Modularidade e Consequencias Evolutivas

‘Modularidade: Conectando padrões e processos em evolução multivariada’

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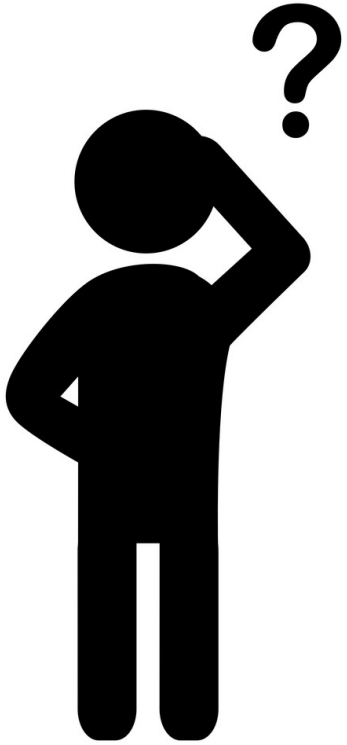
Why study variation in biology?

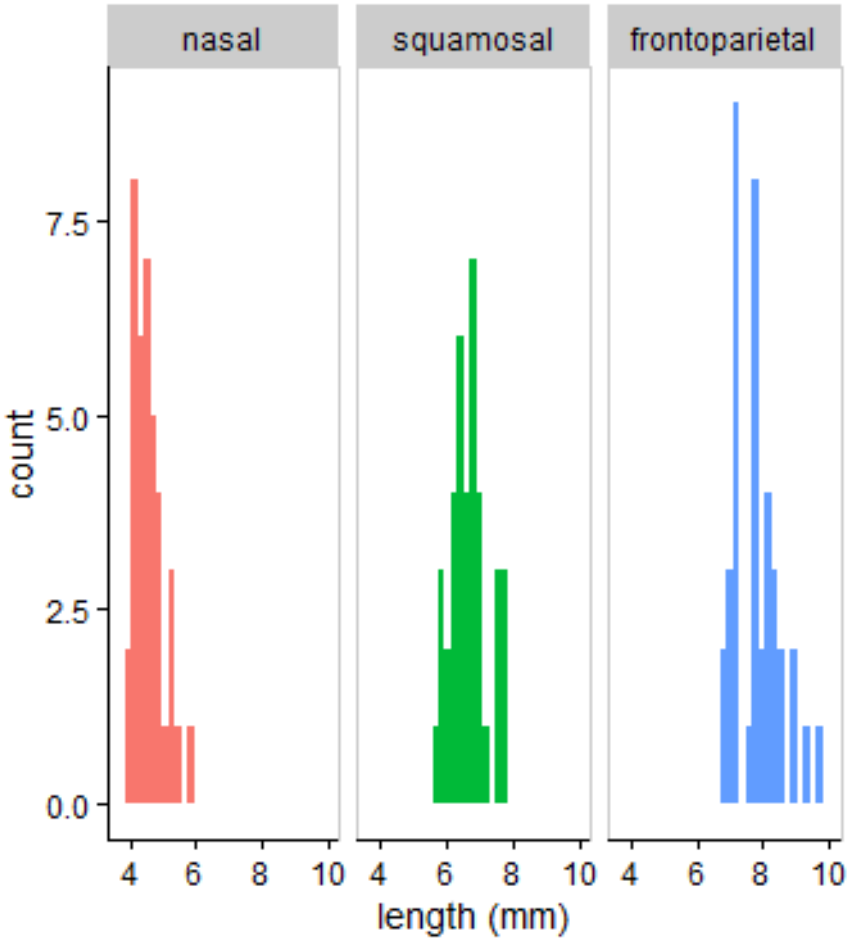


Where does variation comes from?

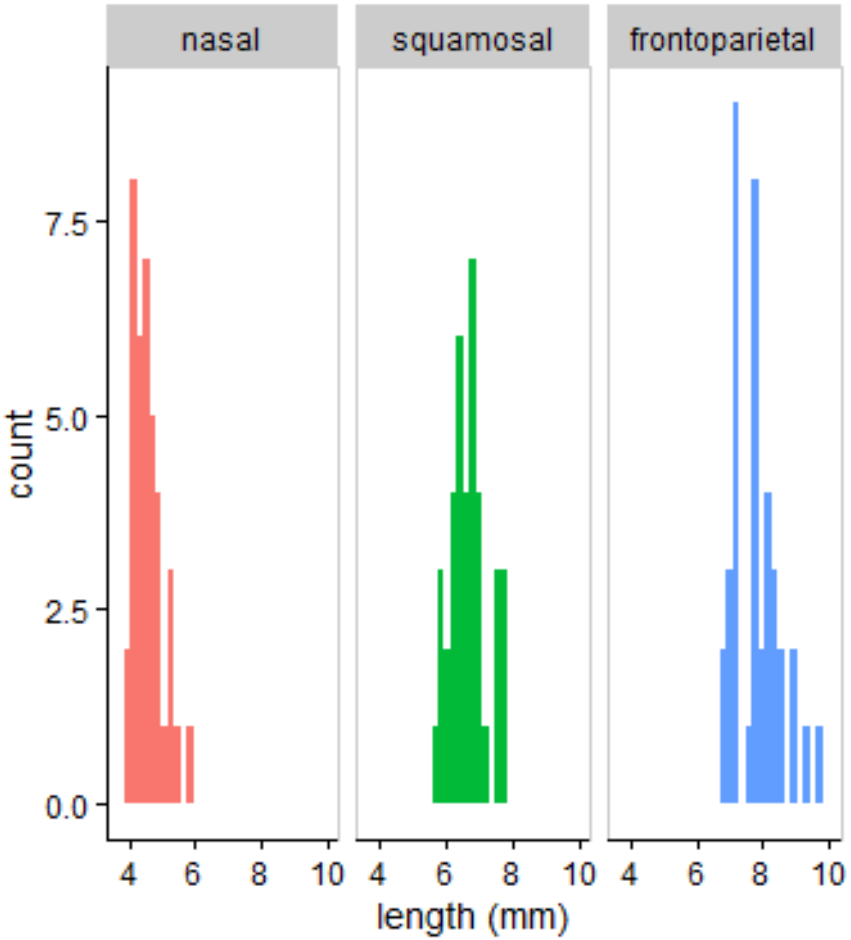
How is variation organized in populations?

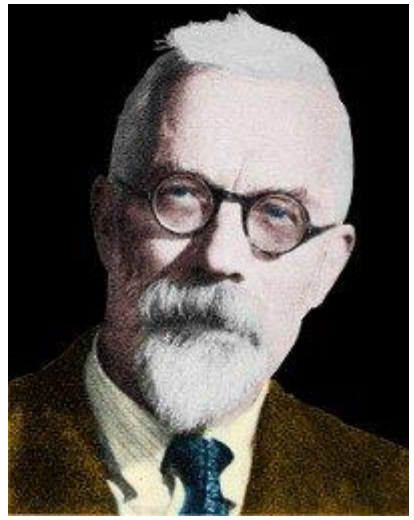
What are the evolutionary consequences of a particular organization of variation?

Quantitative Genetics



Quantitative Genetics





Ronald Fisher

$$P = G + E$$

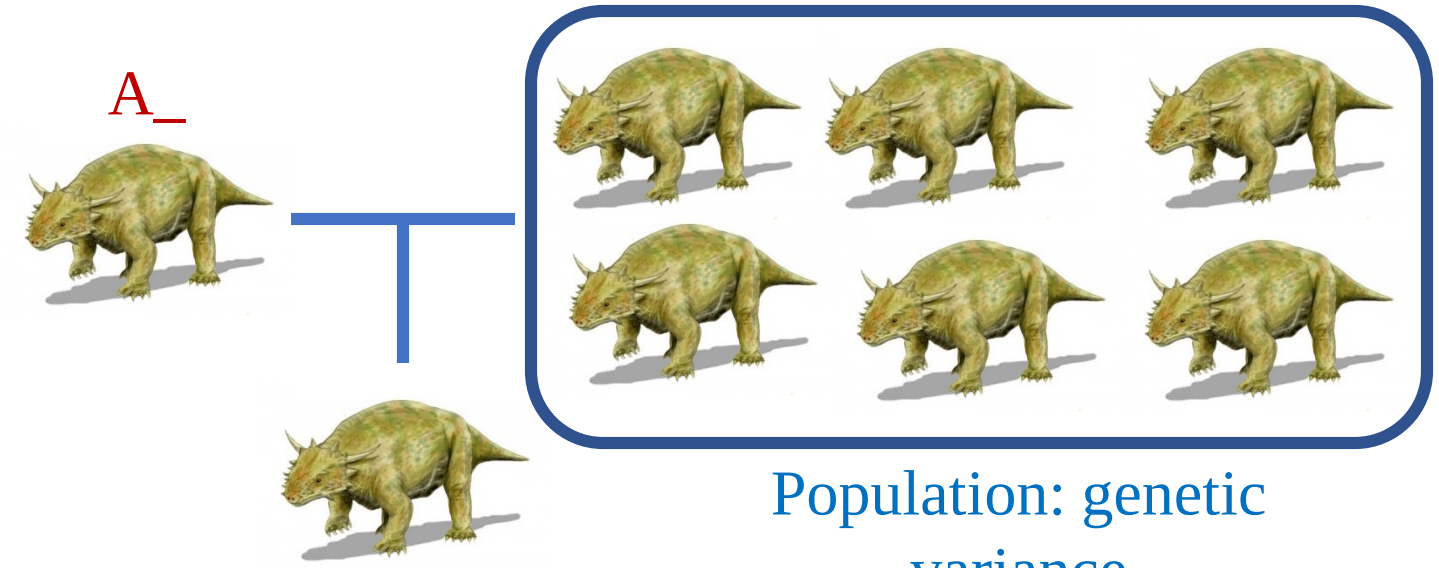
Phenotypic value

Genotypic value

Environmental deviation

Multiple loci with mendelian segregation

Average effect of an allele



p(A1) = p
p(A2) = q

Population: genetic variance

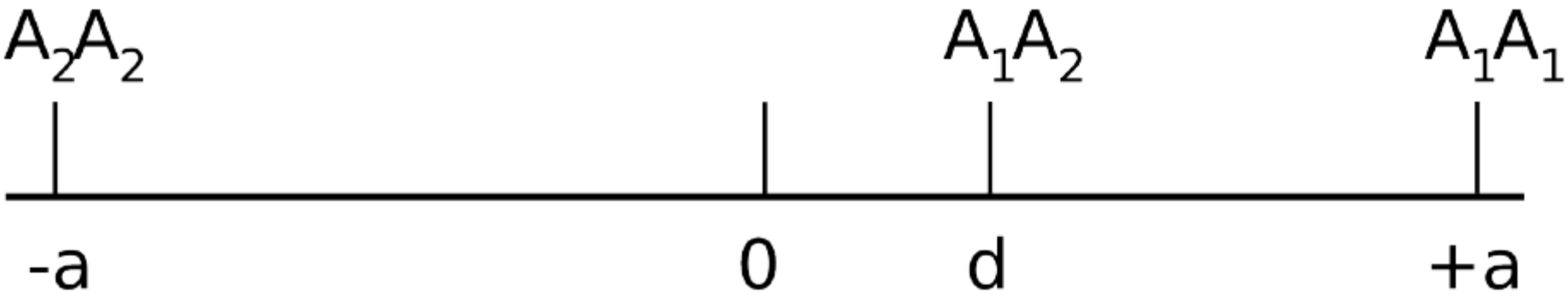
Average phenotypic value in offspring

Populational mean

Difference =
Average contribution of A to the phenotype

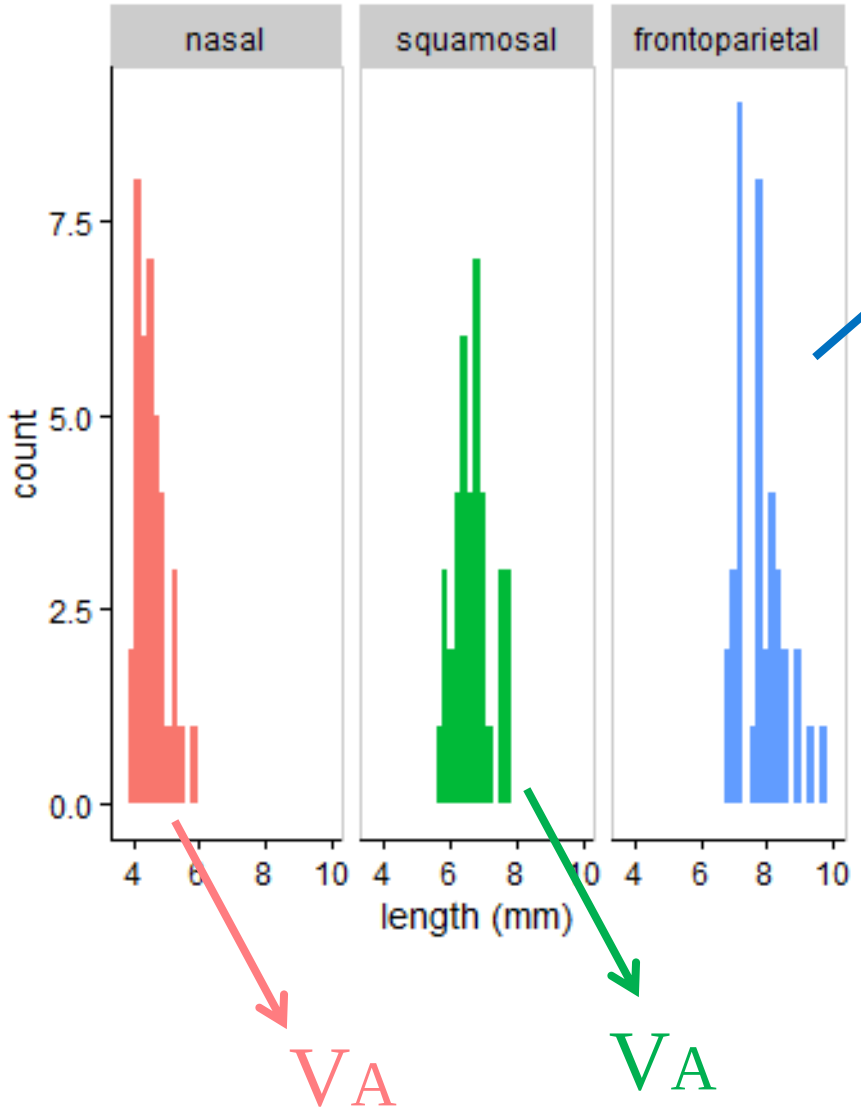
Avg effect: parent-offspring resemblance

Average effect of an allele



$$\alpha = a + d(q - p)$$

Aditive Genetic Variance



Multiple loci affecting the trait

↓

Each allele in each locus has an average effect

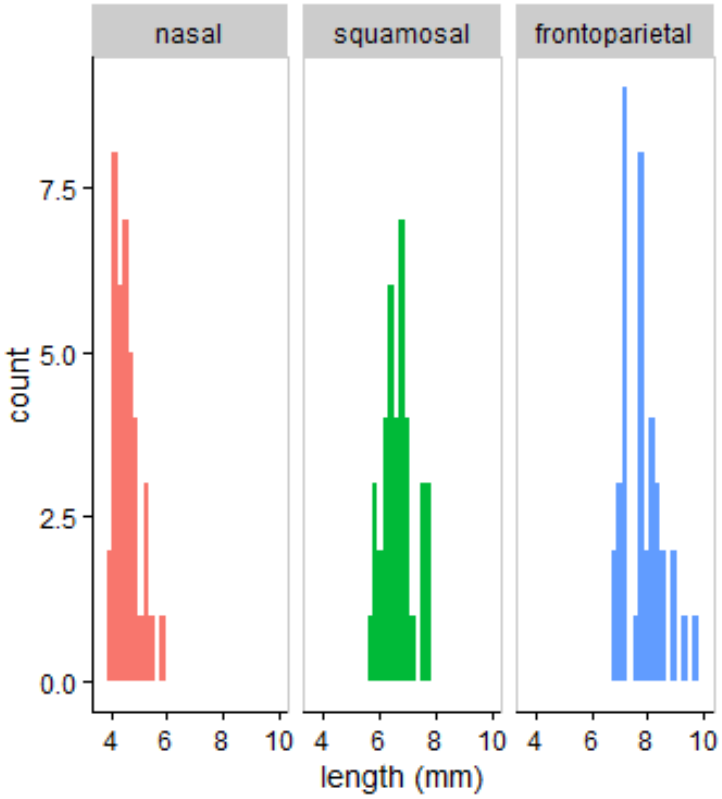
↓

V_A = sum of all average effects of loci that affect the frontoparietal

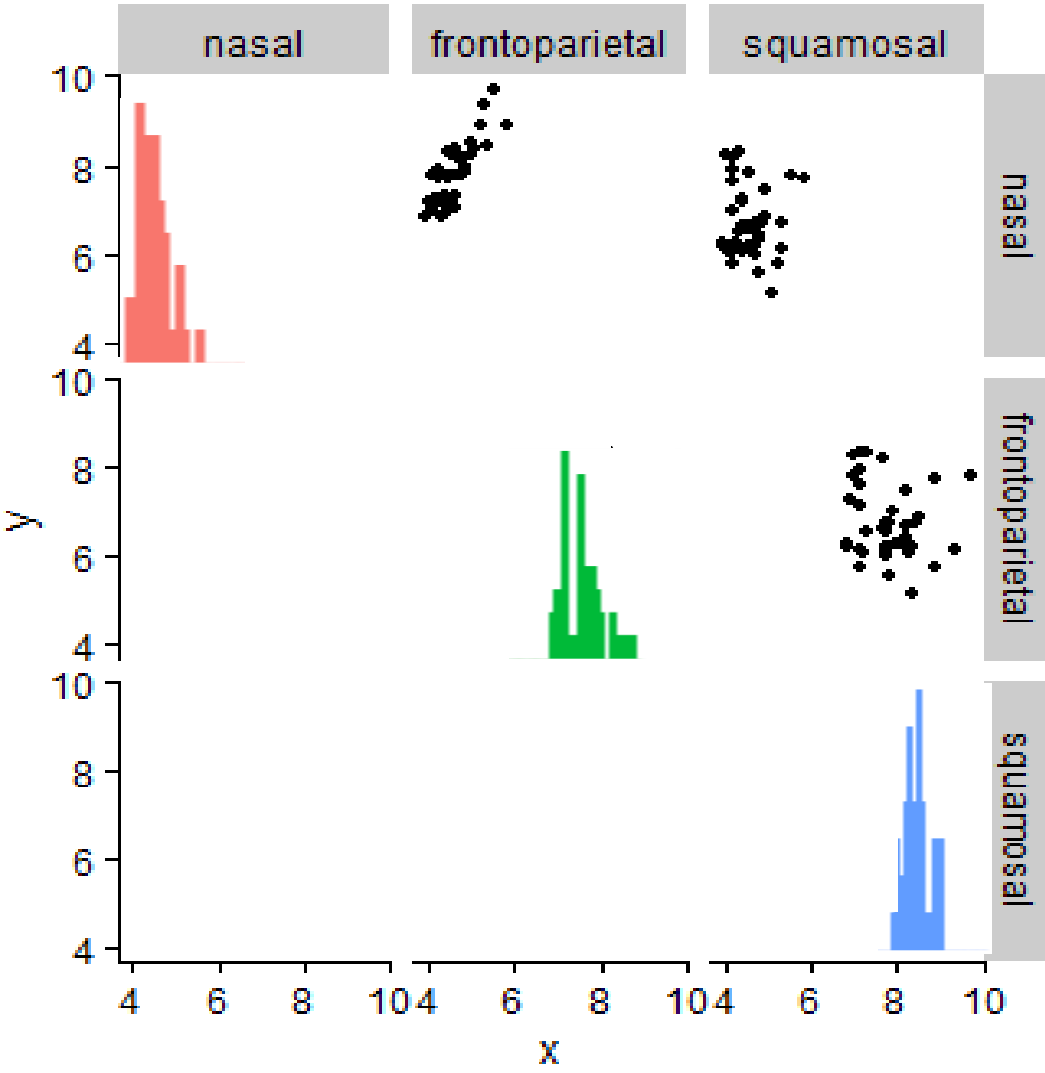
↓

HERITABLE VARIATION

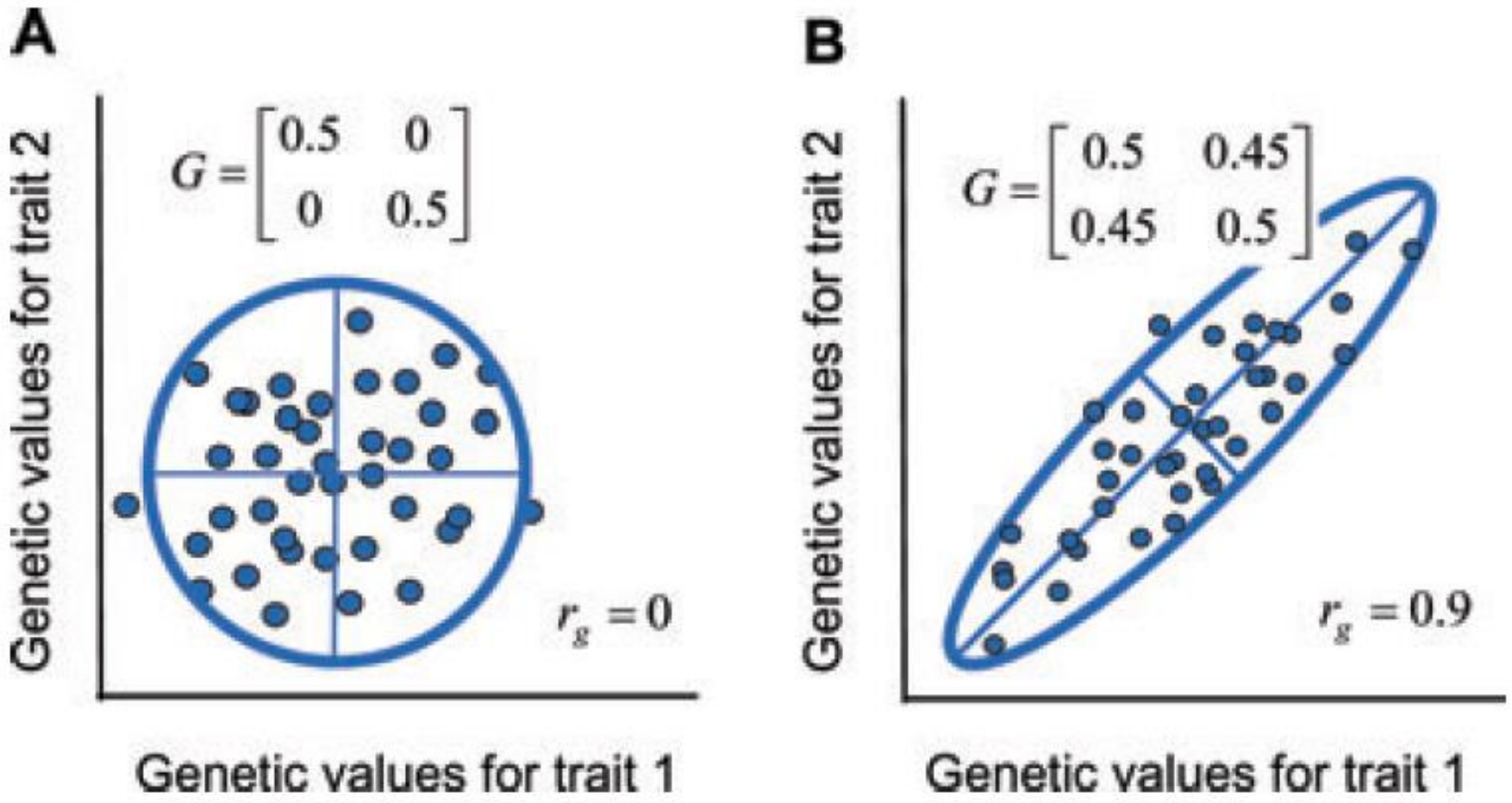
Estimating covariance P-matrix



$$\mathrm{Cov}\,(X, Y) = \frac{\sum(X_i - \bar{X})(Y_j - \bar{Y})}{n}$$

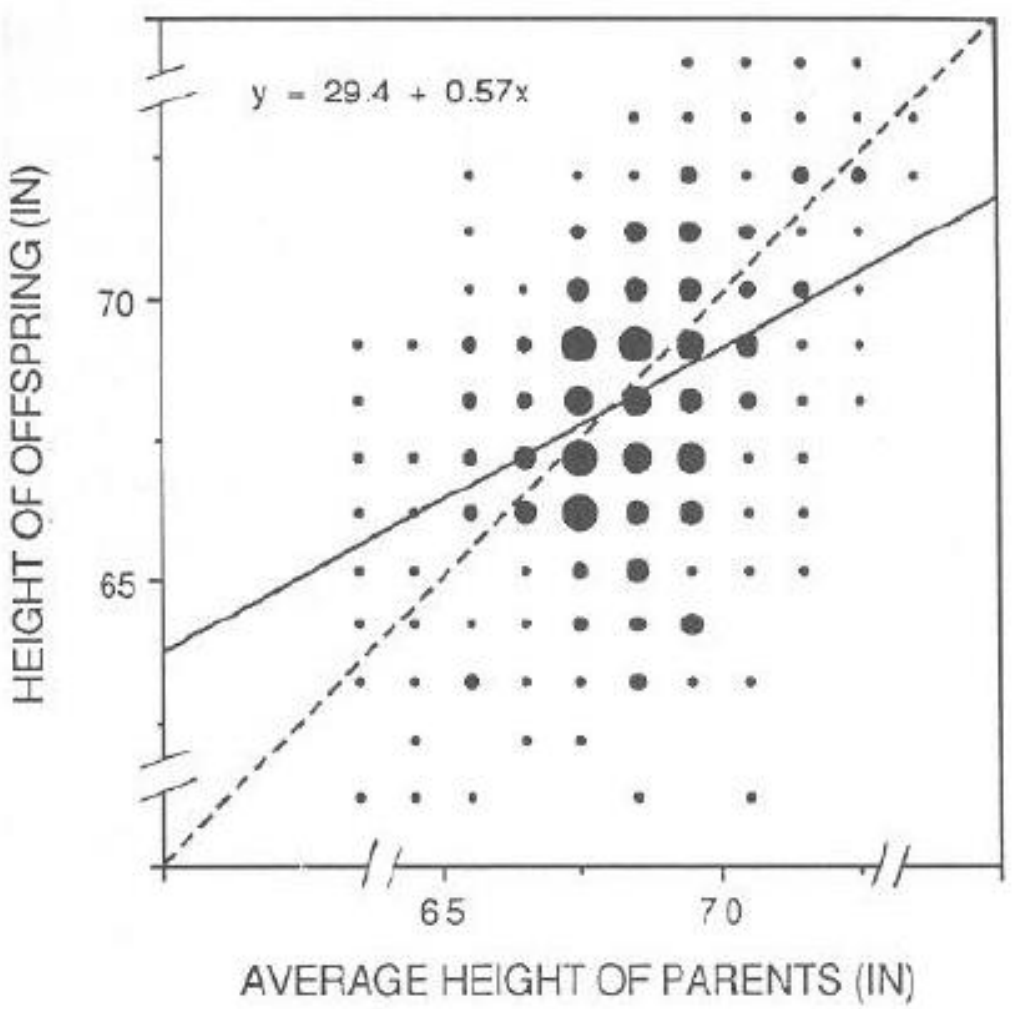


G-matrix = heritable (co)variation



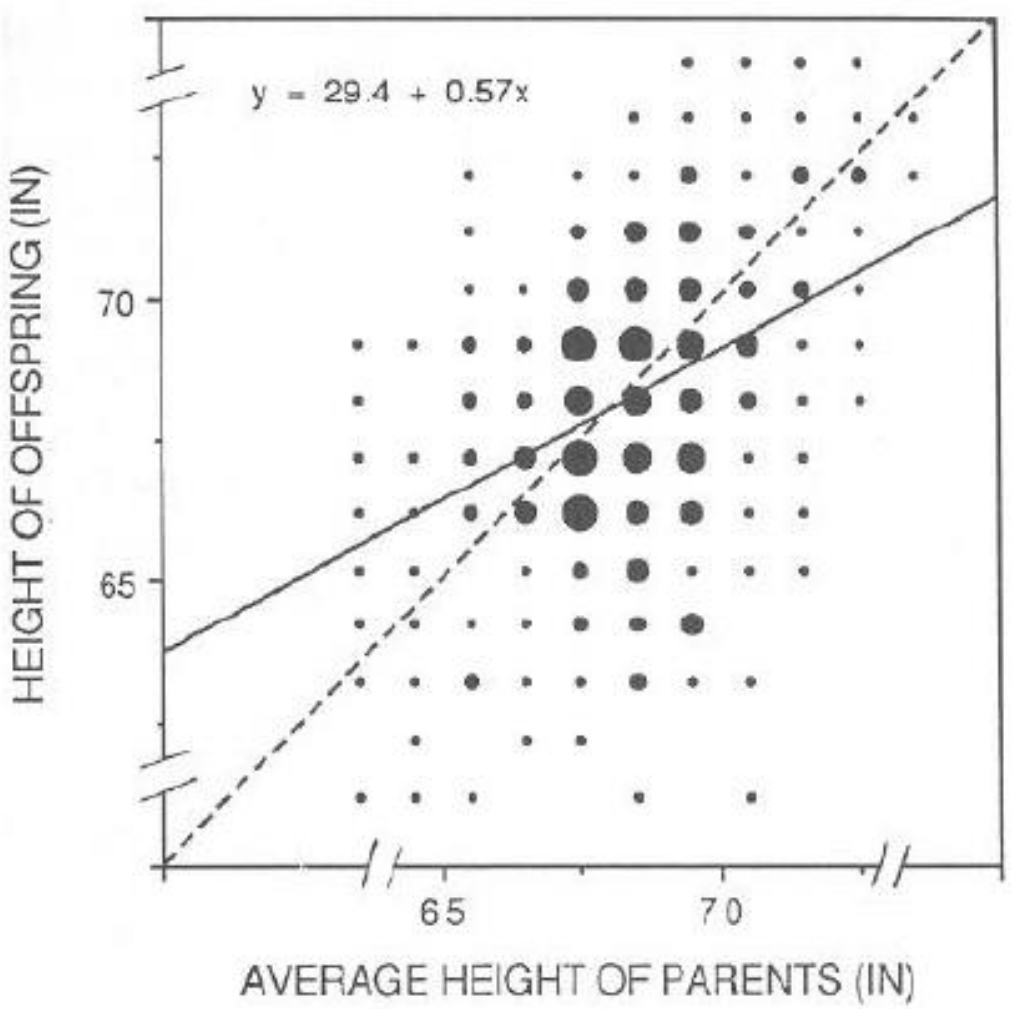
The Breeder's Equation

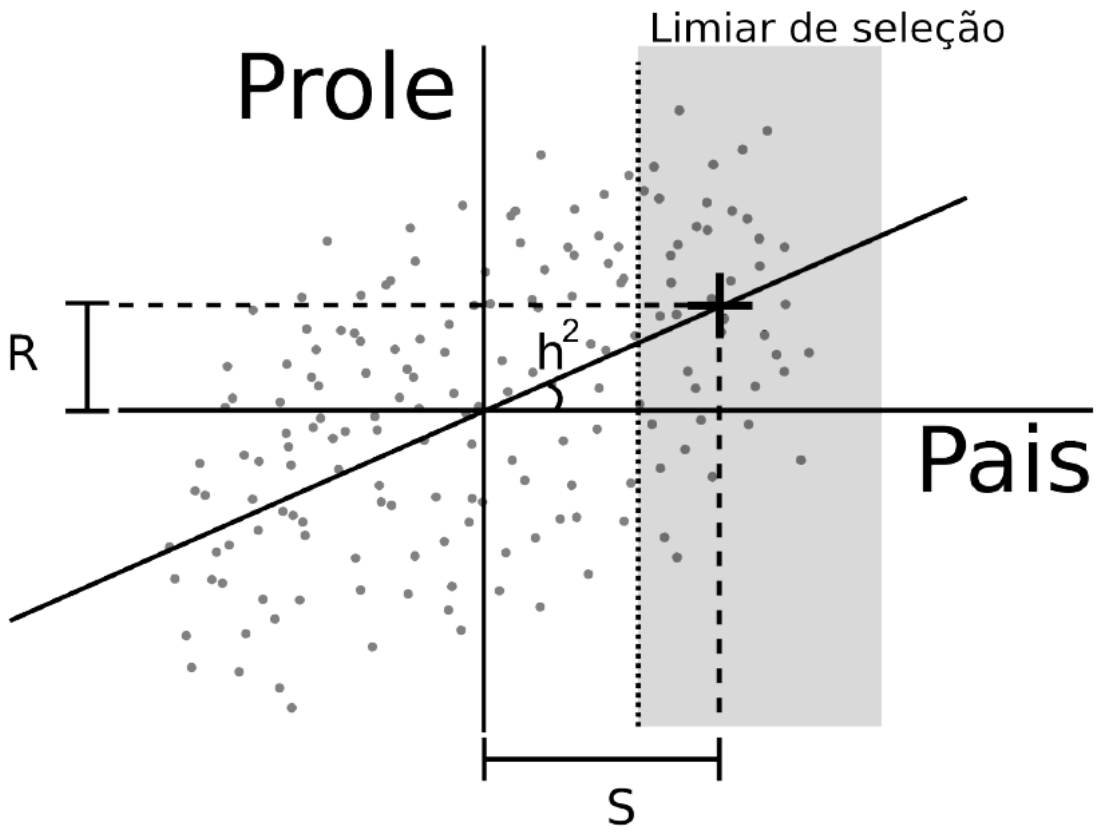
$$R = h^2 S$$

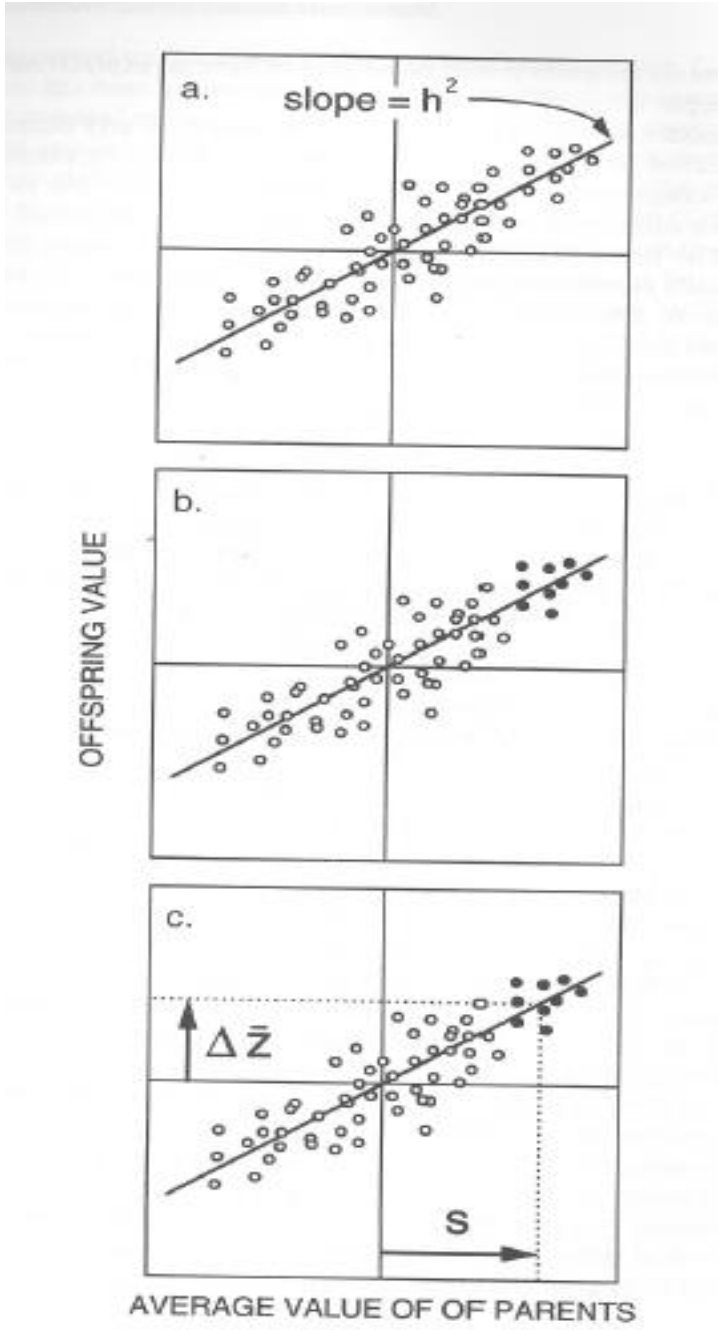


The Breeder's Equation

$$R = h^2 S$$



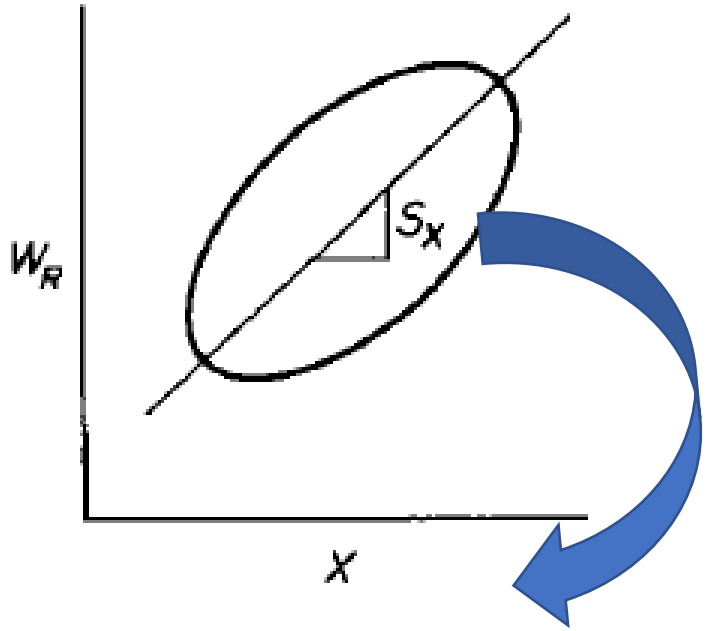




$$\Delta Z = h^2 S$$

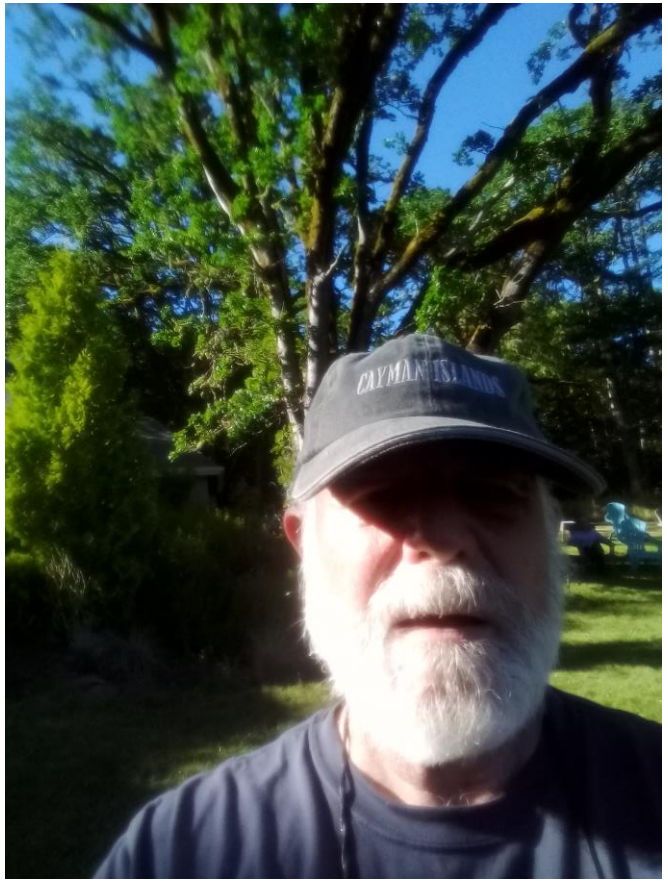
Breeder's equation

$$h^2 = V_A/V_P$$



Price equation: $S_x = \mathrm{cov}(W,x) * \mathrm{Var}(x)$

Multivariate Breeder's Equation



The Measurement of Selection on Correlated Characters
Author(s): Russell Lande and Stevan J. Arnold
Source: *Evolution*, Vol. 37, No. 6 (Nov., 1983), pp. 1210-1226

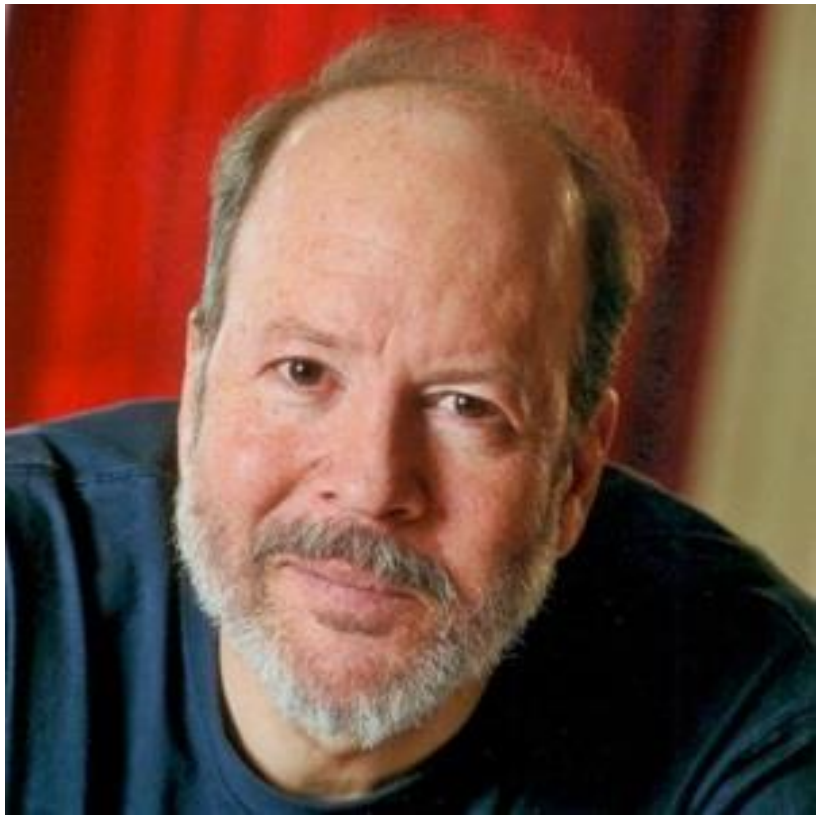
$$\nabla \ln \overline{W} = \mathbf{P}^{-1}\mathbf{S} = \mathbf{G}^{-1}\Delta \mathbf{z}$$

$$\mathbf{S} = \text{cov}(W,x) * \text{Var}(x)$$

$$\Delta \mathbf{z} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S} = \mathbf{G}\beta$$

Vector of partial regression coefficients

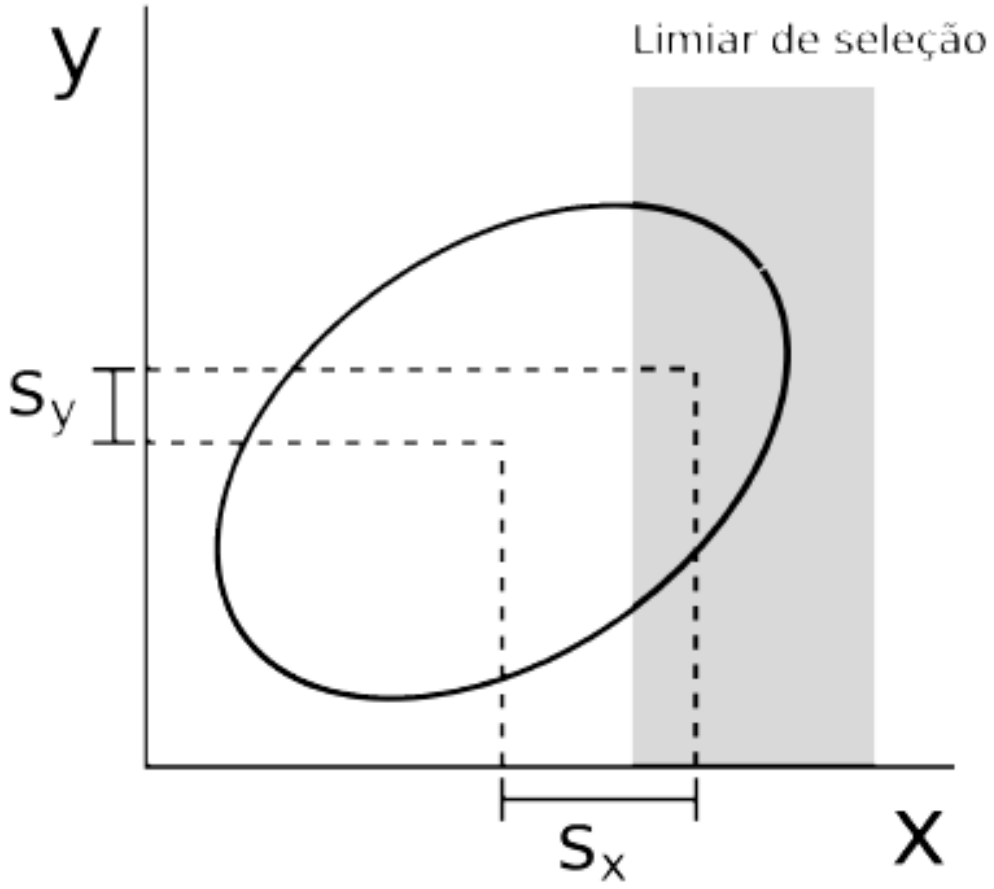
$$\Delta \mathbf{Z} = \mathbf{G}\,\beta$$



Russell Lande

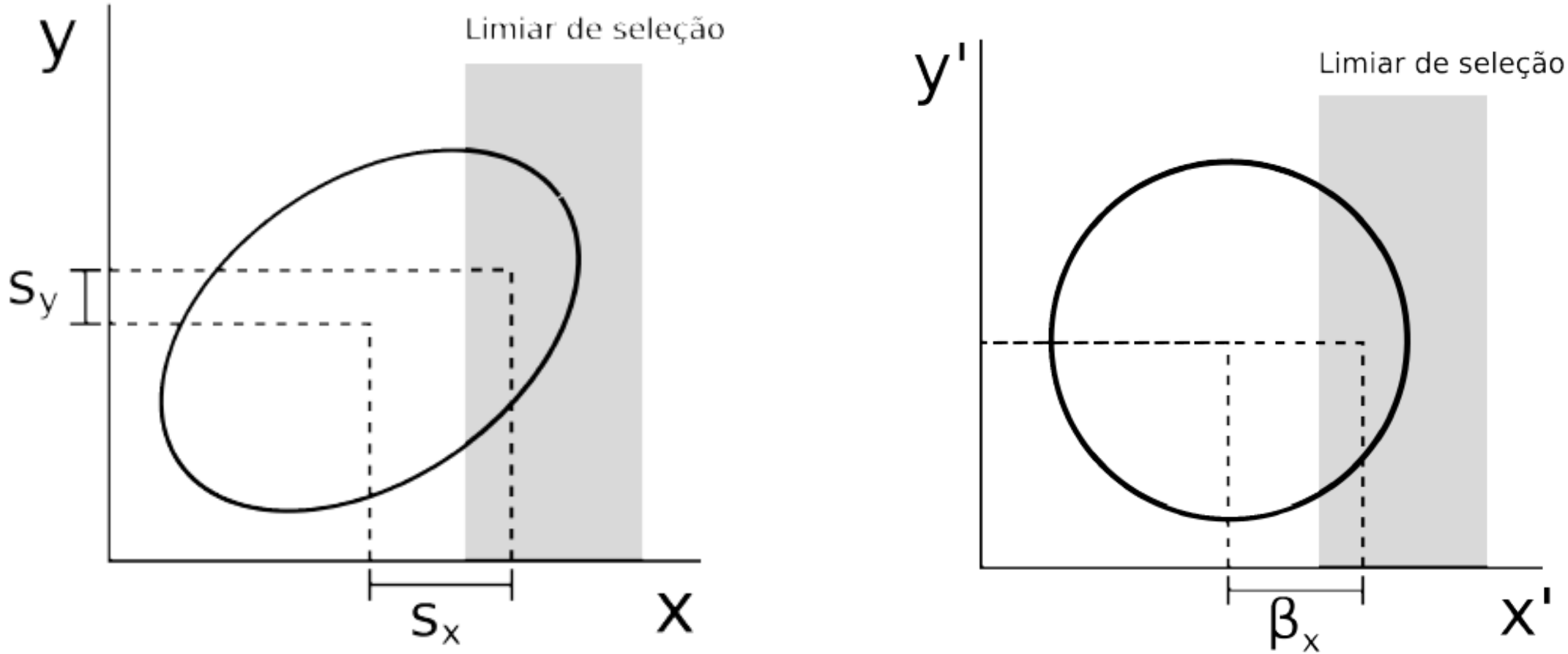
Steve Arnold

Selection differential x Selection gradient



Selection differential x Selection gradient

$$\beta = \mathbf{P}^{-1}\,\mathbf{S}$$



Indirect selection

$$\beta \equiv P^{-1}s = \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix}$$

selection gradient

$$s = P\beta = \begin{bmatrix} P_{11} & P_{12} \\ P_{12} & P_{22} \end{bmatrix}\begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} = \begin{bmatrix} P_{11}\beta_1 + P_{12}\beta_2 \\ P_{12}\beta_1 + P_{22}\beta_2 \end{bmatrix} = \begin{bmatrix} s_1 \\ s_2 \end{bmatrix}$$

selection differential

matrix multiplication!

$$s_1 = P_{11}\beta_1 + P_{12}\beta_2 + P_{13}\beta_3 + \ldots + P_{1n}\beta_n = P_{11}\beta_1 + \sum_{i=2}^{n} P_{1i}\beta_i$$

Indirect selection comes from PHENOTYPIC covariances between the trait that suffered direct selection with other traits.

Indirect response

$$\Delta Z = G \beta$$

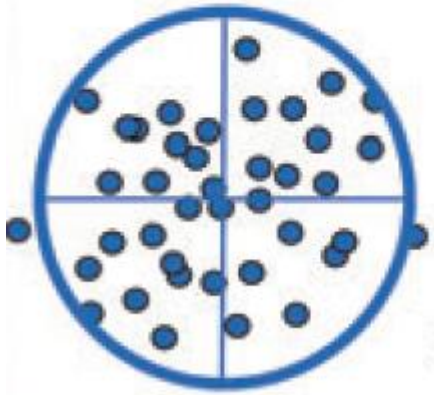
$$\begin{bmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \\ \cdot \\ \cdot \\ \cdot \\ \Delta\bar{z}_p \end{bmatrix} = \begin{bmatrix} G_{11} & G_{12} & \cdots & G_{1p} \\ G_{21} & G_{22} & \cdots & G_{2p} \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ G_{p1} & G_{p2} & \cdots & G_{pp} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \cdot \\ \cdot \\ \cdot \\ \beta_p \end{bmatrix}$$

$$\Delta Z_1 = G_{11}\beta_1 + G_{12}\beta_2 + \ldots + G_{pp}\beta_p$$

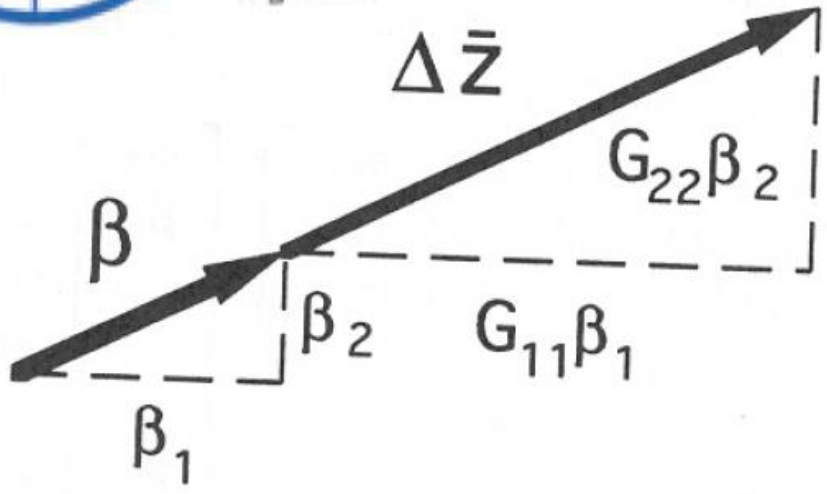
Indirect response comes from GENETIC covariances between the trait that suffered direct selection with other traits.

Indirect response to selection

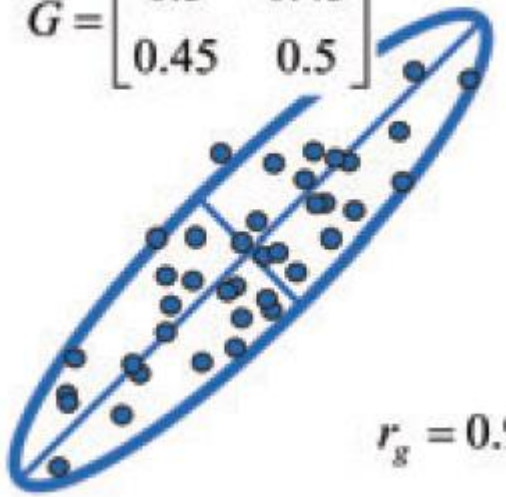
$$G = \begin{bmatrix} 0.5 & 0 \\ 0 & 0.5 \end{bmatrix}$$



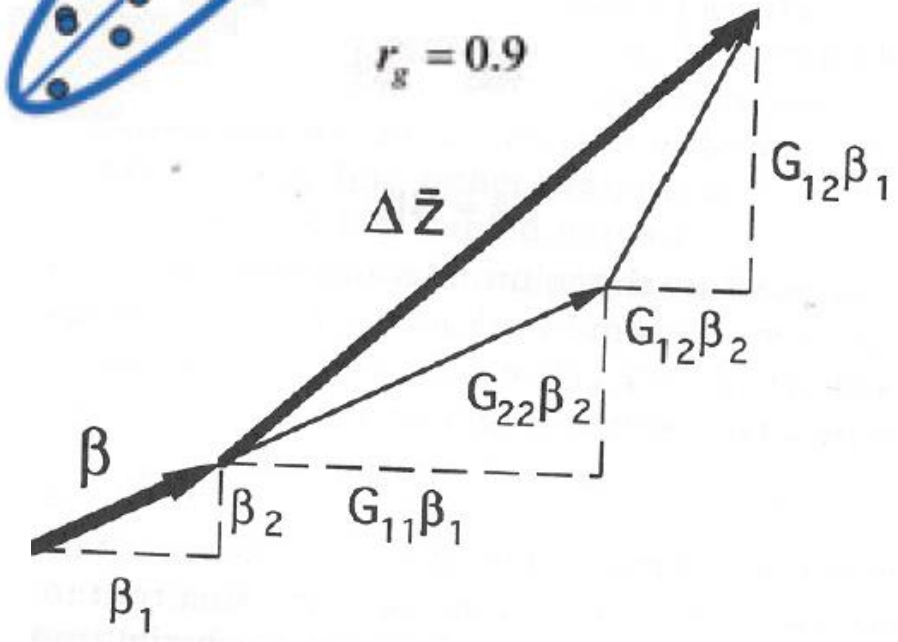
$r_g = 0$



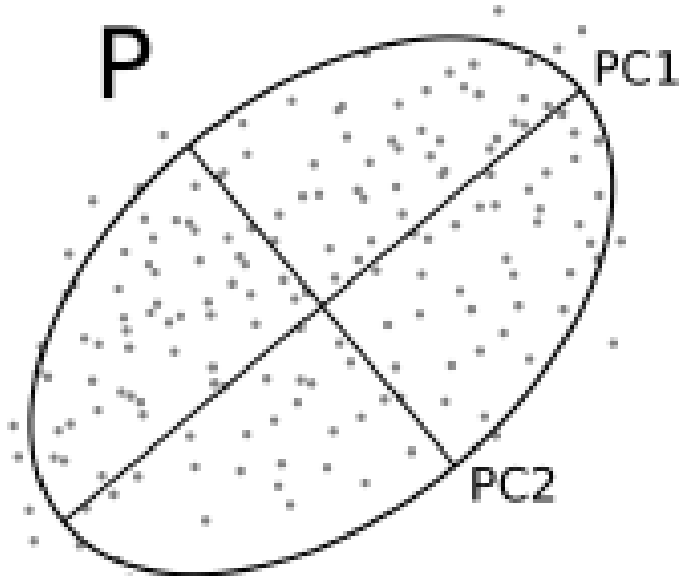
$$G = \begin{bmatrix} 0.5 & 0.45 \\ 0.45 & 0.5 \end{bmatrix}$$

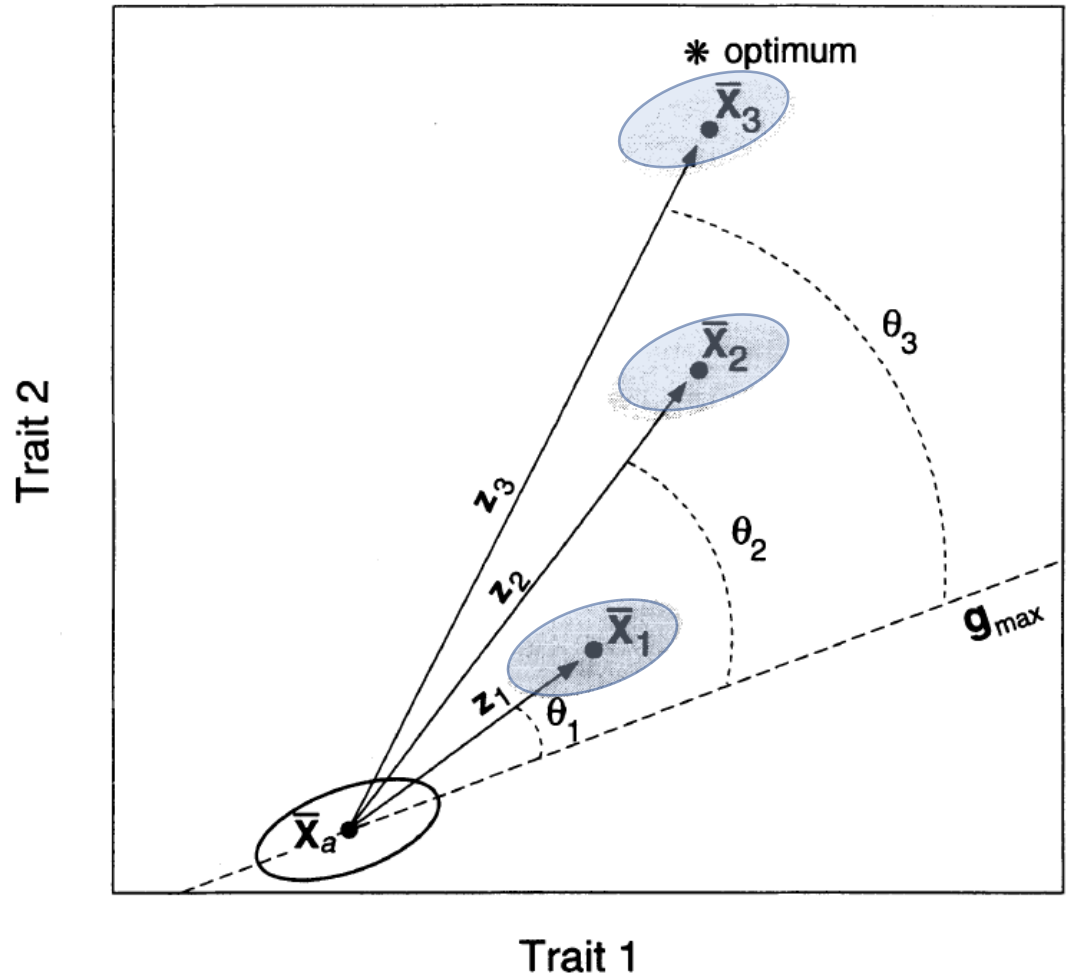


$r_g = 0.9$

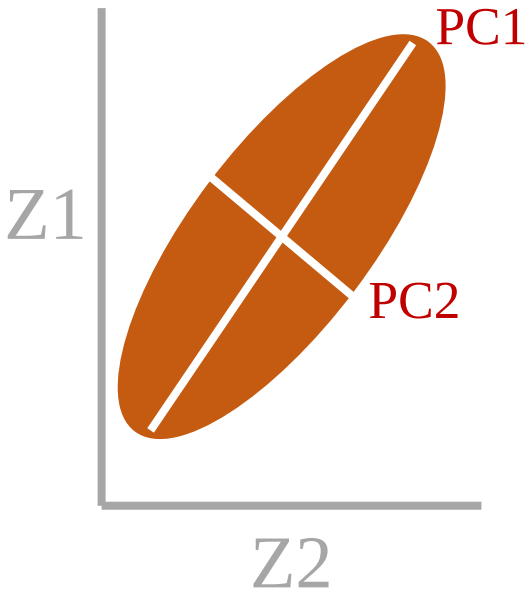


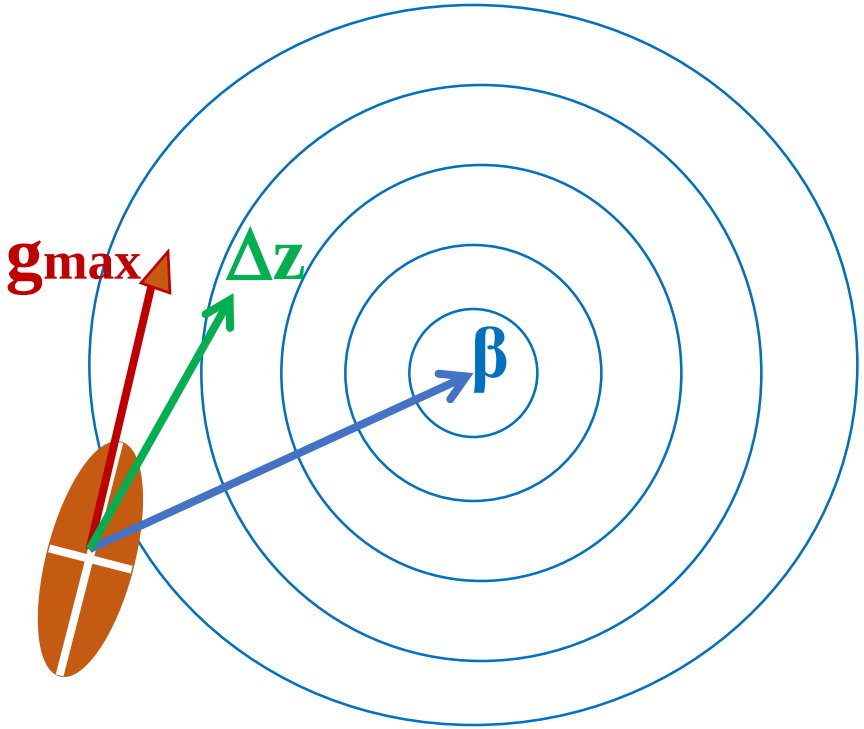
Adaptive Radiation Along Genetic Lines of Least Resistance
Author(s): Dolph Schluter
Source: *Evolution*, Vol. 50, No. 5 (Oct., 1996), pp. 1766-1774

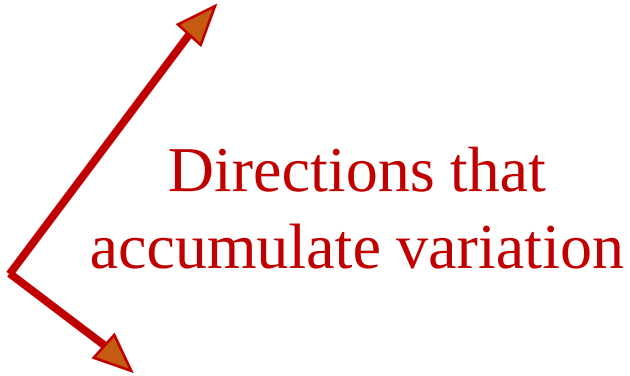




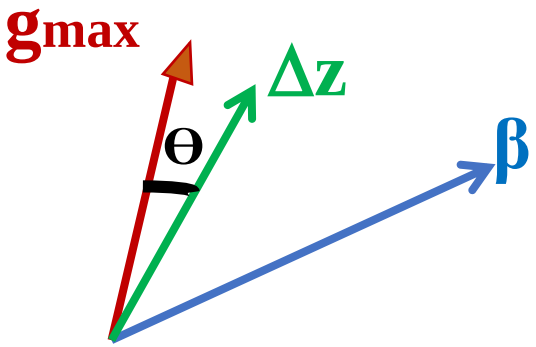
Genetic Constraint





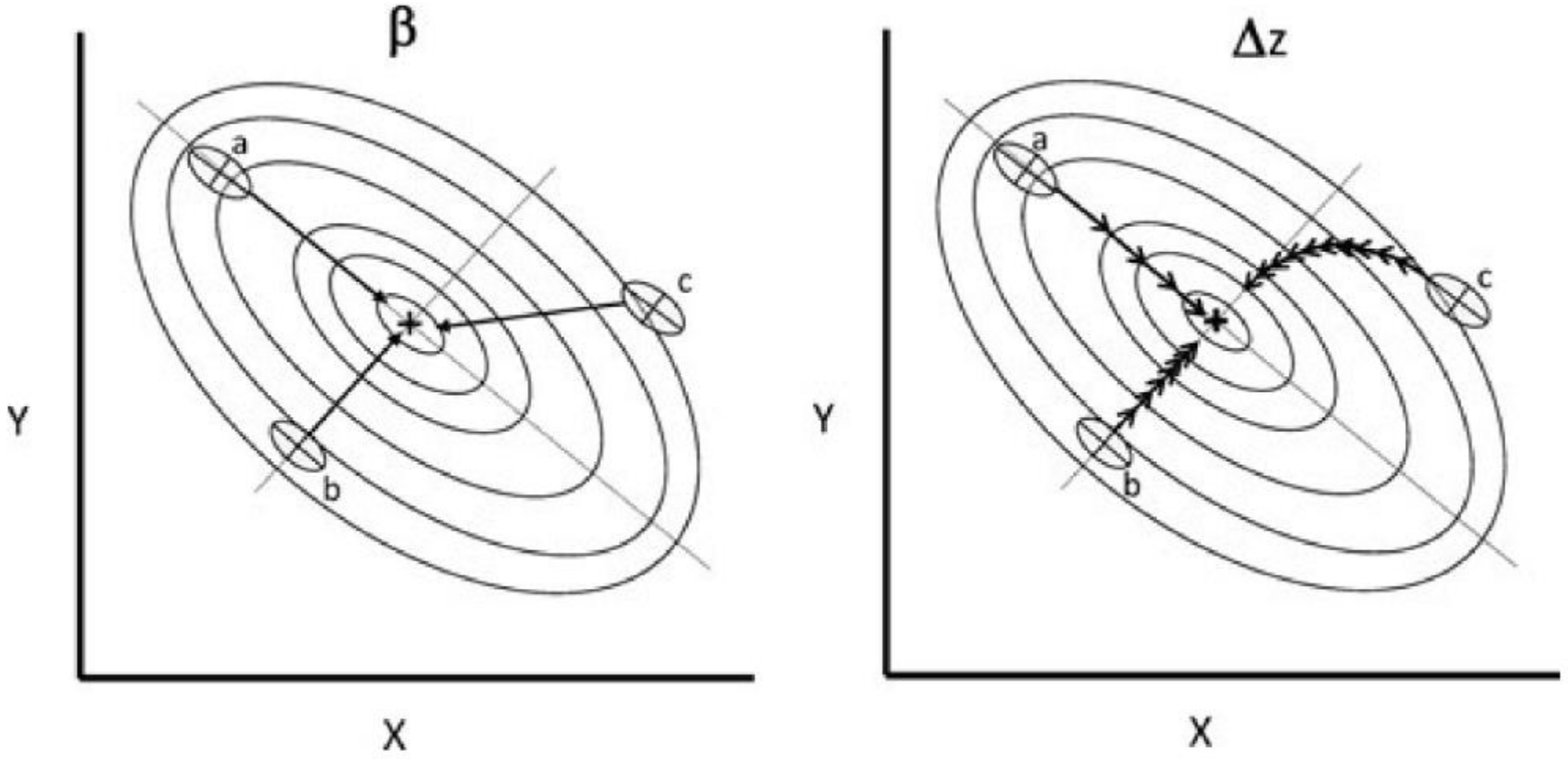


Directions that accumulate variation



Schluter 1996; Walsh and Blows 2009; Futuyma 2010

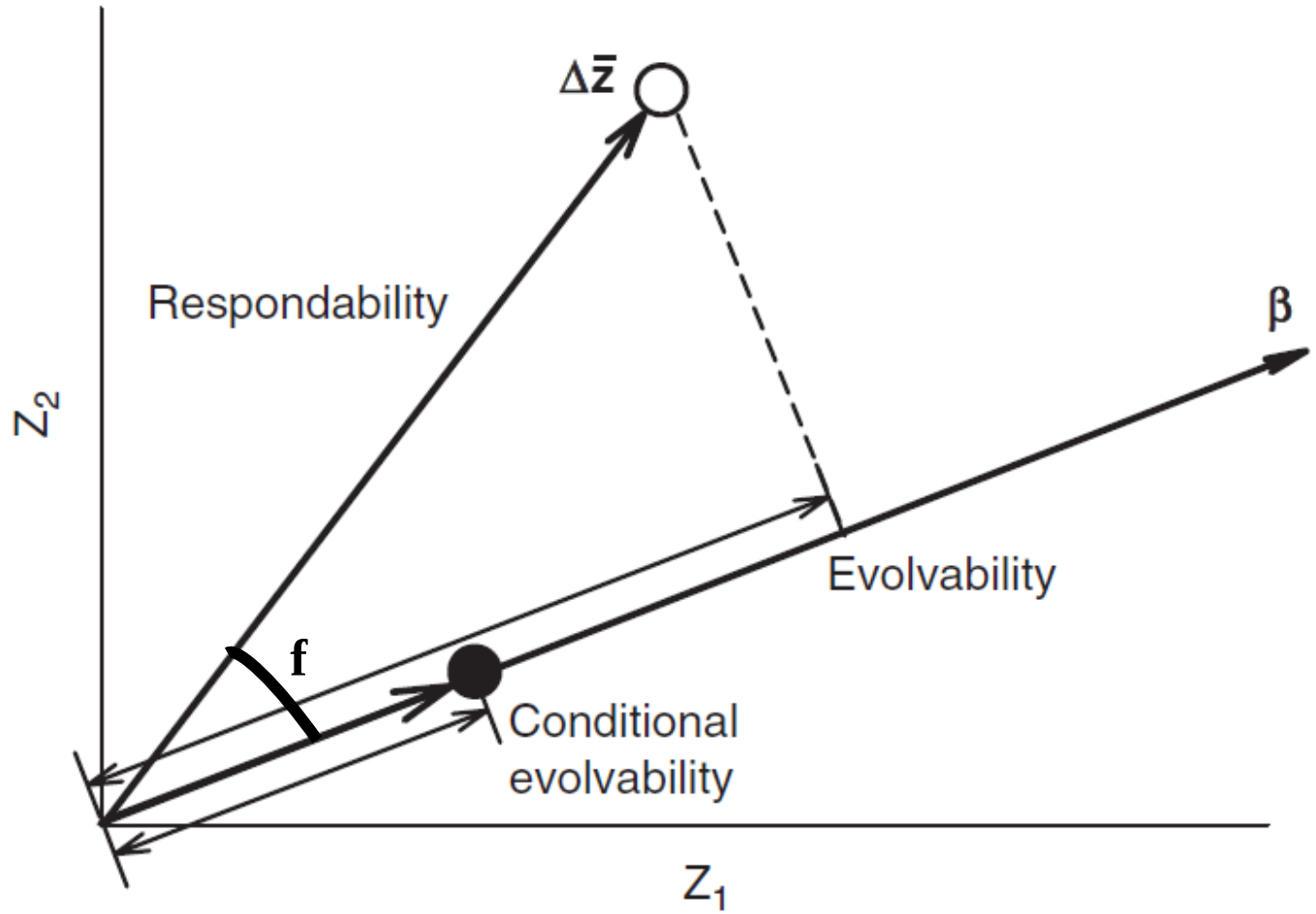
Genetic Constraint: interaction between G and selection



Measuring and comparing evolvability and constraint in multivariate characters

T. F. HANSEN*† & D. HOULE†

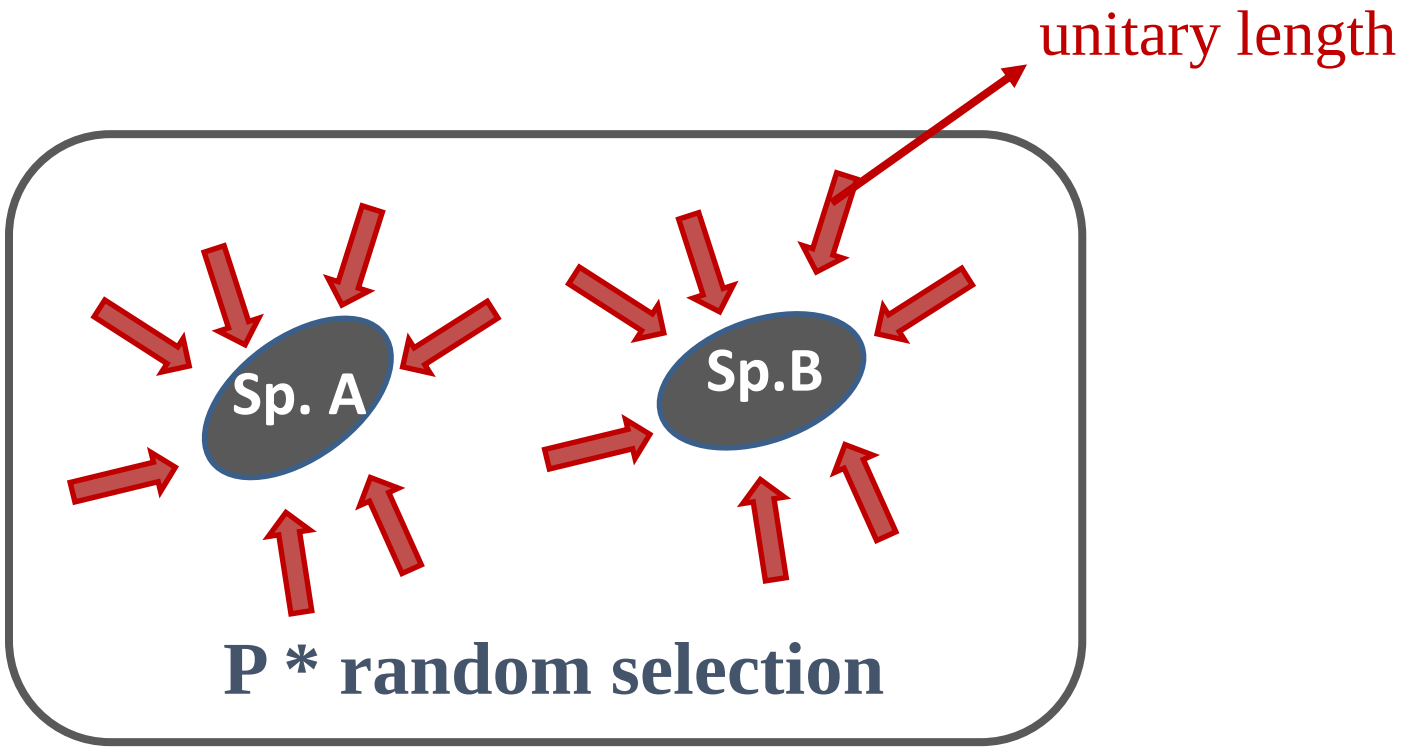
$$e(\boldsymbol{\beta}) \equiv \frac{\boldsymbol{\beta}' \mathbf{G} \boldsymbol{\beta}}{|\boldsymbol{\beta}|^2}$$



What if I don’t know the direction of selection??

Random selection and mean evolvability

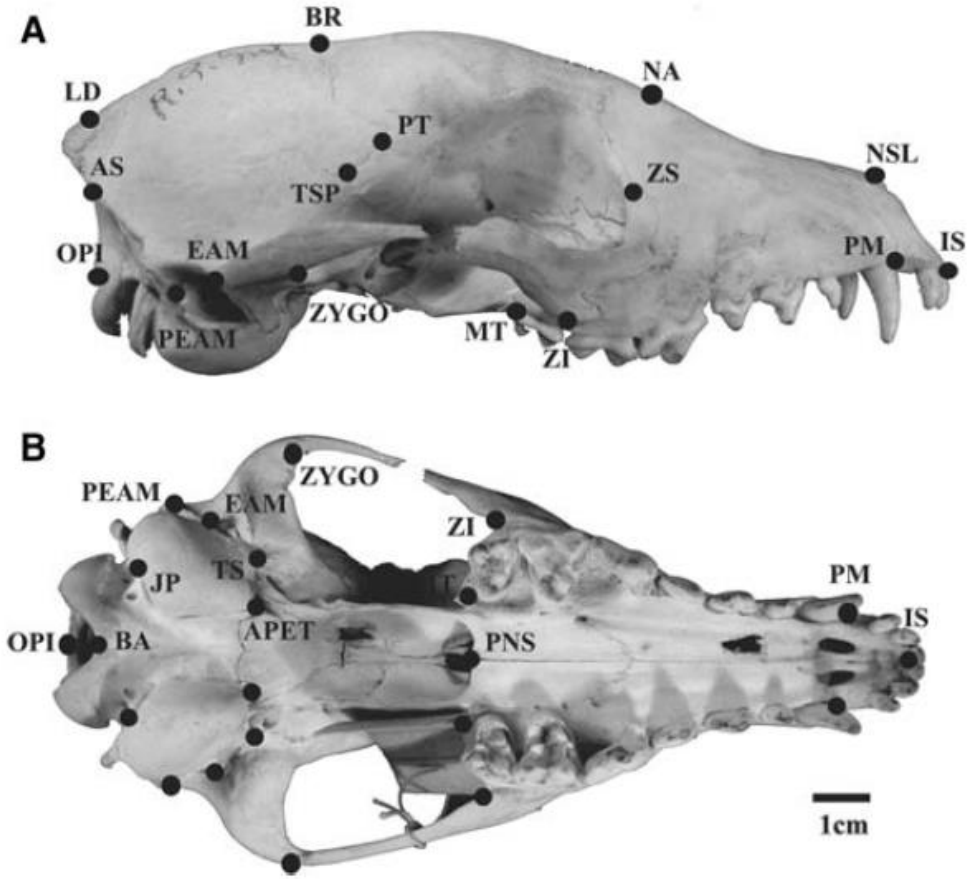
$$\text{mean}(\beta'_i P \beta_i)$$

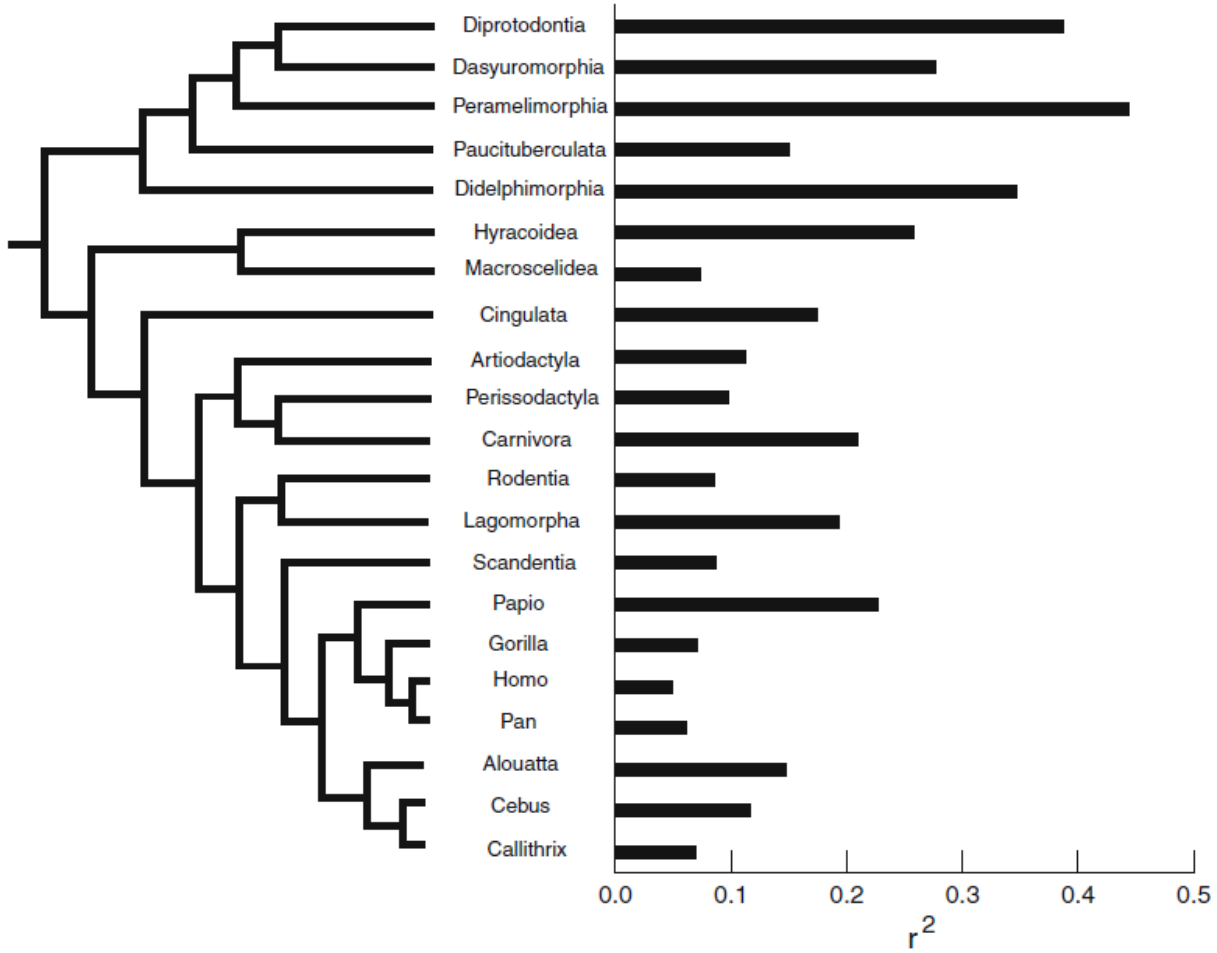


The Evolution of Modularity in the Mammalian Skull I: Morphological Integration Patterns and Magnitudes

Arthur Porto · Felipe B. de Oliveira · Leila T. Shirai · Valderes De Conto · Gabriel Marroig

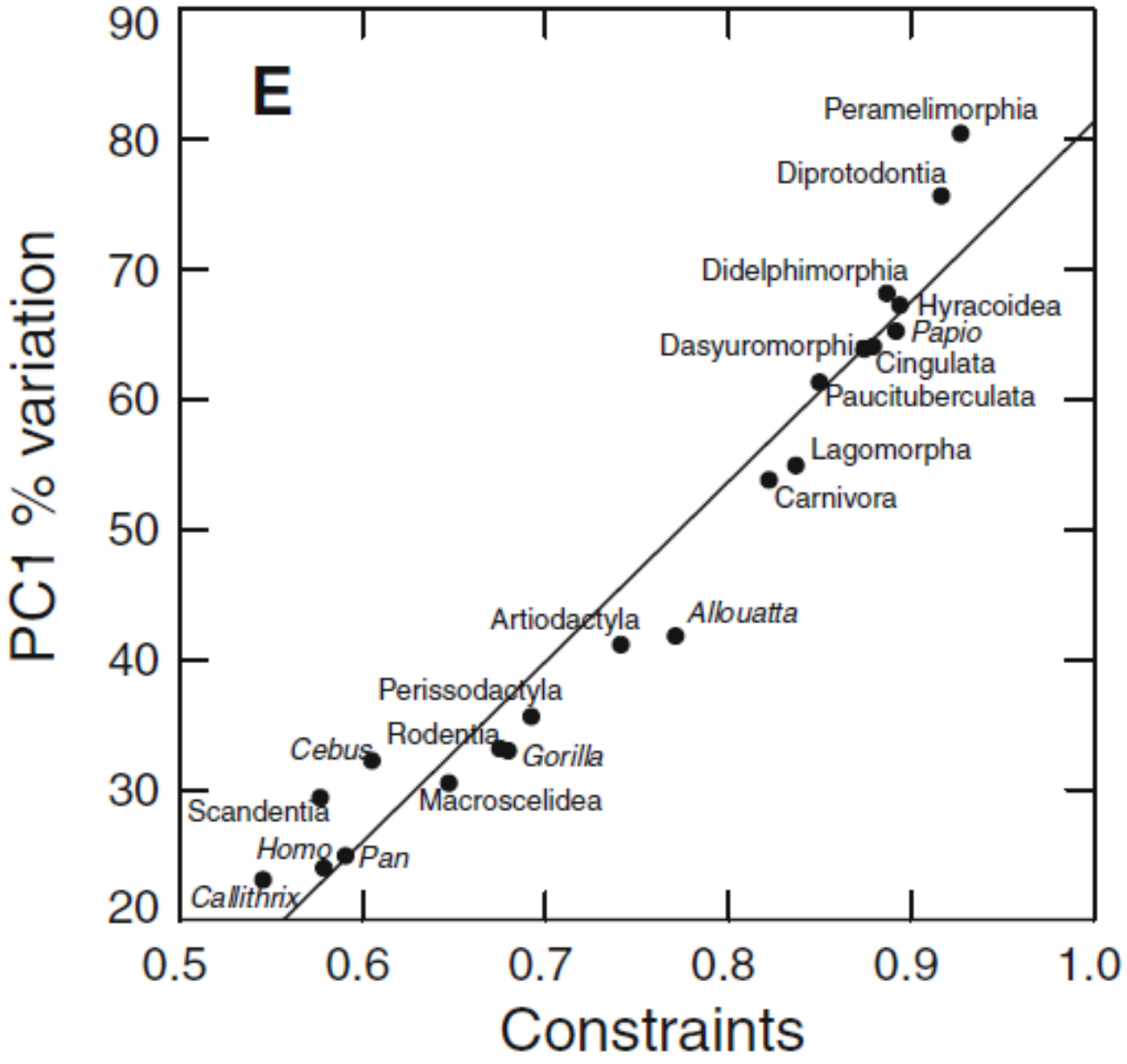
Similar pattern but divergent magnitudes of integrations

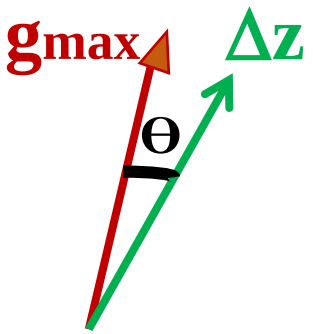


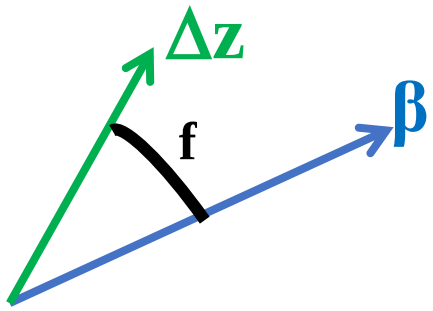


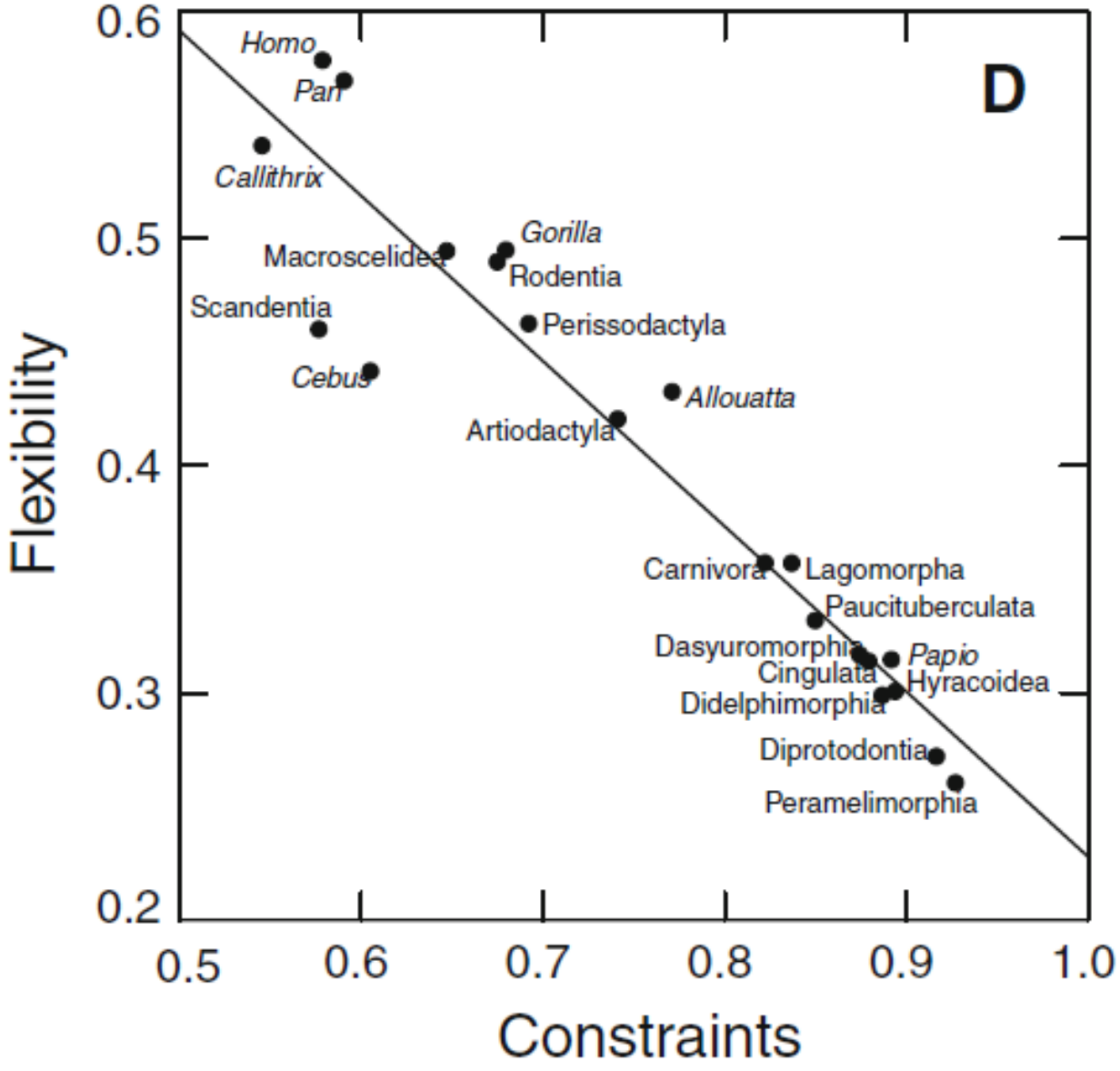
The Evolution of Modularity in the Mammalian Skull II: Evolutionary Consequences

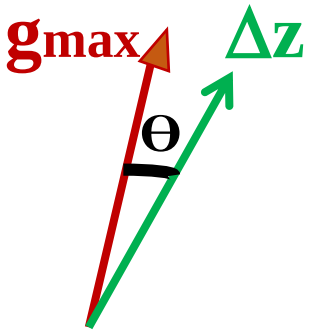
Gabriel Marroig · Leila T. Shirai · Arthur Porto · Felipe B. de Oliveira · Valderes De Conto

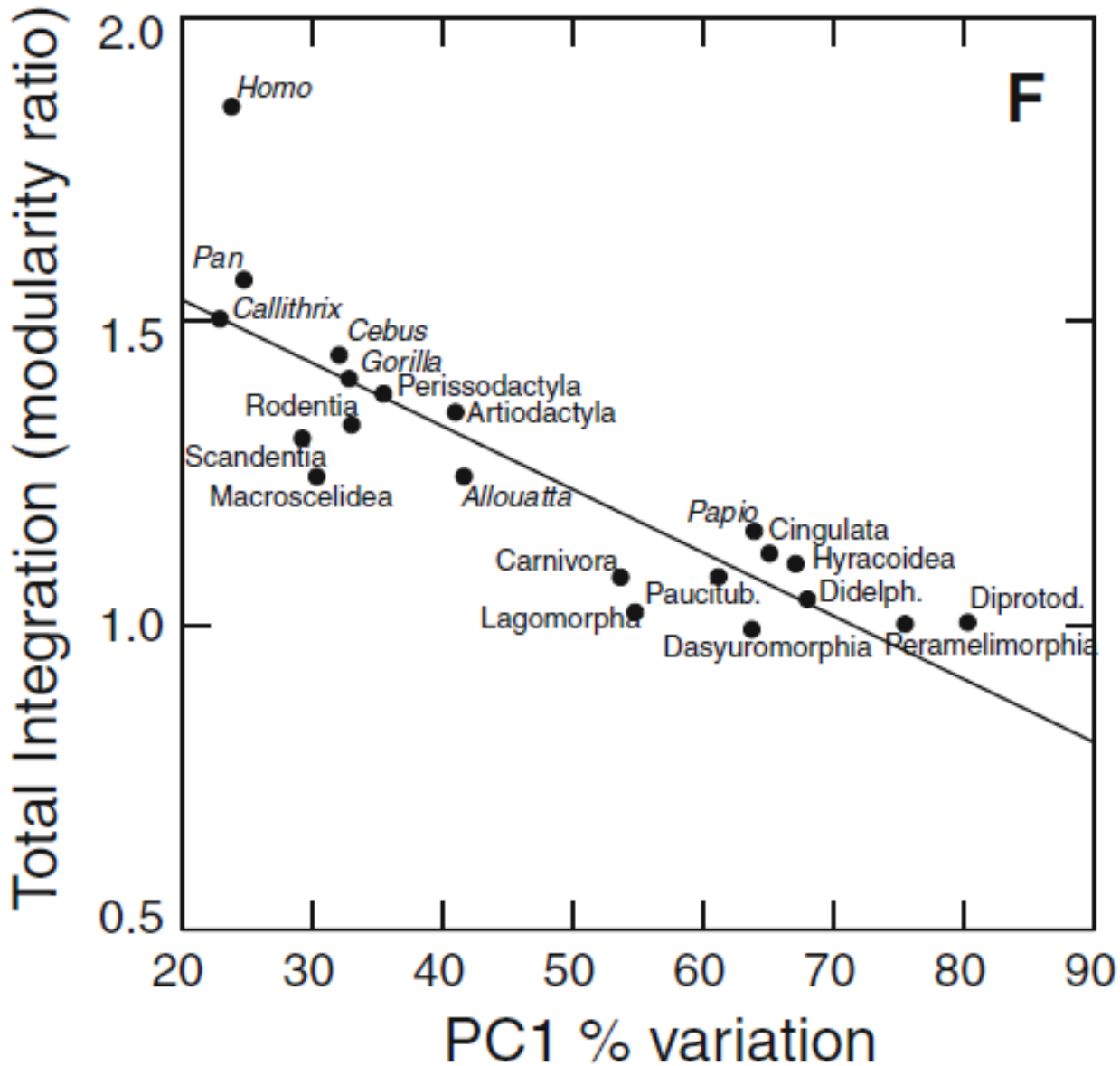

E
PC1 % variation
Constraints
90
80
70
60
50
40
30
20
0.5
0.6
0.7
0.8
0.9
1.0
Peramelimorphia
Diprotodontia
Didelphimorphia
Hyracoidea
Papio
Dasyuromorphi
Cingulata
Paucituberculata
Lagomorpha
Carnivora
Artiodactyla
Allouatta
Perissodactyla
Rodentia
Cebus
Gorilla
Macroscelidea
Scandentia
Homo
Pan
Callithrix

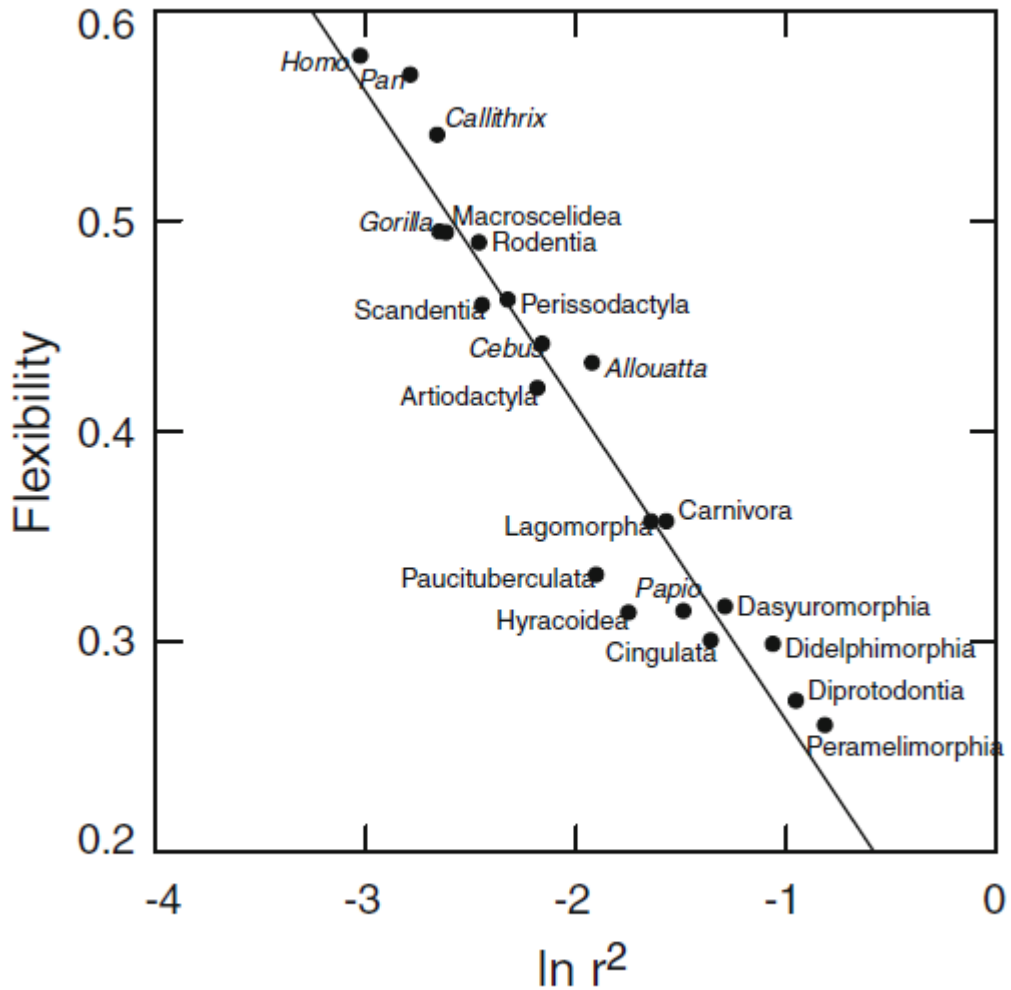

gmax
Δz
θ

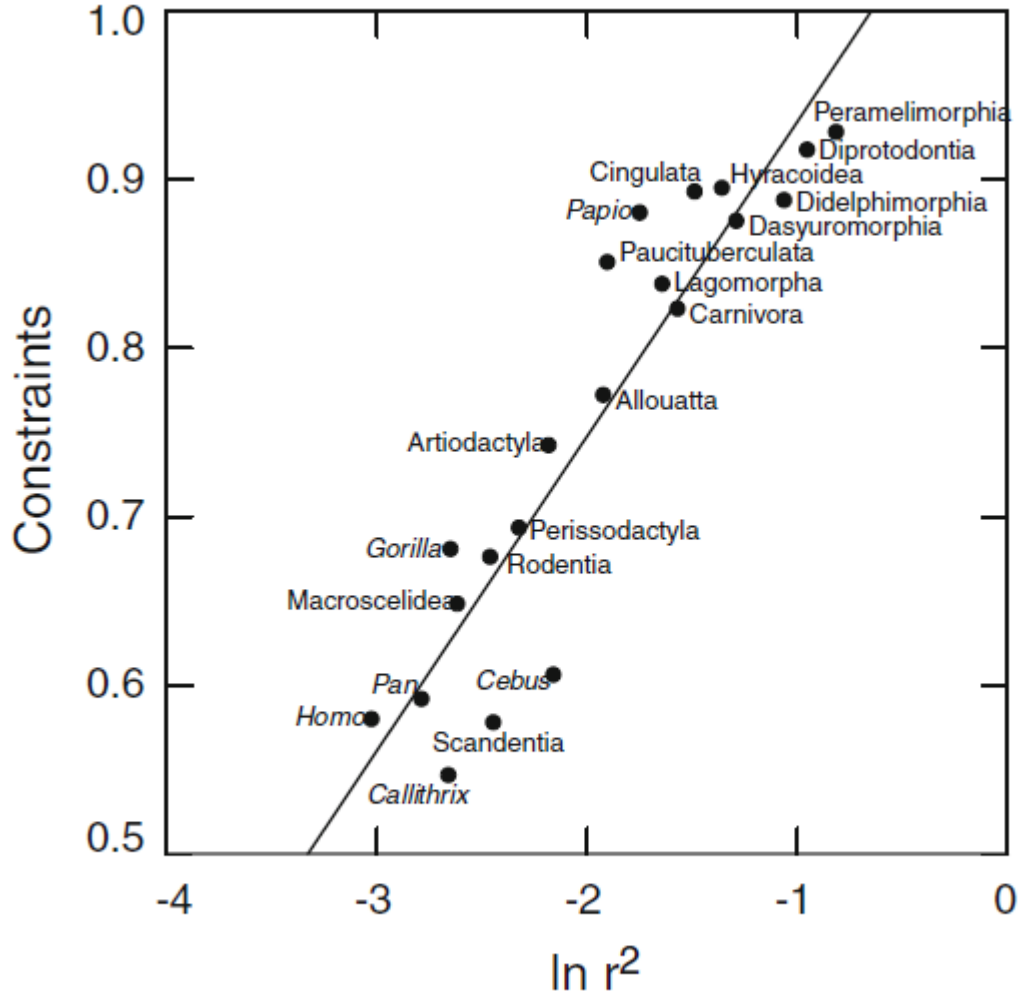

Δz
β
f


D
Flexibility
Constraints
0.6
0.5
0.4
0.3
0.2
0.5
0.6
0.7
0.8
0.9
1.0
Homo
Pan
Callithrix
Gorilla
Macroscelidea
Rodentia
Scandentia
Perissodactyla
Cebus
Allouatta
Artiodactyla
Carnivora
Lagomorpha
Paucituberculata
Dasyuromorphia
Papio
Cingulata
Hyracoidea
Didelphimorphia
Diprotodontia
Peramelimorphia


gmax
Δz
θ


F
Total Integration (modularity ratio)
2.0
1.5
1.0
0.5
20
30
40
50
60
70
80
90
PC1 % variation
Homo
Pan
Callithrix
Cebus
Gorilla
Perissodactyla
Artiodactyla
Rodentia
Scandentia
Macroscelidea
Allouatta
Papio
Cingulata
Hyracoidea
Carnivora
Paucitub.
Didelph.
Diprotod.
Lagomorpha
Dasyuromorphia
Peramelimorphia

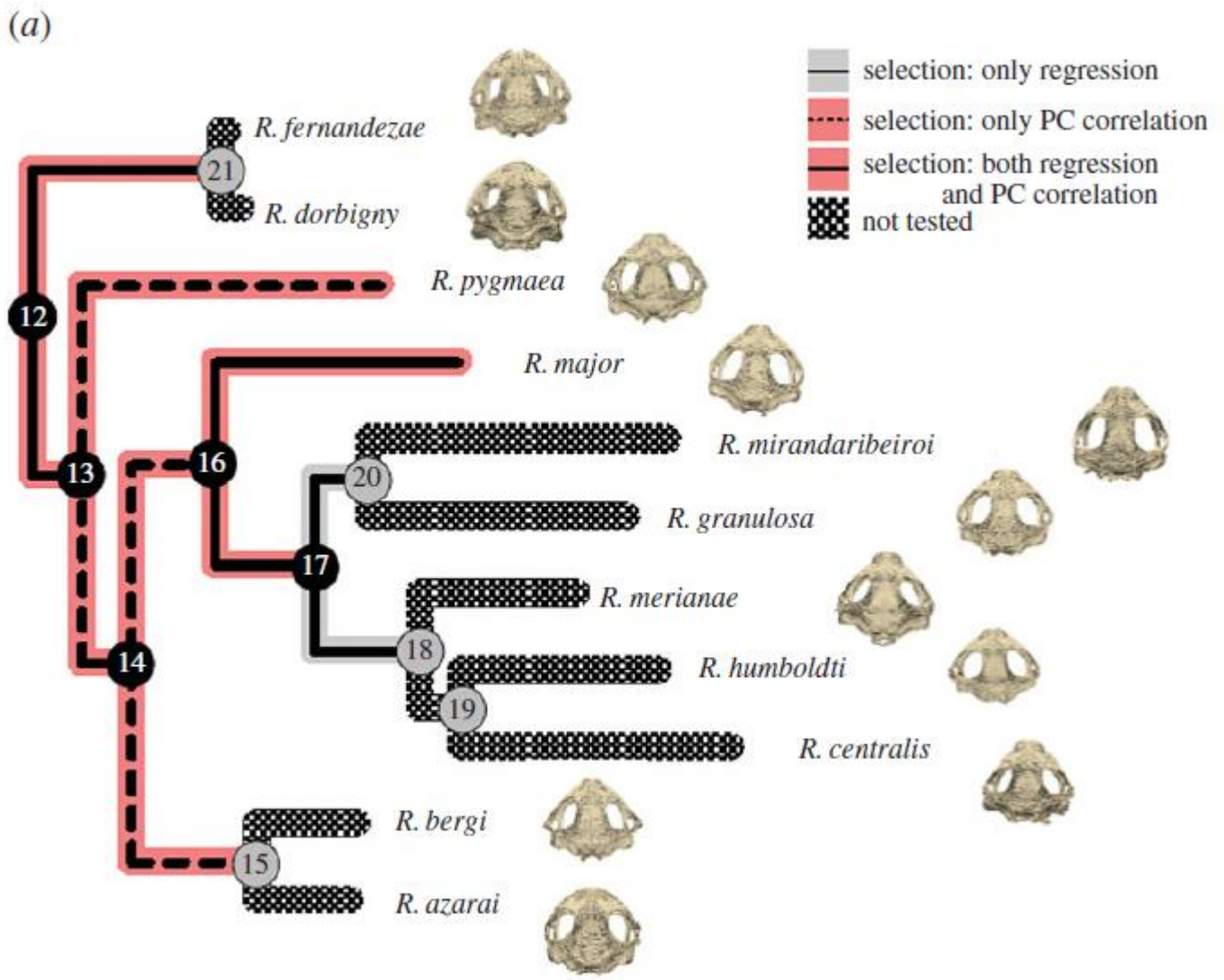

Flexibility
0.6
0.5
0.4
0.3
0.2
-4
-3
-2
-1
0
ln r2
Homo
Pan
Callithrix
Gorilla
Macroscelidea
Rodentia
Scandentia
Perissodactyla
Cebus
Allouatta
Artiodactyla
Lagomorpha
Carnivora
Paucituberculata
Papio
Dasyuromorphia
Hyracoidea
Didelphimorphia
Cingulata
Diprotodontia
Peramelimorphia

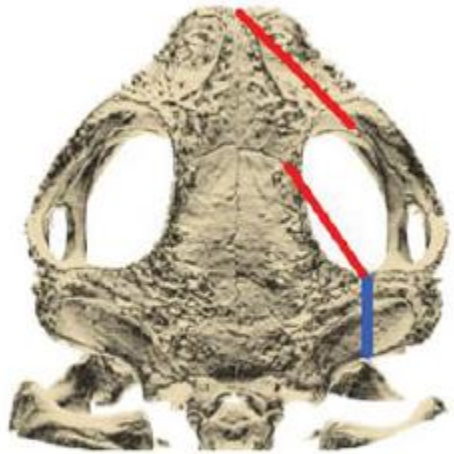

Constraints
1.0
0.9
0.8
0.7
0.6
0.5
-4
-3
-2
-1
0
ln r2
Peramelimorphia
Diprotodontia
Cingulata
Hyracoidea
Didelphimorphia
Papio
Dasyuromorphia
Paucituberculata
Lagomorpha
Carnivora
Allouatta
Artiodactyla
Perissodactyla
Gorilla
Rodentia
Macroscelidea
Pan
Cebus
Homo
Scandentia
Callithrix

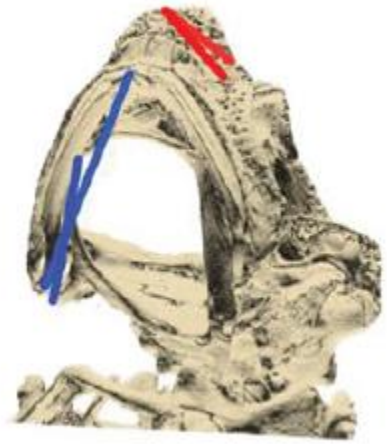
What if I know the direction of past selection??

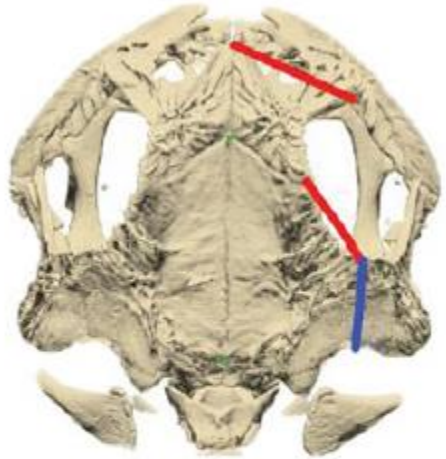
Reconstructing net-selection

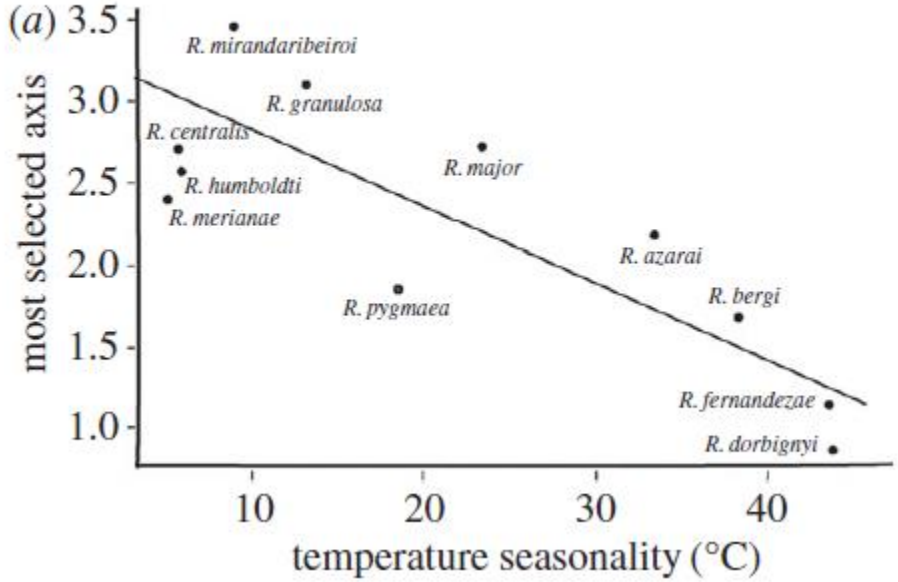
$$\boldsymbol{\beta} = \boldsymbol{W}^{-1}\boldsymbol{\Delta z}$$

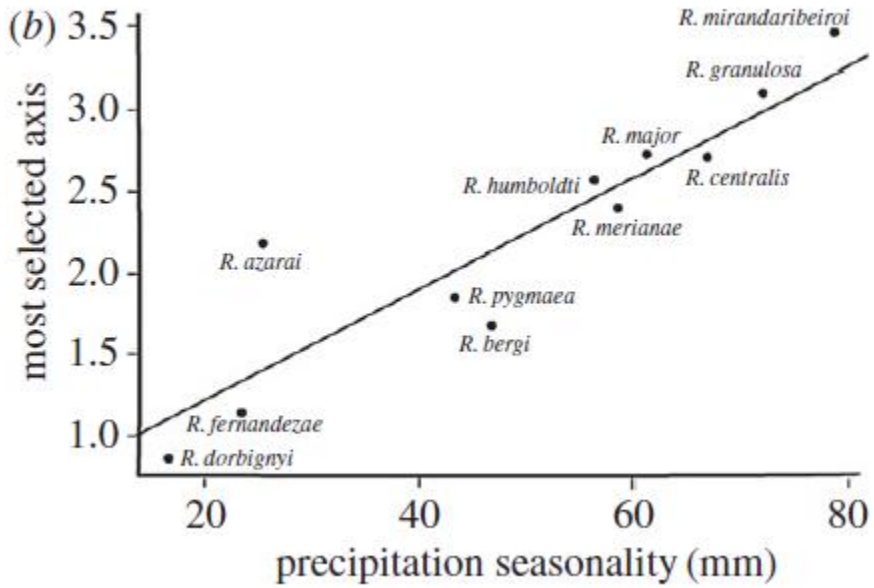






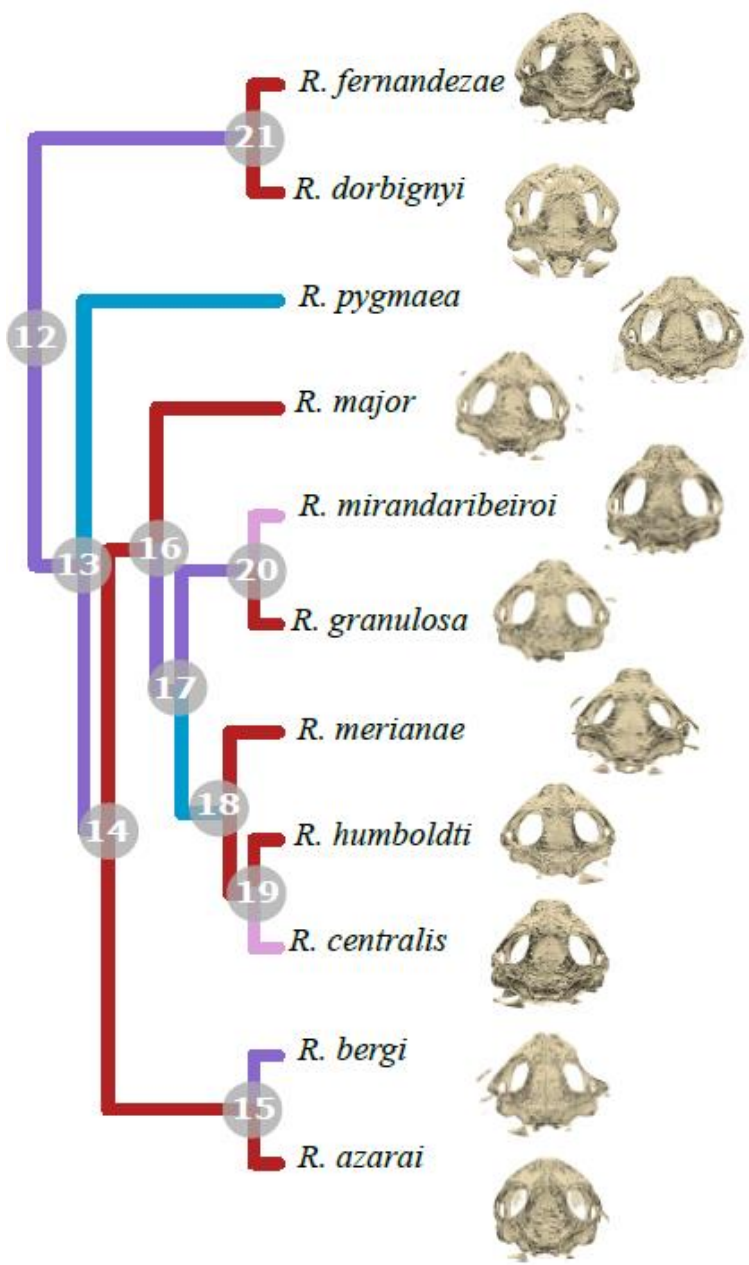


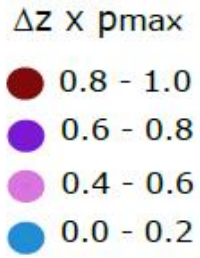

(a)
most selected axis
3.5
3.0
2.5
2.0
1.5
1.0
R. mirandaribeiroi
R. granulosa
R. centralis
R. humboldti
R. merianae
R. major
R. azarai
R. pygmaea
R. bergi
R. fernandezae
R. dorbignyi
10
20
30
40
temperature seasonality (°C)


(b)
most selected axis
3.5
3.0
2.5
2.0
1.5
1.0
R. mirandaribeiroi
R. granulosa
R. major
R. centralis
R. humboldti
R. merianae
R. azarai
R. pygmaea
R. bergi
R. fernandezae
R. dorbignyi
20
40
60
80
precipitation seasonality (mm)

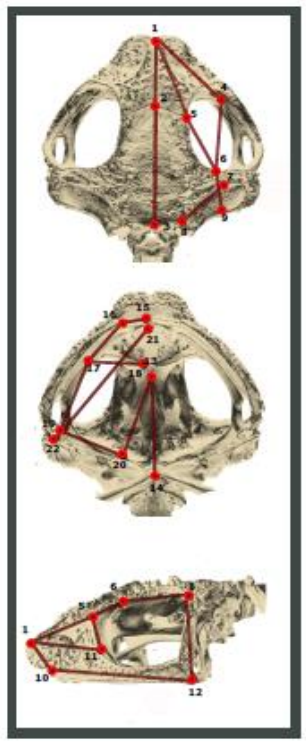
High evolutionary constraints limited adaptive responses to past climate changes in toad skulls

Monique Nouailhetas Simon, Fabio Andrade Machado and Gabriel Marroig

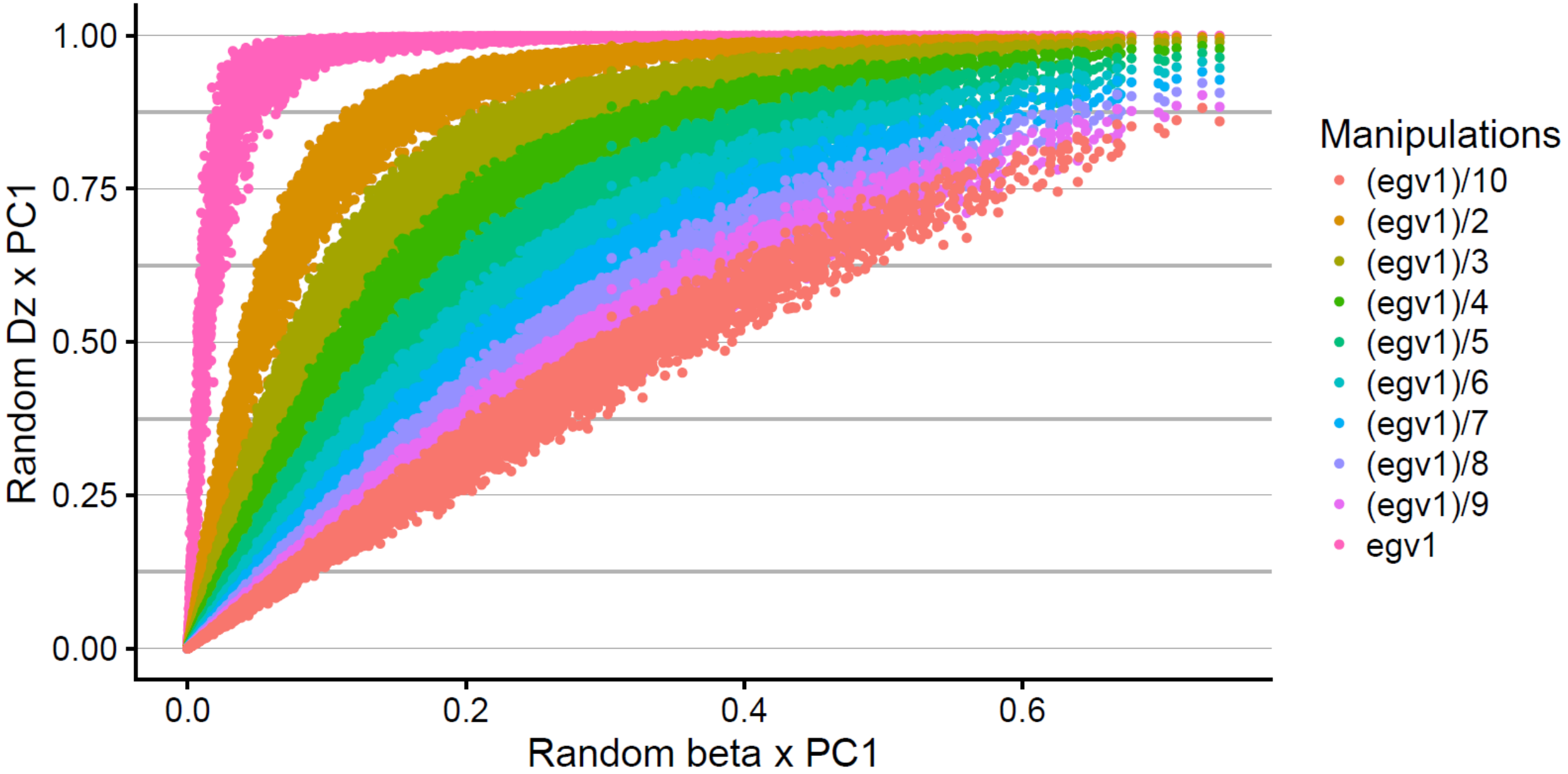




Measurements



vector correlations			
phylogeny branches	$\Delta z \times \beta$	$\Delta z \times$ PC1	PC1 $\times \beta$
1. node 19–*R. centralis*	*0.75*	*0.56*	0.03
2. node 19–*R. humboldti*	0.33	*0.99*	0.17
3. node 18–node 19	0.40	*0.95*	0.12
4. node 18–*R. merianae*	0.36	*0.97*	0.14
5. node 20–*R. granulosa*	*0.57*	*0.83*	0.03
6. node 20–*R. mirandaribeiroi*	*0.88*	0.45	0.01
7. node 17–node 18	*0.95*	0.07	0.00
8. node 17–node 20	*0.68*	*0.74*	0.03
9. node 16–node 17	*0.65*	*0.77*	0.03
10. node 16–*R. major*	0.37	*0.95*	0.07
11. node 15–*R. azarai*	*0.57*	*0.80*	0.02
12. node 15–*R. bergi*	*0.67*	*0.73*	0.02
13. node 14–node 15	0.33	*0.98*	0.13
14. node 14–node 16	0.45	*0.92*	0.05
15. node 13–node 14	*0.75*	*0.66*	0.02
16. node 13–*R. pygmaea*	*0.95*	0.14	0.00
17. node 12–node 13	*0.64*	*0.78*	0.04
18. node 12–node 21	*0.64*	*0.78*	0.04
19. node 21–*R. fernandezae*	0.34	*0.97*	0.12
20. node 21–*R. dorbignyi*	0.35	*0.96*	0.10


1.00
0.75
0.50
0.25
0.00
Random Dz x PC1
0.0
0.2
0.4
0.6
Random beta x PC1
Manipulations
(egv1)/10
(egv1)/2
(egv1)/3
(egv1)/4
(egv1)/5
(egv1)/6
(egv1)/7
(egv1)/8
(egv1)/9
egv1

Take-home messages

- The organization of variation, seen in G and P-matrices, interacts with the selection vector;
- Indirect selection occurs because of phenotypic covariances among traits;
- Indirect response occurs because of genetic covariances among traits;
- The higher the magnitude of integration, the higher is the probability of high constraint (depending on the direction of selection).

THE END!