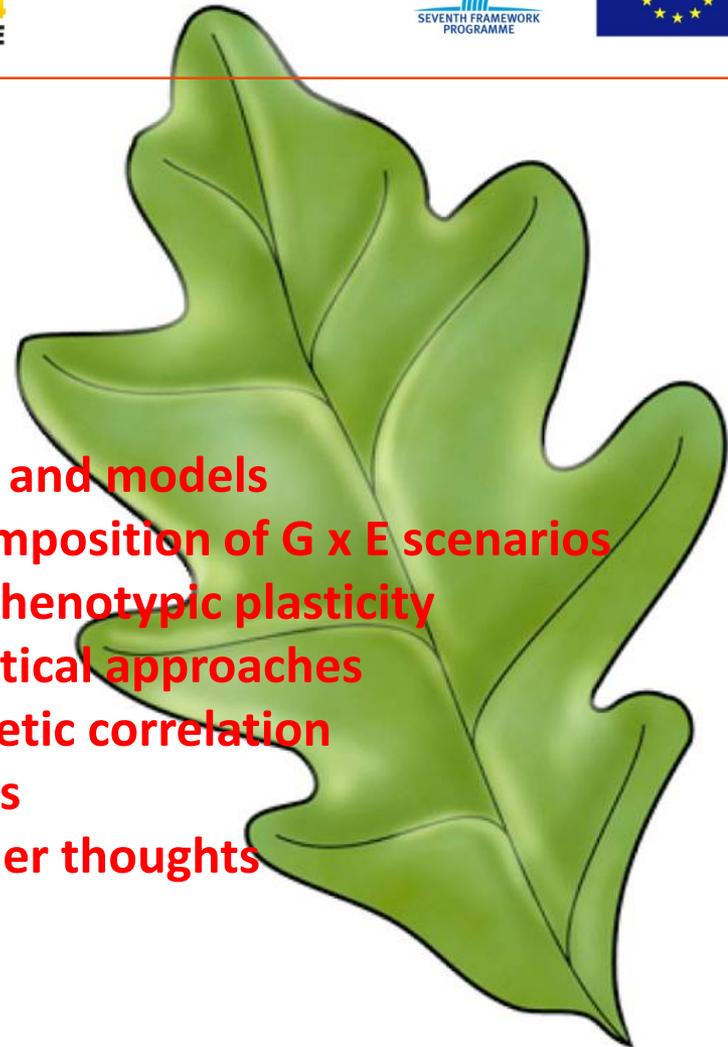


Grown in sun

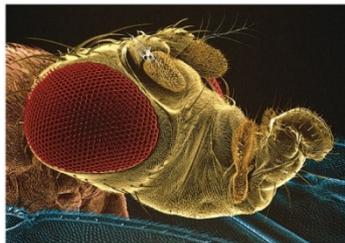
## Contents

- **Definitions and models**
- **Basic decomposition of G x E scenarios**
- **G x E and phenotypic plasticity**
- **Basic analytical approaches**
- **Type B genetic correlation**
- **Ecovalences**
- **Some further thoughts**

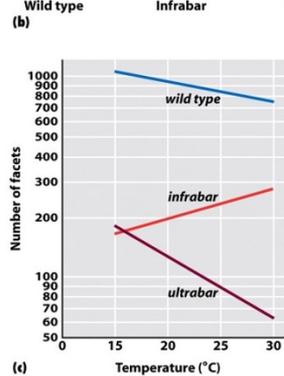
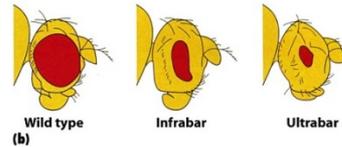


Grown in shade

G × E occurs when changes in environment do not have the same effect on all genotypes:

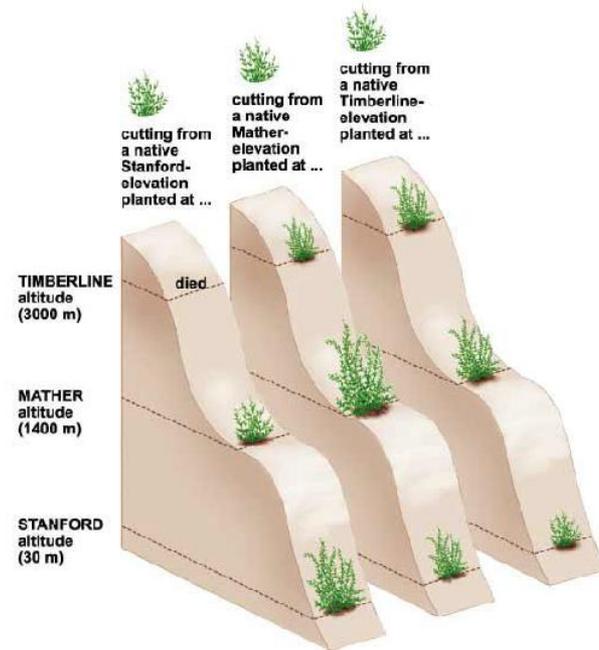


(a)



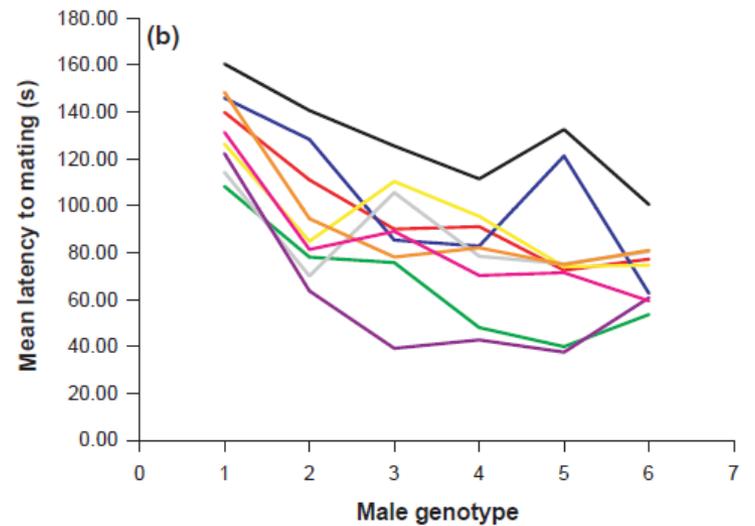
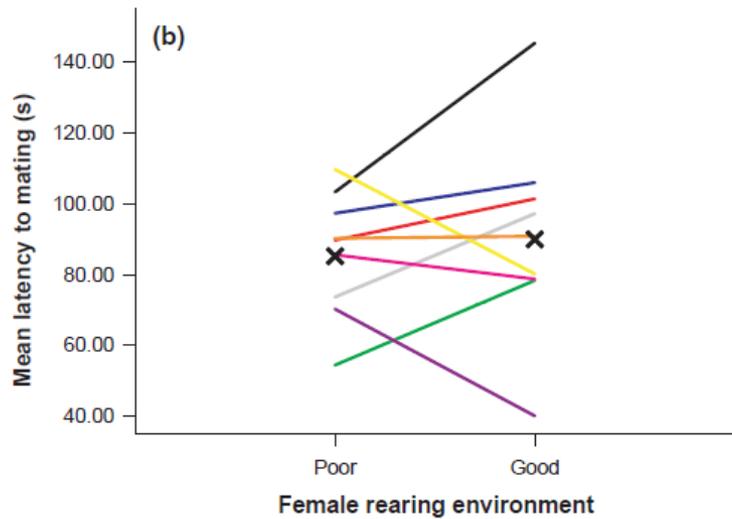
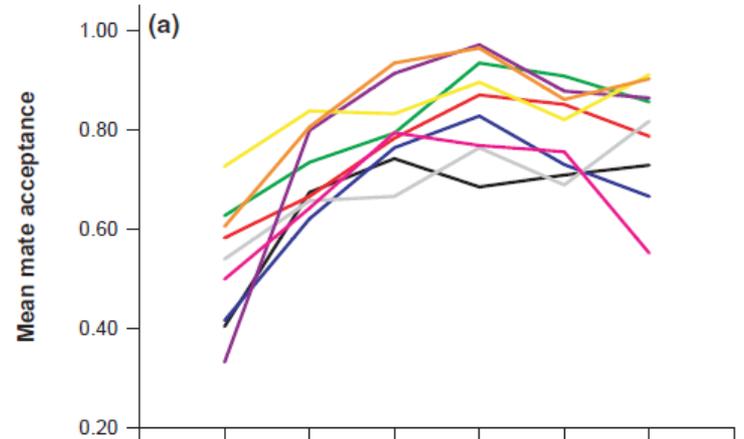
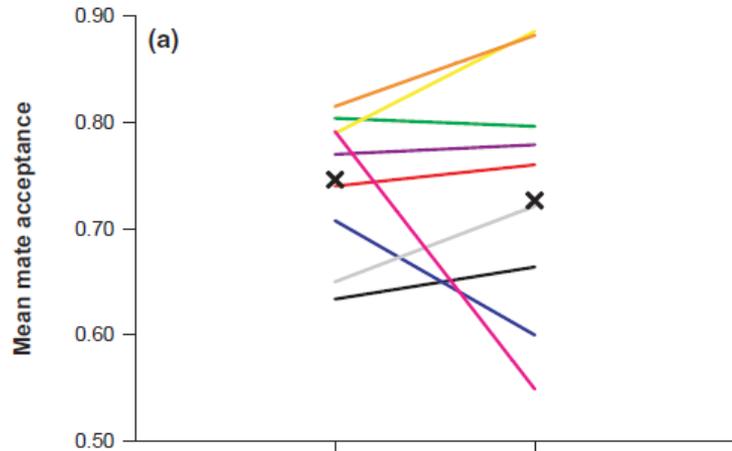
(c)

Figure 1-18  
Introduction to Genetic Analysis, Ninth Edition  
© 2008 W. H. Freeman and Company



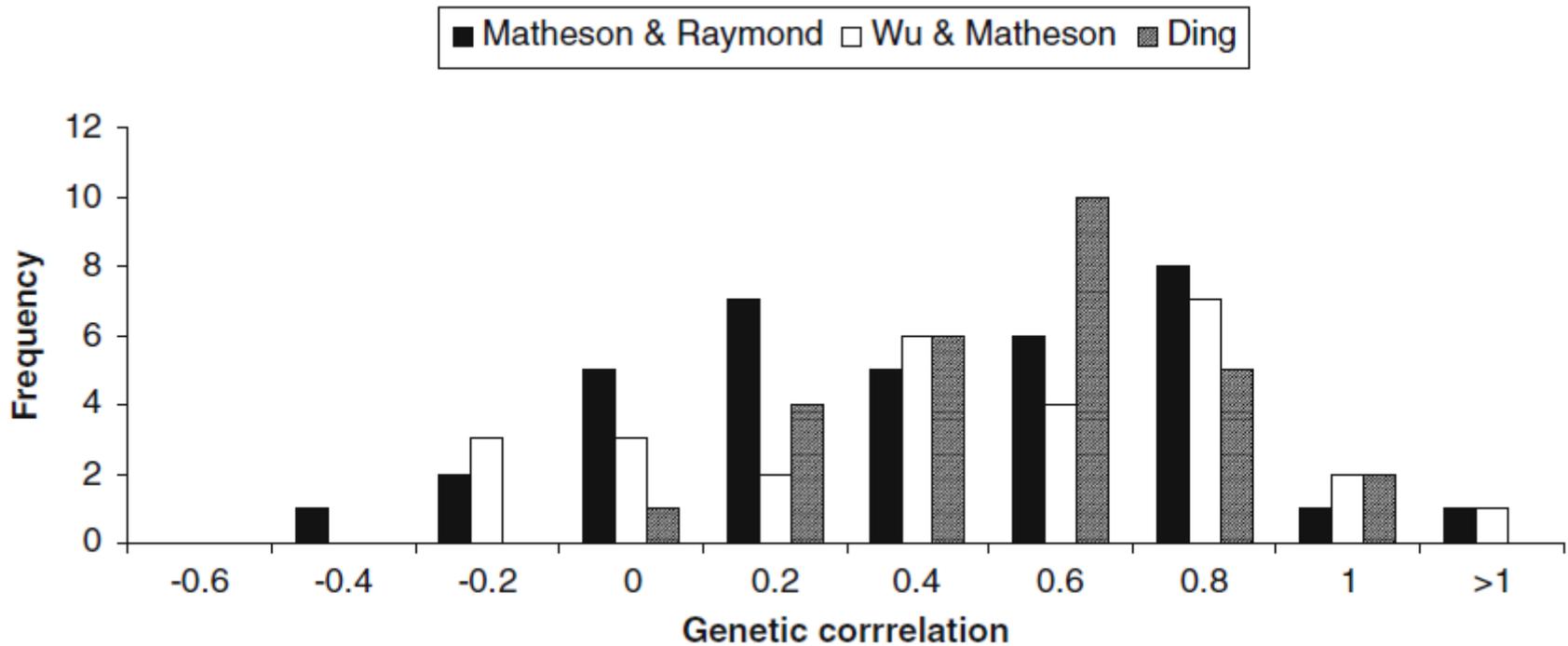
G × E is of great importance for the development of breeds with wide geographical use and/or wide coping capacity to global change

# GxE is common phenomenon



Narraway, C., Hunt, J., Wedell, N., Hosken, D.J., 2010. Genotype-by-environment interactions for female preference. *Journal of Evolutionary Biology* 23, 2550–2557.

## GxE is common phenomenon

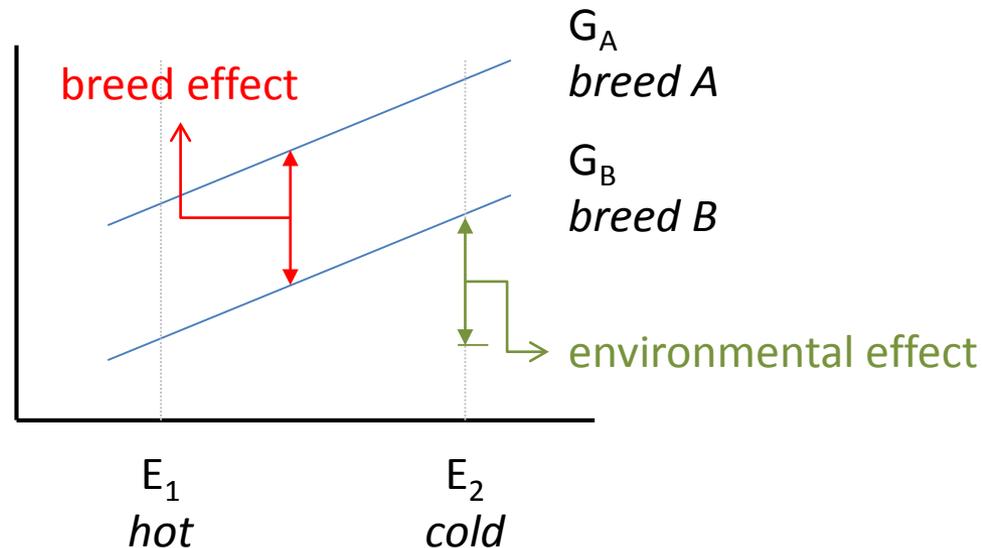


**Raymond, C.A.**, 2011. Genotype by environment interactions for *Pinus radiata* in New South Wales, Australia. *Tree Genetics & Genomes* 7, 819–833.

## The basic model

Breed and environmental effects are combined additively

$$P_{ij} = G_i + E_j$$



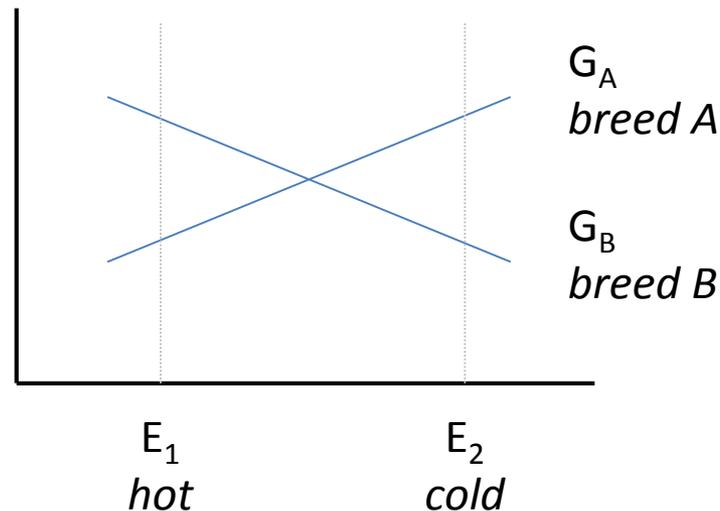
The phenotypic response of a genotype to a change in an environmental factor is often called **Norm of Reaction** (NoR) or simply plasticity

## The extended model

Breed and environmental effects have an additional term of interaction

$$P_{ij} = G_i + E_j + G \times E_{ij}$$

G×E may cause changes in breeds' ranking



### Change in rank:

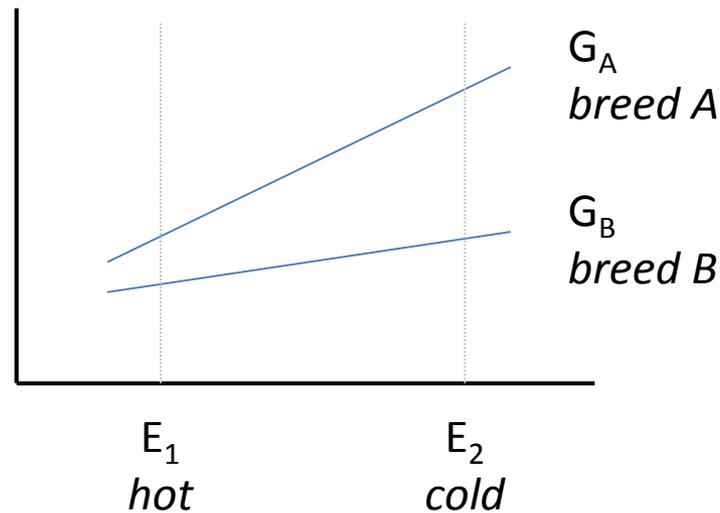
- there is no universal genotype
- a specific genotype is bred for each environment

## The extended model

Breed and environmental effects have an additional term of interaction

$$P_{ij} = G_i + E_j + G \times E_{ij}$$

G×E may cause changes in scale



**Change in scale:**

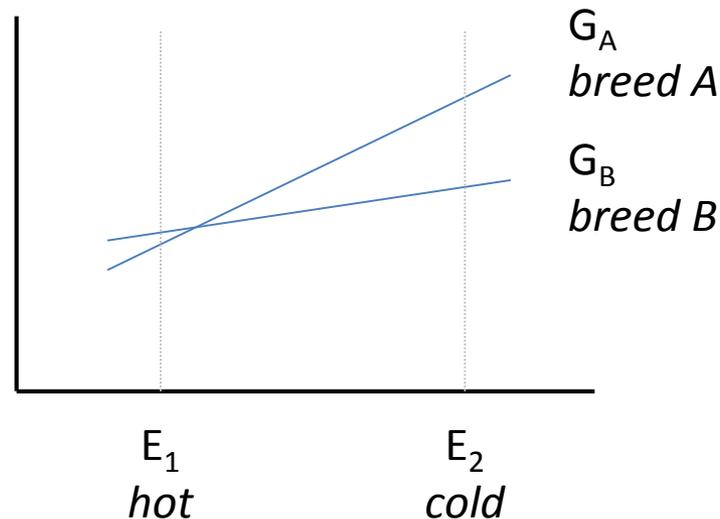
- Breed A is environmentally **sensitive**
- Breed B is environmentally **insensitive**

## The extended model

Breed and environmental effects have an additional term of interaction

$$P_{ij} = G_i + E_j + G \times E_{ij}$$

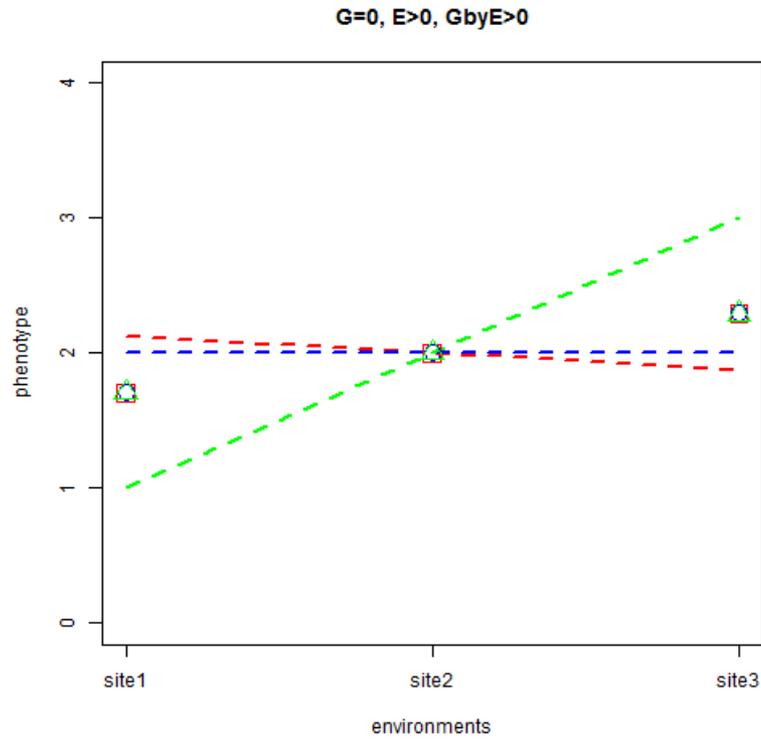
G×E may cause changes in ranking and scale simultaneously



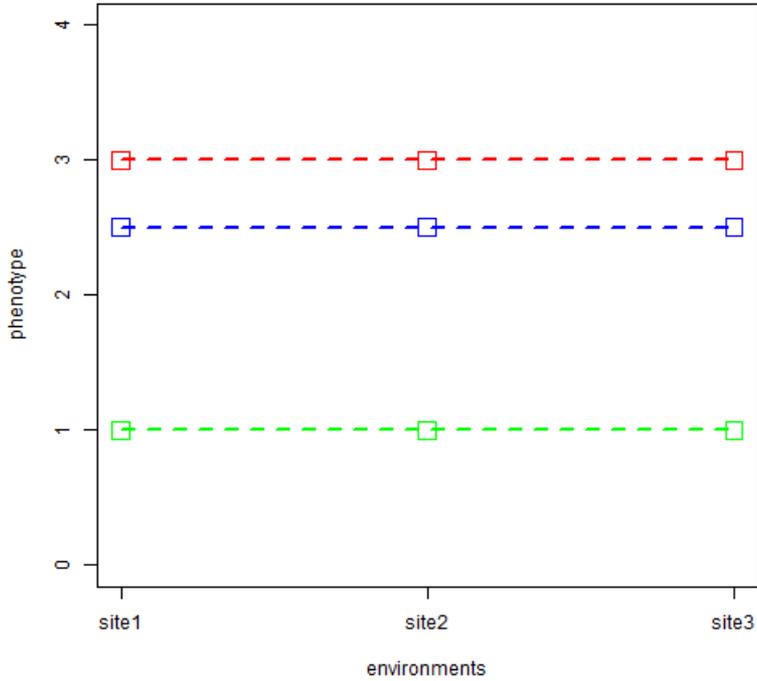
### Changes in ranking and scale:

- Breed A is environmentally **sensitive** and **especially suited to cold**
- Breed B is environmentally **insensitive** but **better suited to hot**

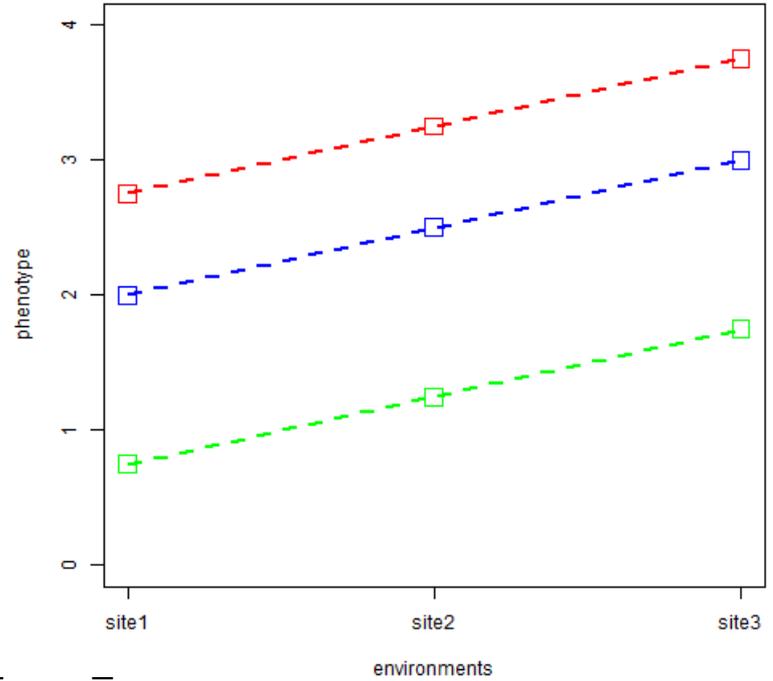
# Genotype, environmental and interaction effects



G>0, E=0, GbyE=0



G>0, E>0, GbyE=0



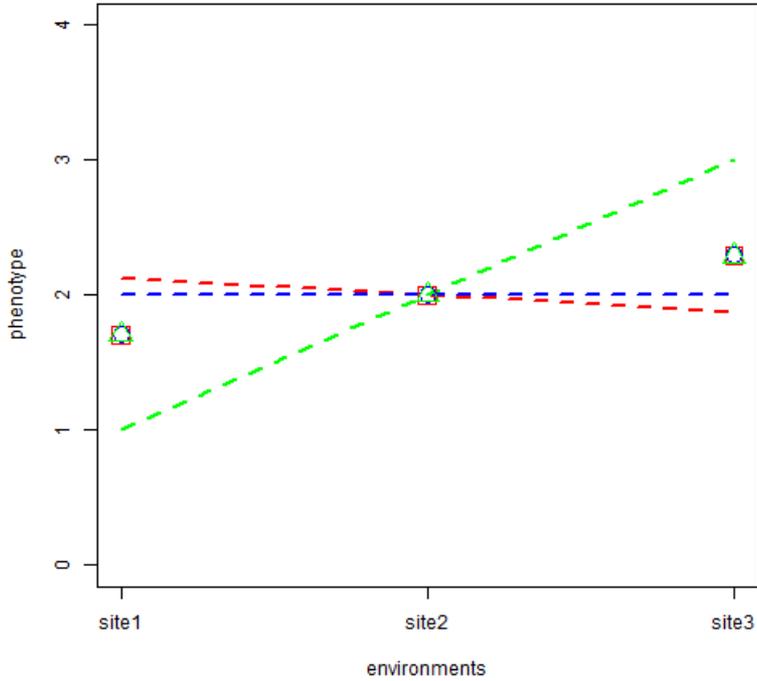
$$g_i = \bar{X}_{i.} - \bar{X}_{..}$$

	s1	s2	s3	mean g	g effect
g1	3.00	3.00	3.00	3.00	0.83
g2	2.50	2.50	2.50	2.50	0.33
g3	1.00	1.00	1.00	1.00	-1.17
mean s	2.17	2.17	2.17	2.17	
s effect	0.00	0.00	0.00		
<b>Interactions g x s</b>					
g1	0.00	0.00	0.00		
g2	0.00	0.00	0.00		
g3	0.00	0.00	0.00		

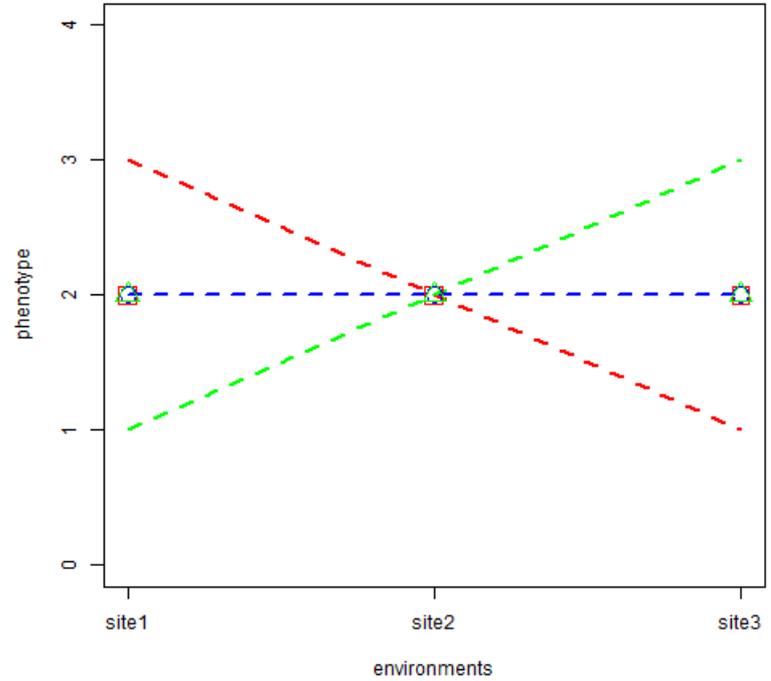
	s1	s2	s3	mean g	g effect
g1	2.75	3.25	3.75	3.25	0.92
g2	2.00	2.50	3.00	2.50	0.17
g3	0.75	1.25	1.75	1.25	-1.08
mean s	1.83	2.33	2.83	2.33	
s effect	-0.50	0.00	0.50		
<b>Interactions g x s</b>					
g1	0.00	0.00	0.00		
g2	0.00	0.00	0.00		
g3	0.00	0.00	0.00		

$$s_j = \bar{X}_{.j} - \bar{X}_{..}$$

G=0, E>0, GbyE>0



G=0, E=0, GbyE>0

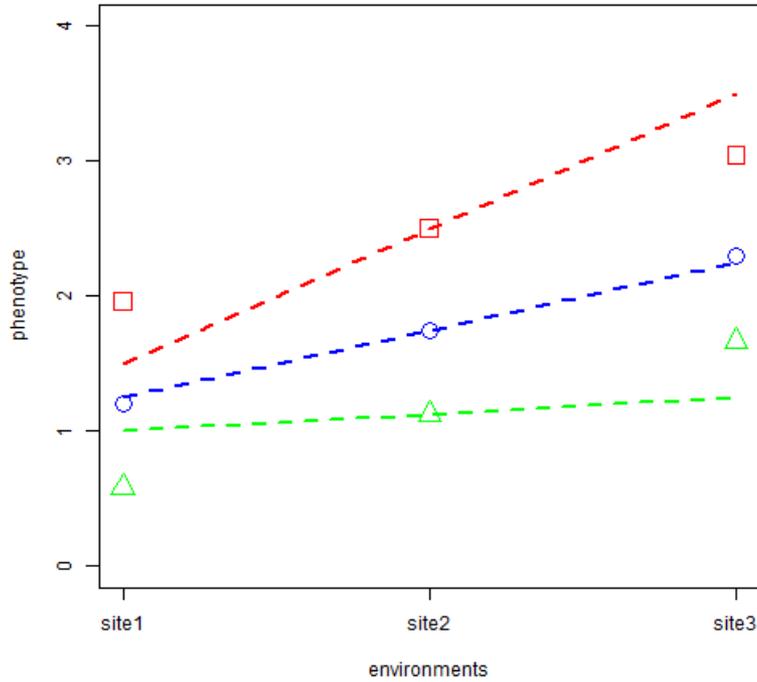


	s1	s2	s3	mean g	g effect
g1	2.13	2.00	1.88	2.00	0.00
g2	2.00	2.00	2.00	2.00	0.00
g3	1.00	2.00	3.00	2.00	0.00
mean s	1.71	2.00	2.29	2.00	
s effect	-0.29	0.00	0.29		
<b>Interactions g x s</b>					
g1	0.42	0.00	-0.42		
g2	0.29	0.00	-0.29		
g3	-0.71	0.00	0.71		

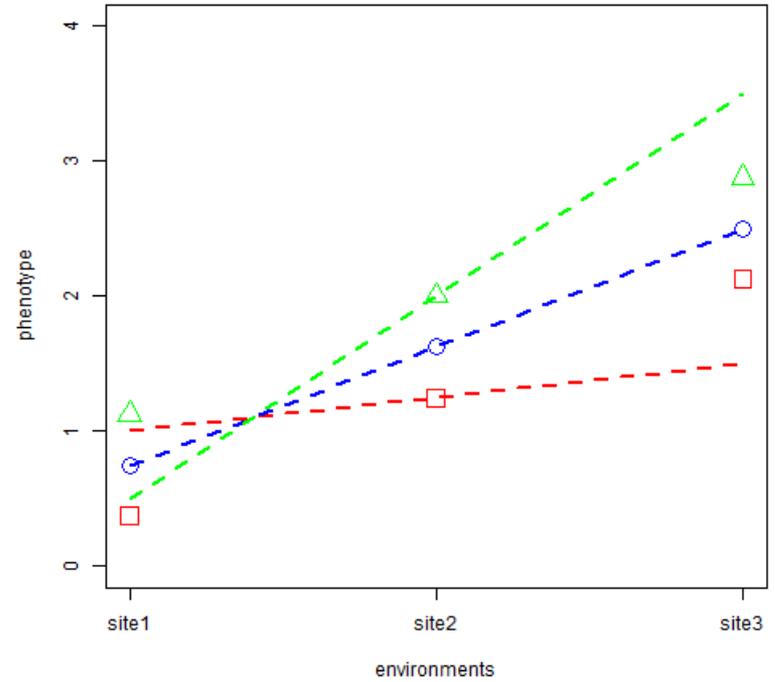
	s1	s2	s3	mean g	g effect
g1	3.00	2.00	1.00	2.00	0.00
g2	2.00	2.00	2.00	2.00	0.00
g3	1.00	2.00	3.00	2.00	0.00
mean s	2.00	2.00	2.00	2.00	
s effect	0.00	0.00	0.00		
<b>Interactions g x s</b>					
g1	1.00	0.00	-1.00		
g2	0.00	0.00	0.00		
g3	-1.00	0.00	1.00		

→  $g \times s_{ij} = X_{ij} - \bar{X}_{i.} - \bar{X}_{.j} + \bar{X}_{..}$

G>0, E>0, GbyE>0



G>0, E>0, GbyE>0

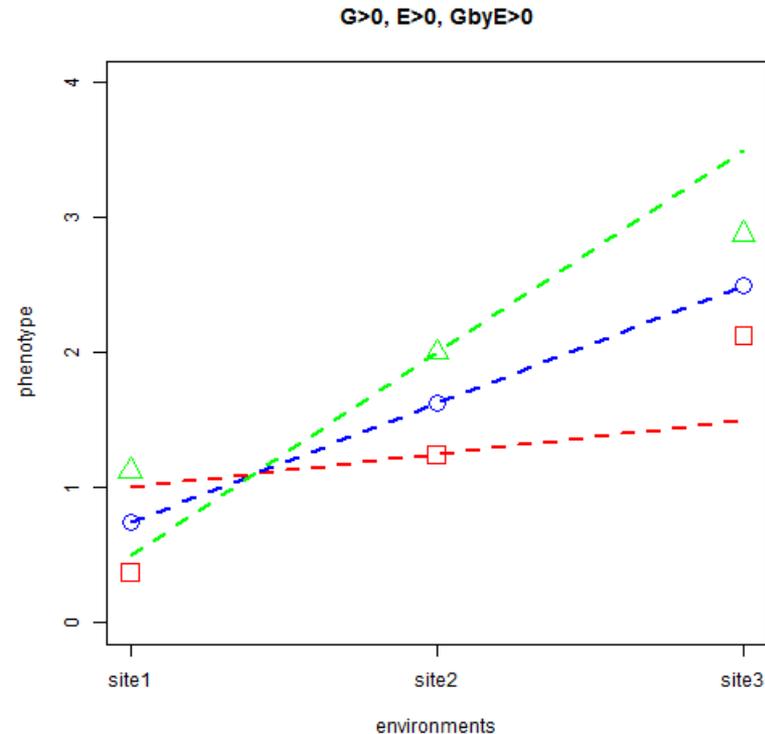


	s1	s2	s3	mean g	g effect
<b>g1</b>	1.50	2.50	3.50	2.50	0.71
<b>g2</b>	1.25	1.75	2.25	1.75	-0.04
<b>g3</b>	1.00	1.13	1.25	1.13	-0.67
<b>mean s</b>	1.25	1.79	2.33	1.79	
<b>s effect</b>	-0.54	0.00	0.54		
	<b>Interactions g x s</b>				
<b>g1</b>	-0.46	0.00	0.46		
<b>g2</b>	0.04	0.00	-0.04		
<b>g3</b>	0.42	0.00	-0.42		

	s1	s2	s3	mean g	g effect
<b>g1</b>	1.00	1.25	1.50	1.25	-0.38
<b>g2</b>	0.75	1.63	2.50	1.63	0.00
<b>g3</b>	0.50	2.00	3.50	2.00	0.38
<b>mean s</b>	0.75	1.63	2.50	1.63	
<b>s effect</b>	-0.88	0.00	0.88		
	<b>Interactions g x s</b>				
<b>g1</b>	0.63	0.00	-0.63		
<b>g2</b>	0.00	0.00	0.00		
<b>g3</b>	-0.63	0.00	0.63		

## G x E and phenotypic plasticity

- G x E implies plasticity in at least one genotype
- Plasticity need not imply G x E
- Phenotypic plasticity is a change in phenotype due to changes in environment
- NoR is the function of phenotypes over environmental changes of a given genotype
- The genetic variation in phenotypic plasticity is G x E and it is identified whenever there are intercrossing NoRs



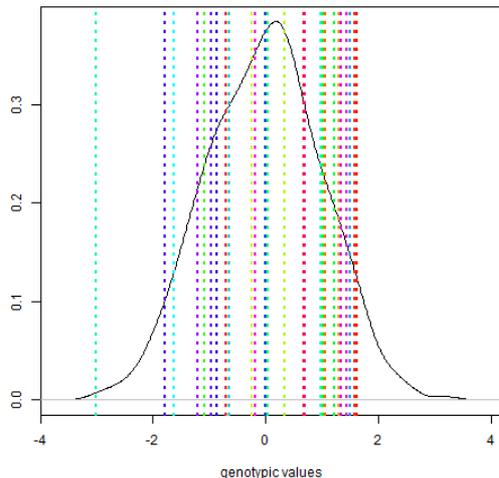
## Assessing G x E

- Two-way (factorial) designs are one of the simplest experimental layouts to detect and assess G x E
- Often genetic groups (families) are sampled randomly from a larger founder population, whose genetic variation we intent to gauge

## Analysis of Variance

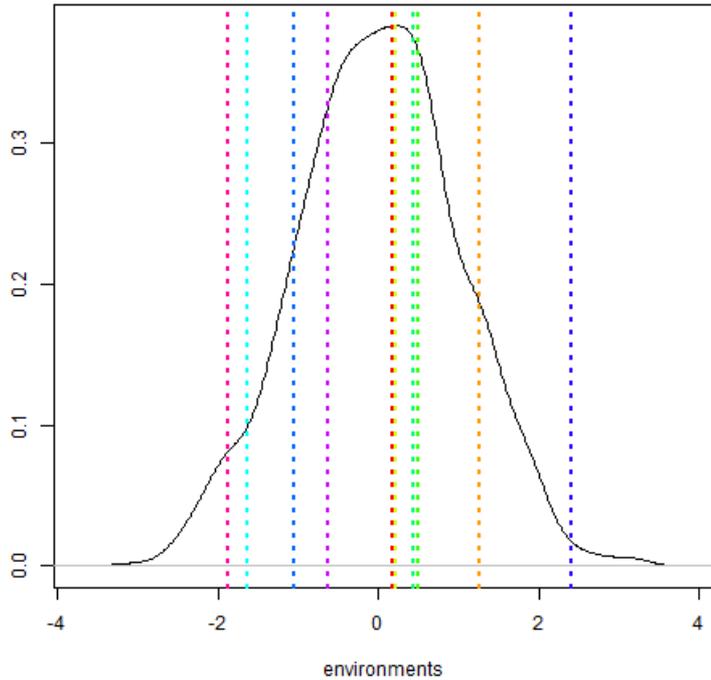
**Table 1.** Analysis of variance and expected mean squares

Source	<i>df</i>	Sum of squares	Mean square	Expected mean square
Environ-ments (E)	<i>e</i> -1			
Genotypes (G)	<i>g</i> -1			
G × E	( <i>g</i> -1) ( <i>e</i> -1)	SS (G × E)	MS (GE)	$\sigma^2 + n\sigma_{GE}^2$
Individuals within	<i>ge</i> ( <i>n</i> -1)	SS (within)	MS (E)	$\sigma^2$

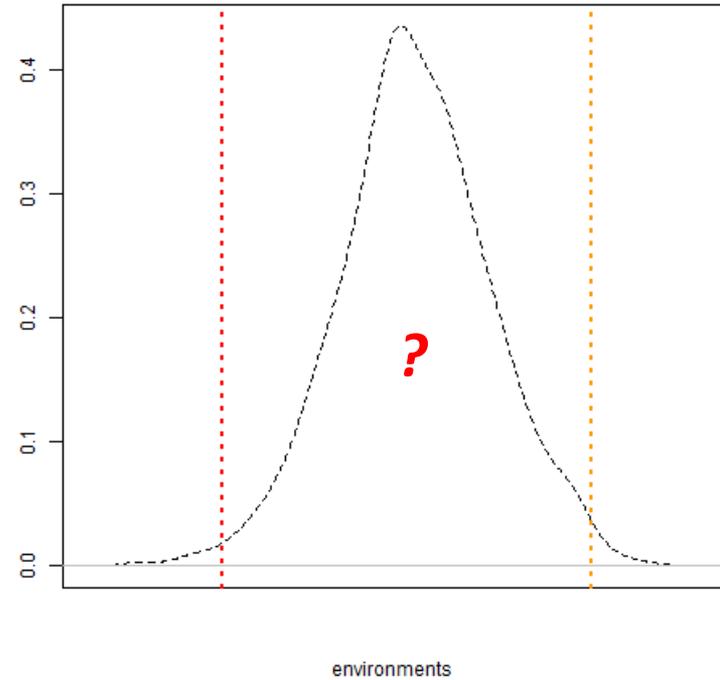


genotypes (families) are assumed to be random effects in the model

## The *issue* with environments being fixed or random



If environments are random samples from *universe* of possible environments & are usually many : niches in a species distribution area, gradient of a climate index, ...



If environments are explicitly selected & are the ones of interest & are often few: typically treatments like irrigated vs. non irrigated, *old trusted* testing sites, ...

# ANOVA: single step *or* double step

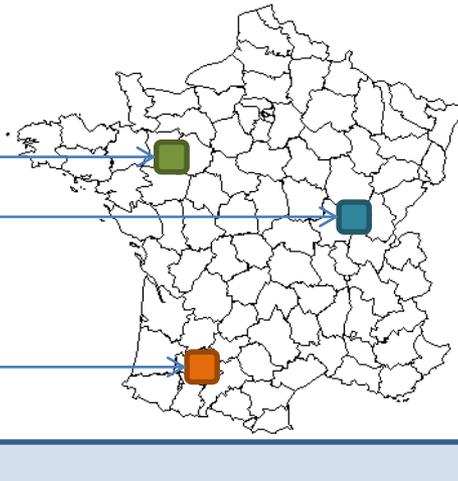
**step 1:** by *macroenv*

$$\text{macroenv.1} \quad y = \mu + \text{spatial} + \text{family} + \varepsilon$$

$$\text{macroenv.k} \quad y = \mu + \text{spatial} + \text{family} + \varepsilon$$

**step 2** on spatially adjusted data

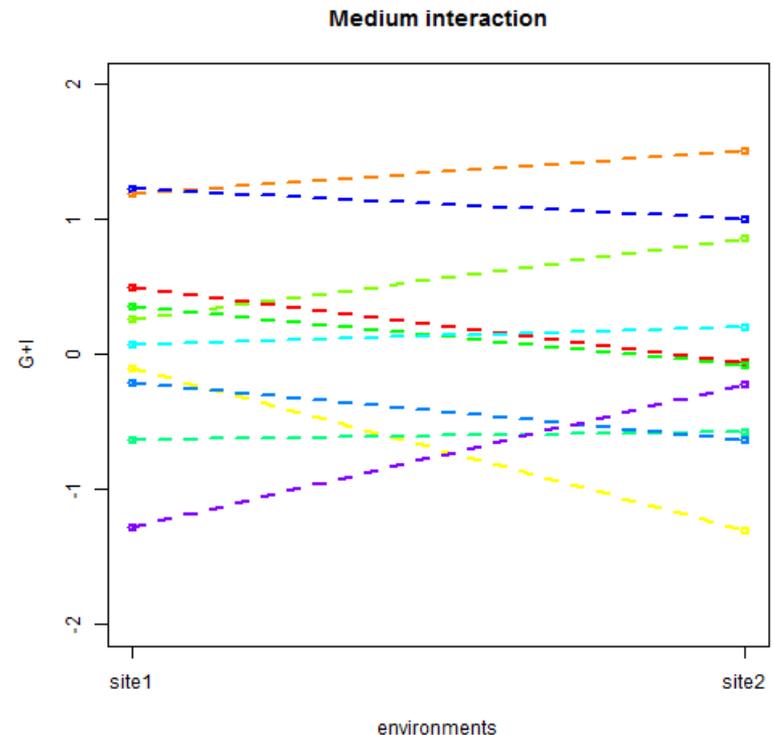
$$\begin{aligned} \hat{y} &= \mu + \text{macroenv} + \text{family} \\ &+ \text{macroenv} \times \text{family} + \varepsilon \end{aligned}$$



$$y = \mu + \text{macroenv} + \text{spatial:macroenv} + \text{family} + \text{family} \times \text{macroenv} + \varepsilon$$

# genetic correlations between traits measured in different environments

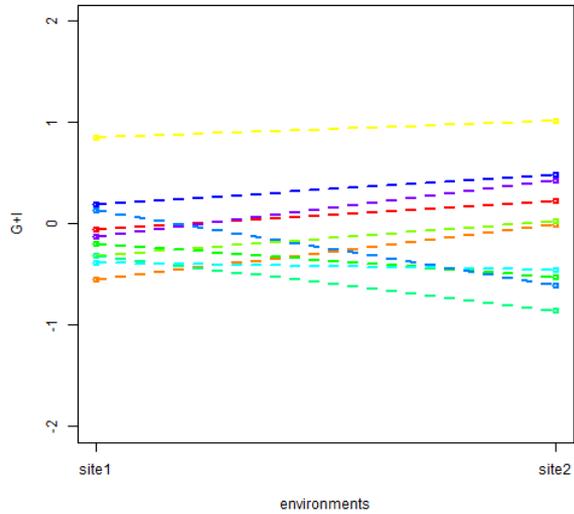
- Same trait measured in two or more environments over same genetic composition can be treated as two different genetically correlated traits
- The resulting correlation between these two traits is often denoted as **type B genetic correlation**
- The simplest formulation is  $\sigma_f^2 / (\sigma_f^2 + \sigma_i^2)$  [1]



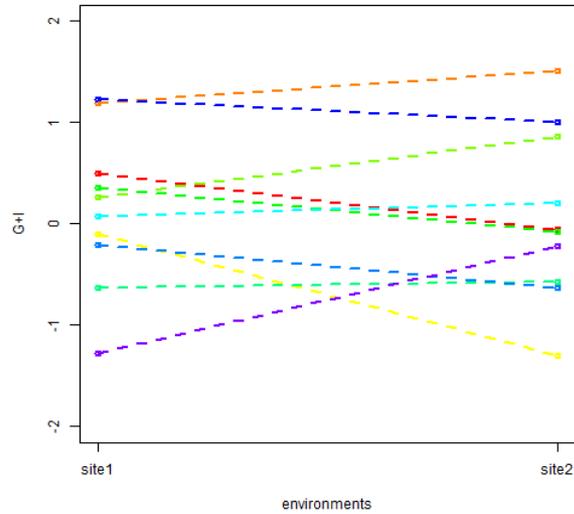
[1] Yamada, Y. 1962. Genotype by environment interaction and genetic correlation of the same trait under different environments. Jap. J. Genet. 37: 498-509.

# genetic correlations between traits measured in different environments

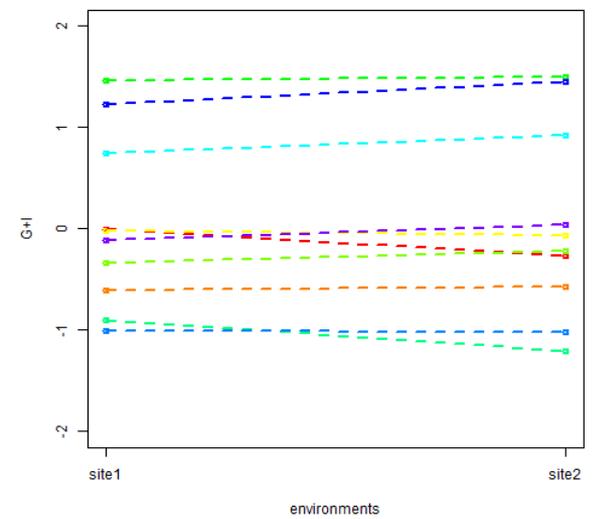
Strong interaction



Medium interaction



Weak interaction



$\sigma^2_f$  0.1397

0.4600

0.6701

$\sigma^2_i$  0.1101

0.1961

0.0219

$\sigma^2_e$  0.2465

0.2441

0.2441

**cor B 0.5592**

**0.7011**

**0.9684**

pearson 0.5959

0.7145

0.9852

```
1 |
2 library(breedR)
3
4 # family effects
5 num_fam <- 12
6 mean_eff_fam <- 0
7 sd_eff_fam <- 0.5
8 fam_eff <- rnorm(num_fam,mean_eff_fam,sd_eff_fam) #generate some random normal deviates
9
10 # family size and residuals
11 fam_size <- 20
12 mean_residuals <- 0
13 sd_residuals <- 0.5
14
15 # site effects
16 num_sites <- 2
17 mean_eff_site <- 0
18 site_eff <- c(-0.5,0.5)
19
20 # global_mean
21 global_mean <- 0
```

```
> samplesize <- 1000
> sub_sample <- 30
> theta <- rnorm(samplesize,0,1) #generate some random normal deviates
> colores <- rainbow(sub_sample)
> s_theta <- sample(theta)
> plot(density(theta), main = " ", xlab="genotypic values", ylab=" ")
> for (i in 1:sub_sample){
+   abline(v = s_theta[i], col = colores[i], lty = 3, lwd = 2)
+ }
> samplesize <- 1000
> sub_sample <- 30
> theta <- rnorm(samplesize,0,1) #generate some random normal deviates
```

## genetic correlations between traits measured in different environments

- type B genetic correlation ( $corr B$ ) =  $\sigma_f^2 / (\sigma_f^2 + \sigma_i^2)$   
when variance among genetic groups (families) is the same in both environments;
- obtained from a two-way mixed model decomposition;
- any  $corr B < 1$  indicates  $G \times E$  and some changes in ranking: the lower the  $corr B$ , the greater the  $G \times E$ ;
- $corr B = 1$  do not necessarily imply absence of  $G \times E$ : there can be scale effects;
- $corr B$  matrix can be used to delineate breeding or deployment zones: threshold levels  $\sigma_i^2 > 0.5 \times \sigma_f^2$ , which is a  $corr B$  of 0.67 **[1]**.

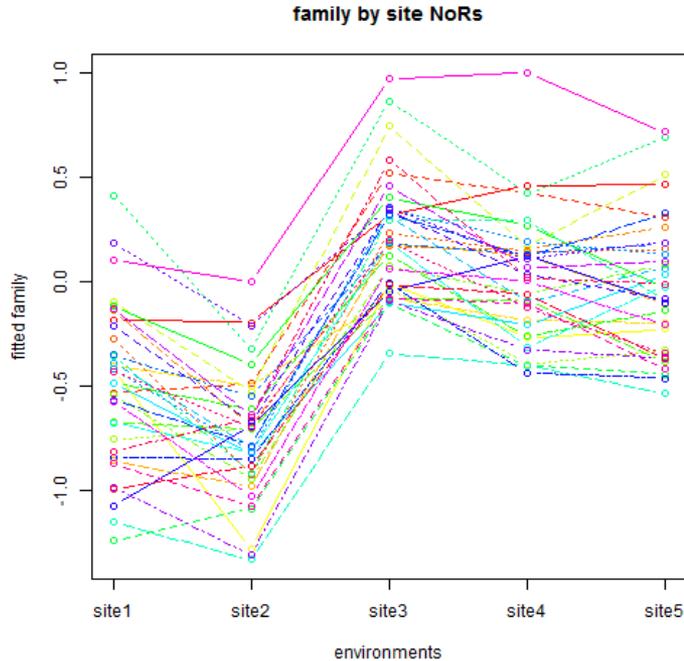
**[1]** Raymond, C.A., 2011. Genotype by environment interactions for *Pinus radiata* in New South Wales, Australia. *Tree Genetics & Genomes* 7, 819–833.

## how families contribute differently to G x E?

Wricke's *ecovale*nce: sum of squared interactions, for a given genotype from a factorial genotype (family) by environment experiment

$$W_i^2 = \sum (X_{ij} - \bar{X}_{i.} - \bar{X}_{.j} + \bar{X}_{..})^2$$

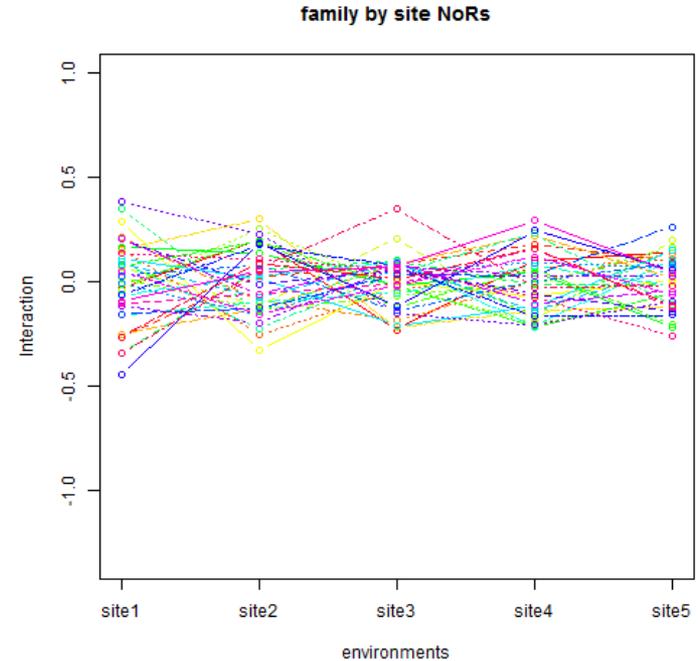
it can be made relative to total sum of squared interactions



$$\sigma_f^2 = 0.07581$$

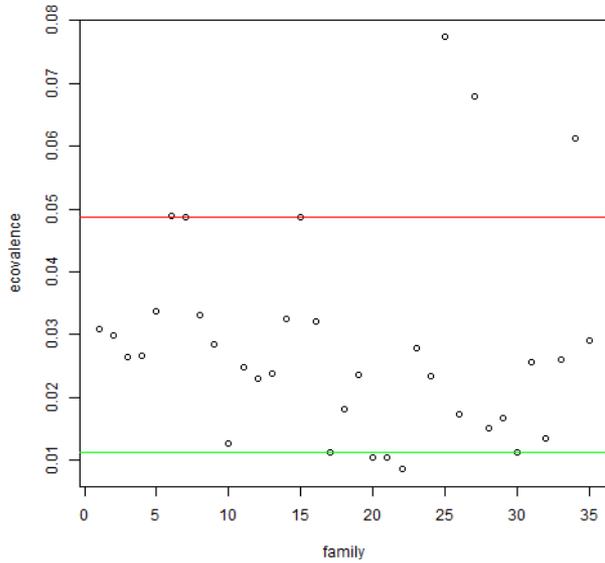
$$\sigma_i^2 = 0.03927$$

$$\sigma_e^2 = 0.29903$$

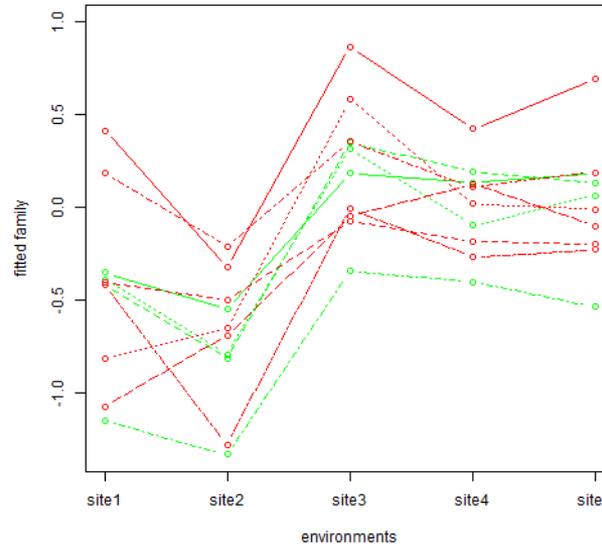


# how families contribute differently to G x E?

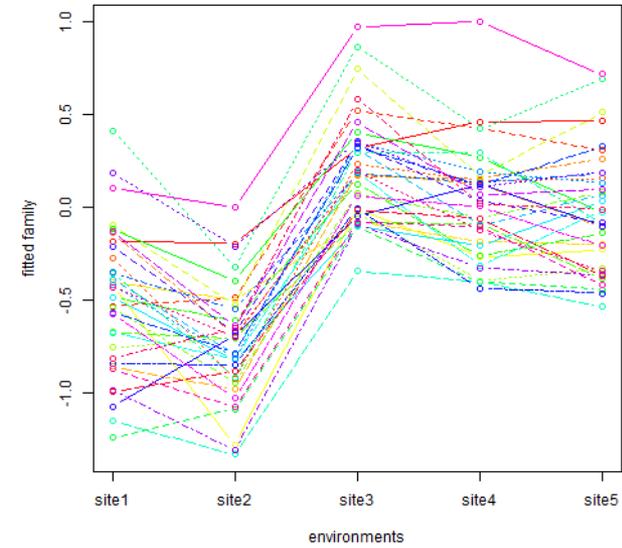
ecovalences per family



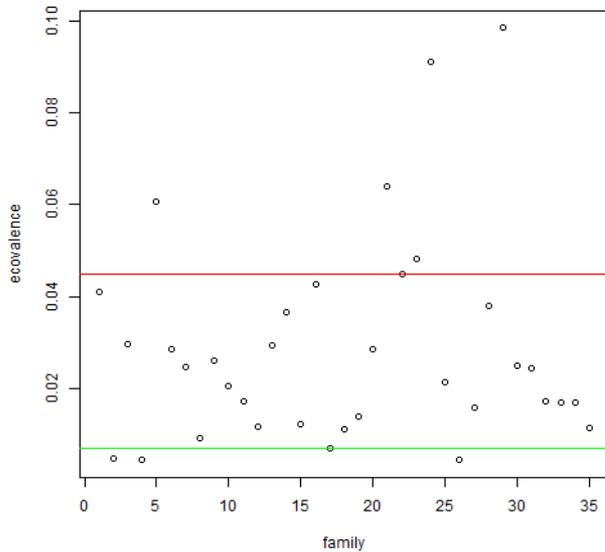
family by site NoRs for highest/lowest ecovalences



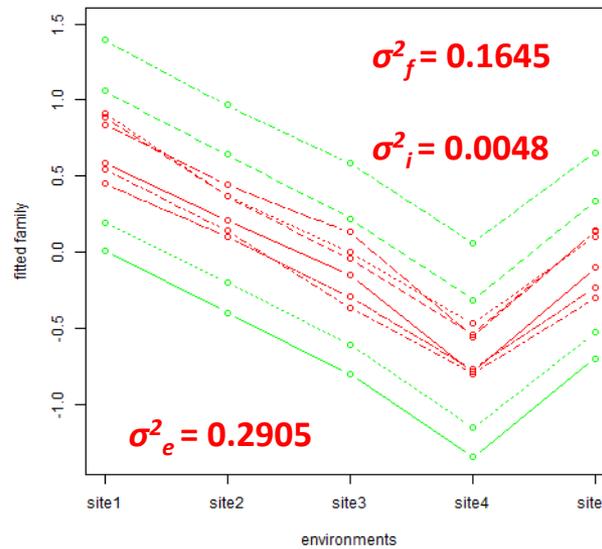
family by site NoRs



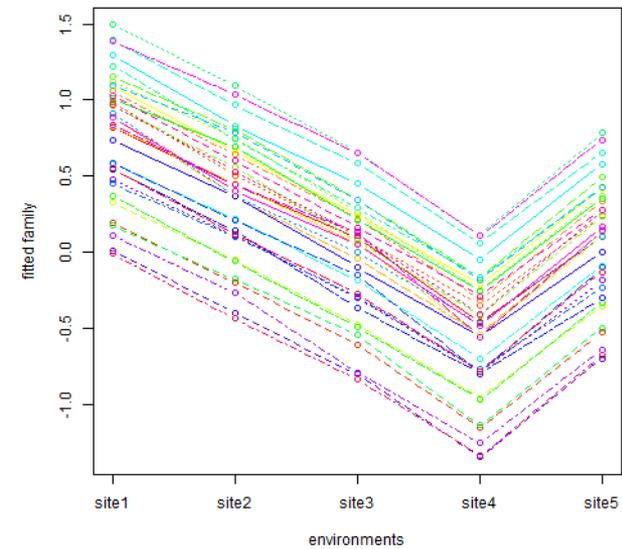
ecovalences per family



family by site NoRs for highest/lowest ecovalences



family by site NoRs



```
toy_examples_gbye_plots.R * first_toy_example.R * simulate_distributions.R * map_france.R * corB_toy_example.R * ecovalences.R *
Source on Save Run Source
124 lines(fam_set$site, fam_set$inter, type="b", lwd=1.5,
125       lty=linetype[i], col=colores[i])
126 }
127 dev.off()
128
129 # calculates ecovalences from interaction blups
130 aggdata$sq_inter <- aggdata$inter^2
131 aggdata_inter <- data.frame(aggregate(aggdata$sq_inter, by=list(aggdata$fam), FUN=sum))
132 names(aggdata_inter) <- c("fam", "sq_inter")
133 total_sq_inter <- sum(aggdata_inter$sq_inter)
134 aggdata_inter$ecoval <- aggdata_inter$sq_inter/total_sq_inter
135
136 # rank in ascending order families by their ecovalence
137 rank <- aggdata_inter$fam[order(aggdata_inter$ecoval)]
138 upper_rank <- 4
139 upper_threshold <- aggdata_inter$ecoval[rank[upper_rank]]
140 lower_rank <- num_fam-upper_rank-1
141 lower_threshold <- aggdata_inter$ecoval[rank[lower_rank]]
142
143 heading <- "ecovalences per family"
144 tiff(filename="ecovalences_by_family.tif",width=500,height=500,compression = c("none"))
136:22 (Top Level) R Script
```

```
Console D:/Leopoldo/LeoJob/INRA/Proyectos_financiados_en_curso/FP7 Tree4future/WP6/workshops/Jaca/contents/gbye/
> summary(two_way)
Linear Mixed Model with pedigree and spatial effects fit by AI-REMLF90 ver. 1.110
  Data: data_toy
  AIC   BIC logLik
5981 5999  -2987

Variance components:
              Estimated variances      S.E.
factor(fam)      0.215030 0.051402
factor(inter)    0.001255 0.000000
Residual         0.306700 0.007332

Fixed effects:
              value  s.e.
factor(site).1 -0.025904 0.0813
factor(site).2  0.762004 0.0813
factor(site).3  0.155000 0.0813
```

## Alternatives to univariate analyses for G x E and type B correlations

Univariate two-way analysis are:

- prone to biased type B correlations due to unbalanced-ness in data and heterogeneous variances across environments
- frequently producing correlation estimates out of the theoretical parametrical space
- unable to account for relatedness between genetic groups

Multivariate methods can estimate genetic variances (within environments) and covariances (between environments) simultaneously and properly.

- This latter feature will be ready soon in breedR via multiple trait analyses