

rP=rE -ALL

Number of Observations Read	6290
Number of Observations Used	6290

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	424.12059	424.12059	14787.9	<.0001
Error	6288	180.34108	0.02868		
Corrected Total	6289	604.46167			

Root MSE	0.16935	R-Square	0.7017
Dependent Mean	0.15790	Adj R-Sq	0.7016
Coeff Var	107.25201		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.04250	0.00234	18.19	<.0001
rE	1	0.82326	0.00677	121.61	<.0001

Part F. Simple Regression of rA on rP

Phenotypic correlation as predictor of genetic correlation

The REG Procedure
Model: MODEL1
Dependent Variable: rA

Number of Observations Read	6290
Number of Observations Used	6290

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	781.01307	781.01307	12931.1	<.0001
Error	6288	379.78362	0.06040		
Corrected Total	6289	1160.79669			

Root MSE	0.24576	R-Square	0.6728
Dependent Mean	0.19490	Adj R-Sq	0.6728
Coeff Var	126.09348		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	0.01542	0.00348	4.43	<.0001
rP	1	1.13670	0.01000	113.71	<.0001

Part G. Test of heterogeneity of regression coefficients

Results of the test that the regression coefficients of Model 1 (involving the coheritability and coenvironmentability as regressors) are not different than zero

rP=hxy exy -ALL

The REG Procedure
Model: MODEL1

Test test00 Results for Dependent Variable rP

Source	DF	Mean Square	F Value	Pr > F
Numerator	2	299.12757	4.221E9	<.0001
Denominator	6207	7.086589E-8		

Results of the test that the regression coefficients of Model 1 (involving the coheritability and coenvironmentability as regressors) are not different than unity

rP=hxy exy -ALL

The REG Procedure
Model: MODEL1

Test test01 Results for Dependent Variable rP

Source	DF	Mean Square	F Value	Pr > F
Numerator	2	4.57815E-9	0.06	0.9374
Denominator	6207	7.086589E-8		

Test of Heterogenetity of slopes by partition model 1
The GLM Procedure

Dependent Variable: rP

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	12	598.2551448	49.8545954	7.033E8	<.0001
Error	6197	0.0004393	0.0000001		
Corrected Total	6209	598.2555841			

R-Square	Coeff Var	Root MSE	rP Mean
0.999999	0.166491	0.000266	0.159914

Source	DF	Type I SS	Mean Square	F Value	Pr > F
hxy	1	381.6300961	381.6300961	5.384E9	<.0001
exy	1	216.6250481	216.6250481	3.056E9	<.0001
hxy*partition	5	0.0000002	0.0000000	0.64	0.6681
exy*partition	5	0.0000004	0.0000001	1.02	0.4038

Parameter	Estimate		Standard Error	t Value	Pr > |t|
Intercept	0.0000078329		0.00000561	1.40	0.1625
hxy	0.9997105089	B	0.00025964	3850.43	<.0001
exy	0.9998122234	B	0.00010991	9096.53	<.0001
hxy*partition S+1	0.0002540093	B	0.00026188	0.97	0.3321
hxy*partition S+2	0.0002920603	B	0.00027023	1.08	0.2798
hxy*partition S+3	0.0005000960	B	0.00040304	1.24	0.2147
hxy*partition S-1	0.0003553349	B	0.00027009	1.32	0.1884
hxy*partition S-2	0.0004238301	B	0.00027890	1.52	0.1287
hxy*partition S-3	0.0000000000	B	.	.	.
exy*partition S+1	0.0002021176	B	0.00011064	1.83	0.0678
exy*partition S+2	0.0000516191	B	0.00022539	0.23	0.8189
exy*partition S+3	0.0002783650	B	0.00017860	1.56	0.1191
exy*partition S-1	0.0001797528	B	0.00012612	1.43	0.1541
exy*partition S-2	0.0004022520	B	0.00026639	1.51	0.1311
exy*partition S-3	0.0000000000	B	.	.	.

Test of Heterogenetity of slopes by partition model 2
The GLM Procedure

Dependent Variable: rP

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	12	566.8512326	47.2376027	9321.37	<.0001
Error	6197	31.4043515	0.0050677		
Corrected Total	6209	598.2555841			

R-Square	Coeff Var	Root MSE	rP Mean
0.947507	44.51616	0.071188	0.159914

Source	DF	Type I SS	Mean Square	F Value	Pr > F
rA	1	406.6296609	406.6296609	80240.0	<.0001
rE	1	148.6597054	148.6597054	29334.9	<.0001
rA*partition	5	3.5007162	0.7001432	138.16	<.0001
rE*partition	5	8.0611501	1.6122300	318.14	<.0001

Parameter	Estimate		Standard Error	t Value	Pr > |t|
Intercept	-.0067448116		0.00159477	-4.23	<.0001
rA	0.0511668388	B	0.01525943	3.35	0.0008
rE	0.4257233458	B	0.01474941	28.86	<.0001
rA*partition S+1	0.3388508491	B	0.01622625	20.88	<.0001
rA*partition S+2	0.2303500082	B	0.01747176	13.18	<.0001
rA*partition S+3	0.0170564459	B	0.02716135	0.63	0.5300
rA*partition S-1	0.3184734467	B	0.01765384	18.04	<.0001
rA*partition S-2	0.1628277772	B	0.01849852	8.80	<.0001
rA*partition S-3	0.0000000000	B	.	.	.
rE*partition S+1	0.1717135371	B	0.01563650	10.98	<.0001
rE*partition S+2	-.4235432624	B	0.02471607	-17.14	<.0001
rE*partition S+3	-.0673930605	B	0.02460769	-2.74	0.0062
rE*partition S-1	0.1769540581	B	0.01952937	9.06	<.0001
rE*partition S-2	-.4605367454	B	0.02774716	-16.60	<.0001
rE*partition S-3	0.0000000000	B	.	.	.

Part H. Correlation between the squared disparity and sampling variance of the genetic correlation

Simple Statistics						
Variable	N	Mean	Std Dev	Sum	Minimum	Maximum
D2	3234	0.06406	0.12350	207.16323	0	0.96040
V_rA	3241	0.04516	0.15385	146.36436	0	3.79080

Pearson Correlation Coefficients Prob > |r| under H0: Rho=0 Number of Observations		
	D2	V_rA
D2	1.00000 3234	0.17093 <.0001 3233
V_rA	0.17093 <.0001 3233	1.00000 3241

Part I. Wilcoxon Rank Test of the squared disparity and the sampling variance of the genetic correlation

The NPAR1WAY Procedure

partition	N	Sum of Scores	Expected Under H0	Std Dev Under H0	Mean Score
S+1	1862	2539773.00	3011785.00	26240.6879	1364.00269
S+2	251	608568.00	405992.50	14206.0000	2424.57371
S+3	171	344470.00	276592.50	11881.7354	2014.44444
S-1	454	607333.50	734345.00	18444.1501	1337.73899
S-2	192	449557.50	310560.00	12546.9608	2341.44531
S-3	304	681293.00	491720.00	15494.5485	2241.09539

Wilcoxon Scores (Rank Sums) for Variable D^2 Classified by Variable partition

Average scores were used for ties.

Kruskal-Wallis Test

Chi-Square	647.5628
DF	5
Pr > Chi-Square	<.0001

Distribution of Wilcoxon Scores for D2
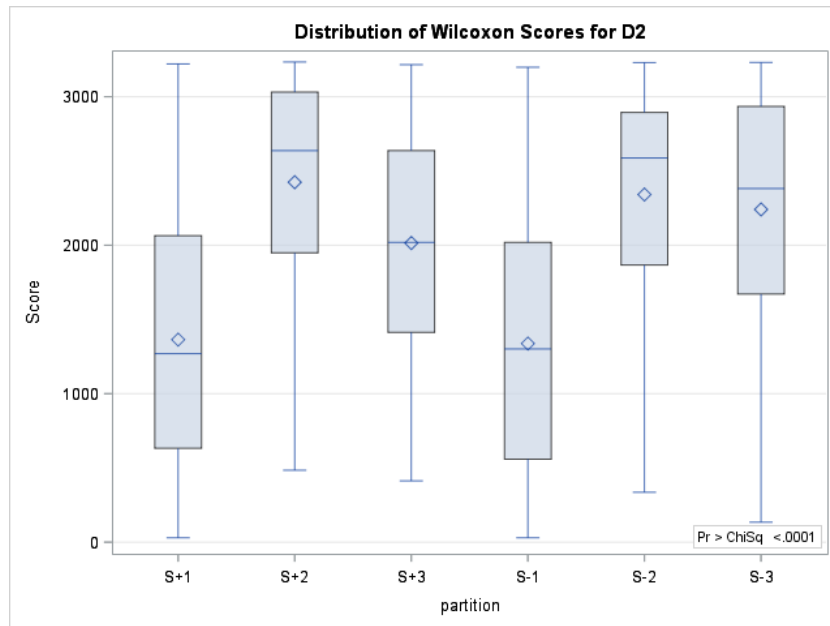
The NPAR1WAY Procedure

Wilcoxon Scores (Rank Sums) for Variable Var(rA) Classified by Variable partition					
partition	N	Sum of Scores	Expected Under H0	Std Dev Under H0	Mean Score
S+1	1865	2477918.00	3023165.0	26324.8233	1328.64236
S+2	251	507142.50	406871.0	14236.0428	2020.48805
S+3	171	349740.00	277191.0	11906.4988	2045.26316
S-1	455	796619.50	737555.0	18501.7617	1750.81209
S-2	194	436730.00	314474.0	12634.3796	2251.18557
S-3	305	685511.00	494405.0	15550.5149	2247.57705
Average scores were used for ties.					

Kruskal-Wallis Test	
Chi-Square	496.6782
DF	5
Pr > Chi-Square	<.0001

Distribution of Wilcoxon Scores for V_rA
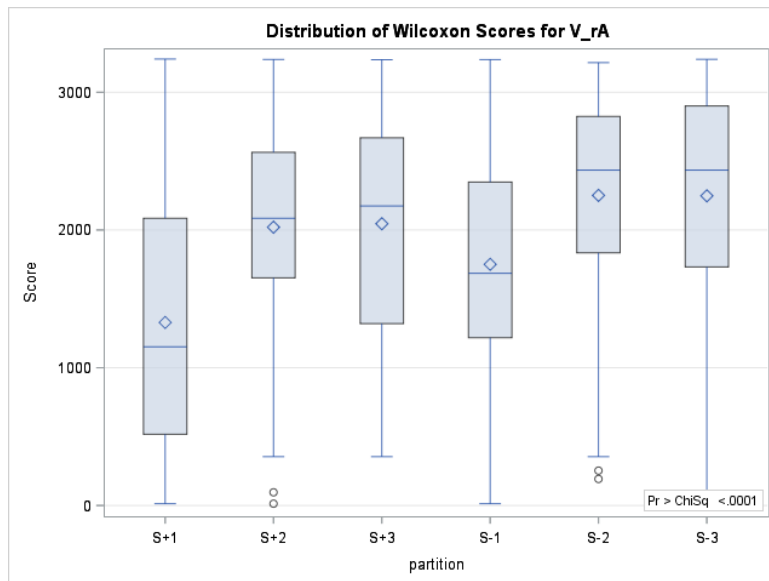
Results:

Wilcoxon signed rank test with continuity correction

Test statistic V : 3138479

p-value : 2.971110e-31

There are ties in the ranks, so the exact p-value cannot be computed. The p-value shown is inexact but fairly robust when the number of ties is small.

null hypothesis $\mu_0 = 0.0$

alternative hypothesis: two sided, $\hat{\mu} \neq \mu_0$

95% confidence interval : 0.0056 --------- 0.0088

sample estimate of pseudo-median $\hat{\mu}$: 0.00711298393513

Results from http://astatsa.com/WilcoxonTest/Result/

Wilcoxon Signed-Rank test, using Normal tables (n=3183) (two-tailed)

Since n > 25, **normal approximation** is used.

1. H$_0$ hypothesis
Since p-value<α, H$_0$ is rejected.
The value of the **After minus Before's** population is considered to be **not equal to** the Expected difference (μ0)
In other words, the difference between the value of the **After minus Before** and Expected difference (μ0) is big enough to be statistically significant.

2. P-value
p-value equals **0.00000**, (p(x≤Z) = 1.000000). This means that the chance of type1 error (rejecting a correct H$_0$) is small: 0.000 (0.0%)
The smaller the p-value the more it supports H$_1$

3. The statistics
The test statistic Z equals **11.653362**, is not in the 95% critical value accepted range: [-1.9600 : 1.9600]
W.=3137919.50, is not in the 95% accepted range: [2432039.7200 : 2635296.2800]

Normal Distribution

reject(α/2) accept Z

After minus Before wilcoxon signed-rank

value Expected difference (μ0)

Histogram

After minus Before (count) undefined (count)
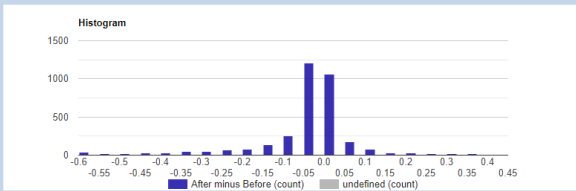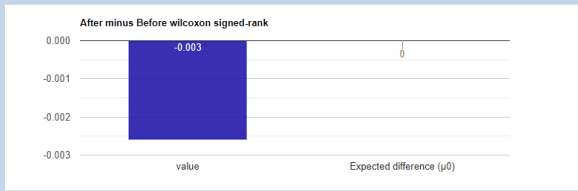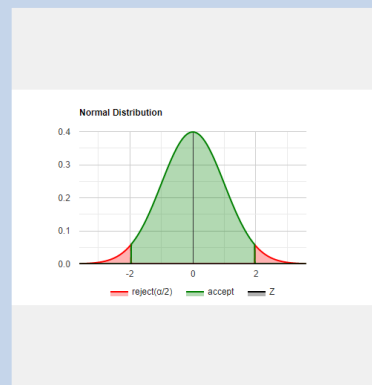
Results from http://www.statskingdom.com/175wilcoxon_signed_ranks.html

Figure S1. Abundance, dispersion and distribution of coheritability, coenvironmentability, and phenotypic correlation, overall and by partition. A single datum determined by $\{\, h_{x,y}\, ,\, e_{x,y}\, ,\, r_{P_{x,y}}\, \}$ is represented by a dot in the scatter plot.

Distribution of Genetic Parameters

Distribution of Genetic Parameters
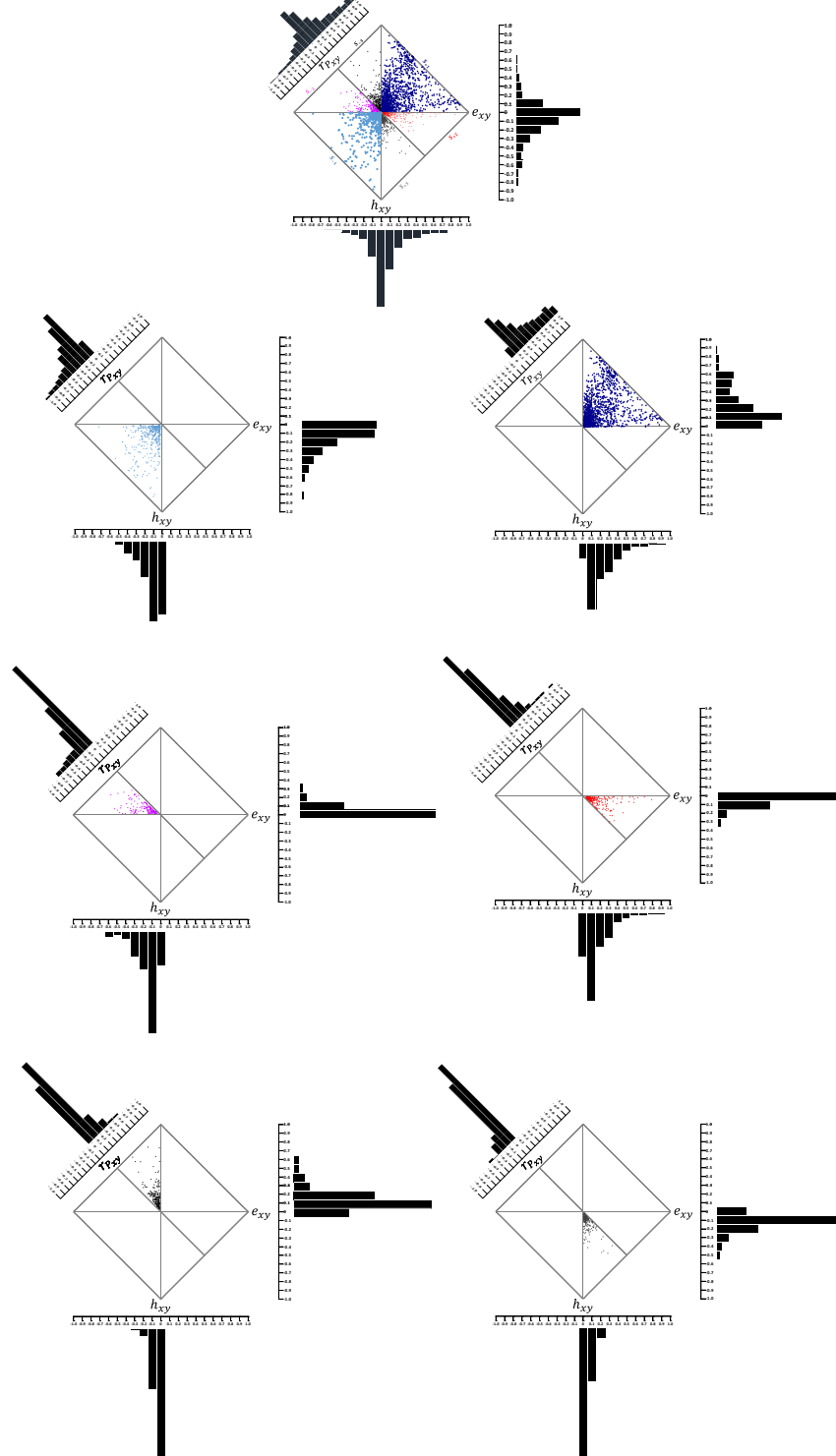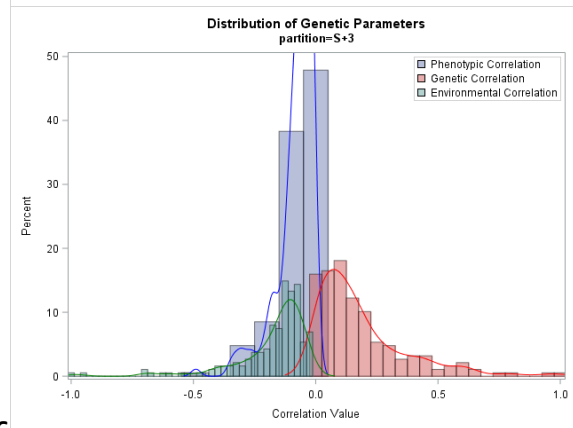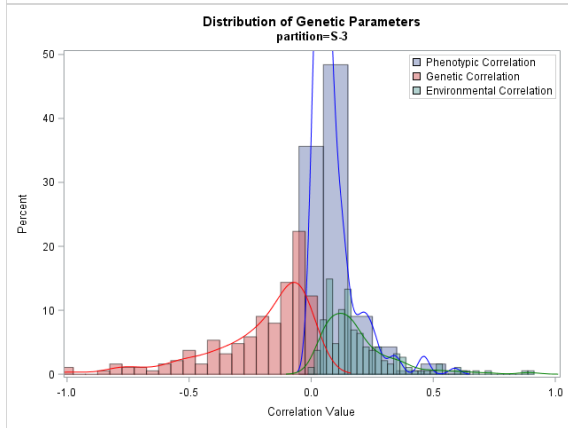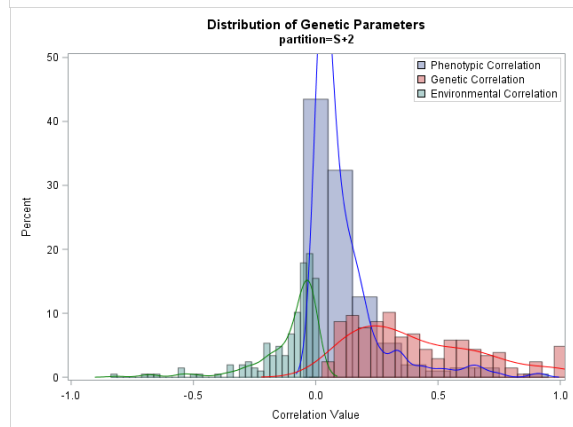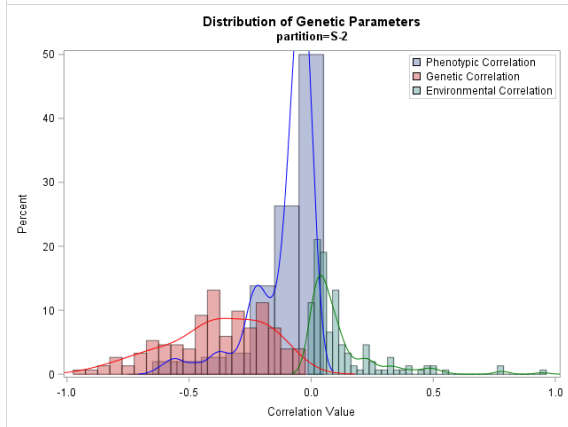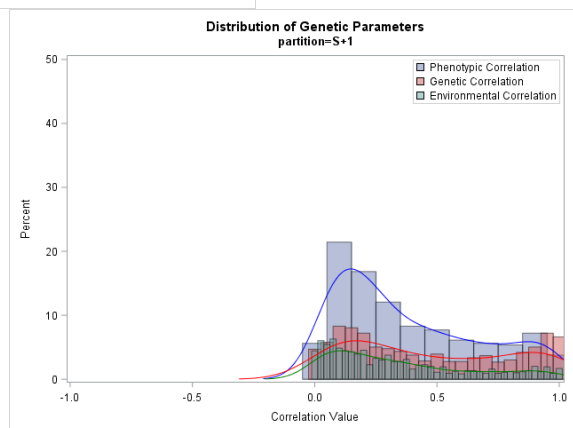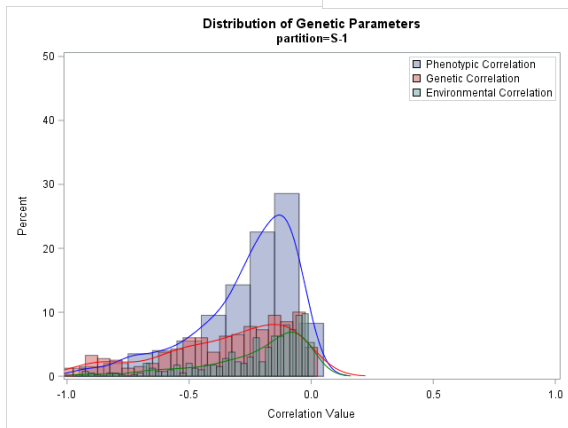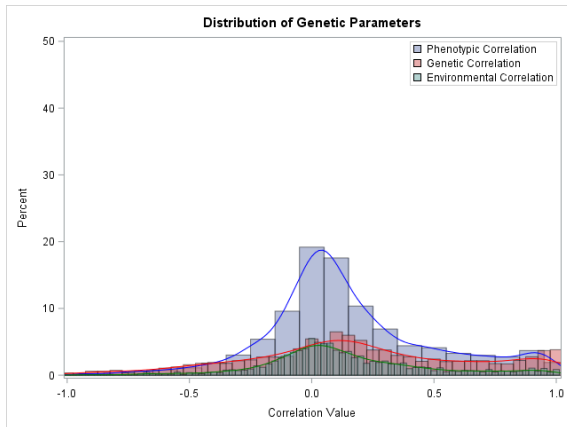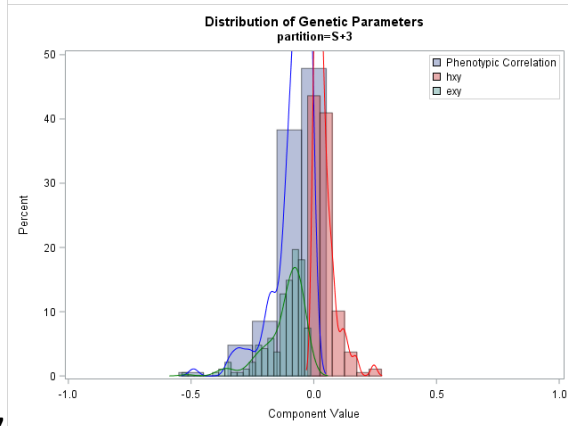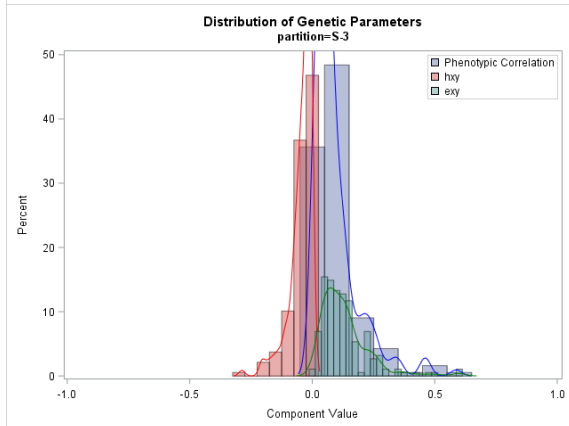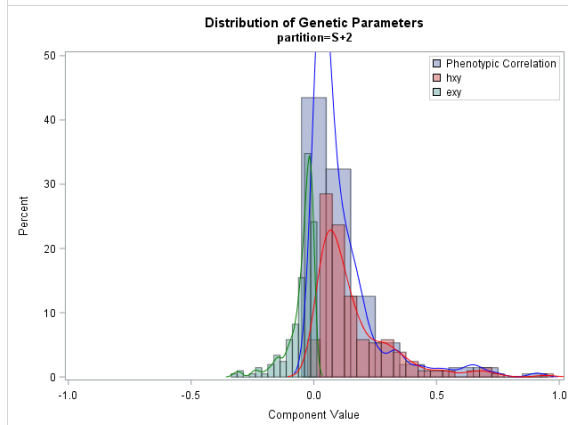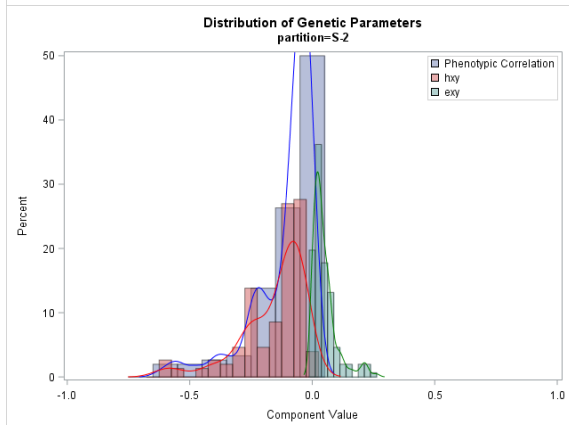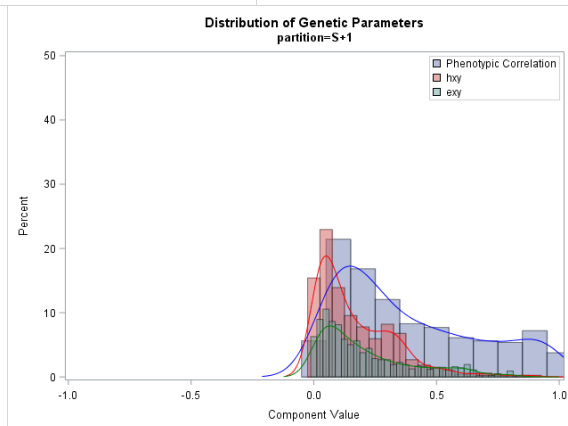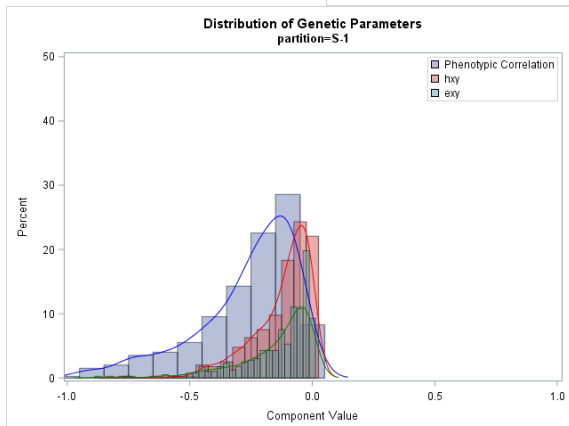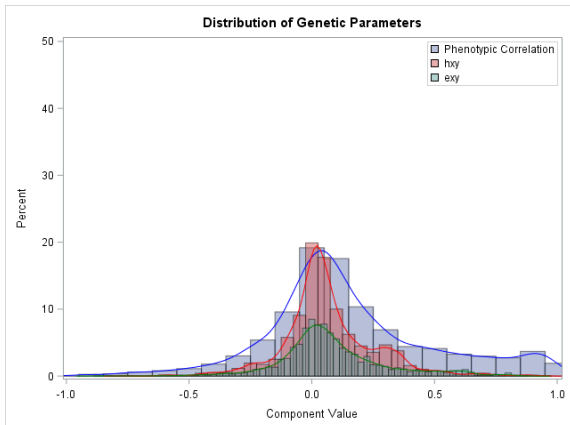
Figure S2. Scatter plot and regression of genetic correlation (A) and environmental correlation (B) against the phenotypic correlation. (C) Regression of environmental correlation on genetic correlation.
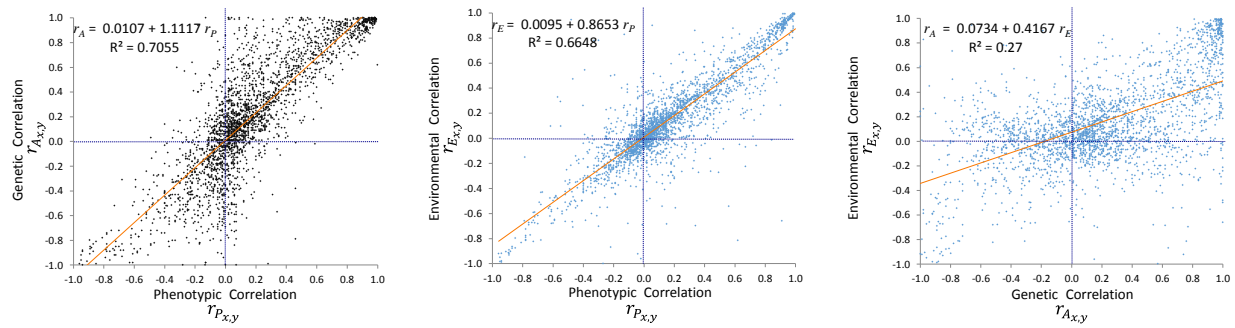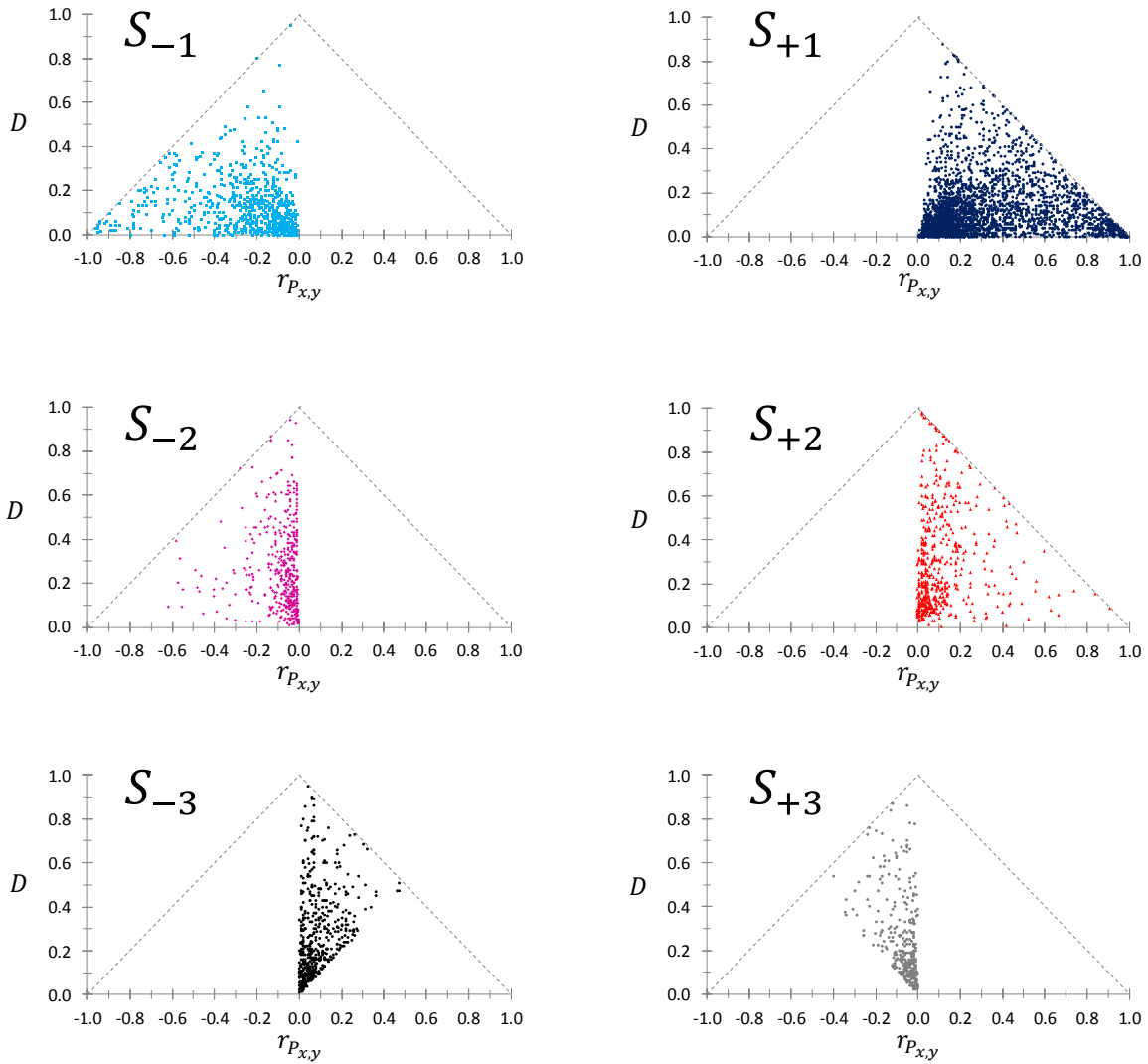
Figure S3. Disparity Index by partition

Figure S4. Supplementary Examples

Pick et al. (2016) studied the role of egg size as a maternal effector (a mother's trait causing maternal effects). Despite the positive association between egg size and fitness, a significant amount of additive genetic variation is maintained in natural populations, which lead to an evolutionary stasis in egg size. The authors hypothesized that this variation is kept by genetic constraints due to shared genetics among maternal resource investment on egg components. They assessed this hypothesis by performing artificial selection in a captive population of Japanese quail (*Coturnix japonica*). They found effectively that the high maternal egg investment line produced eggs with more albumen, yolk and shell mass than low-line eggs.
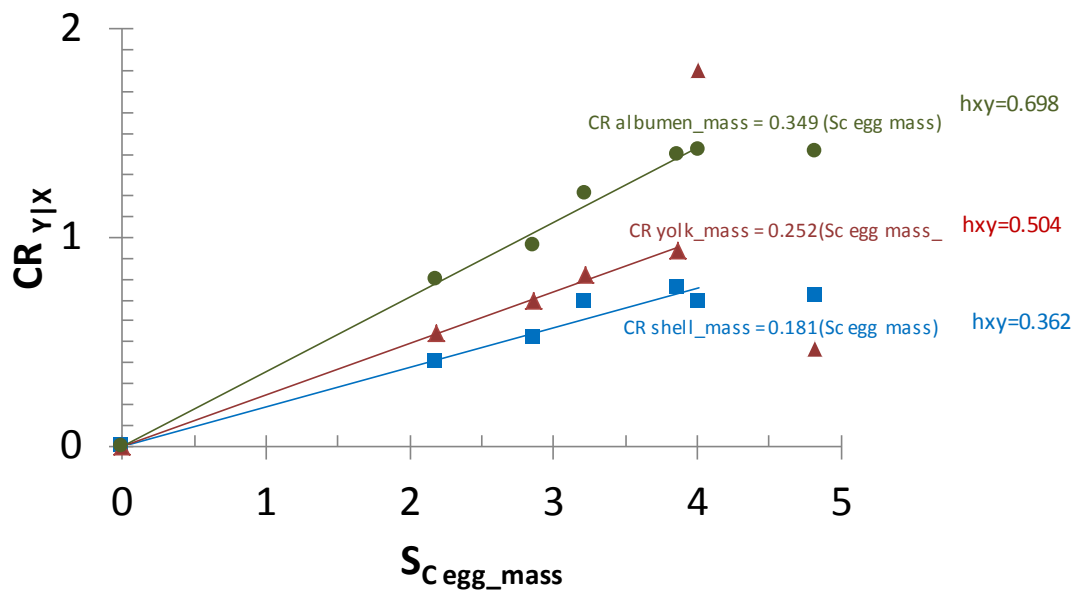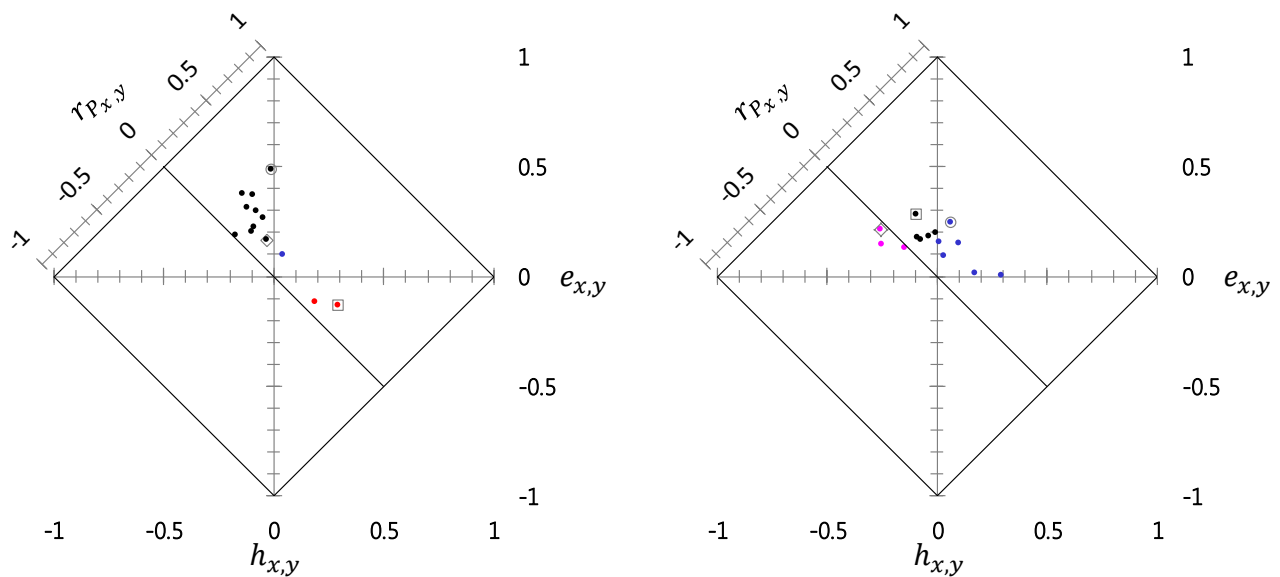
Figure S4-1. Coheritability, coenvironmentability and phenotypic correlation from pairwise analyses of morphological traits in house sparrow, *Passer domesticus*. (A) male, (B) female. The pair of traits highlighted are: tarsus length-bill length (square), tarsus length-body mass (circle), bill length-body mass (rhomboid). (Data source: Jensen et al. 2003). Notice the comparison of the phenotypic correlations of tarsus length and bill length in males ($r_m = 0.161, n = 407$) and females ($r_f = 0.185, n = 364$) were similar (Ho: $r_m = r_f$ was retained based on Zou's confidence interval of the difference -0.1609 and 0.1136 which included zero), the relative contribution of the coheritabilities and coenvironmentabilities were dramatically different in each sex. The coheritability (in males 0.295, in females -0.095) and and coenvironmentability (0.134 males, 0.280 females) were significantly different between each other. This tells of a differential genetic and environmental influence on these traits by sex.

Figure S5 Coheritability surface as a function of the heritabilities of the traits given a genetic correlation.
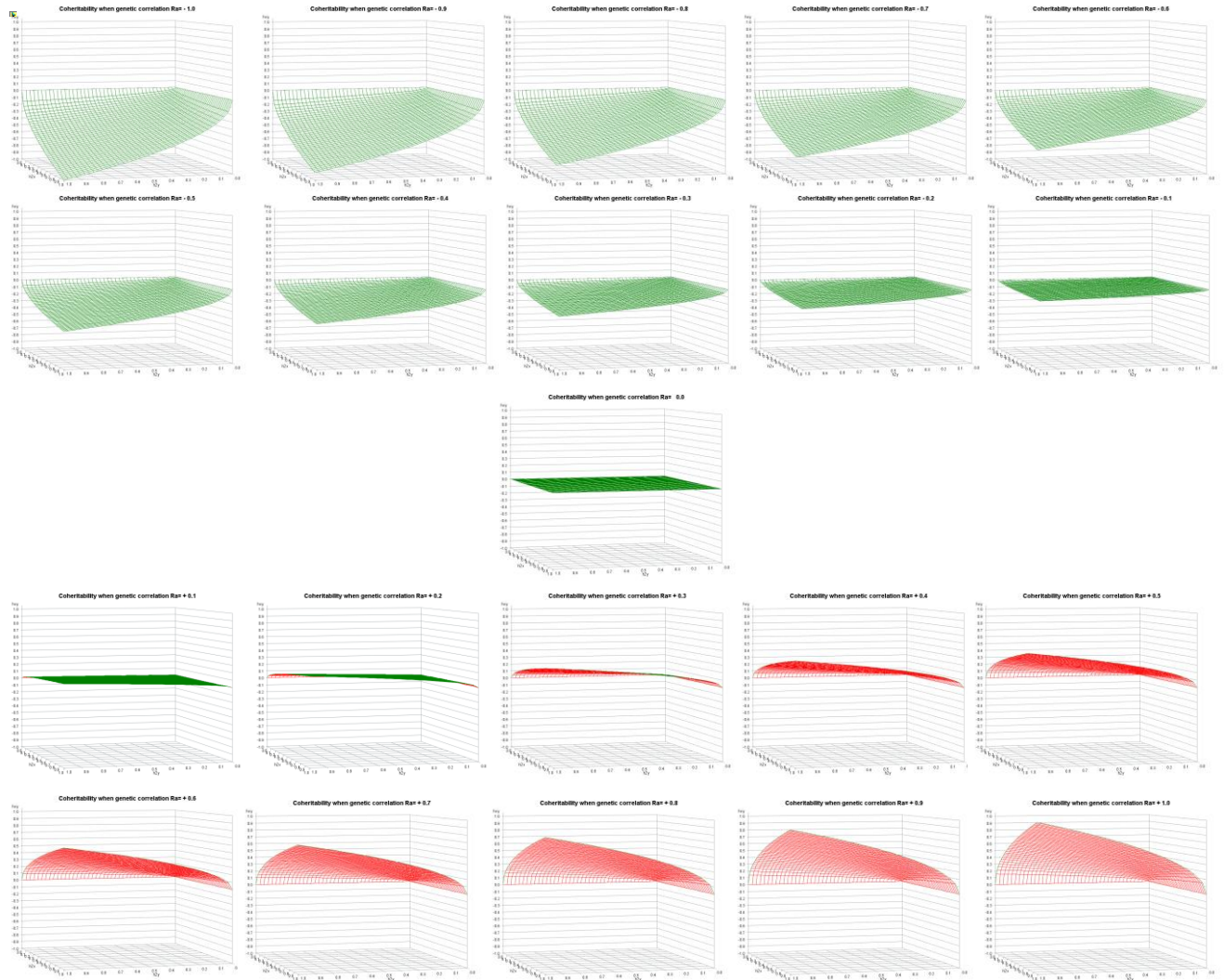
Table T2. Definitions

	heritability h^2	environmentability e^2	genetic correlation $r_{A_{xy}}$	environmental correlation $r_{E_{xy}}$	phenotypic correlation $r_{P_{xy}}$	coheritability h_{xy}	coenvironmentability e_{xy}
definition	• Proportion of the total phenotypic variance that is attributed to variability of breeding values. $$h^2 = \frac{V_{A_x}}{V_{P_x}}$$	• Residual proportion of the total phenotypic variance that is attributed to factors not accounted by breeding values. $$e^2 = 1 - h^2$$	Linear association between breeding values of two traits. Degree to which two characters are influenced by same loci. $$r_{A_{x,y}} = \frac{C_{A_{x,y}}}{\sqrt{V_{A_x} V_{A_y}}}$$	$$r_{E_{x,y}} = \frac{r_{P_{x,y}} - h_{xy}}{\sqrt{(1-h_x^2)(1-h_y^2)}}$$	• Linear association between phenotypic values of two traits. $$r_{P_{x,y}} = \frac{C_{P_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}}$$ $$= \sqrt{h_x^2 h_y^2}\; r_{A_{x,y}} + \sqrt{(1-h_x^2)(1-h_y^2)}\; r_{E_{x,y}}$$	• Proportion of total phenotypic variability of two traits attributed to the additive covariance of the traits. $$h_{xy} = \frac{C_{A_{x,y}}}{\sqrt{V_{P_x} V_{P_y}}}$$ $$= \sqrt{h_x^2 h_y^2}\; r_{A_{x,y}}$$	• Proportion of total phenotypic variability of two traits attributed to non genetic covariance of the traits. $$e_{xy} = r_{P_{x,y}} - h_{xy}$$ $$= \sqrt{(1-h_x^2)(1-h_y^2)}\; r_{E_{x,y}}$$
data	• breeding values of the trait • population with known genetic structure		• breeding values of each traits	• residual	• phenotypic values of each trait	• heritabilities of each trait, and genetic correlation, or • phenotypic variances, and additive genetic covariance	• heritabilities of each trait, and environmental correlation, or • phenotypic variances, and environmental covariance
range , domain	$0 < h^2 < 1$	$0 < e^2 < 1$	$-1 < r_{A_{xy}} < 1$	$-1 < r_{E_{xy}} < 1$	$-1 < r_{P_{xy}} < 1$	$-1 < h_{xy} < 1$	$-1 < e_{xy} < 1$
cause	• degree of resemblace between relatives	•	• pleiotropic action of genes • linkage disequilibrium		•	•	•
graphical depiction							

Appendix 5. Hypergeometric function

$_2F_1$ is the generalized hypergeometric function

$$_2F_1(a_1, a_2 ; b_1; x) = \sum_{m=0}^{\infty} \frac{(a_1)_m (a_2)_m}{(b_1)_k} \frac{x^m}{m!}$$

where $(q)_m$ denotes the rising Pochhammer symbol

$$(q)_m = \begin{cases} 1 & m = 0 \\ q(q-1) \dots (q+m-1) & m > 0 \end{cases}$$

	Hypergeometric function $_2F_1(a_1, a_2 ; b_1; x) = \sum_{m=0}^{\infty} \frac{(a_1)_m (a_2)_m}{(b_1)_k} \frac{x^m}{m!}$	Pochhammer function $(a_1)_0 = (a_2)_0$ $(b_1)_0$	Hypergeometric function associated to the density distribution of the sample correlation coefficient $_2F_1\left(\frac{1}{2},\frac{1}{2}; n-\frac{1}{2};\frac{1+\rho r}{2}\right)$
$m = 0$	$\frac{(a_1)_0(a_2)_0 x^0}{(b_1)_0 \; 0!}$	$(a_1)_0 = (a_2)_0 = \left(\frac{1}{2}\right)_0 = 1$ $(b_1)_0 = \left(n-\frac{1}{2}\right)_0 = 1$	1
$m = 1$	$\frac{(a_1)_1(a_2)_1 x^1}{(b_1)_1 \; 1!} = \frac{a_1 a_2}{b_1} \frac{x^1}{1!}$	$(a_1)_1 = (a_2)_1 = \left(\frac{1}{2}\right)_1 = \frac{1}{2}$ $(b_1)_1 = \left(n-\frac{1}{2}\right)_1 = \left[n-\frac{1}{2}\right] = \frac{1}{2}(2n-1)$	$\frac{\frac{1}{2}\cdot\frac{1}{2}}{\frac{(2n-1)}{2}}\left(\frac{1+\rho r}{2}\right)^1\frac{1}{1} = \frac{1}{4}\frac{(1+\rho r)}{(2n-1)}$
$m = 2$	$\frac{(a_1)_2(a_2)_2 x^2}{(b_1)_2 \; 2!} = \frac{a_1(a_1+1)a_2(a_2+1)}{b_1(b_1+1)} \frac{x^2}{2!}$	$(a_1)_2 = (a_2)_2 = \left(\frac{1}{2}\right)_2 = \frac{1}{2}\cdot\left[\frac{1}{2}+1\right] = \frac{3}{4}$ $(b_1)_2 = \left(n-\frac{1}{2}\right)_2 = \left[n-\frac{1}{2}\right]\left[n+\frac{1}{2}\right] = \frac{1}{4}(2n-1)(2n+1)$	$\frac{\frac{3}{2}\cdot\frac{3}{2}}{\frac{(2n-1)(2n+1)}{4}}\left(\frac{1+\rho r}{2}\right)^2\frac{1}{2} = \frac{9}{32}\frac{(1+\rho r)^2}{(2n-1)(2n+1)}$
$m = 3$	$\frac{(a_1)_3(a_2)_3 x^3}{(b_1)_3 \; 3!} = \frac{a_1(a_1+1)(a_1+2)a_2(a_2+1)(a_2+2)}{b_1(b_1+1)(b_1+2)} \frac{x^3}{3!}$	$(a_1)_3 = (a_2)_3 = \left(\frac{1}{2}\right)_3 = \frac{1}{2}\cdot\left[\frac{1}{2}+1\right]\left[\frac{1}{2}+2\right] = \frac{15}{8}$ $(b_1)_3 = \left(n-\frac{1}{2}\right)_3 = \left[n-\frac{1}{2}\right]\left[n+\frac{1}{2}\right]\left[n+\frac{3}{2}\right]$ $= \frac{1}{8}(2n-1)(2n+1)(2n+3)$	$\frac{\frac{15}{8}\cdot\frac{15}{8}}{\frac{(2n-1)(2n+1)(2n+3)}{8}}\left(\frac{1+\rho r}{2}\right)^3\frac{1}{6} = \frac{225}{384}\frac{(1+\rho r)^3}{(2n-1)(2n+1)(2n+3)}$
$m = 4$	$\frac{(a_1)_4(a_2)_4 x^4}{(b_1)_4 \; 4!} = \frac{a_1(a_1+1)(a_1+2)(a_1+3)a_2(a_2+1)(a_2+2)(a_2+3)}{b_1(b_1+1)(b_1+2)(b_1+3)} \frac{x^4}{4!}$	$(a_1)_4 = (a_2)_4 = \left(\frac{1}{2}\right)_4 = \frac{1}{2}\cdot\left[\frac{1}{2}+1\right]\left[\frac{1}{2}+2\right]\left[\frac{1}{2}+3\right] = \frac{105}{16}$ $(b_1)_4 = \left(n-\frac{1}{2}\right)_4 = \left[n-\frac{1}{2}\right]\left[n+\frac{1}{2}\right]\left[n+\frac{3}{2}\right]\left[n+\frac{5}{2}\right]$ $= \frac{1}{16}(2n-1)(2n+1)(2n+3)(2n+5)$	$\frac{\frac{105}{16}\cdot\frac{105}{16}}{\frac{(2n-1)(2n+1)(2n+3)(2n+5)}{16}}\left(\frac{1+\rho r}{2}\right)^4\frac{1}{24}$ $= \frac{11025}{6144}\frac{(1+\rho r)^4}{(2n-1)(2n+1)(2n+3)(2n+5)}$
$m = 5$	$\frac{(a_1)_5(a_2)_5 x^5}{(b_1)_5 \; 5!}$ $= \frac{a_1(a_1+1)(a_1+2)(a_1+3)(a_1+4)a_2(a_2+1)(a_2+2)(a_2+3)(a_2+4)}{b_1(b_1+1)(b_1+2)(b_1+3)(b_1+4)} \frac{x^5}{5!}$	$(a_1)_5 = (a_2)_5 = \left(\frac{1}{2}\right)_5 = \frac{1}{2}\cdot\left[\frac{1}{2}+1\right]\left[\frac{1}{2}+2\right]\left[\frac{1}{2}+3\right]\left[\frac{1}{2}+4\right] = \frac{945}{32}$ $(b_1)_5 = \left(n-\frac{1}{2}\right)_5 = \left[n-\frac{1}{2}\right]\left[n+\frac{1}{2}\right]\left[n+\frac{3}{2}\right]\left[n+\frac{5}{2}\right]\left[n+\frac{7}{2}\right]$ $= \frac{1}{32}(2n-1)(2n+1)(2n+3)(2n+5)(2n+7)$	$\frac{\frac{945}{32}\cdot\frac{945}{32}}{\frac{(2n-1)(2n+1)(2n+3)(2n+5)(2n+7)}{32}}\left(\frac{1+\rho r}{2}\right)^5\frac{1}{120}$ $= \frac{893025}{122880}\frac{(1+\rho r)^5}{(2n-1)(2n+1)(2n+3)(2n+5)(2n+7)}$
$m = 6$	$\frac{(a_1)_6(a_2)_6 x^6}{(b_1)_6 \; 6!}$ $= \frac{a_1(a_1+1)(a_1+2)(a_1+3)(a_1+4)a_2(a_2+1)(a_2+2)(a_2+3)(a_2+4)(a_2+5)}{b_1(b_1+1)(b_1+2)(b_1+3)(b_1+4)(b_1+5)} \frac{x^6}{6!}$	$(a_1)_6 = (a_2)_6 = \left(\frac{1}{2}\right)_6 = \frac{1}{2}\cdot\left[\frac{1}{2}+1\right]\left[\frac{1}{2}+2\right]\left[\frac{1}{2}+3\right]\left[\frac{1}{2}+4\right]\left[\frac{1}{2}+5\right] = \frac{10395}{64}$ $(b_1)_6 = \left(n-\frac{1}{2}\right)_6 = \left[n-\frac{1}{2}\right]\left[n+\frac{1}{2}\right]\left[n+\frac{3}{2}\right]\left[n+\frac{5}{2}\right]\left[n+\frac{7}{2}\right]\left[n+\frac{9}{2}\right]$ $= \frac{1}{64}(2n-1)(2n+1)(2n+3)(2n+5)(2n+7)(2n+9)$	$\frac{\frac{10395}{64}\cdot\frac{10396}{64}}{\frac{(2n-1)(2n+1)(2n+3)(2n+5)(2n+7)(2n+9)}{64}}\left(\frac{1+\rho r}{2}\right)^6\frac{1}{720}$ $= \frac{108056025}{2949120}\frac{(1+\rho r)^6}{(2n-1)(2n+1)(2n+3)(2n+5)(2n+7)(2n+9)}$
$m > 7$	$\sum_{m=7}^{\infty} \frac{(a_1)_m (a_2)_m}{(b_1)_k} \frac{x^m}{m!}$		$O(n^{-8})$

Appendix 6. Delta Method

Taylor Expansion of a trivariate function around its means

$$f(x,y,z) = f(x_o,y_o,z_o) + f_x^1(x_o,y_o,z_o)(x - x_o) + f_y^1(x_o,y_o,z_o)(y - y_o) + f_z^1(x_o,y_o,z_o)(z - z_o)$$

where x_o, y_o, z_o are constants (considered here as means). The first term is the actual estimate of the function. Terms of the form $f_\blacksquare^1(x_o, y_o, z_o)$ are the first-order derivatives evaluated around x_o, y_o, z_o.

Expected value

$$E[f(x,y,z)] = E[f(x_o,y_o,z_o) + f_x^1(x_o,y_o,z_o)(x - x_o) + f_y^1(x_o,y_o,z_o)(y - y_o) + f_z^1(x_o,y_o,z_o)(z - z_o)]$$

$$= E[f(x_o,y_o,z_o)] + f_x^1(x_o,y_o,z_o)E(x - x_o) + f_y^1(x_o,y_o,z_o)E(y - y_o) + f_z^1(x_o,y_o,z_o)E(z - z_o)$$

Since the expected value of a variable around its mean is zero,

$$E[f(x,y,z)] = f(x_o,y_o,z_o)$$

Variance

Here we define the variance of a variable as the squared deviations around its mean

$$Var[f(x,y,z)] = E(f(x,y,z) - E[f(x,y,z)])^2$$

$$= [f(x_o,y_o,z_o) + f_x^1(x_o,y_o,z_o)(x - x_o) + f_y^1(x_o,y_o,z_o)(y - y_o) + f_z^1(x_o,y_o,z_o)(z - z_o) - f(x_o,y_o,z_o)]^2$$

$$= [f_x^1(x_o,y_o,z_o)(x - x_o) + f_y^1(x_o,y_o,z_o)(y - y_o) + f_z^1(x_o,y_o,z_o)(z - z_o)]^2$$

$$= E[f_x^1(x_o,y_o,z_o)(x - x_o) + f_y^1(x_o,y_o,z_o)(y - y_o) + f_z^1(x_o,y_o,z_o)(z - z_o)]^2$$

Squaring the terms within the brackets, we obtain

$$= E\left[\left(f_x^1(x_o,y_o,z_o)\right)^2(x - x_o)^2 + \left(f_y^1(x_o,y_o,z_o)\right)^2(y - y_o)^2 + \left(f_z^1(x_o,y_o,z_o)\right)^2(z - z_o)^2\right.$$

$$+ 2 f_x^1(x_o,y_o,z_o) f_y^1(x_o,y_o,z_o)(x - x_o)(y - y_o)$$

$$+ 2 f_x^1(x_o,y_o,z_o) f_z^1(x_o,y_o,z_o)(x - x_o)(z - z_o)$$

$$+ 2 f_y^1(x_o,y_o,z_o) f_z^1(x_o,y_o,z_o)(y - y_o)(z - z_o)\left.\right]$$

Taking the expectation of the terms involving variables

$$= \left(f_x^1(x_o,y_o,z_o)\right)^2 E(x - x_o)^2 + \left(f_y^1(x_o,y_o,z_o)\right)^2 E(y - y_o)^2 + \left(f_z^1(x_o,y_o,z_o)\right)^2 E(z - z_o)^2$$

$$+ 2 f_x^1(x_o,y_o,z_o) f_y^1(x_o,y_o,z_o)E[(x - x_o)(y - y_o)]$$

$$+ 2 f_x^1(x_o,y_o,z_o) f_z^1(x_o,y_o,z_o)E[(x - x_o)(z - z_o)]$$

$$+ 2 f_y^1(x_o,y_o,z_o) f_z^1(x_o,y_o,z_o)E[(y - y_o)(z - z_o)]$$

Finally, the variance of the function can be approximated

$$Var[f(x,y,z)] = \left(f_x^1(x_o,y_o,z_o)\right)^2 Var(x) + \left(f_y^1(x_o,y_o,z_o)\right)^2 Var(y) + \left(f_z^1(x_o,y_o,z_o)\right)^2 Var(z)$$

$$+ 2 f_x^1(x_o,y_o,z_o) f_y^1(x_o,y_o,z_o) Cov(x,y)$$

$$+ 2 f_x^1(x_o,y_o,z_o) f_z^1(x_o,y_o,z_o) Cov(x,z)$$

$$+ 2 f_y^1(x_o,y_o,z_o) f_z^1(x_o,y_o,z_o) Cov(y,z)$$

		Estimator			
		phenotypic correlation	coheritability	coenvironmentability	heritability
function	$f = f(x_0,y_0,z_0)$	$r_{P_{x,y}} = \dfrac{s_{P_{x,y}}}{\sqrt{s_{P_x}^2\, s_{P_y}^2}}$	$h_{x,y} = \sqrt{h_x^2 h_y^2}\, r_{A_{x,y}}$	$e_{x,y} = \sqrt{(1-h_x^2)(1-h_y^2)}\, r_{E_{x,y}}$	$h^2 = \dfrac{V_A}{V_P}$
elements	x_0	$s_{P_{x,y}}$	h_x^2	h_x^2	V_A
	y_0	$s_{P_x}^2$	h_x^2	h_x^2	V_P
	z_0	$s_{P_y}^2$	$r_{A_{x,y}}$	$r_{E_{x,y}}$	
first-order derivatives	$f_x^1 = \dfrac{\delta f}{\delta x}\Big|_{x_0,y_0,z_0}$	$\dfrac{\delta r_{P_{x,y}}}{\delta s_{P_{x,y}}} = (s_{P_x}^2 s_{P_y}^2)^{-\frac{1}{2}}$	$\dfrac{\delta h_{x,y}}{\delta h_x^2} = \dfrac{1}{2} h_y^2\, r_{A_{x,y}}\, (h_x^2 h_y^2)^{-\frac{1}{2}}$	$\dfrac{\delta e_{x,y}}{\delta h_x^2} = -\dfrac{(1-h_y^2)}{2\sqrt{(1-h_x^2)(1-h_y^2)}}\, r_{E_{x,y}}$	$\dfrac{\delta h^2}{\delta V_A} = \dfrac{1}{V_P}$
	$f_x^1 = \dfrac{\delta f}{\delta y}\Big|_{x_0,y_0,z_0}$	$\dfrac{\delta r_{P_{x,y}}}{\delta s_{P_x}^2} = -\dfrac{1}{2}(s_{P_{x,y}} s_{P_y}^2)(s_{P_x}^2 s_{P_y}^2)^{-\frac{3}{2}}$	$\dfrac{\delta h_{x,y}}{\delta h_y^2} = \dfrac{1}{2} h_x^2\, r_{A_{x,y}}\, (h_x^2 h_y^2)^{-\frac{1}{2}}$	$\dfrac{\delta e_{x,y}}{\delta h_y^2} = -\dfrac{(1-h_x^2)}{2\sqrt{(1-h_x^2)(1-h_y^2)}}\, r_{E_{x,y}}$	$\dfrac{\delta h^2}{\delta V_P} = -\dfrac{V_A}{V_P}$
	$f_x^1 = \dfrac{\delta f}{\delta z}\Big|_{x_0,y_0,z_0}$	$\dfrac{\delta r_{P_{x,y}}}{\delta s_{P_y}^2} = -\dfrac{1}{2}(s_{P_{x,y}} s_{P_x}^2)(s_{P_x}^2 s_{P_y}^2)^{-\frac{3}{2}}$	$\dfrac{\delta h_{x,y}}{\delta r_{A_{x,y}}} = (h_x^2 h_y^2)^{\frac{1}{2}}$	$\dfrac{\delta e_{x,y}}{\delta r_{E_{x,y}}} = \sqrt{(1-h_x^2)(1-h_y^2)}$	

Note on the Taylor expansion of a function involving three variables

Taylor series are polynomials that approximate functions. For functions of three variables, the Taylor series depends upon first, second, third, etc. partial derivatives at some point (x_o, y_o, z_o), which involve taking sequential derivatives with respect to the same or different variables. The following is the expansion of the function up to the fourth-order.

$$f(x, y, z) = f(x_o, y_o, z_o)$$

$$+ \frac{1}{1!} \left[f_x^1(x_o, y_o, z_o)(x - x_o) + f_y^1(x_o, y_o, z_o)(y - y_o) + f_z^1(x_o, y_o, z_o)(z - z_o) \right]$$

$$+ \frac{1}{2!} \left[f_{xx}^2(x_o, y_o, z_o)(x - x_o)^2 + 2f_{xy}^2(x_o, y_o, z_o)(x - x_o)(y - y_o) + 2f_{xz}^2(x_o, y_o, z_o)(x - x_o)(z - z_o) + 2f_{yy}^2(x_o, y_o, z_o)(y - y_o)^2 + 2f_{yz}^2(x_o, y_o, z_o)(y - y_o)(z - z_o) + 2f_{zz}^2(x_o, y_o, z_o)(z - z_o)^2 \right]$$

$$+ \frac{1}{3!} \left[f_{xxx}^3(x_o, y_o, z_o)(x - x_o)^3 + 3f_{xxy}^3(x_o, y_o, z_o)(x - x_o)^2(y - y_o) + 3f_{xxz}^3(x_o, y_o, z_o)(x - x_o)^2(z - z_o) + 3f_{yyx}^3(x_o, y_o, z_o)(y - y_o)^2(x - x_o) + f_{yyy}^3(x_o, y_o, z_o)(y - y_o)^3 + 3f_{yyz}^3(x_o, y_o, z_o)(y - y_o)^2(z - z_o) + 3f_{zzx}^3(x_o, y_o, z_o)(z - z_o)^2(x - x_o) + 3f_{zzy}^3(x_o, y_o, z_o)(z - z_o)^2(y - y_o) + f_{zzz}^3(x_o, y_o, z_o)(z - z_o)^3 + 6f_{xyz}^3(x_o, y_o, z_o)(x - x_o)(y - y_o)(z - z_o) \right]$$

$$+ \frac{1}{4!} \left[f_{xxxx}^4(x_o, y_o, z_o)(x - x_o)^4 + 4f_{xxxy}^4(x_o, y_o, z_o)(x - x_o)^3(y - y_o) + 6f_{xxyy}^4(x_o, y_o, z_o)(x - x_o)^2(y - y_o)^2 + 4f_{xxxz}^4(x_o, y_o, z_o)(x - x_o)^3(z - z_o) + 4f_{xyyy}^4(x_o, y_o, z_o)(x - x_o)(y - y_o)^3 + 12f_{xxyz}^4(x_o, y_o, z_o)(x - x_o)^2(y - y_o)(z - z_o) + 6f_{xxzz}^4(x_o, y_o, z_o)(x - x_o)^2(z - z_o)^2 + 12f_{xyyz}^4(x_o, y_o, z_o)(x - x_o)(y - y_o)^2(z - z_o) + 12f_{xyzz}^4(x_o, y_o, z_o)(x - x_o)(z - z_o)(y - y_o)^2 + 4f_{xzzz}^4(x_o, y_o, z_o)(x - x_o)(z - z_o)^3 + f_{yyyy}^4(x_o, y_o, z_o)(y - y_o)^4 + 4f_{yyyz}^4(x_o, y_o, z_o)(y - y_o)^3(z - z_o) + 6f_{yyzz}^4(x_o, y_o, z_o)(y - y_o)^2(z - z_o)^2 + 4f_{yzzz}^4(x_o, y_o, z_o)(y - y_o)(z - z_o)^3 + f_{zzzz}^4(x_o, y_o, z_o)(z - z_o)^4 \right]$$

$$+ O(n^{-5})$$

Appendix 7. Web resources

The URLs of online resources relevant to this work are presented below:

Testing the significance of correlations

https://www.psychometrica.de/correlation.html

1. Comparison of correlations from independent samples. 2. Comparison of correlations from dependent samples. 3. Testing linear independence (Testing against 0). 4. Testing correlations against a fixed value. 5. Calculation of confidence intervals of correlations. 6. Fisher-Z-Transformation. 7. Calculation of the weighted mean of a list of correlations. 8. Transformation of the effect sizes r, d, f, Odds Ratio and eta square. 9. Calculation of Linear Correlations.

Citation

Lenhard, W. & Lenhard, A. 2014 . *Hypothesis Tests for Comparing Correlations*. Available: Bibergau (Germany): Psychometrica. DOI: 10.13140/RG.2.1.2954.1367
https://www.psychometrica.de/correlation.html.

The confidence interval of rho (the correlation coefficient)

http://vassarstats.net/rho.html

1. Calculation of the 0.95 and 0.99 confidence intervals for rho, based on the Fisher r-to-z transformation. The values of *r* and *n* are required. Note that the confidence interval of rho is symmetrical around the observed r only with large values of n.
2. *- Free, full-length, and interactive statistics textbook. It is a companion site of "VassarStats: Web Site for Statistical Computation"*

Citation
Lowry, R 2015. Concepts and Applications of Inferential Statistics.
http://vassarstats.net/textbook/

Confidence Interval

http://www.psyctc.org/cgi-bin/R.cgi/CI_correln.R

Sample size calculators for designing clinical research

http://www.sample-size.net/correlation-sample-size

1. Total sample size required to determine whether a correlation coefficient differs from zero.

Citation
Hulley SB, Cummings SR, Browner WS, Grady D, Newman TB 2013 . Designing clinical research : an epidemiologic approach. 4th ed. Philadelphia, PA: Lippincott Williams & Wilkins. Appendix 6C, page 79.

Fisher r-to-Z transformation

http://vassarstats.net/tabs_rz.html

For any particular value of r, the Pearson product-moment correlation coefficient, this section will perform the Fisher r-to-z transformation according to the formula

$$Z_r = \frac{1}{2} \ln\left(\frac{1 + r}{1 - r}\right)$$

If a value of N is entered (optional), it will also calculate the standard deviation of z_r as

$$\sigma_{Z_r} = \frac{1}{n - 3}$$

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Cocor Comparing correlations

http://comparingcorrelations.org

1. Tests for comparing two correlations based on independent groups: Fisher's z; Zou's confidence interval.

2. Tests for comparing two correlations based on dependent groups with overlapping variables: Pearson and Filon's; Hotelling's; Williams; Olkin's; Dunn and Clark's; Hendrickson's modification of Williams'; Steiger's modification of Dunn and Clark's; Hittner's modification of Dunn and Clark's; Zou's.

3. Tests for comparing two correlations based on dependent groups with nonoverlapping variables: Pearson and Filon's; Dunn and Clark's; Steiger's modification of Dunn and Clark's; Raghunathan, Rosenthal, and Rubin's modification of Pearson and Filon's; Silver, Hittner, and May's modification of Dunn and Clark's; Zou's confidence interval.

Citation:
Diedenhofen B, Musch J 2015 . cocor: A Comprehensive Solution for the Statistical Comparison of Correlations. PLoS ONE 10(4): e0121945. doi:10.1371/journal.pone.0121945. http://journals.plos.org/plosone/article/file?id=10.1371/journal.pone.0121945&type=printabl e

Package documentation
http://comparingcorrelations.org/repo/pckg/cocor/cocor.pdf

Useful online blogs and information

Fisher's transformation of the correlation coefficient

https://blogs.sas.com/content/iml/2017/09/20/fishers-transformation-correlation.html?utm_source=feedburner&utm_medium=feed&utm_campaign=Feed%3A+TheDoLoop+%28The+DO+Loop%29

By Rick Wicklin on The DO Loop |September 20, 2017

This article shows that Fisher's "z transformation," which is z = arctanh(r), is a normalizing transformation for the Pearson correlation of bivariate normal samples of size N. The transformation converts the skewed and bounded sampling distribution of r into a normal distribution for z. The standard error of the transformed distribution is 1/sqrt(N-3), which does not depend on the correlation.

One can download the SAS program that creates all the graphs in this article.

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Simulate correlations by using the Wishart distribution

https://blogs.sas.com/content/iml/2017/10/11/simulate-correlations-wishart-distribution.html

By Rick Wicklin on The DO Loop October 11, 2017

There is a simpler ways to simulate the correlation estimates: One can directly simulate from the Wishart distribution. Each draw from the Wishart distribution is a sample covariance matrix for a multivariate normal sample of size N. If you convert that covariance matrix to a correlation matrix, you can immediately extract the off-diagonal elements.

Coverage probability of confidence intervals: A simulation approach

https://blogs.sas.com/content/iml/2016/09/08/coverage-probability-confidence-intervals.html

By Rick Wicklin on The DO Loop

The article uses the SAS DATA step and Base SAS procedures to estimate the coverage probability of the confidence interval for the mean of normally distributed data. This discussion is based on Section 5.2 (p. 74–77) of Simulating Data with SAS.

http://keisan.casio.com/exec/system/1359533867

http://www.emathhelp.net/calculators/probability-statistics/