

Behavior of PL metric

KE Lotterhos, M Albecker, G Trussel

April 2023

Overview

This supplemental file compares the PL metric of Stamp and Hadfield 2020 (hereafter SH2020, doi: 10.1111/ele.13565) with the Cov-GE metric of Albecker, Trussell, and Lotterhos 2022 (hereafter ATL2022 <https://doi.org/10.1111/ele.14020>).

In the first section *Behavior of PL Metric*, we review what the PL metric is and use 6 case datasets to show that the PL metric has some weird behavior. For instance, it can give vastly different values for very similar reaction norm patterns.

In the second section, *Compare PL to CovGE*, we show that the two metrics are related for a 2x2 reciprocal transplant design. We show that using the median PL to infer how common co- vs. countergradient variation is in nature will lead to biased inference, but that the median CovGE is unbiased. We show that the median PL is always biased in the direction of cogradients because the PL metric is bimodally distributed under countergradient variation, and countergradient cases effectively cancel each other out in the calculation of median PL. Both metrics, however, can be used to calculate the proportion of datasets showing co-gradient or counter-gradient patterns.

In the third section, *Summary of PL vs CovGE*, we compare the two metrics. Only the PL metric can be used for inference of hyperplasticity and wrong-sign plasticity, although as a ratio it has some weird behavior as described in the first section. We discuss the advantages of CovGE over PL for the study of gradient variation, which include the application to more complex experimental designs, the availability of statistical tests for a single dataset, and more straightforward interpretation.

Behavior of PL Metric

Description of PL metric

The PL metric was developed in SH2020. The metric can be calculated for a 2 population x 2 environment reciprocal transplant scenario (reciprocal transplant experiments are those in which two populations are assayed in their own and each other's environment). They used the metric to test whether phenotypic differences between populations are due to genetic differences or a plastic response to environmental variation. They also used the metric to test the prevalence of co-gradient vs. countergradient variation in the datasets. It is this latter application of the PL metric that we explore here.

The *in situ* divergence is the difference in mean phenotypes of two populations raised in their home environments ($P_A E_A - P_B E_B$, where $P_i E_j$ refers to the average phenotype of individuals from population i raised in the environment of population of j).

They define PL as:

$$PL = \Delta E / \Delta H$$

where

$$\Delta E_A = P_A E_A - P_A E_B$$

In SH2020 they state “the difference in phenotype between individuals from Population B in Environment A (P_BE_A) and from Population B in Environment B (P_BE_B) can be ascribed to plasticity (ΔE_B),” so it is a little ambiguous whether then mean $\Delta E_B = P_BE_B - P_BE_A$ or $\Delta E_B = P_BE_A - P_BE_B$. We use the latter definition because it would give $PL = 1$ under a “perfect plasticity” scenario, and would be consistent with the outcomes and interpretation in the paper.

$$\Delta E_B = P_BE_A - P_BE_B$$

$$\Delta E = (\Delta E_A + \Delta E_B)/2 = ((P_AE_A - P_AE_B) + (P_BE_A - P_BE_B))/2$$

$$\Delta H = P_AE_A - P_BE_B$$

They also define:

$\Delta A = P_BE_A - P_AE_B$ (the estimated difference in the two populations phenotypes when away in each other’s environment)

Interpretation of PL:

SH2020 interpret the plasticity metric $PL = \Delta E/\Delta H$ as lying between zero and one if there is co-gradient variation, negative if there is wrong-sign plasticity, or greater than one if there is hyperplasticity.

| Value of PL | Interpretation |
|--------------|---|
| $PL > 1$ | countegradient with hyperplasticity |
| $0 < PL < 1$ | cogradient variation |
| $PL = 1$ | perfect plasticity (Figure 4 in paper) |
| $PL < 1$ | countegradient with wrong-sign plasticity |

$$PL = \Delta E/\Delta H = (((P_AE_A - P_AE_B) + (P_BE_A - P_BE_B))/2)/(P_AE_A - P_BE_B)$$

When 100% of the divergence is due to plasticity with no genetic differentiation, in Environment A both populations would have the same trait value ($P_BE_A = P_AE_A$) and in Environment B both populations would have the same trait value ($P_AE_B = P_BE_B$).

In this case, plugging in the equivalencies to the PL equations shows that the numerator of PL reduces to 1: $PL = (((P_AE_A - P_BE_B) + (P_AE_A - P_BE_B))/2)/(P_AE_A - P_BE_B) = (2(P_AE_A - P_BE_B)/2)/(P_AE_A - P_BE_B) = 1$

Therefore, values of $PL = 1$ are interpreted as “perfect plasticity” in the paper. (Below, we show that scenarios with GxE can also give $PL = 1$).

Function

This function takes a vector of the (hypothetical) measured phenotypes from a 2x2 reciprocal transplant and plots them with the calculated PL metric.

```
makeplot <- function(a, letr, main){
  # a is vector of "PAEA", "PAEB", "PBEA", "PBEB"
  a <- as.numeric(a)
  plot(0:1, c(a[1:2]), ylim=c(-2,2),
        xaxt="n", type="l", col="blue", xlab="",
        ylab="Std. phenotype", bty="l",
        main=main, lwd=2, xlim=c(0,1.5))
  mtext("EA", side=1, line=1, adj=0, col="blue")
  points(0:1, c(a[3:4]), type="l", col="green", xlab="", lwd=1, lty=2)
  mtext("EB", side=1, line=1, adj=0.66, col="green")
}
```

```

D_H <- a[1] - a[4]
(D_EA <- a[1]-a[2]) #  $\Delta E_A = P_{AE_A} - P_{AE_B}$ 
(D_EB <- a[3]-a[4]) #  $\Delta E_B = P_{BE_A} - P_{BE_B}$ 
(D_E <- mean(c(D_EA, D_EB)))

text(1.1,1.5,"D_H", cex=0.8)
if (D_H!=0){arrows(1.1,a[4], 1.1,
                  a[1], length=0.1)}

text(1.4, 1.5, "D_E", cex=0.8)
if (D_E!=0){
arrows(1.4, mean(c(a[2], a[4])),
      1.4, mean(c(a[2], a[4]))+D_E,
      length=0.1)
}

PL <- D_E/D_H
text(1,-1.9,paste("PL =",PL),adj=1)

text(0,2, letr)
return(data.frame(D_H=D_H, D_EA = D_EA,
                  D_EB=D_EB,D_E=D_E, PL=PL))
}

```

Cases 1 and 2: drastically different PL metrics for similar reaction norms

These two cases show how slight differences in the mean fitness in the home population can give extremely opposite values of the PL statistic.

- PAEA is the phenotype value for genotype A in Environment A
- PAEB is the phenotype value for genotype A in Environment B
- PBEA is the phenotype value for genotype B in Environment A
- PBEB is the phenotype value for genotype B in Environment B

Case 1 and Case 2 are both countergradient scenarios, with almost the exact same reaction norms. In both cases, PAEA = 0 and PAEB = 1.

However, there are very small differences in PBEA and PBEB, which generate large differences in the PL metric. In Case 1 PBEA = -0.99 while in Case 2 PBEA = -1.01 (a difference of -0.02), and in Case 1 PBEB = 0.01 while in Case 2 PBEB = -0.01 (a difference of +0.02).

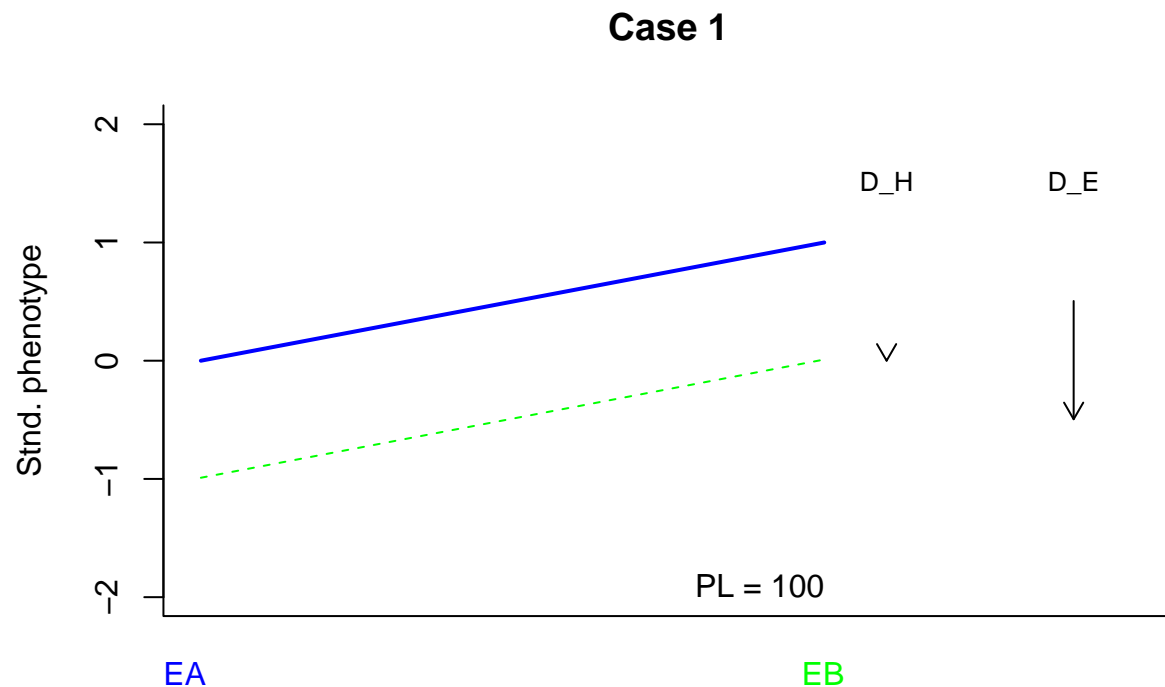
Case 1

This is a case of almost perfect countergradient variation that give a PL of 100.

```
# Case 1
case1 <- rep(NA, 4)
names(case1) <- c("PAEA", "PAEB", "PBEA", "PBEB")
a <- 0
case1[1:4] <- c(a, a+1, a-1+0.01, a+0.01)
case1
```

```
## PAEA PAEB PBEA PBEB
## 0.00 1.00 -0.99 0.01
```

```
makeplot(case1, "", "Case 1")
```



```
## D_H D_EA D_EB D_E PL
## 1 -0.01 -1 -1 -1 100
```

In the above figure, the D_H arrow represents the difference between the trait value of the the blue genotype in the blue habitat (EA) and the green genotype in the green habitat (EB). The D_E arrow represents the average effect of moving genotypes from environment B to environment A.

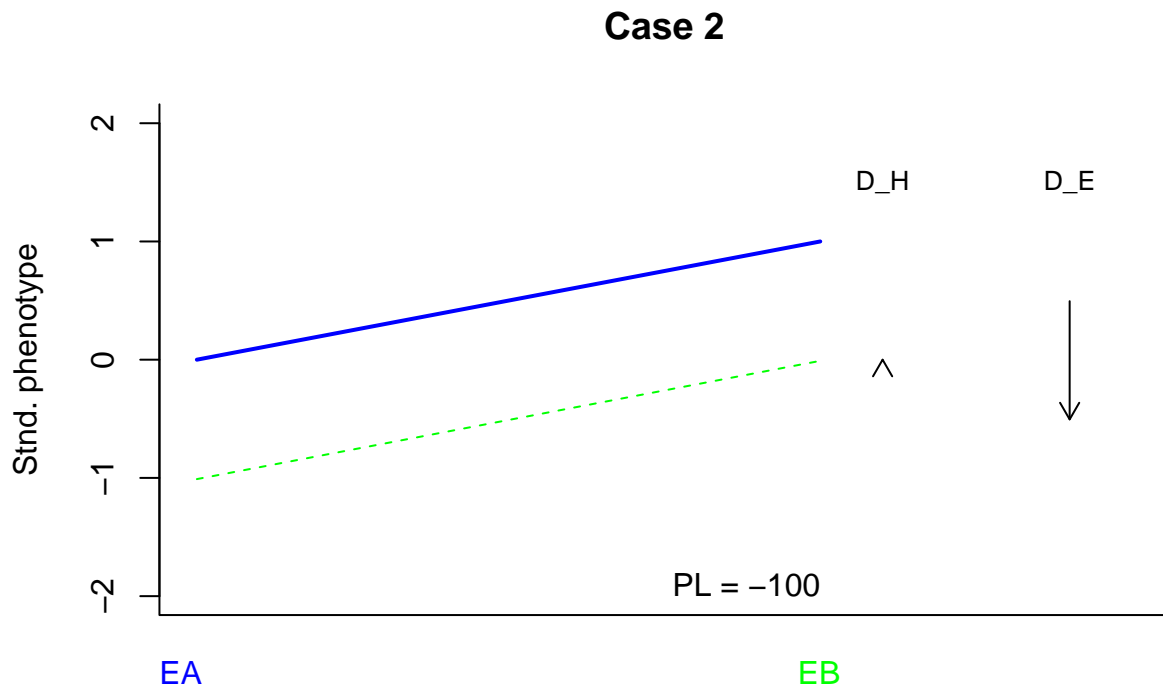
Case 2

This is a case of almost perfect countergradient variation, with trait values very close to Case 1, but that give a PL of -100. In this case, D_E is the same as Case 1, but D_H is slightly different in the opposite direction.

```
# Case 2
case2 <- rep(NA, 4)
names(case2) <- names(case1)
a <- 0
case2[1:4] <- c(a, a+1, a-1-0.01, a-0.01)
case2
```

```
## PAEA PAEB PBEA PBEB
## 0.00 1.00 -1.01 -0.01
```

```
makeplot(case2, "", "Case 2")
```



```
## D_H D_EA D_EB D_E PL
## 1 0.01 -1 -1 -1 -100
```

In the above figure, the D_H arrow represents the difference between the trait value of the the blue genotype in the blue habitat (EA) and the green genotype in the green habitat (EB). The D_E arrow represents the average effect of moving genotypes from environment B to environment A.

Compare Case 1 and Case 2

The following plot shows how Case 1 and Case 2 have almost equivalent reaction norms, and therefore similar plastic responses to the environment and similar amount of countergradient variation.

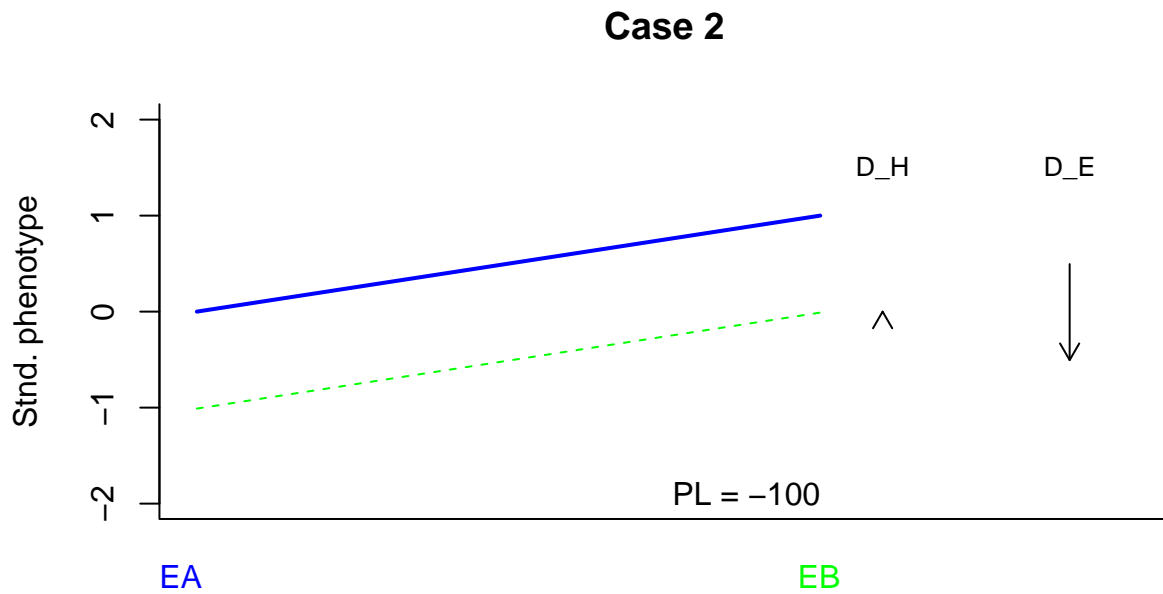
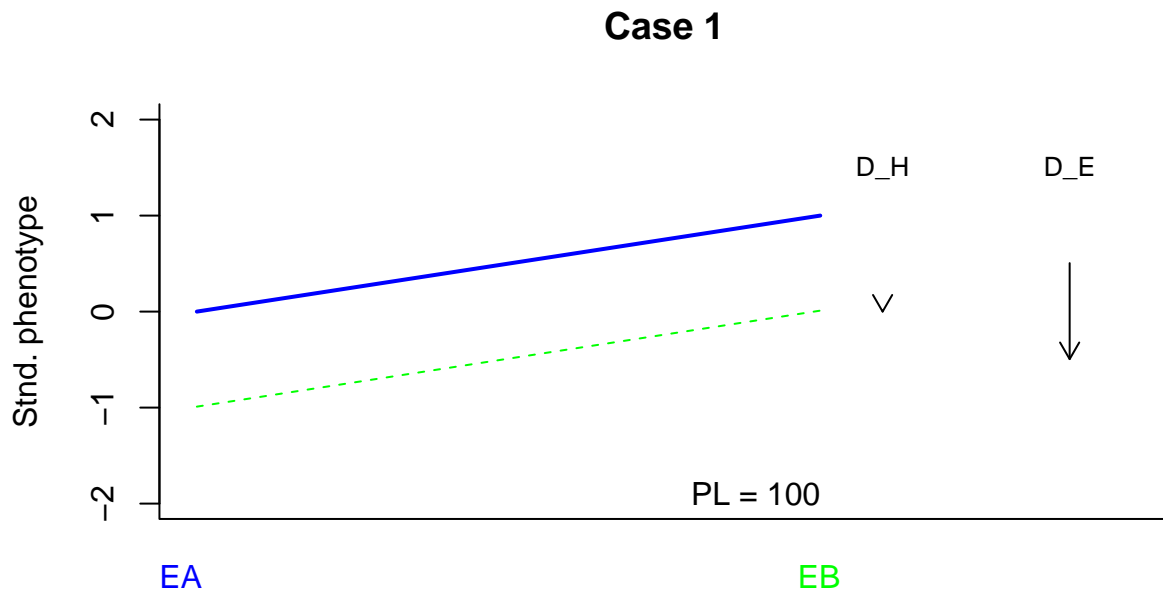
Despite these datasets being almost identical, Case 1 has PL=100 (implying extreme hyperplasticity) while Case 2 has PL= -100 (implying extreme wrong-sign plasticity).

Note that the difference in means for the two cases are very small and are within the range expected by sampling error, but the PL metric implies that they are very different cases.

```
par(mfrow=c(2,1))
makeplot(case1, "", "Case 1")
```

```
##      D_H D_EA D_EB D_E  PL
## 1 -0.01  -1   -1  -1  100
```

```
makeplot(case2, "", "Case 2")
```



```
##      D_H D_EA D_EB D_E  PL
## 1  0.01  -1   -1  -1 -100
```

Cases 3 and 4: $PL = 1$ for $G \times E$ reaction norms

In SH2020, $PL = 1$ is interpreted as “perfect plasticity” (which is interpreted as adaptive plasticity in which there is no genotype divergence, see Cases 5 and 6). In this section we show that datasets with $G \times E$ reaction norms can also give $PL=1$ due to the averaging of the ΔE_A and ΔE_B .

In Cases 3 and 4, we compare two very different patterns of reaction norms that both give $PL=1$. In both cases, there is a pattern of $G \times E$ reaction norms, that results from the “A” genotype being plastic and the “B” genotype having little-to-no plasticity.

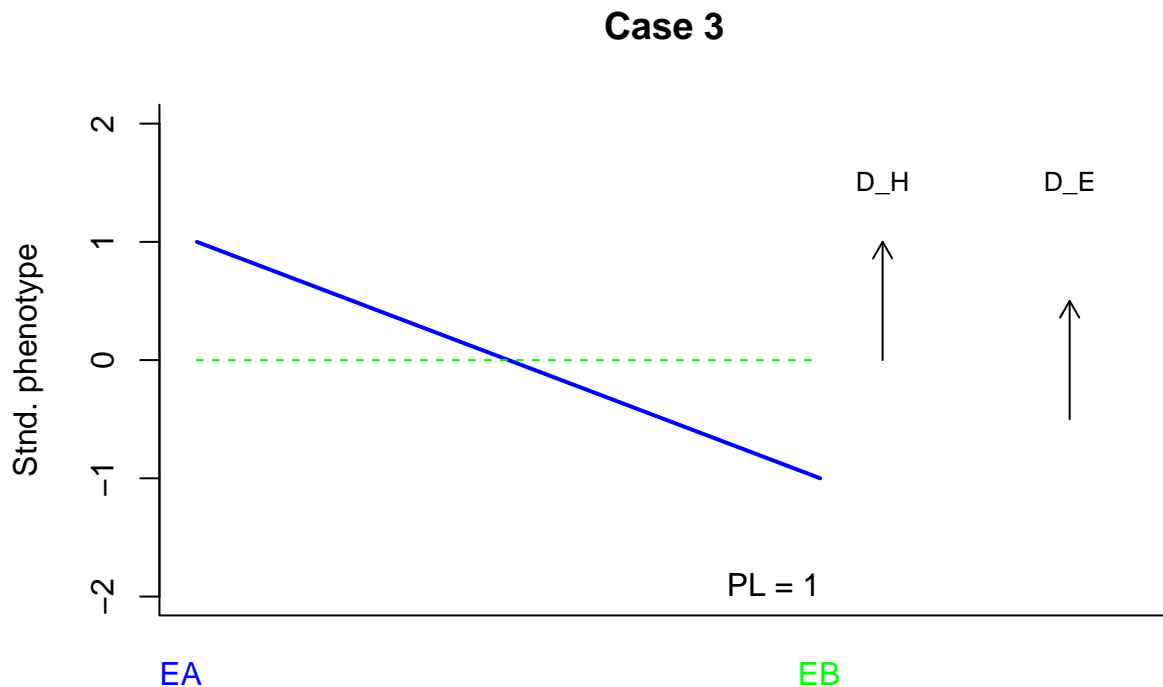
Case 3

In Case 3, the A genotype in blue is highly plastic while the B genotype in green has zero plasticity.

```
case3 <- rep(NA, 4)
names(case3) <- names(case1)
case3[1:4] <- c(1,-1,0,0)
case3

## PAEA PAEB PBEA PBEB
##    1  -1   0   0

par(mfrow=c(1,1))
makeplot(case3, "", "Case 3")
```



```
##    D_H D_EA D_EB D_E PL
## 1    1    2    0    1  1
```

In the above figure, the D_H arrow represents the difference between the trait value of the the blue genotype in the blue habitat (EA) and the green genotype in the green habitat (EB). The D_E arrow represents the average effect of moving genotypes from environment B to environment A. **Since $D_H = D_E$ in Case 4, the PL statistic equals 1.** Thus, PL can equal 1 even when there is not perfect plasticity in the dataset.

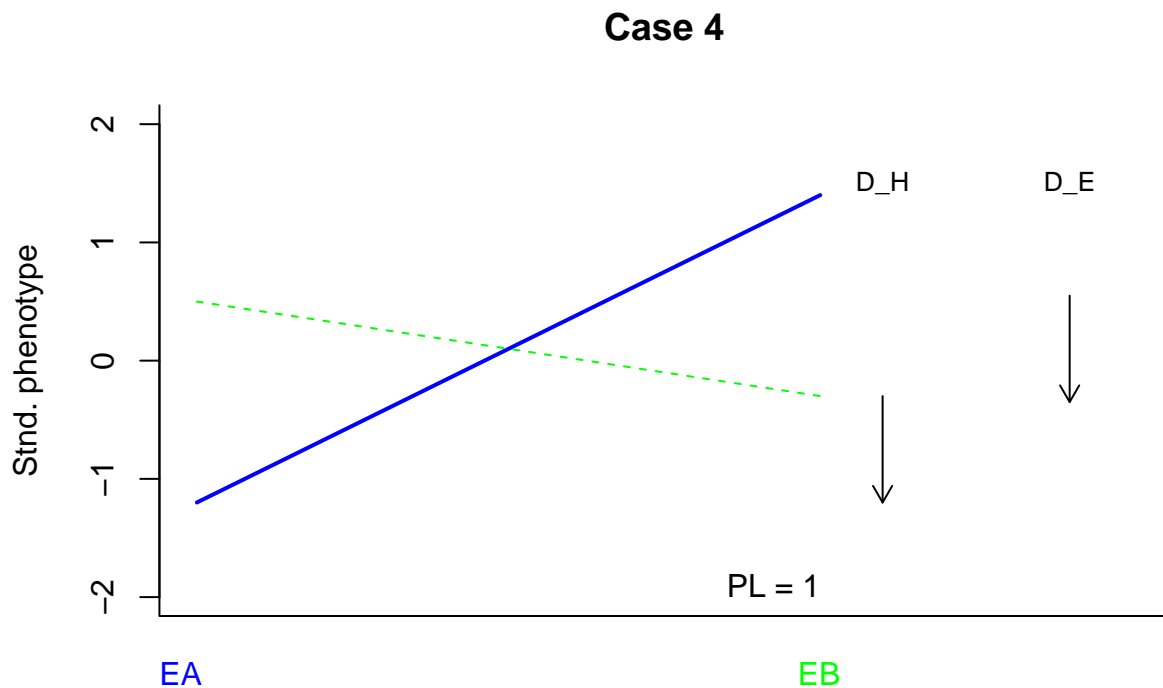
Case 4

In case 4, the A genotype in blue is highly plastic, while the B genotype in green has a little plasticity in the opposite direction of the A genotype.

```
case4 <- rep(NA, 4)
names(case4) <- names(case1)
case4[1:4] <- c(-1.2, +1.4, +0.5, -0.3)
case4
```

```
## PAEA PAEB PBEA PBEB
## -1.2 1.4 0.5 -0.3
```

```
makeplot(case4, "", "Case 4")
```



```
## D_H D_EA D_EB D_E PL
## 1 -0.9 -2.6 0.8 -0.9 1
```

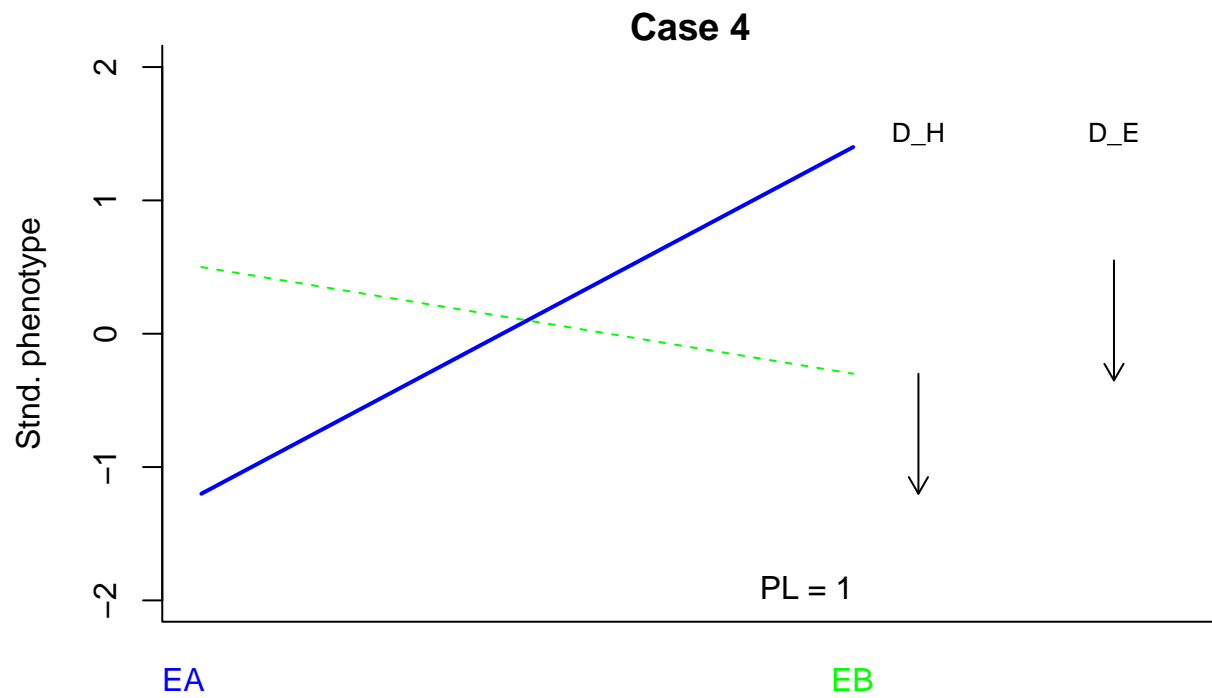
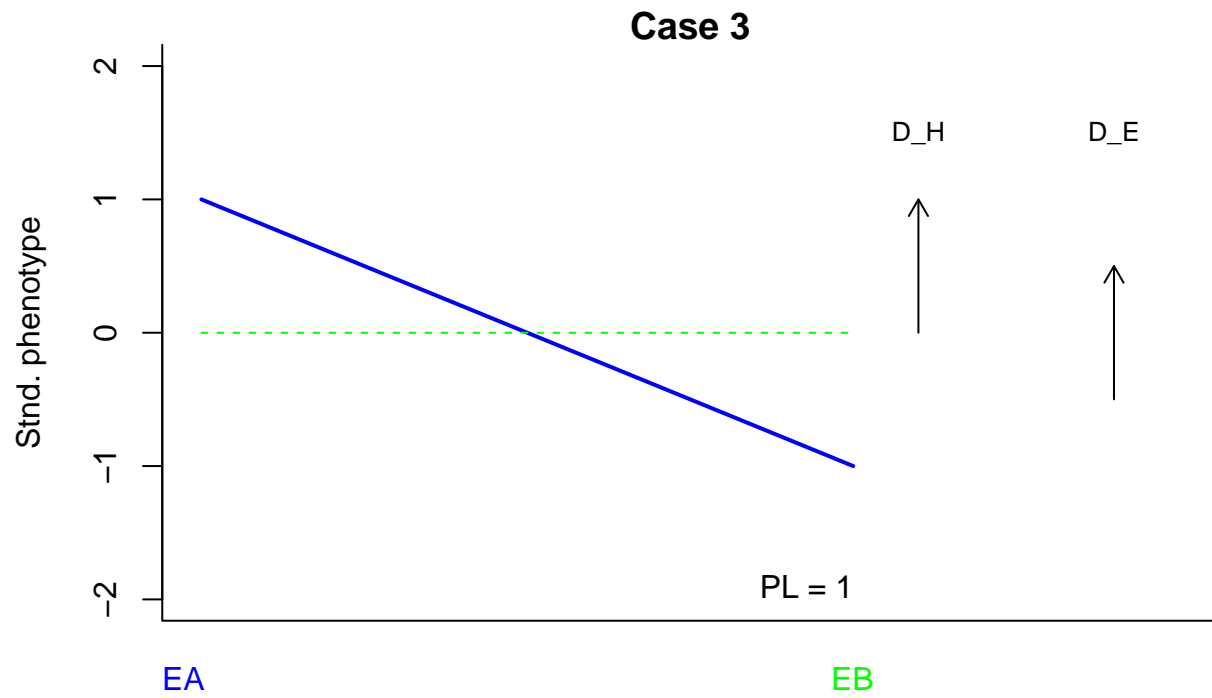
In the above figure, the D_H arrow represents the difference between the trait value of the blue genotype in the blue habitat (EA) and the green genotype in the green habitat (EB). The D_E arrow represents the average effect of moving genotypes from environment B to environment A. **Since $D_H = D_E$ in Case 4, the PL statistic equals 1.** Thus, PL can equal 1 even when there is not perfect plasticity in the dataset.

Compare Case 3 and Case 4

```
par(mfrow=c(2,1), mar=c(4,4,1,1))
makeplot(case3, "", "Case 3")
```

```
## D_H D_EA D_EB D_E PL
## 1 1 2 0 1 1
```

```
makeplot(case4, "", "Case 4")
```

```
##      D_H D_EA D_EB  D_E PL
## 1 -0.9 -2.6  0.8 -0.9  1
```

The above comparison of Cases 3 and 4 show that PL can equal 1 even when there is not perfect plasticity in the dataset.

Cases 5 and 6: $PL = 1$ for “perfect” plasticity scenario

In Cases 5 and 6, we show that the perfect plasticity scenario produces $PL = 1$. In both cases, there is no genetic differentiation between the genotypes (both genotypes have the same reaction norms).

In Case 5, there is almost no plasticity as there is a very small change in the phenotype from one environment to the other.

In Case 6, there is a lot of plasticity because there is a relatively large change in the phenotype from one environment to the other.

Both cases give $PL = 1$ because D_H equals D_E .

Both these cases are considered “perfect plasticity” under the PL framework, since trait value of the local genotype is equal to the trait value of the foreign genotype in both environments.

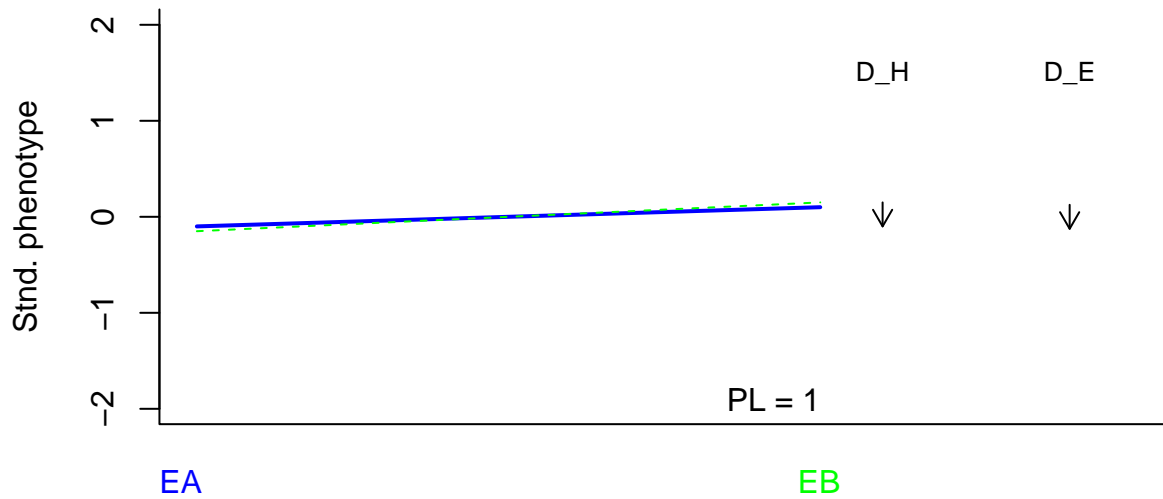
```
case5 <- c(-0.1, 0.1, -0.15, 0.15)
case6 <- c(-1, 1, -1.05, 1.05)
```

```
par(mfrow=c(2,1))
makeplot(case5, "", "Case 5")
```

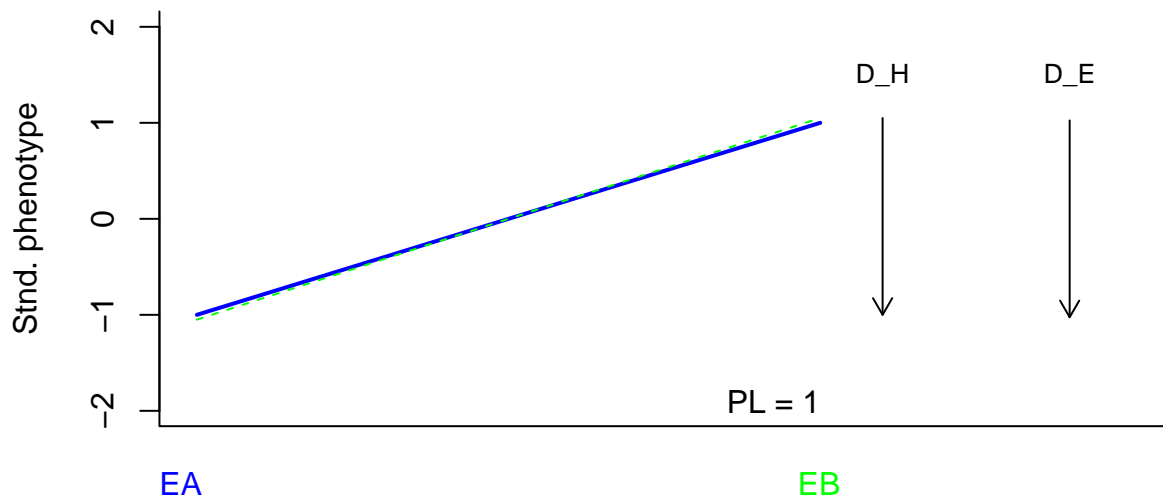
```
##      D_H D_EA D_EB  D_E PL
## 1 -0.25 -0.2 -0.3 -0.25  1
```

```
makeplot(case6, "", "Case 6")
```

Case 5



Case 6



```
##      D_H D_EA D_EB  D_E PL
## 1 -2.05  -2 -2.1 -2.05  1
```

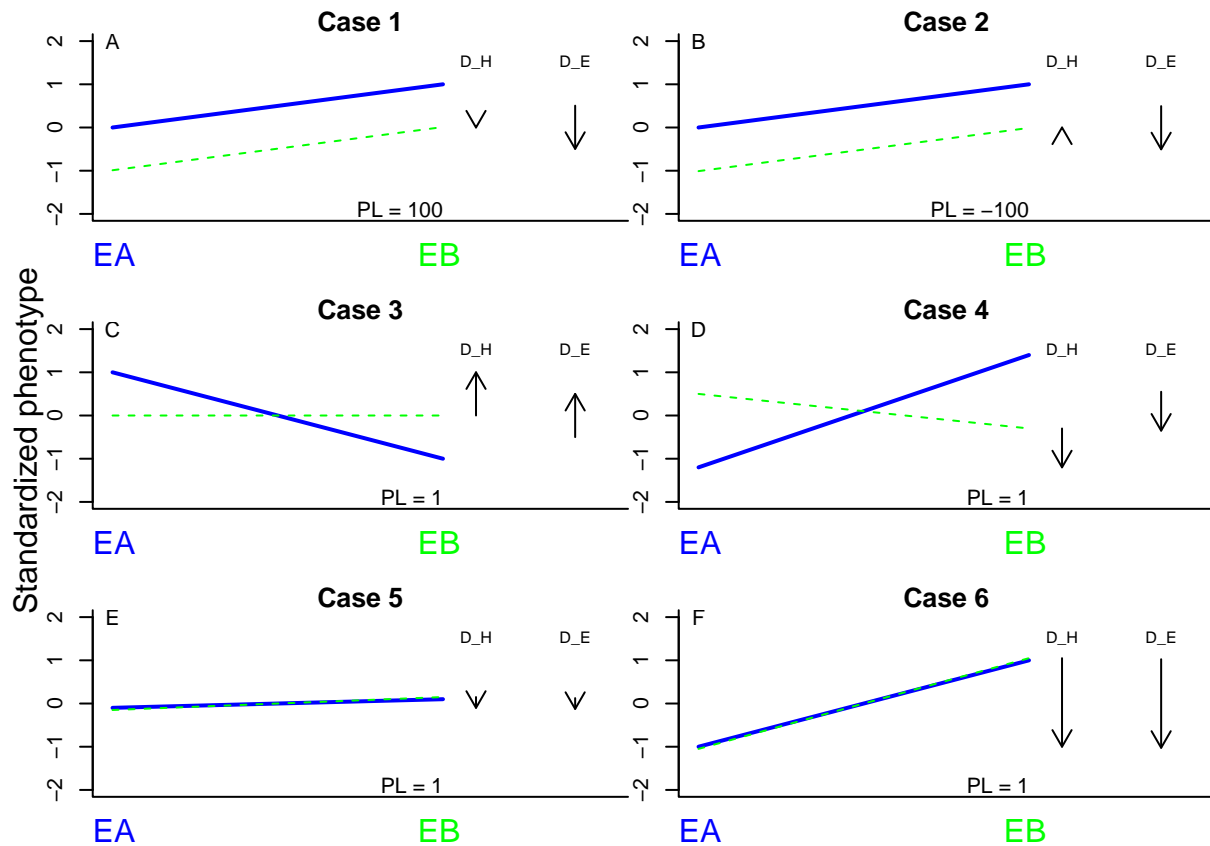
In the above figure, the D_H arrow represents the difference between the trait value of the blue genotype in the blue habitat (EA) and the green genotype in the green habitat (EB). The D_E arrow represents the average effect of moving genotypes from environment B to environment A. **Since $D_H = D_E$ in Cases 5 and 6, the PL statistic equals 1, even though there isn't a lot of plasticity in Case 5.**

Summary of PL behavior

Under countergradient variation, PL is bimodal and can give extremely different values for datasets with very similar reaction norms (Cases 1-2). In the next section, we discuss the consequences of this property for inferring the prevalence of co- vs. countergradient variation in a metaanalysis.

PL can also give the same value for very different patterns of reaction norms, varying from those with high genetic variation and GxE (Cases 3-4) to those with no genetic differentiation (Cases 5-6). Therefore, $PL = 1$ cannot be used to infer “perfect plasticity” in all scenarios.

```
# Make plot
#pdf("")
par(mfrow=c(3,2), mar=c(3,1,1,1), oma=c(0,3,0,0))
a <- makeplot(case1, "A", "Case 1")
b <- makeplot(case2, "B", "Case 2")
c <- makeplot(case3, "C", "Case 3")
d <- makeplot(case4, "D", "Case 4")
e <- makeplot(case5, "E", "Case 5")
f <- makeplot(case6, "F", "Case 6")
mtext("Standardized phenotype", side=2,
      outer=TRUE, line=1)
```



```
#dev.off()

final_1 <- rbind(case1, case2, case3, case4, case5, case6)

final_2 <- rbind(a,b,c,d,e, f)

(final <- cbind(final_1, final_2))
```

| ## | | PAEA | PAEB | PBEA | PBEB | D_H | D_EA | D_EB | D_E | PL |
|----|-------|------|------|-------|-------|-------|------|------|-------|------|
| ## | case1 | 0.0 | 1.0 | -0.99 | 0.01 | -0.01 | -1.0 | -1.0 | -1.00 | 100 |
| ## | case2 | 0.0 | 1.0 | -1.01 | -0.01 | 0.01 | -1.0 | -1.0 | -1.00 | -100 |
| ## | case3 | 1.0 | -1.0 | 0.00 | 0.00 | 1.00 | 2.0 | 0.0 | 1.00 | 1 |
| ## | case4 | -1.2 | 1.4 | 0.50 | -0.30 | -0.90 | -2.6 | 0.8 | -0.90 | 1 |
| ## | case5 | -0.1 | 0.1 | -0.15 | 0.15 | -0.25 | -0.2 | -0.3 | -0.25 | 1 |
| ## | case6 | -1.0 | 1.0 | -1.05 | 1.05 | -2.05 | -2.0 | -2.1 | -2.05 | 1 |

Compare PL to CovGE

We compare the PL metric to the CovGE metric from ATL2022 to show how the two are related for 2x2 reciprocal transplant designs.

SH2020 only shows how to calculate PL for a 2x2 reciprocal transplant, however the CovGE metric can be calculated for any reciprocal transplant experiment as well as a specifically designed common garden experiment with at least 2 common gardens and multiple genotypes (see ATL2022 for details).

First, we load a complete results of the simulations from Albecker, which included a calculation of the PL metric for 2 x 2 reciprocal transplant designs.

MOLLY - CAN YOU DOUBLE CHECK ALL THE FILES BELOW ARE ARCHIVED ONLINE WITH BCO-DMO AND IF NOT, CREATE A NEW BCO-DMO PROJECT FOR THIS PAPER AND ARCHIVE THEM. THEN WE WILL ADD THE LINK HERE. THANKS!

(To replicate this code, readers should change the path to where the files are stored on their computer.)

```
powdf <- read.csv("../results/Results_10.06.2020/Archive/Power_output_results.csv")
vardf <- read.csv("../results/Results_10.06.2020/Archive/Variance_output_results.csv")
PLdf <- read.csv("../results/Results_10.06.2020/Archive/PL_output_results.csv")
phendf <- read.csv("../results/Results_10.06.2020/Archive/phenotype_output_results.csv")

#head(powdf)
#head(vardf)
#head(PLdf)
#head(phendf)
```

First, we have to subset the data to cases with 2 genotypes and 2 environments because SH2020 only derived the PL metric for those cases. However, note that CovGE can be calculated for many different designs.

```
cases <- powdf$row[powdf$n_env==2 & powdf$n_pop==2]
length(cases)
```

```
## [1] 800
```

There are 800 cases that met this criteria in our simulations.

Let's subset the data to those cases:

```
powdf2 <- powdf[powdf$row %in% cases,]
vardf2 <- vardf[vardf$row %in% cases,]

#dim(powdf2)
#head(PLdf)

newdf <- merge(powdf2, PLdf, by = "row")
#dim(newdf)
#str(newdf)
```

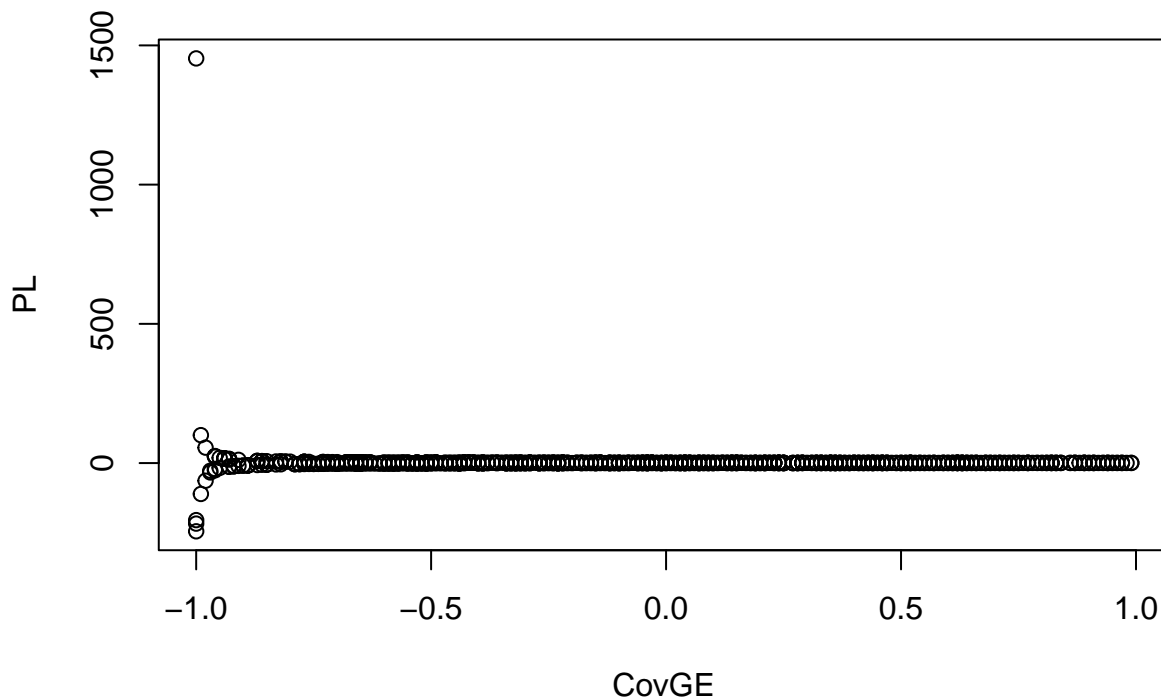
Here is an example of how to extract the mean phenotype value for 2 genotypes grown in 2 environments:

```
i = 1001 # simulation ID
cond <- which(phendf$row==i)
tapply(phendf$phen_corrected[cond], as.character(phendf$GE_factor[cond]), mean, na.rm=TRUE)
```

```
##          G1E1          G1E2          G2E1          G2E2
## -0.7891405  0.6349688 -2.4337788  0.6584051
```

First, let's compare CovGE and PL for all the simulations:

```
## compare CovGE and PL
plot(newdf$covariance.x, newdf$PL, xlab="CovGE", ylab="PL"
)
```

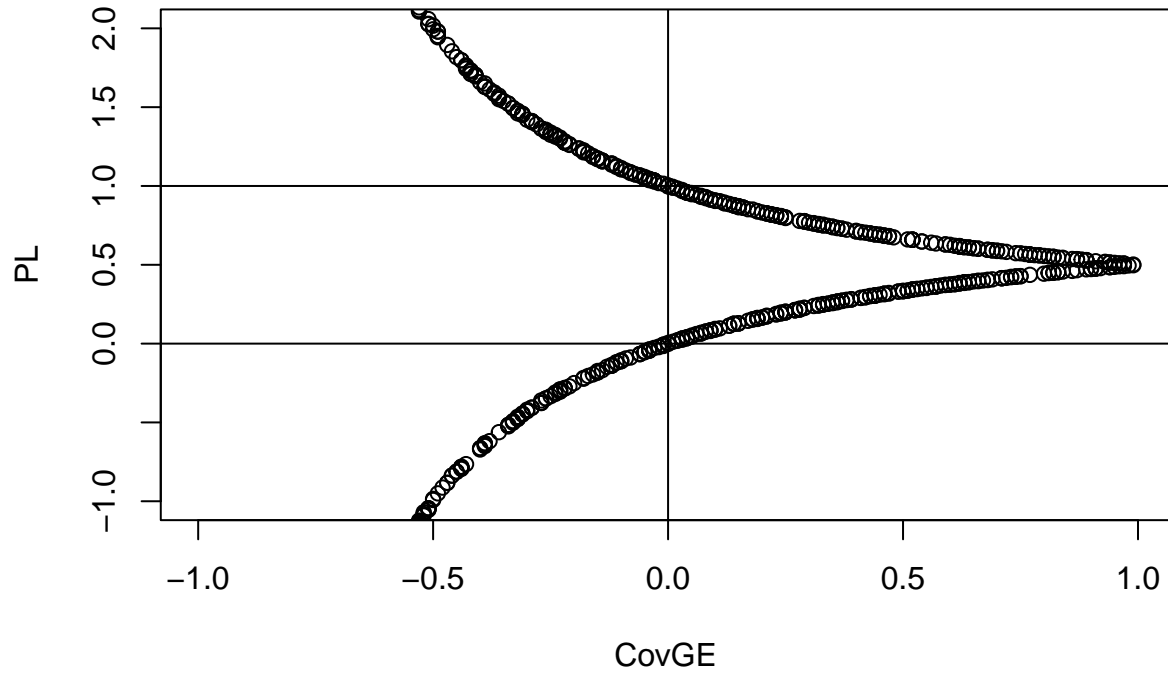


The above plot shows that as the dataset approaches countergradient variation ($\text{CovGE} = -1$), the PL metric can have very large positive or negative values.

Let's zoom in on the y-axis:

```
plot(newdf$covariance.x, newdf$PL, ylim=c(-1,2),
     xlab="CovGE", ylab="PL", main="Figure 1")
abline(1,0)
abline(0,0)
abline(v=0)
```

Figure 1



The above plot shows that in 2x2 cases, the PL metric is directly related to CovGE. At $PL = 0$ or $PL = 1$, there is no gradient variation ($CovGE=0$). The vertical line shows where $CovGE = 0$ (no gradient variation). The horizontal lines show where $PL = 0$ and $PL = 1$ (perfect plasticity).

Can PL be used to infer the overall distribution of cogradients or countergradient variation in nature?

The last figure shows that PL is bimodally distributed for countergradient variation.

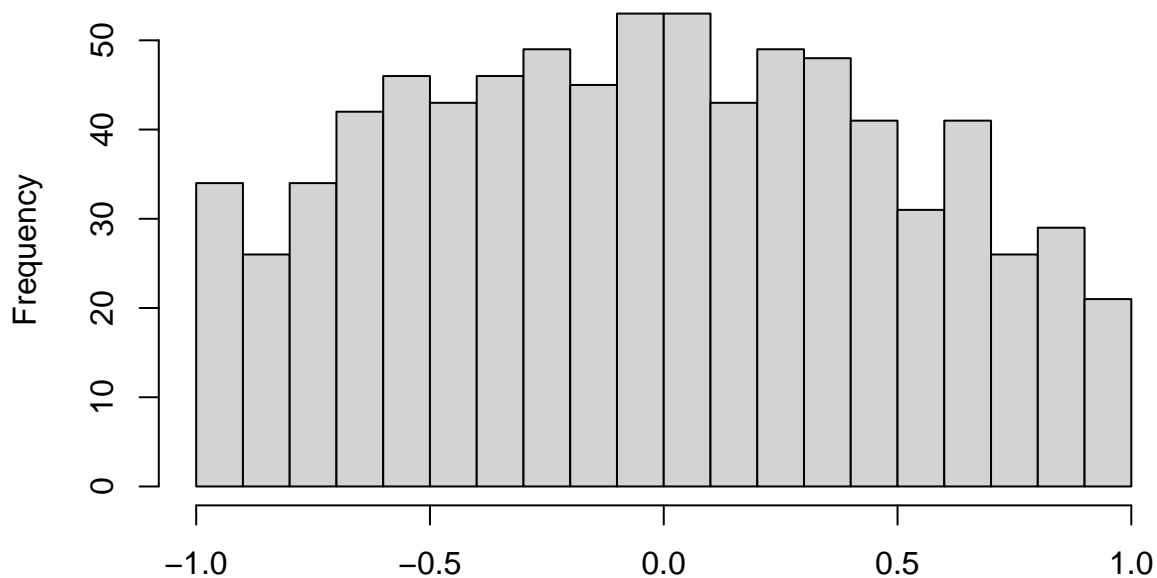
The ATL2022 simulations were designed to capture a range of possible patterns that may arise in 2 genotype x 2 environment experiments in nature. The distribution of simulated parameters gave an approximately uniform distribution from extreme countergradient, to no gradient variation, to extreme cogradients variation. (The distribution was not perfectly uniform because varying amounts of noise were added to the trait values.)

We can visualize this with the distribution of CovGE in the simulations:

```
summary(newdf$covariance.x)
```

```
##      Min.   1st Qu.   Median     Mean  3rd Qu.     Max.
## -1.00000 -0.44000 -0.03000 -0.02753  0.37000  0.99000
```

```
hist(newdf$covariance.x, main="", xlab="Distribution of CovGE in simulations", breaks=seq(-1,1,0.1))
```



Distribution of CovGE in simulations

Note that the distribution is symmetric around 0, with a slight skew toward countergradient scenarios.

The proportion of cogradients scenarios in the simulations is:

```
sum(newdf$covariance.x>0)/length(newdf$covariance.x) # proportion of cogradients simulations
```

```
## [1] 0.4775
```

The proportion of countergradient scenarios in the simulations is:

```
sum(newdf$covariance.x<0)/length(newdf$covariance.x) # proportion of countergradient simulations
```

```
## [1] 0.515
```

Comparison of the median CovGE to the median PL shows that the median CovGE is not biased and that median PL is biased

We can compare the distribution of CovGE to the distribution of the PL metric from the same simulations.

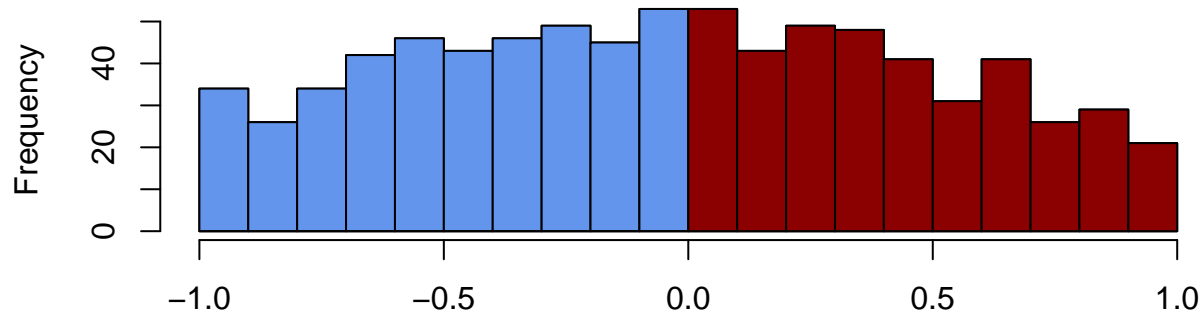
```
summary(newdf$PL)
```

```
##      Min.   1st Qu.   Median     Mean   3rd Qu.    Max.
## -245.0634 -0.0121   0.4889   1.4148   1.0360 1453.2121
```

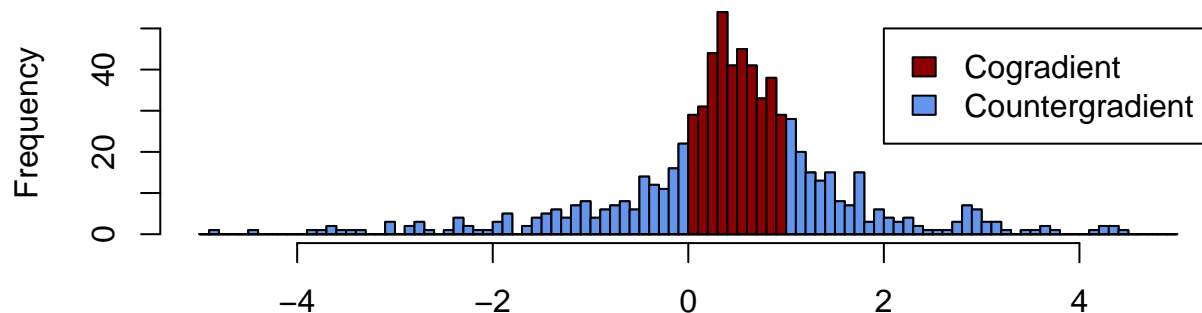
```
par(mfrow=c(2,1), mar=c(4,4,1,1))
hist(newdf$covariance.x, main="",
     xlab="Distribution of CovGE in simulations", breaks=seq(-1,1,0.1))
hist(newdf$covariance.x[newdf$covariance.x<=0],
     main="", xlab="Distribution of CovGE in simulations",
     breaks=seq(-1,1,0.1), col="cornflowerblue", add=TRUE)
hist(newdf$covariance.x[newdf$covariance.x>0],
     main="", xlab="Distribution of CovGE in simulations",
     breaks=seq(-1,1,0.1), col="darkred", add=TRUE)

hist(newdf$PL[newdf$PL>-5 & newdf$PL<5], main="",
     xlab="Distribution of PL in simulations", breaks=seq(-5,5,0.1))
hist(newdf$PL[newdf$PL>-5 & newdf$PL<0], main="",
     xlab="Distribution of PL in simulations",
     breaks=seq(-5,5,0.1), col="cornflowerblue", add=TRUE)
hist(newdf$PL[newdf$PL>1 & newdf$PL<5], main="",
     xlab="Distribution of PL in simulations",
     breaks=seq(-5,5,0.1), col="cornflowerblue", add=TRUE)
hist(newdf$PL[newdf$PL<1 & newdf$PL>0], main="",
     xlab="Distribution of PL in simulations",
     breaks=seq(-5,5,0.1), col="darkred", add=TRUE)

legend(2, 50, c("Cogradient", "Countergradient"),
     fill=c("darkred", "cornflowerblue"))
```



Distribution of CovGE in simulations



Distribution of PL in simulations

In the above plot, cogradient cases are colored red and countergradient cases are colored blue.

- The above plot shows that median CovGE is near 0, which implies a roughly equal number of cogradient and countergradient datasets (which is consistent with what was simulated).
- The above plot shown that the median PL metric is near 0.5, which implies that co-gradient variation is the most common scenario in the datasets (which is not consistent with what was simulated). This happens because when $PL < 0$ (countergradient variation) it is bimodally distributed, and these values essentially cancel each other out. The consequence is that even when the average pattern in nature is no gradient variation (as it was in the simulations), the PL metric erroneously infers cogradient variation as having the highest probability of occurring.

Thus, while the median CovGE in the simulations is near 0, the median PL in the simulations is near 0.5 (wrongly implying cogradient) because PL is bimodally distributed for countergradient variation as shown above. The true median of gradient variation in the simulated datasets is near 0.

Therefore, the median CovGE can be used in a metanalysis to get an average effect size for gradient variation, but the median PL should not be used for that purpose.

Both CovGE and PL can be used to calculate the proportion of datasets that are cogradient or countergradient

Both metrics can be used to infer the proportion of datasets with co- vs. countergradient variation in a metanalysis.

- The proportion of datasets of PL between 0 and 1 gives an unbiased estimate of the proportion of cogradient simulations:

```
sum(newdf$PL>0 & newdf$PL<1)/nrow(newdf)
```

```
## [1] 0.48125
```

- The proportion of datasets with CovGE greater than 0 gives an unbiased estimate of the proportion of cogradient simulations:

```
sum(newdf$covariance.x>0)/nrow(newdf)
```

```
## [1] 0.4775
```

There are some slight differences in the two proportions due to rounding in the calculations.

Summary of PL vs CovGE

The below table summarizes the differences between PL and CovGE.

PL gives insight into hyperplasticity and wrong-sign plasticity, but because it is a ratio it has some weird behavior as described in cases 1-6.

Both metrics can be used to infer whether a dataset exhibits co-gradient or counter-gradient variation for a 2 x 2 reciprocal transplant, but only CovGE can be applied to more complex designs. Also, ATL2022 shows how to calculate confidence intervals and P-values for CovGE on a single dataset, so it is possible to test the null hypothesis that $\text{CovGE} = 0$. It would be difficult to design a statistical test for PL on a single dataset because it is bimodally distributed under countergradient variation, and can give extremely opposite values for the same pattern in the data as shown in Cases 1-2.

| Context | PL | CovGE |
|---|---|--|
| sampling design | 2x2 reciprocal transplant only | n x n reciprocal transplant and some common garden designs |
| Median when the distribution of gradient variation is uniform | 0.5 (wrongly inferring cogradient) | 0 (correctly inferring equal number of counter and co-gradient datasets) |
| Values giving no gradient variation | near 0 or 1 | near 0 |
| Values giving cogradient variation | between 0 and 1 | greater than 0 |
| Values giving countergradient variation | less than 0 or greater than 1 | less than 0 |
| Confidence intervals and P-value for a single dataset | No | Yes |
| Shape of distribution under countergradient variation | Bimodal (can create extremely opposite values for similar reaction norms) | Unimodal (creates similar values for similar reaction norms) |
| Gives insight into hyperplasticity and wrong-sign plasticity | Yes | No |