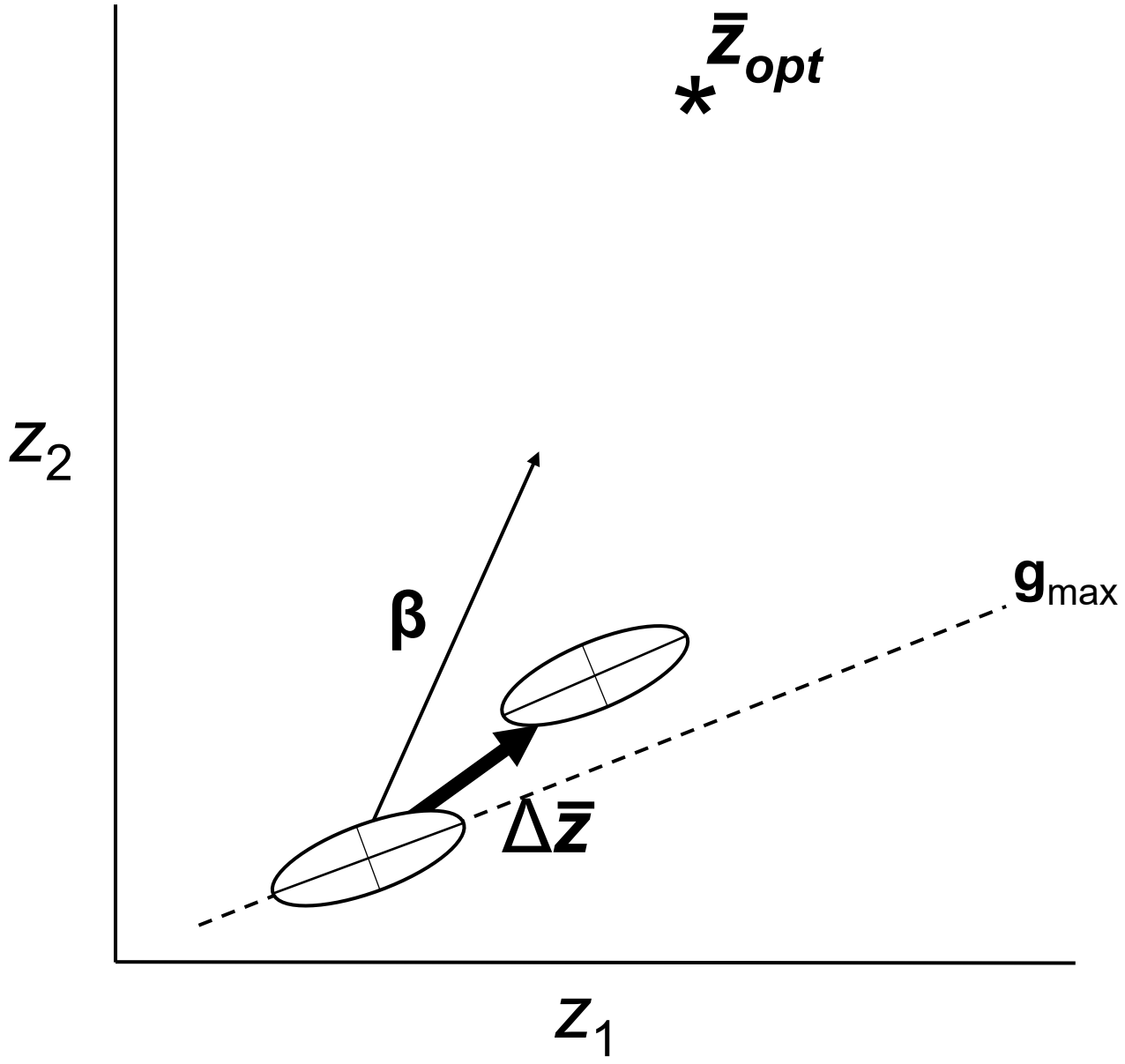
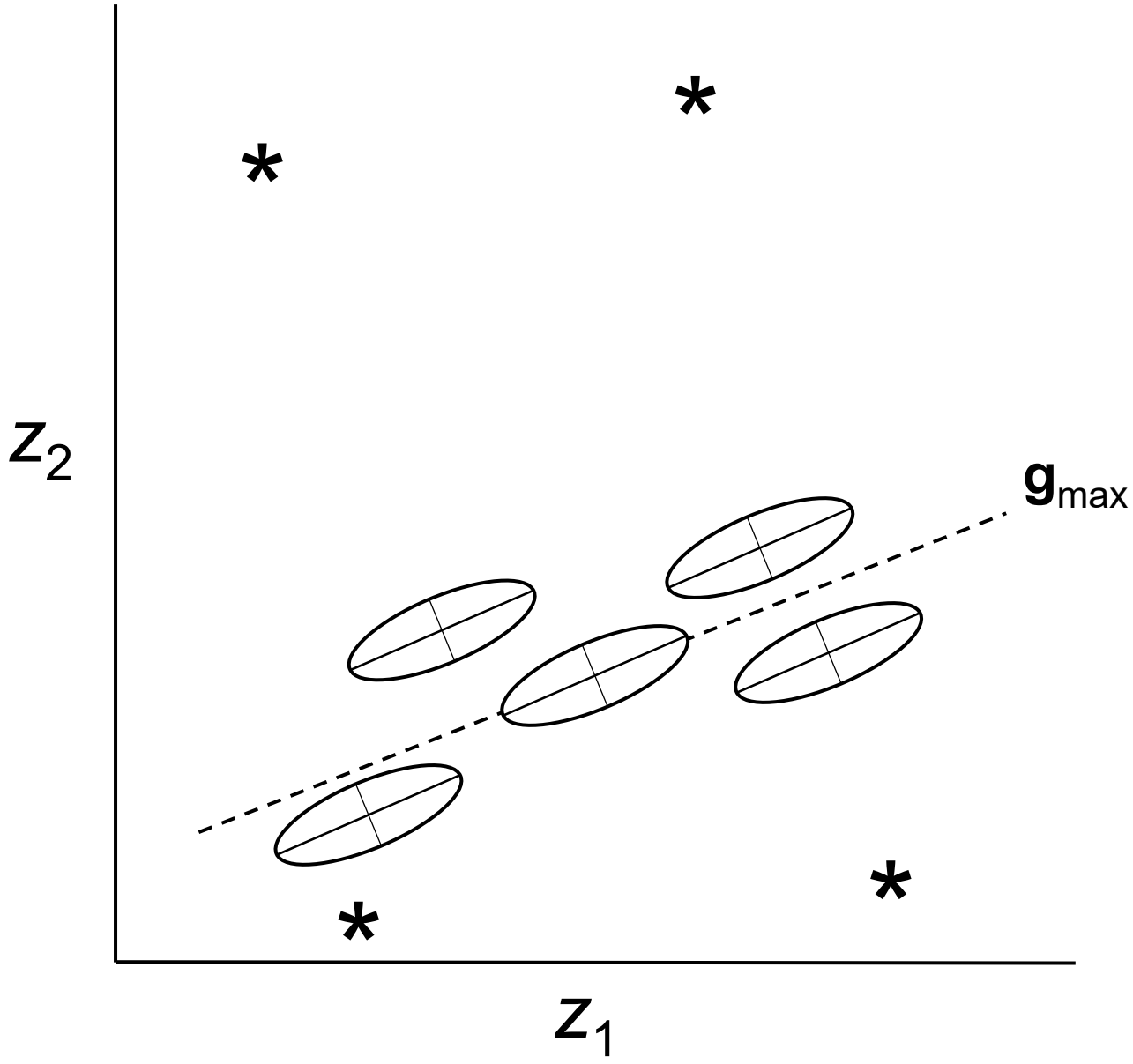
Evolution of **G**

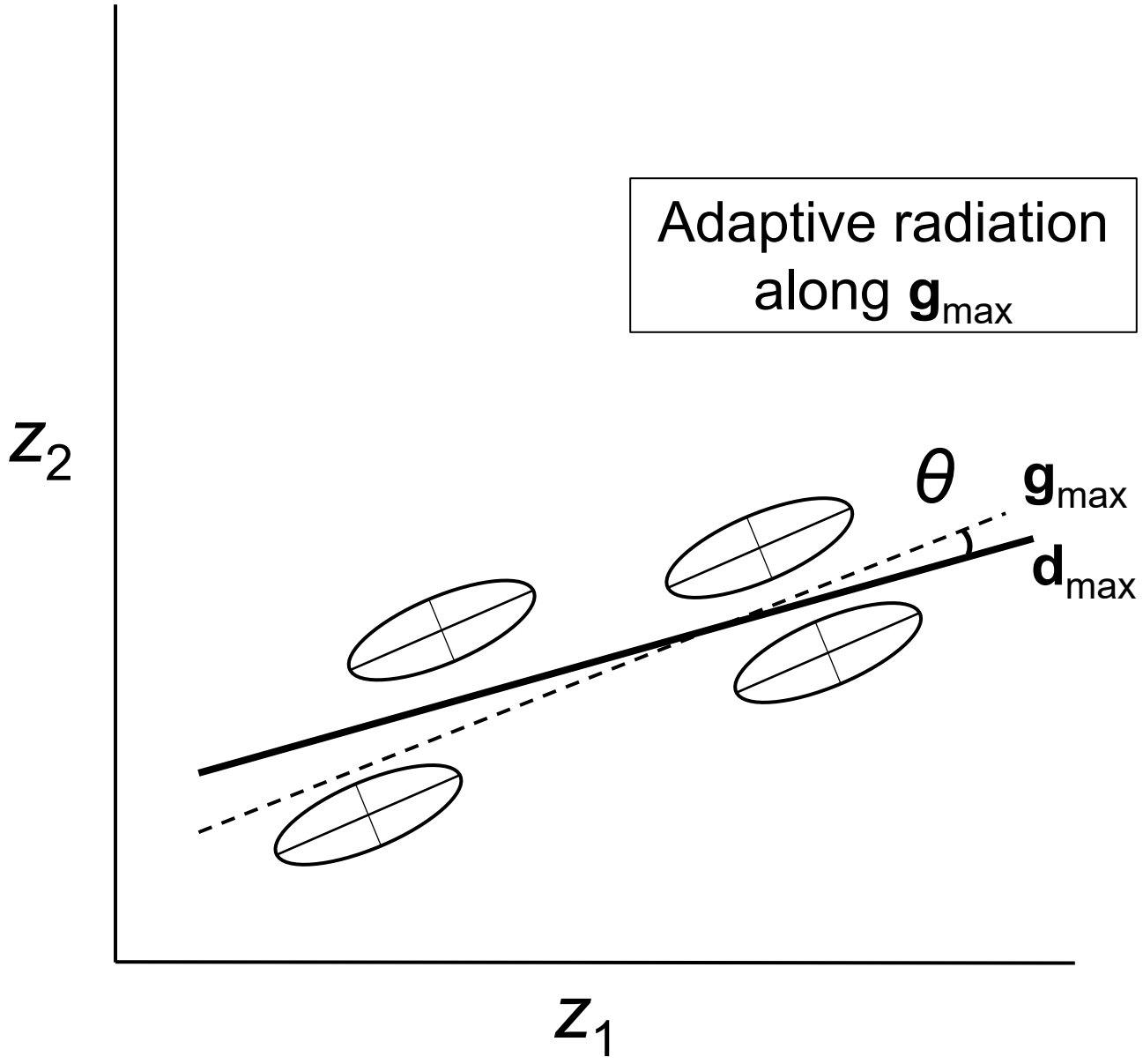
Joel McGlothlin



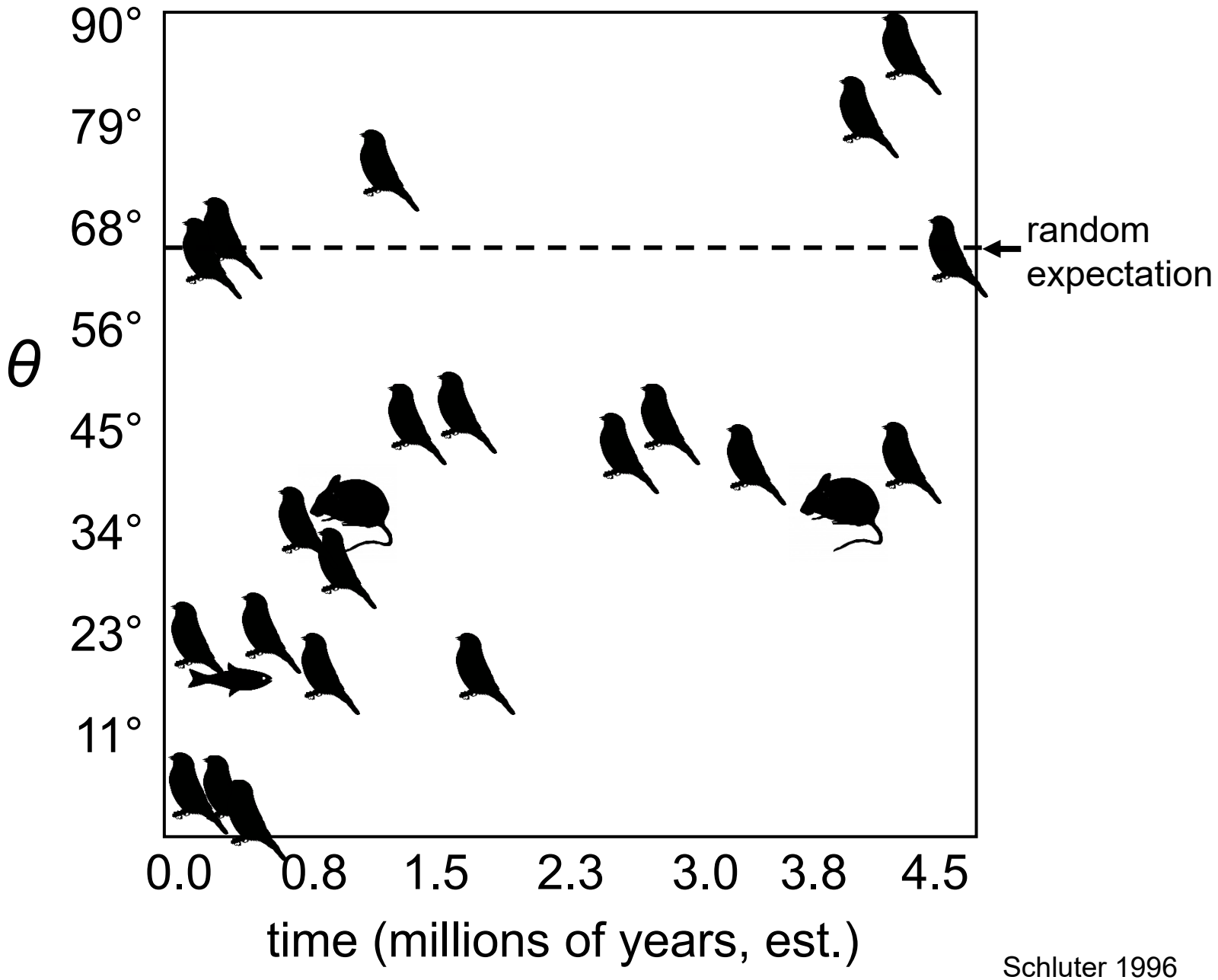
Schluter 1996



Schluter 1996



Schluter 1996



Schluter 1996

Does microevolution predict macroevolution?

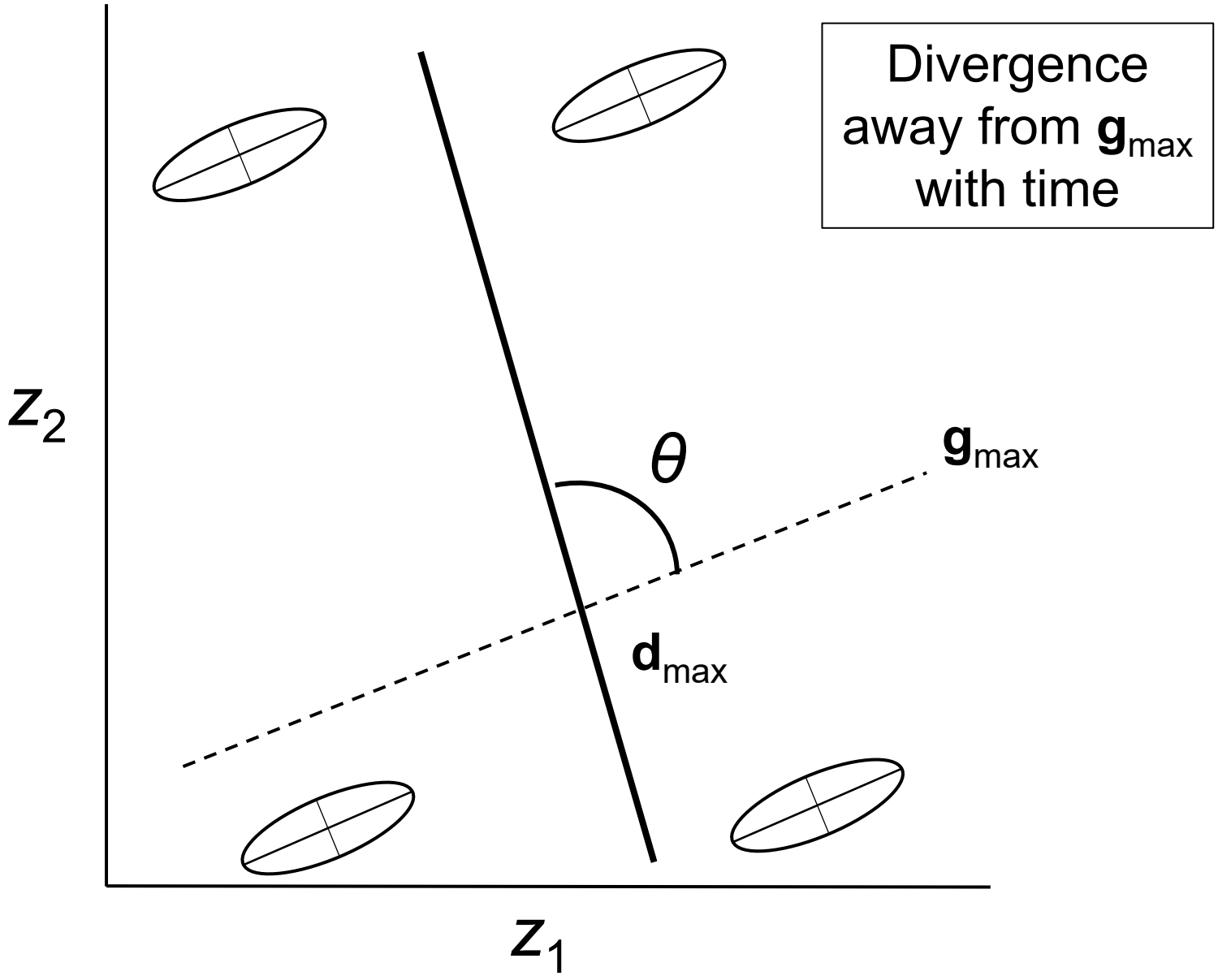
Can we predict species divergence (**D**) from within-population variance (**G**)?

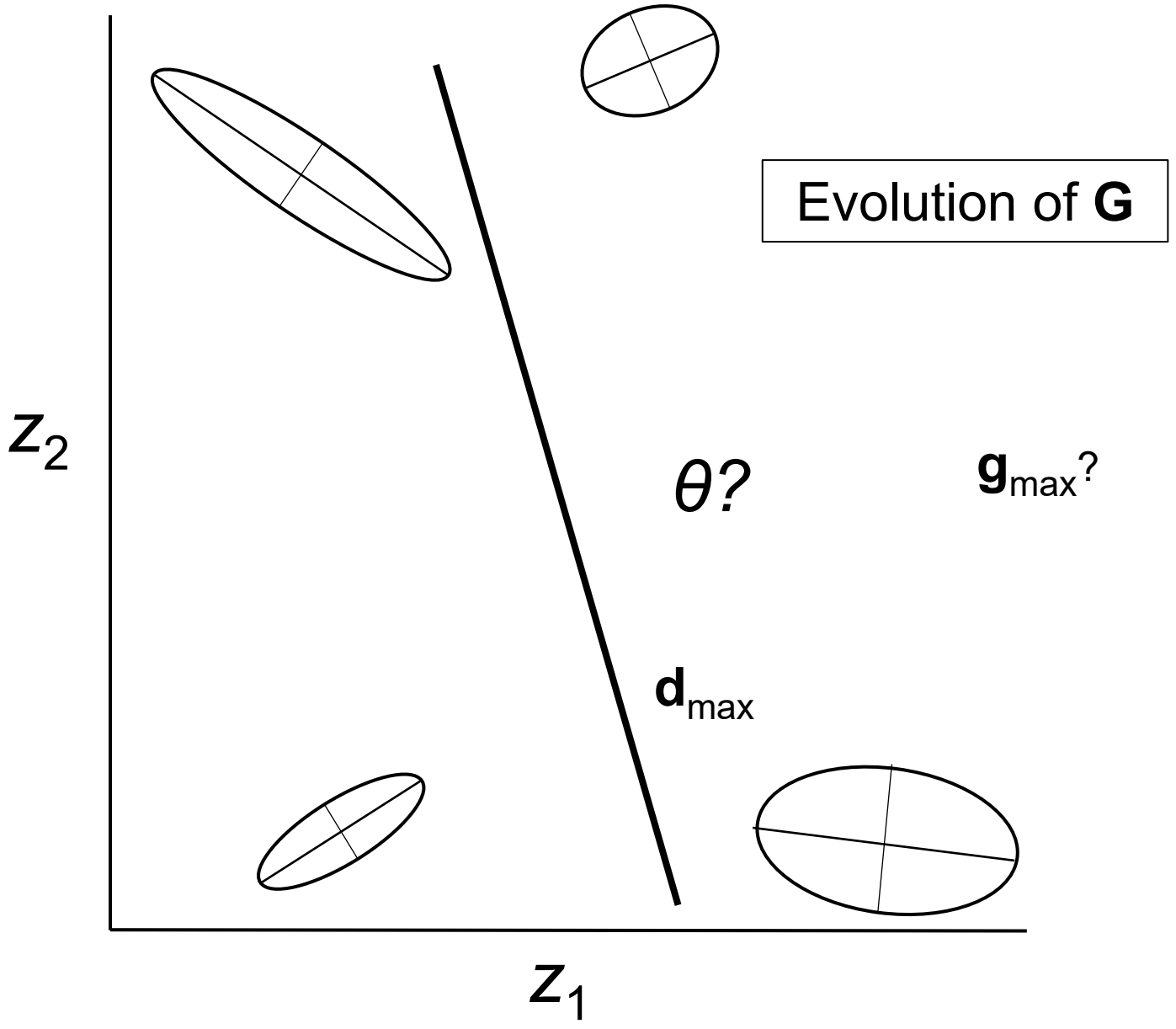
Does divergence maintain its alignment with $\mathbf{g}_{max}$?

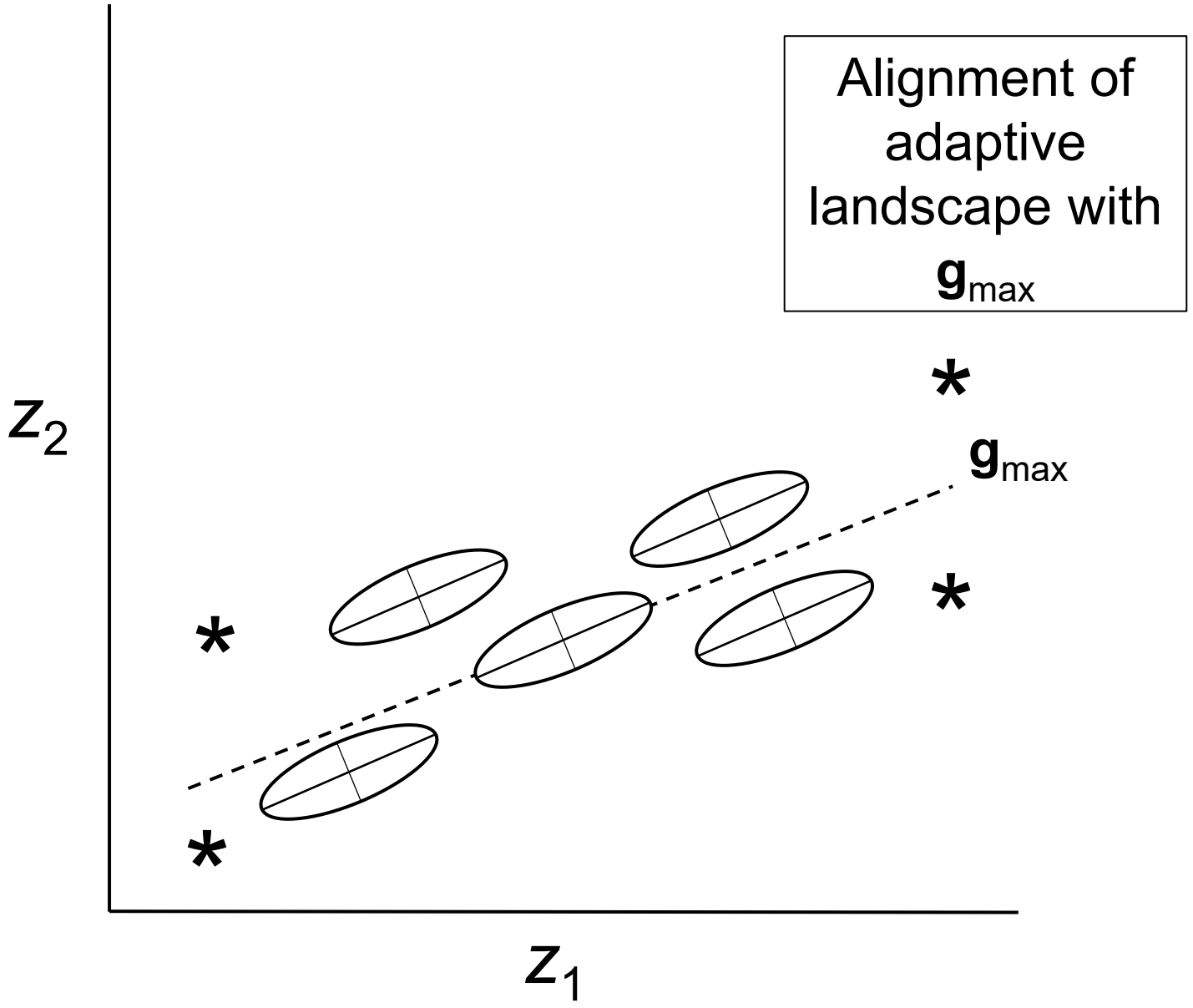
What do we expect?

1. Reasons to expect alignment

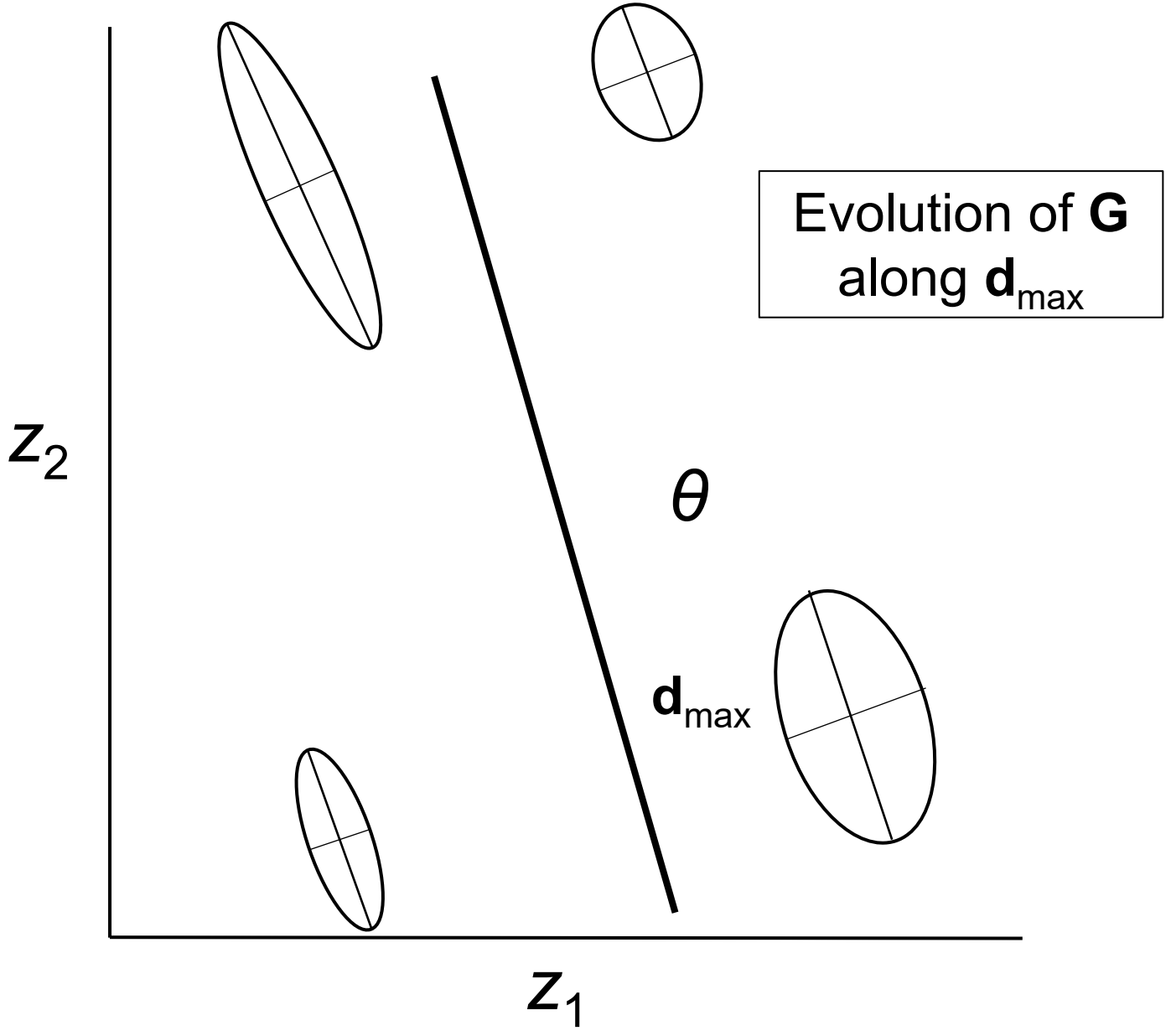
2. Reasons to expect no alignment


Divergence away from $\mathbf{g}_{max}$ with time
z_2
θ
$\mathbf{g}_{max}$
$\mathbf{d}_{max}$
z_1


Evolution of **G**
z_2
θ?
$\mathbf{g}_{max}$?
$\mathbf{d}_{max}$
z_1



Schluter 1996


Evolution of **G** along $\mathbf{d}_{max}$
z_2
θ
$\mathbf{d}_{max}$
z_1

Evolution of **G**

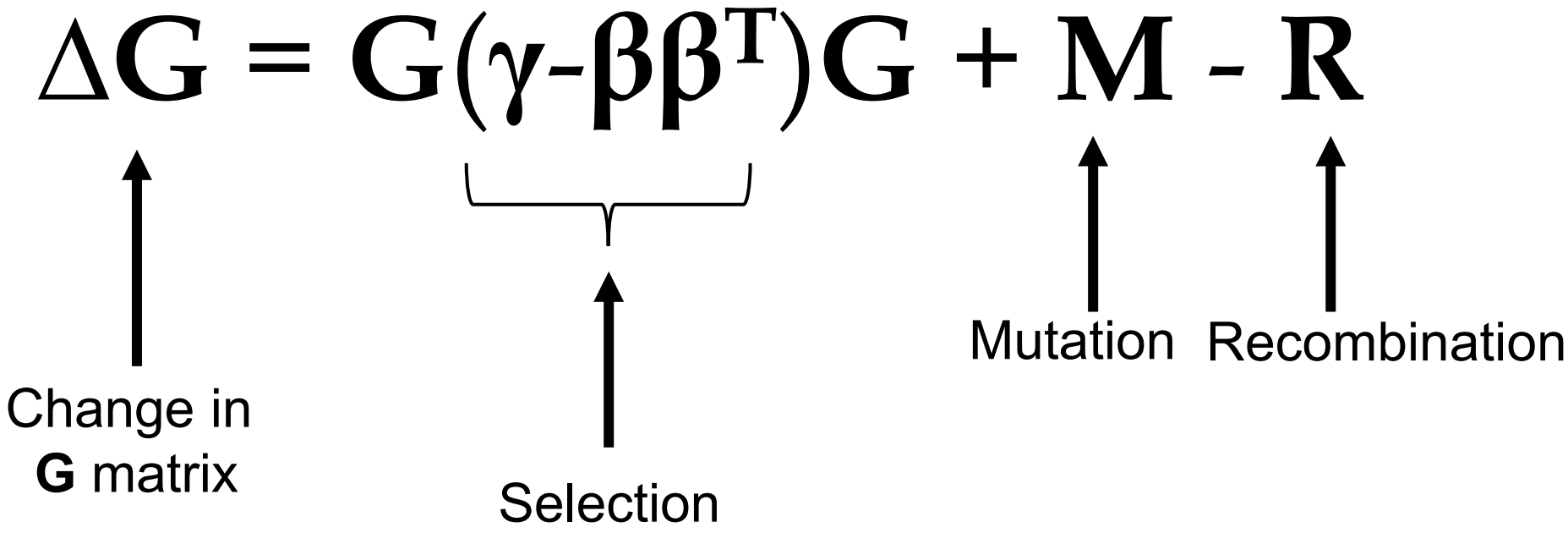
- Simple theory
- Simulations
- Data from *Anolis*
- Implications for macroevolution

$$\Delta \mathbf{G} = \mathbf{G}(\boldsymbol{\gamma} - \boldsymbol{\beta}\boldsymbol{\beta}^{T})\mathbf{G}$$

Change in **G** matrix

Selection

Lande 1980, Phillips & Arnold 1989

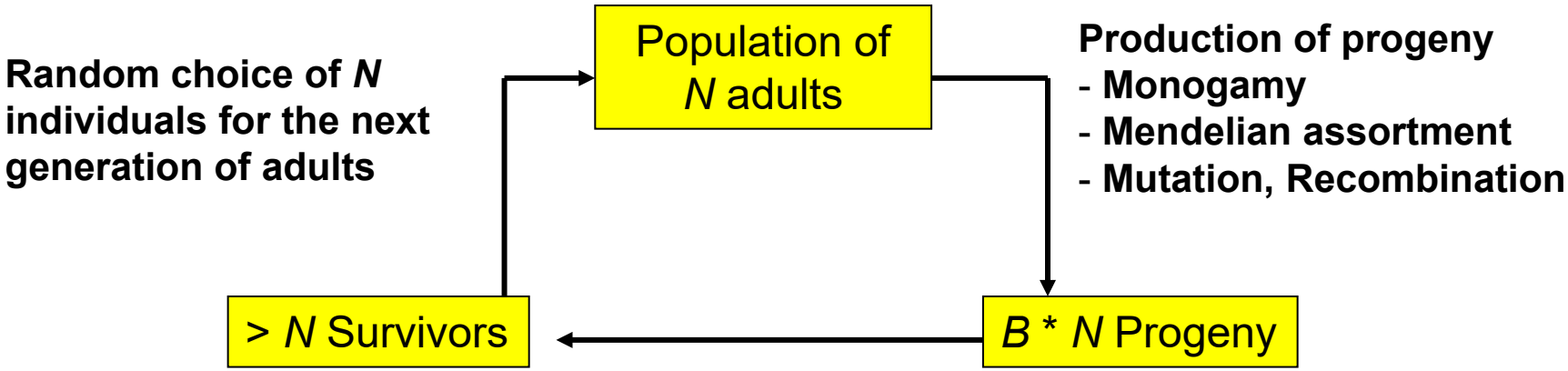


Lande 1980, Phillips & Arnold 1989

$$\Delta \mathbf{G} = \mathbf{G}(\boldsymbol{\gamma} - \boldsymbol{\beta}\boldsymbol{\beta}^{\mathrm{T}})\mathbf{G} + \mathbf{M} - \mathbf{R}$$

Predictions of this model?
Problems with this model?

Jones et al. **G** simulation models

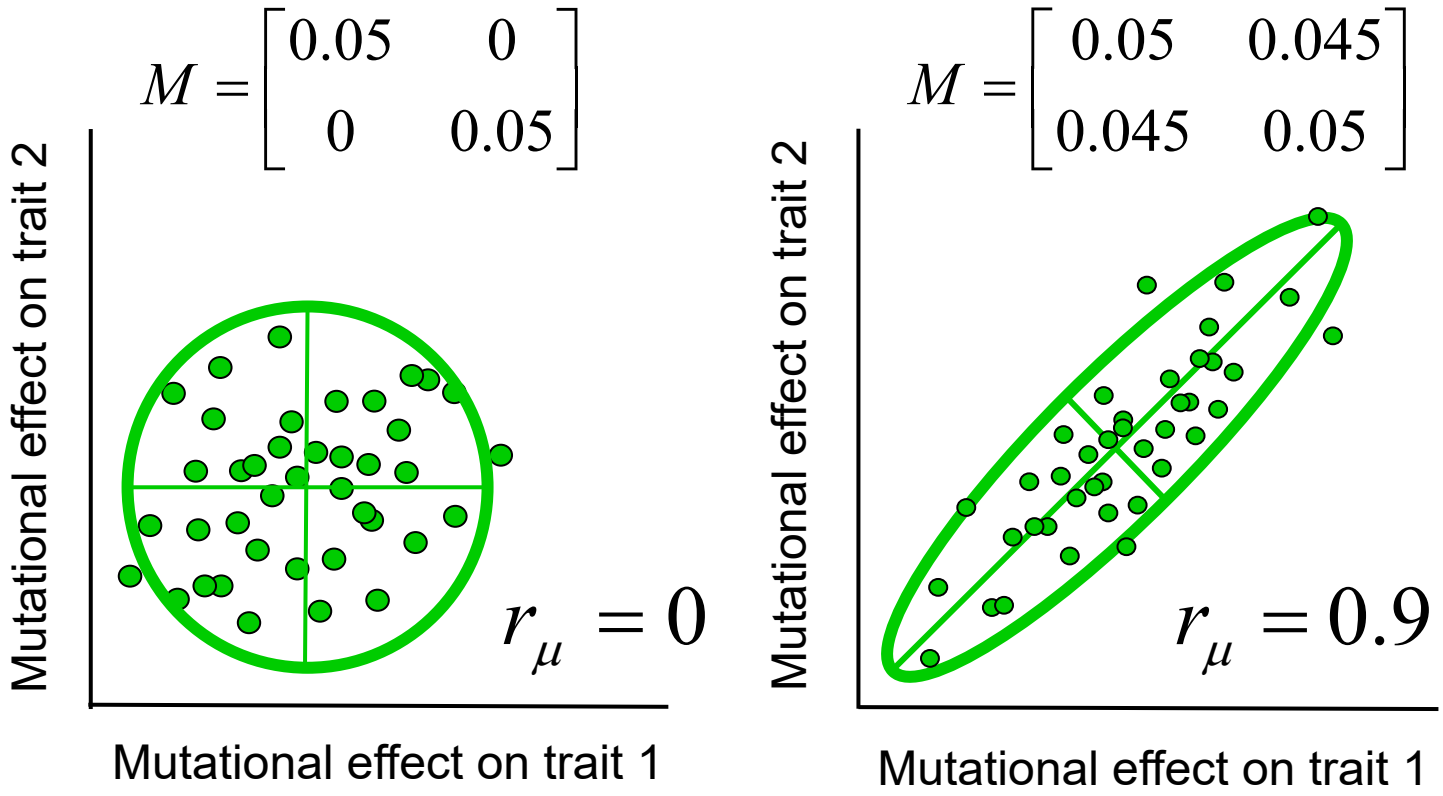


https://github.com/JonesLabIdaho

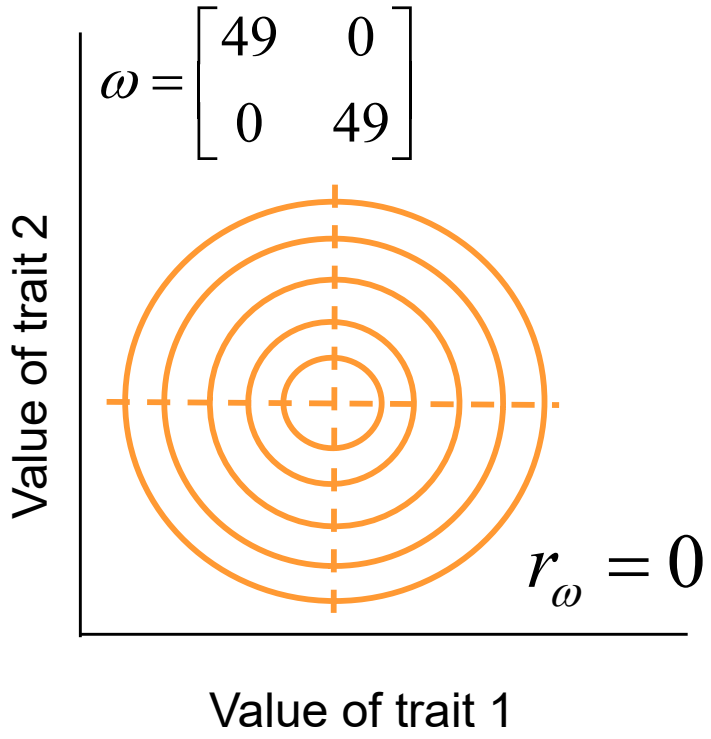
Jones et al. model details

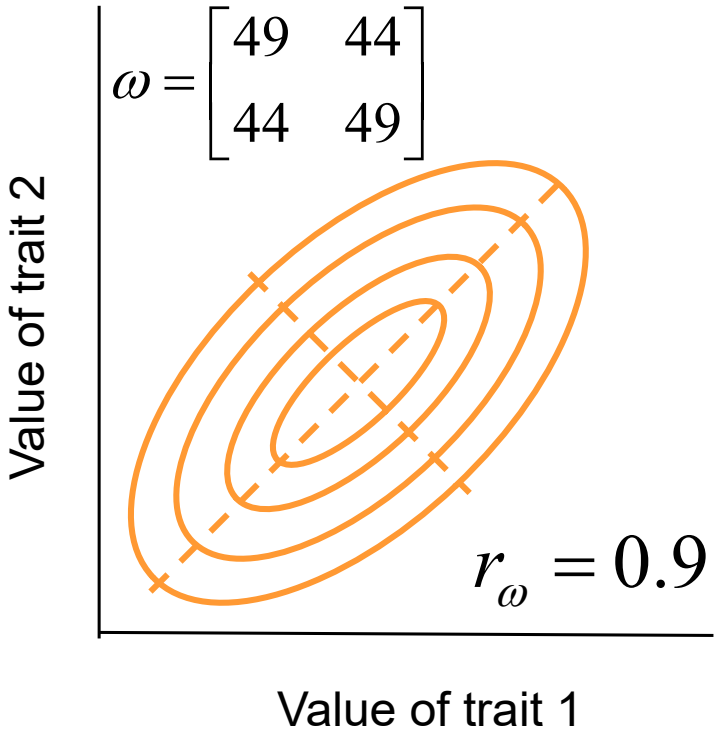
- Direct Monte Carlo simulation with each gene and individual specified
- Two traits affected by 50 pleiotropic loci
- Additive inheritance with no dominance or epistasis
- Allelic effects drawn from a bivariate normal distribution with means = 0, variances = 0.05, and mutational correlation r_μ = 0.0-0.9
- Mutation rate = 0.0002 per haploid locus
- Environmental effects drawn from a bivariate normal distribution with mean = 0, variances = 1
- Gaussian individual selection surface, with a specified amount of correlational selection and ω = 9 or 49
- Each simulation run equilibrated for 10,000 (non-overlapping) generations, followed by several thousand of experimental generations

Mutation


$M = \begin{bmatrix} 0.05 & 0 \\ 0 & 0.05 \end{bmatrix}$
Mutational effect on trait 2
$r_\mu = 0$
Mutational effect on trait 1
$M = \begin{bmatrix} 0.05 & 0.045 \\ 0.045 & 0.05 \end{bmatrix}$
Mutational effect on trait 2
$r_\mu = 0.9$
Mutational effect on trait 1

Selection

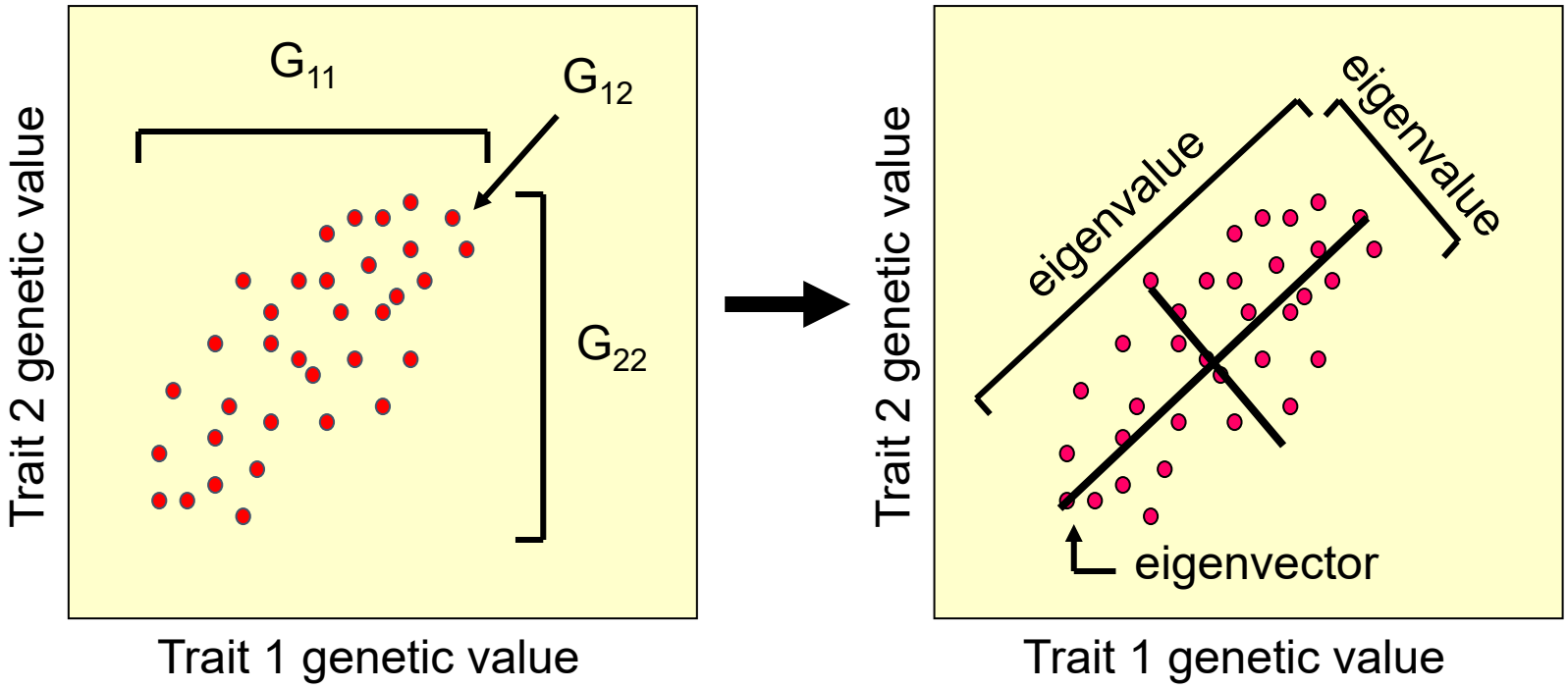




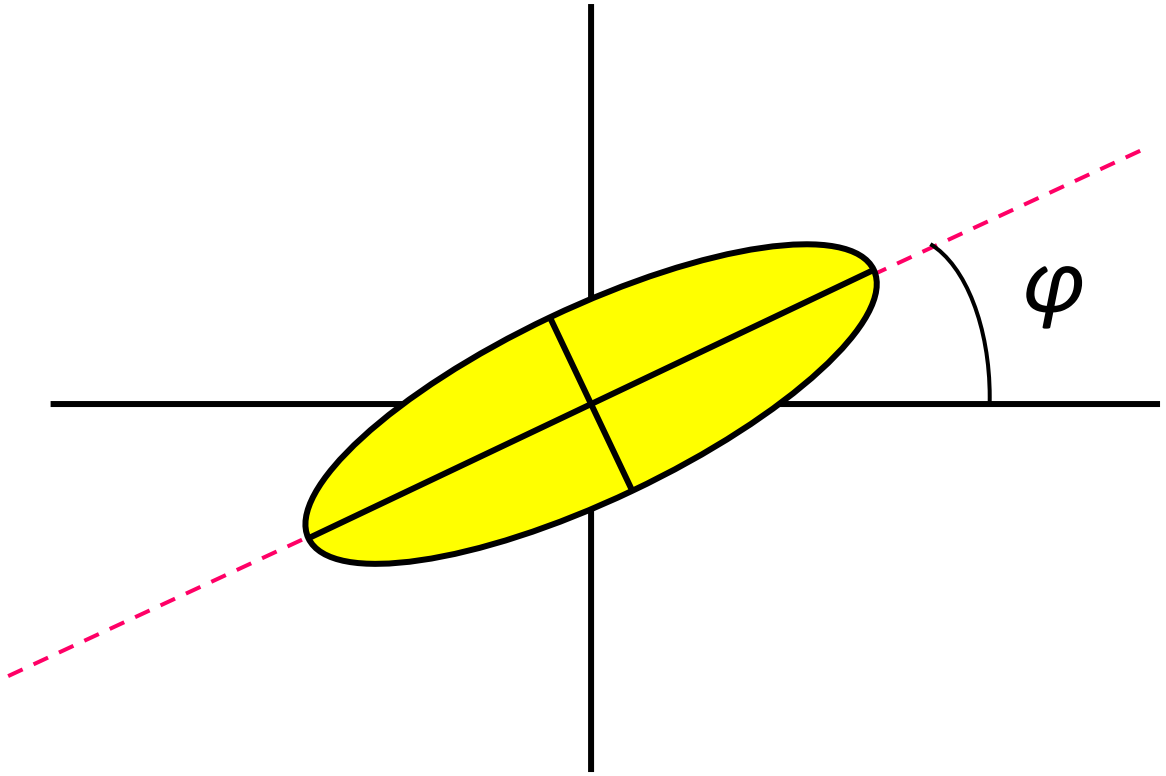
Individual selection surfaces

Visualizing the **G**-matrix

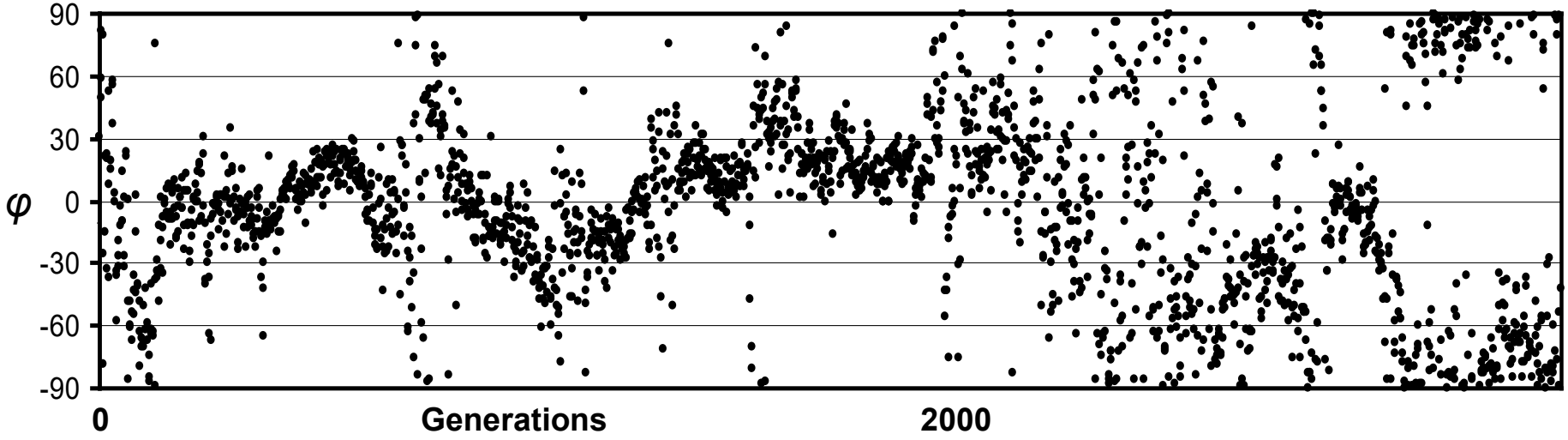
$$\mathbf{G} = \begin{bmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{bmatrix}$$



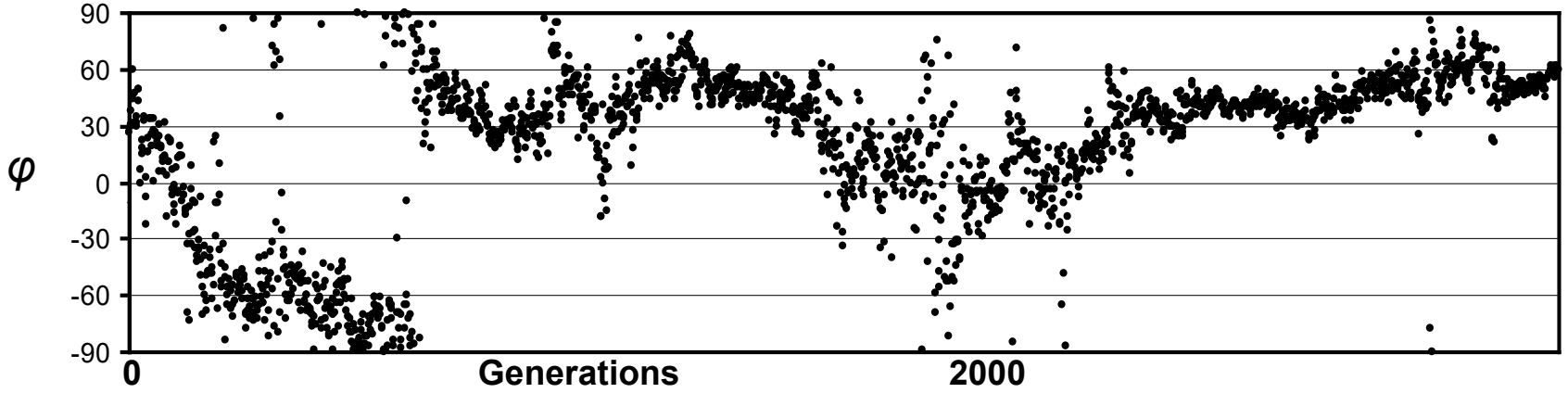
Effect on the **G**-matrix



Stationary Optimum
(selectional correlation = 0, mutational correlation = 0)

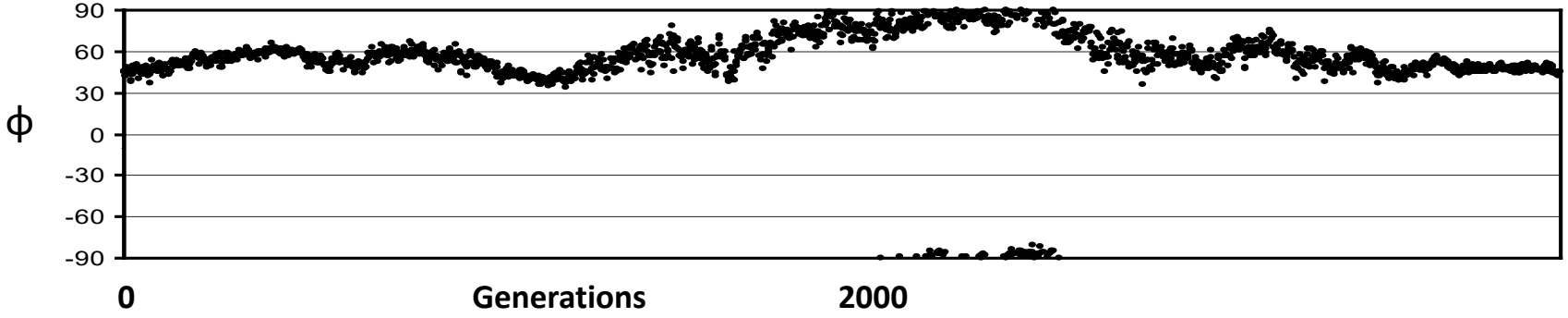


Stronger correlational selection produces a more stable **G**-matrix
(selectional correlation = 0.75, mutational correlation = 0)



ω (trait 1)	ω (trait 2)	r (ω)	r (μ)	Δφ
49	49	0	0	9.1
49	49	0.25	0	9.2
49	49	0.50	0	8.9
49	49	0.75	0	7.8
49	49	0.85	0	5.4
49	49	0.90	0	4.3

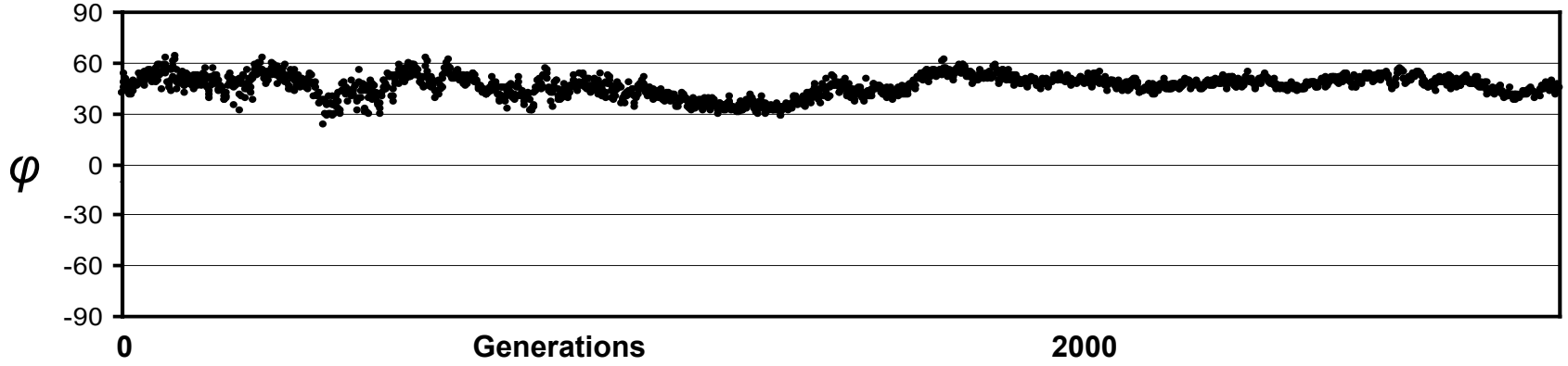
A high correlation between mutational effects produces stability (selectional correlation = 0, mutational correlation = 0.5)



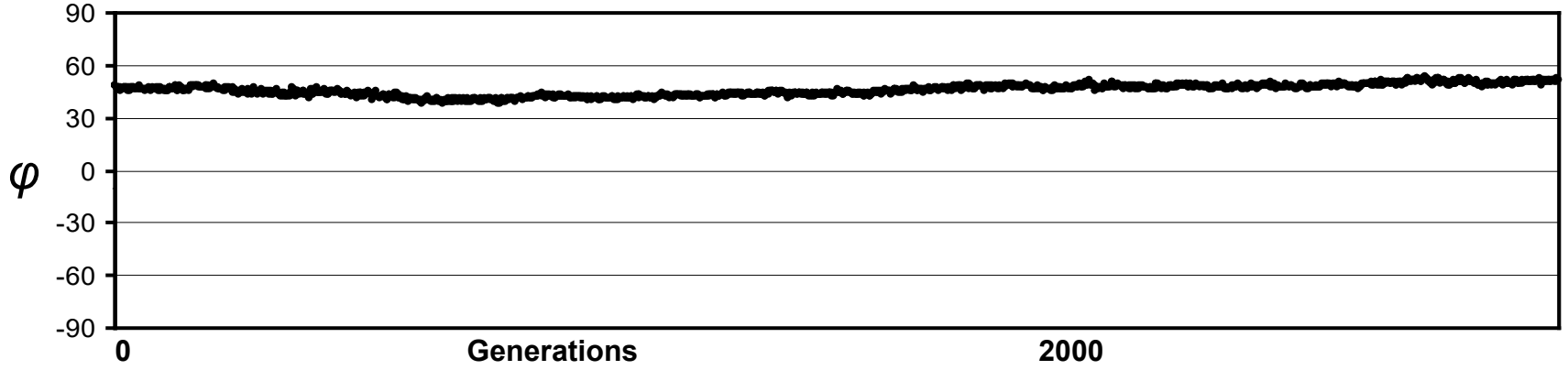
ω (trait 1)	ω (trait 2)	r (ω)	r (μ)	Δφ
49	49	0	0	9.9
49	49	0	0.25	7.9
49	49	0	0.50	3.6
49	49	0	0.75	1.5
49	49	0	0.85	1.1
49	49	0	0.90	0.9

When the selection matrix and mutation matrix are aligned, **G** can be very stable

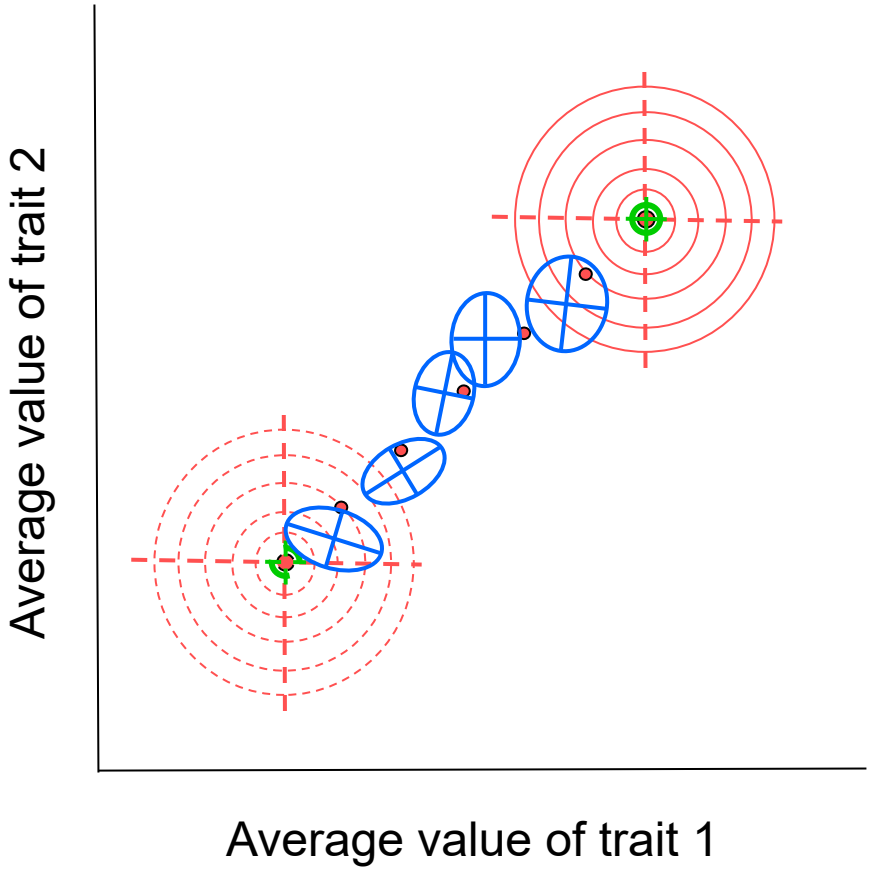
selectional correlation = 0.75, mutational correlation = 0.5



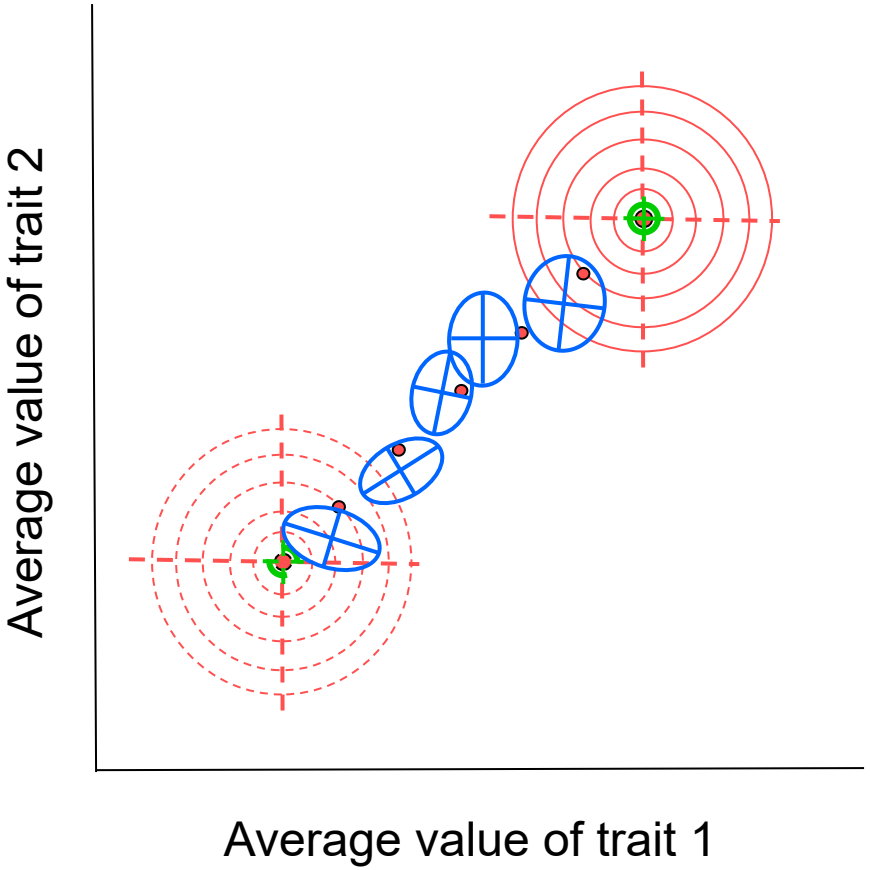
selectional correlation = 0.9, mutational correlation = 0.9

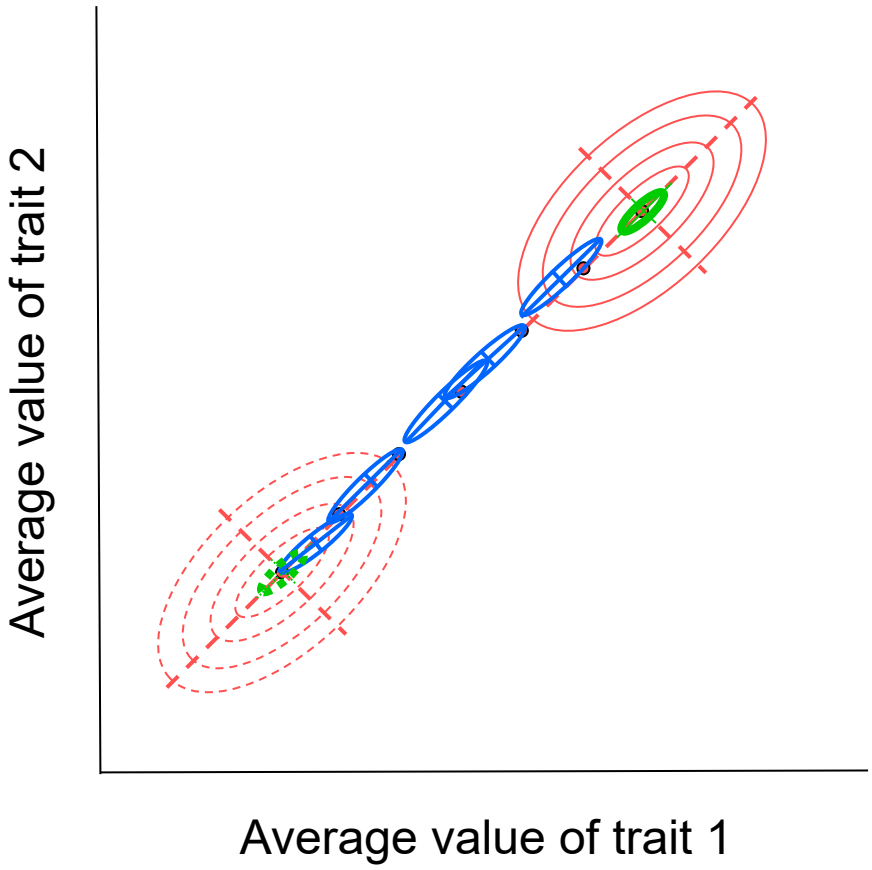


What happens when the optimum moves?



Peak movement along a genetic line of least resistance stabilizes the **G**-matrix





$$\Delta \mathbf{G} = \mathbf{G}(\boldsymbol{\gamma} - \boldsymbol{\beta}\boldsymbol{\beta}^{\mathrm{T}})\mathbf{G} + \mathbf{M}$$

Epistasis – The Multilinear Model

Multivariate extension of the multilinear model of Hansen and Wagner (2001):

Additive model:

$$z = a_1 + a_2 + a_3 + \ldots + e$$

Multilinear model:

$$z = a_1 + a_2 + \varepsilon a_1 a_2 + \ldots + e$$

Only slightly more complex for the multivariate case

Epistasis Results

- Epistasis allows selection to shape the distribution of new mutations

N	r_ω	V_1	V_2	r_V	M_1	M_2	r_μ
128	0	0.77	0.79	0.05	0.71	0.82	0.02
256	0	0.80	0.84	-0.02	0.46	0.50	-0.01
1024	0	0.70	0.70	0.00	0.17	0.16	-0.01
2048	0	0.68	0.65	-0.02	0.14	0.14	-0.01
128	0.90	0.33	0.32	0.41	0.43	0.42	0.08
256	0.90	0.33	0.33	0.45	0.24	0.26	0.14
1024	0.90	0.28	0.28	0.40	0.11	0.12	0.16
2048	0.90	0.26	0.27	0.40	0.10	0.10	0.18

Generations = 5000, ε variance = 1.0, ω = 49, μ = 0.0005

$$\omega = \begin{bmatrix} 93 & 0 \\ 0 & 5 \end{bmatrix}$$

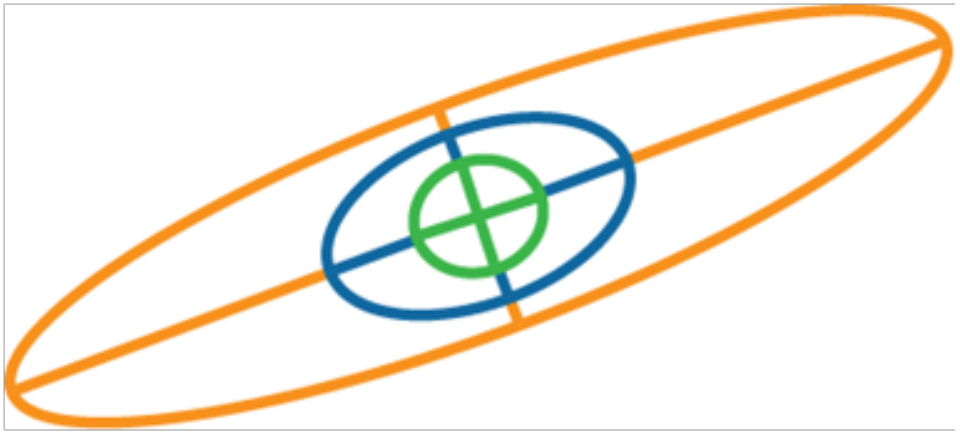
$$G = \begin{bmatrix} 0.262 & 0.000 \\ 0.000 & 0.079 \end{bmatrix}$$

$$M = \begin{bmatrix} 0.103 & 0.000 \\ 0.000 & 0.072 \end{bmatrix}$$

$$\omega = \begin{bmatrix} 82 & 30.0 \\ 30.0 & 16 \end{bmatrix}$$

$$G = \begin{bmatrix} 0.239 & 0.060 \\ 0.060 & 0.102 \end{bmatrix}$$

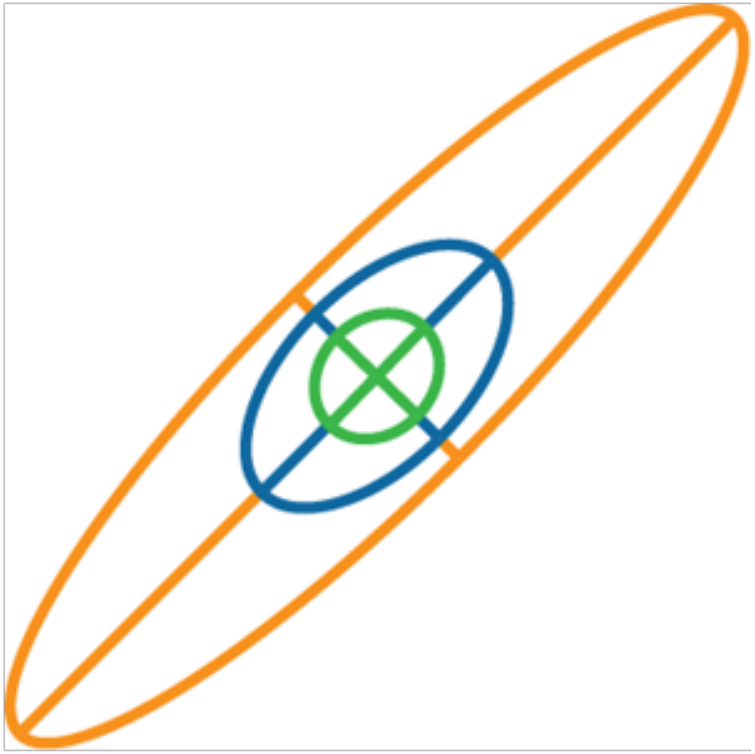
$$M = \begin{bmatrix} 0.097 & 0.008 \\ 0.008 & 0.075 \end{bmatrix}$$



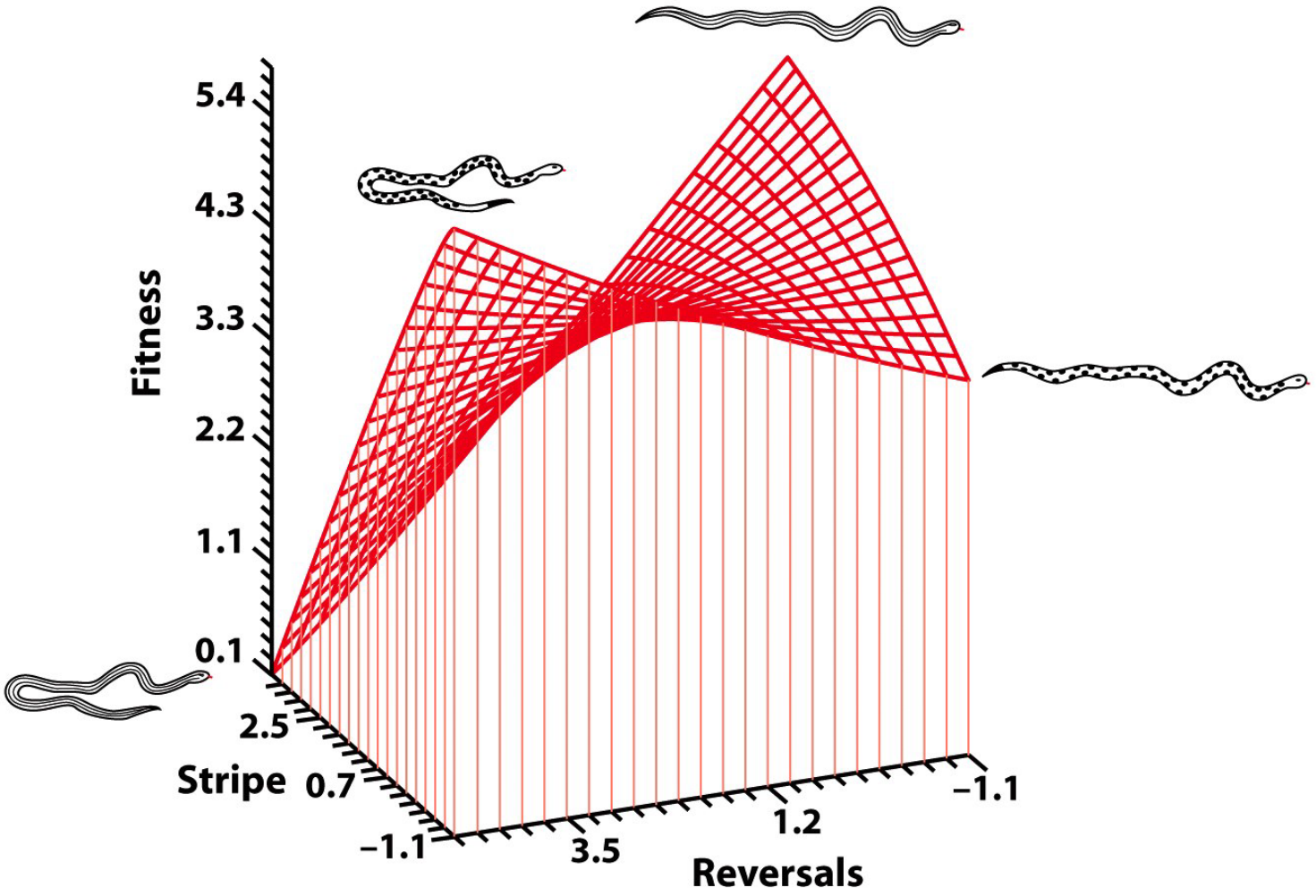
$$\omega = \begin{bmatrix} 49 & 44.1 \\ 44.1 & 49 \end{bmatrix}$$

$$G = \begin{bmatrix} 0.174 & 0.096 \\ 0.096 & 0.175 \end{bmatrix}$$

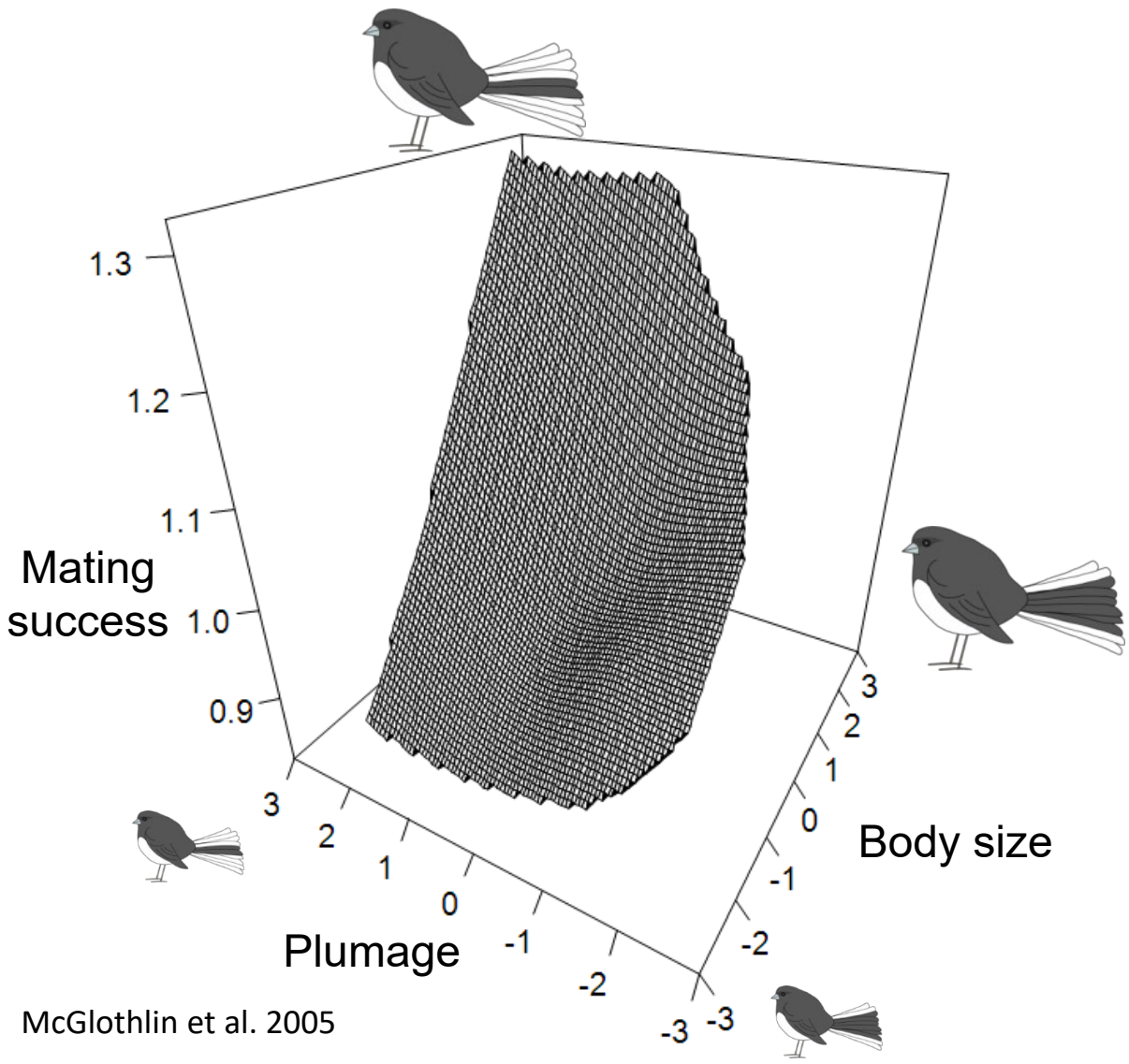
$$M = \begin{bmatrix} 0.089 & 0.016 \\ 0.016 & 0.090 \end{bmatrix}$$



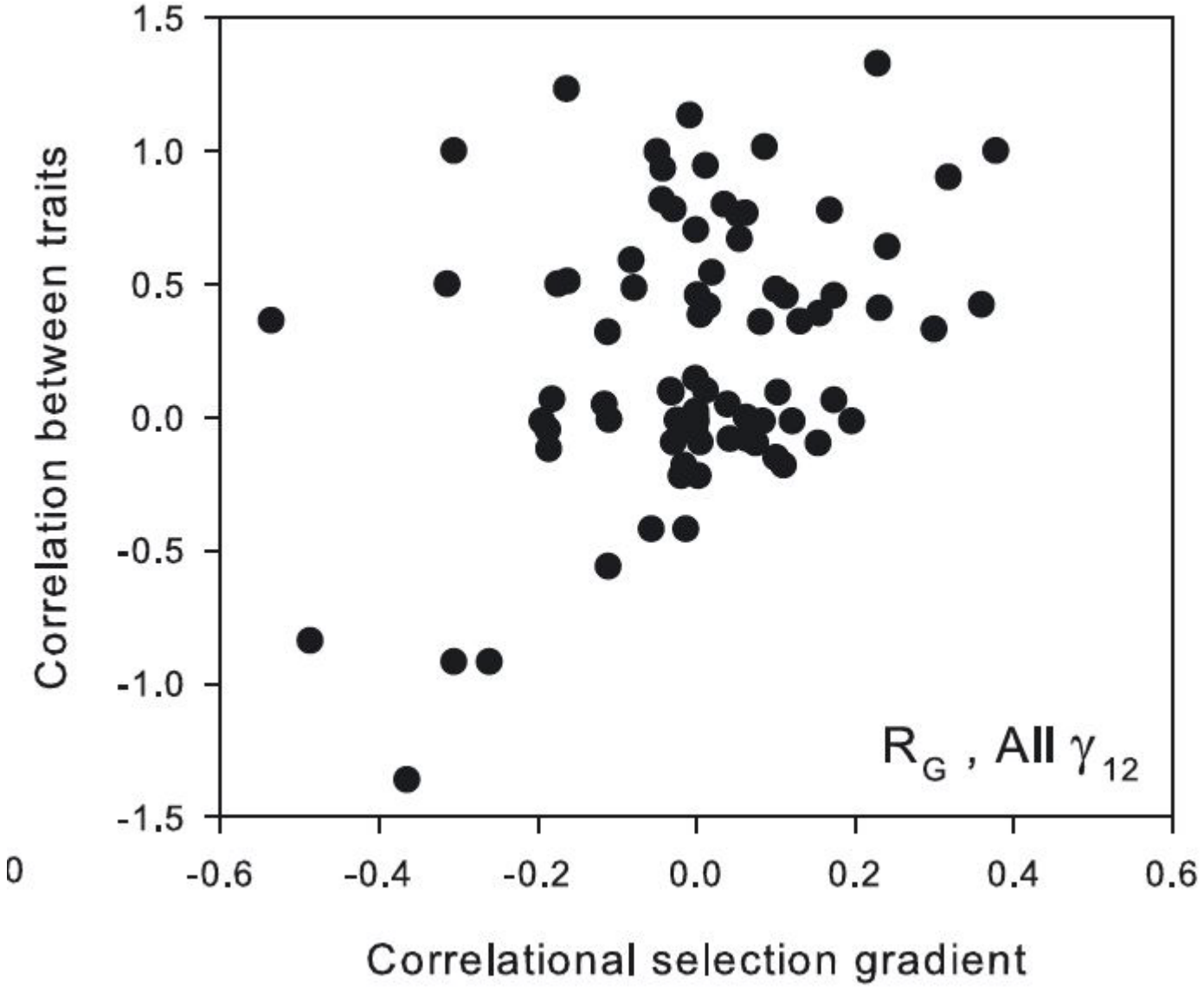
Conclusions from **G** matrix simulations



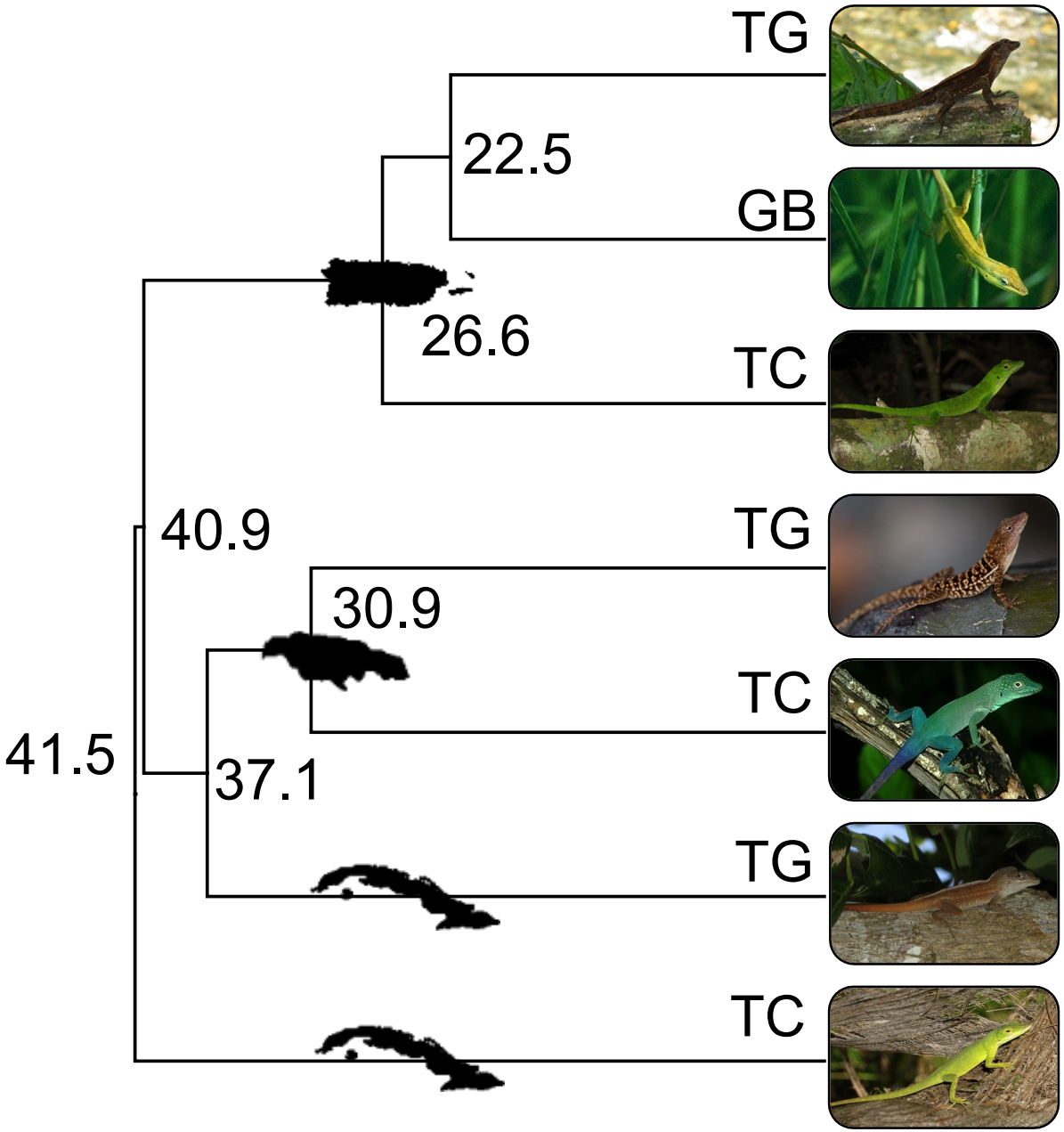
Brodie 1992

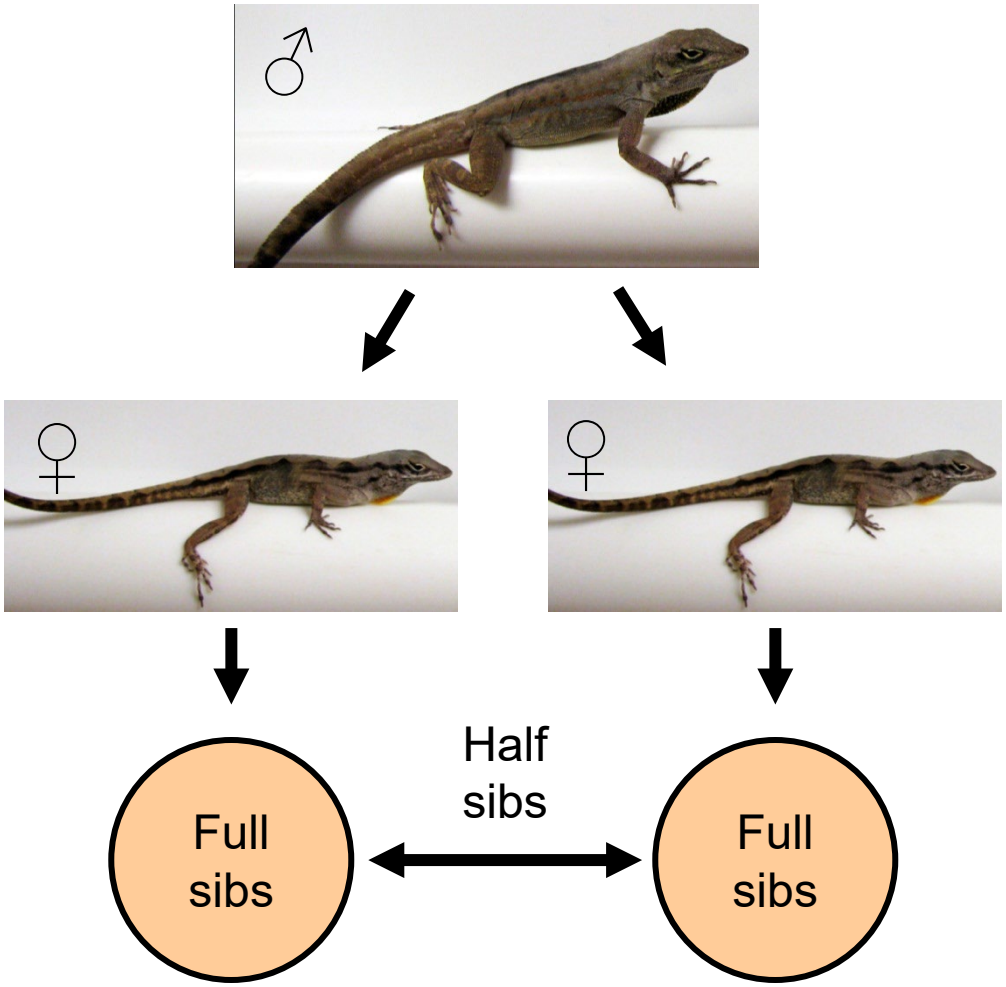


McGlothlin et al. 2005

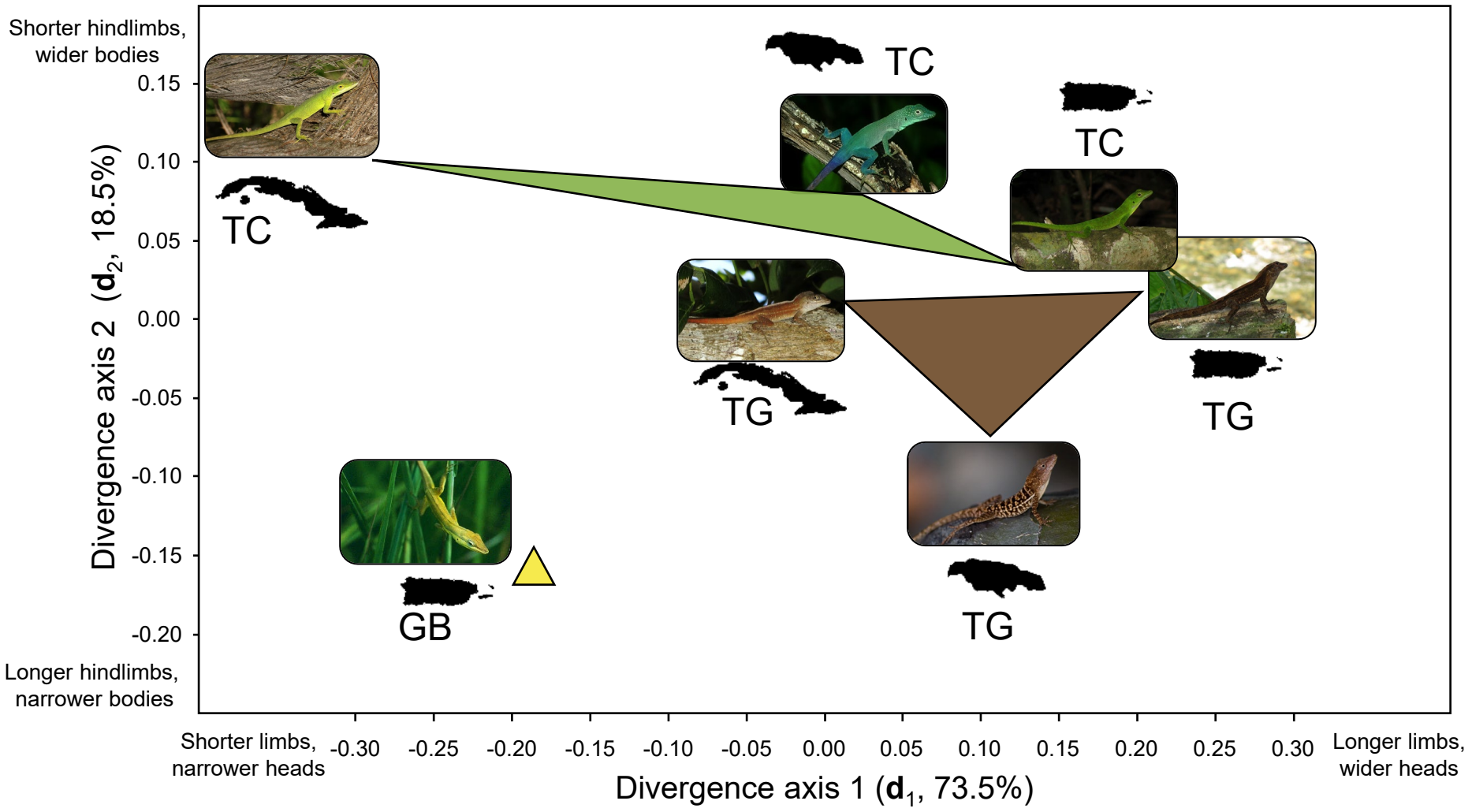


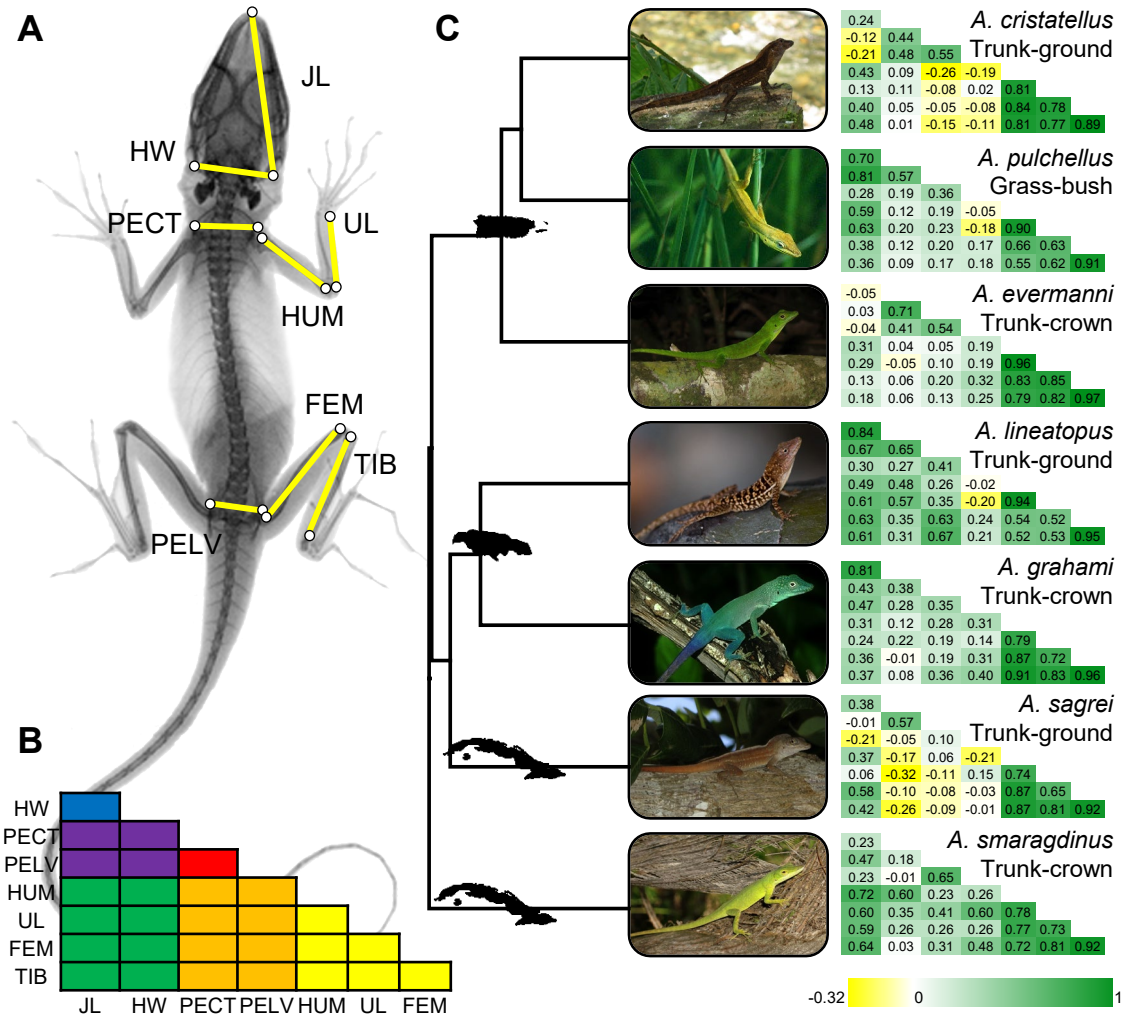
Roff & Fairbairn 2012

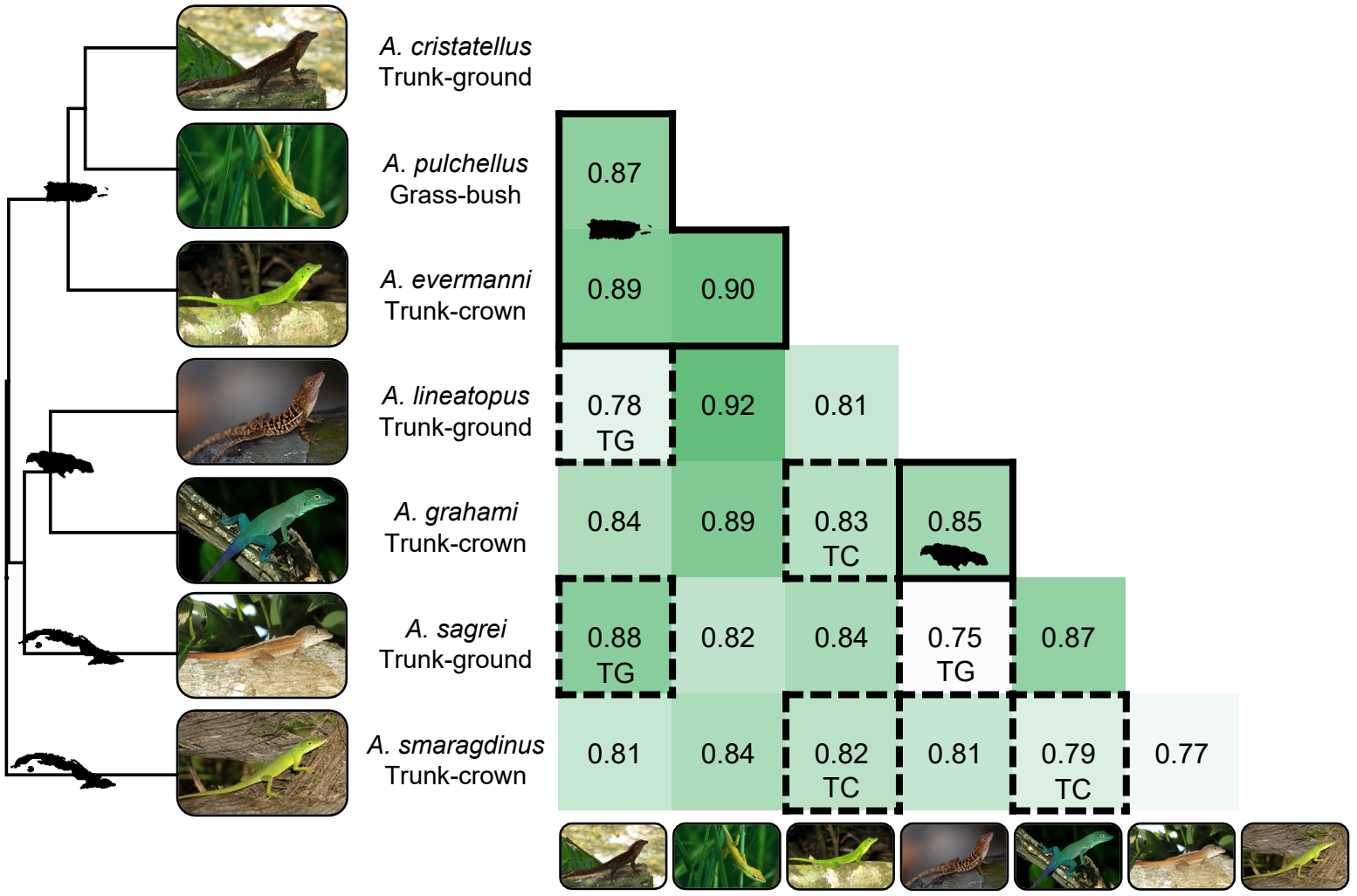

TG
22.5
GB
26.6
TC
40.9
TG
30.9
TC
41.5
37.1
TG
TC

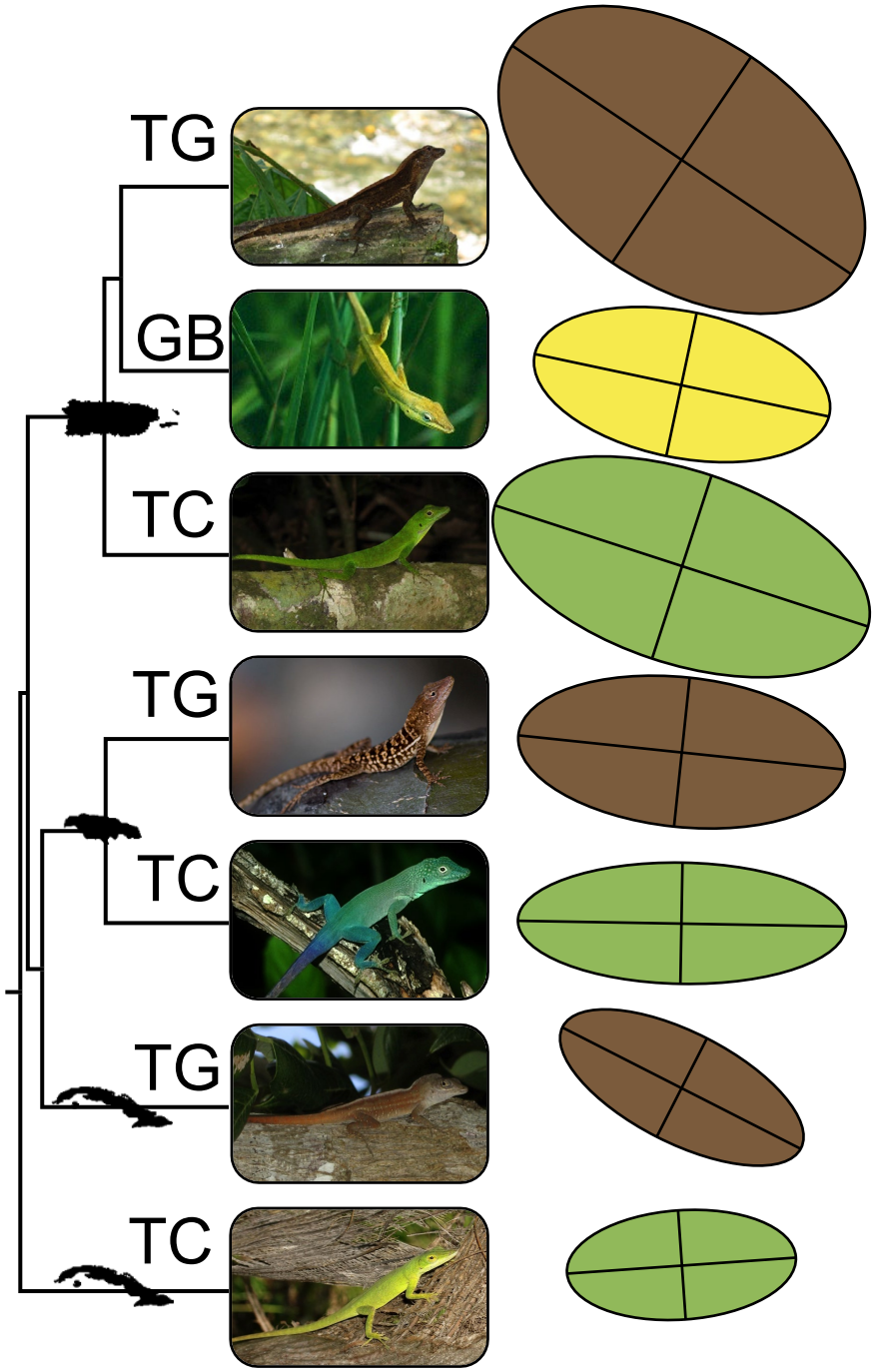

♂
♀
♀
Full sibs
Half sibs
Full sibs


2845 juveniles,
reared to 6 months


Shorter hindlimbs, wider bodies
Longer hindlimbs, narrower bodies
Divergence axis 2 (d2, 18.5%)
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
TC
TC
TC
TG
TG
TG
GB
Shorter limbs, narrower heads
-0.30
-0.25
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Longer limbs, wider heads
Divergence axis 1 (d1, 73.5%)


A
JL
HW
PECT
UL
HUM
FEM
TIB
PELV
B
HW
PECT
PELV
HUM
UL
FEM
TIB
JL HW PECT PELV HUM UL FEM
C
A. cristatellus
Trunk-ground
A. pulchellus
Grass-bush
A. evermanni
Trunk-crown
A. lineatopus
Trunk-ground
A. grahami
Trunk-crown
A. sagrei
Trunk-ground
A. smaragdinus
Trunk-crown
-0.32
0
1


A. cristatellus
Trunk-ground
A. pulchellus
Grass-bush
A. evermanni
Trunk-crown
A. lineatopus
Trunk-ground
A. grahami
Trunk-crown
A. sagrei
Trunk-ground
A. smaragdinus
Trunk-crown
0.87
0.89
0.90
0.78
TG
0.92
0.81
0.84
0.89
0.83
TC
0.85
0.88
TG
0.82
0.84
0.75
TG
0.87
0.81
0.84
0.82
TC
0.81
0.79
TC
0.77



G matrix evolution

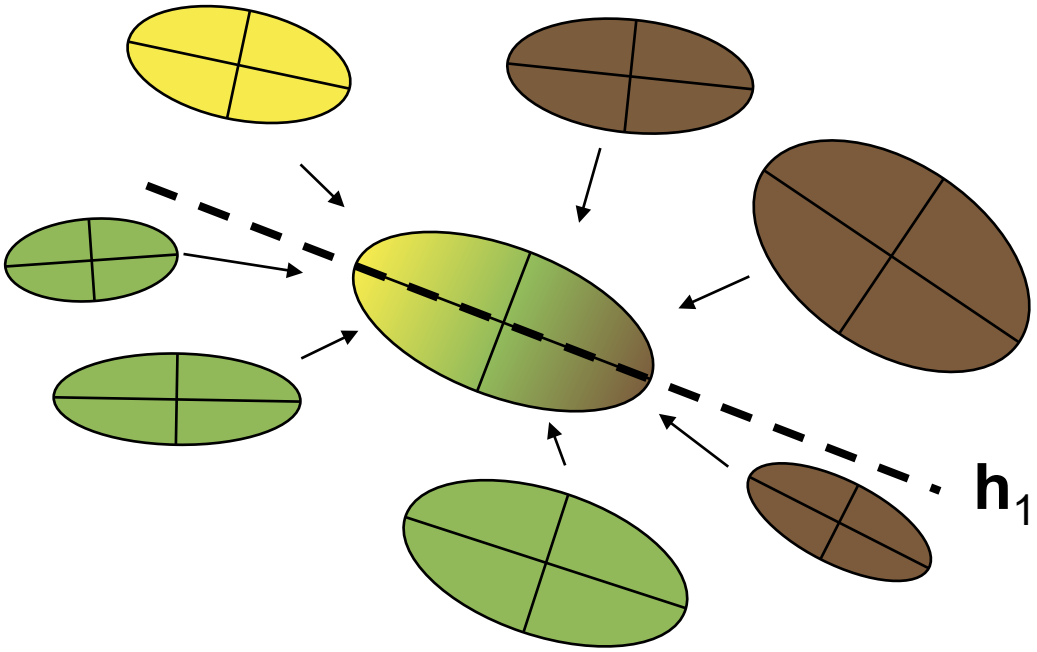
Matrices differ in size, shape, and orientation

Most matrices share no common PCs

Phylogenetic signal

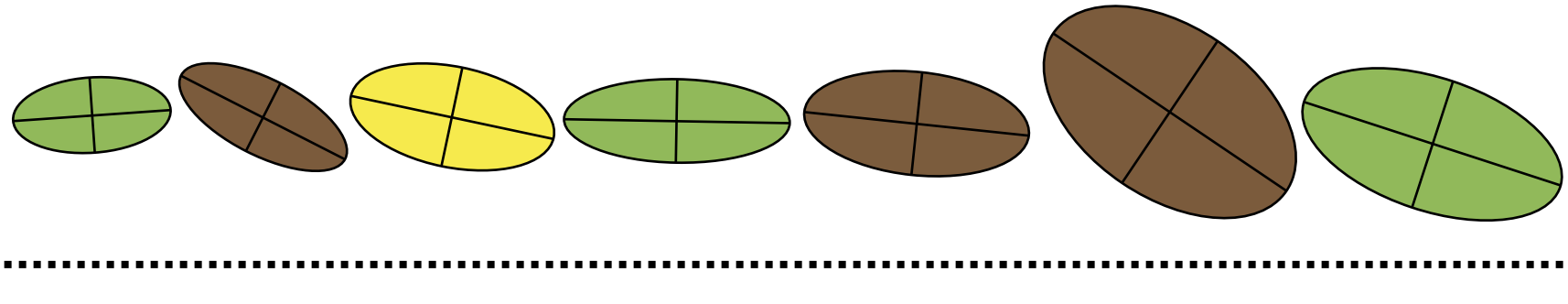
Ecomorph effect

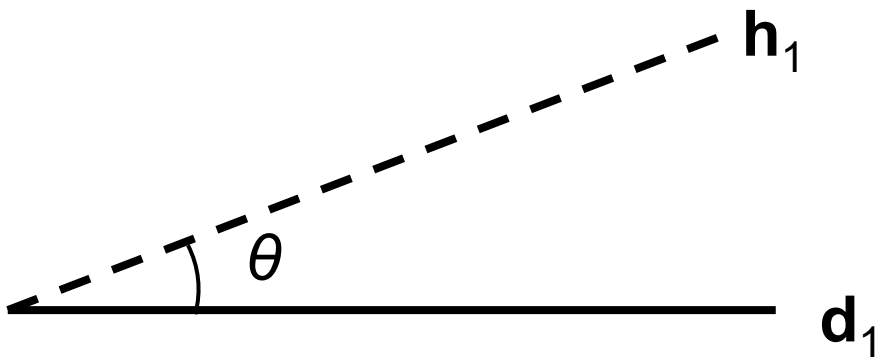
Is there a signature of genetic constraint in the *Anolis* radiation?



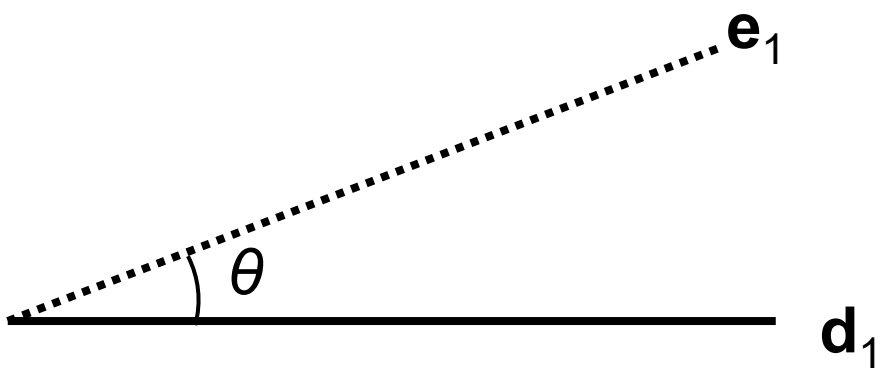
Common subspace analysis:
How are **G** matrices most similar?

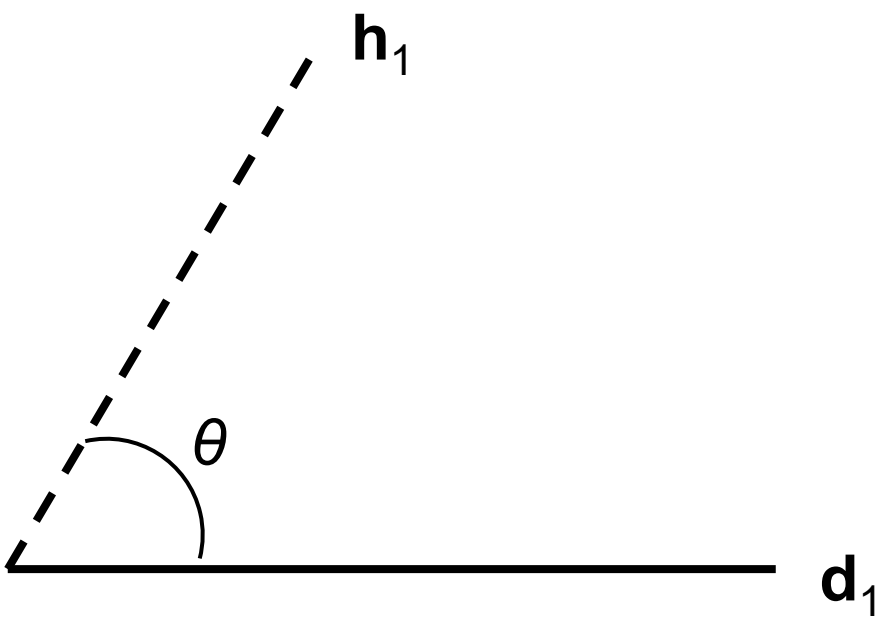
Tensor analysis:
How do **G** matrices differ the most?



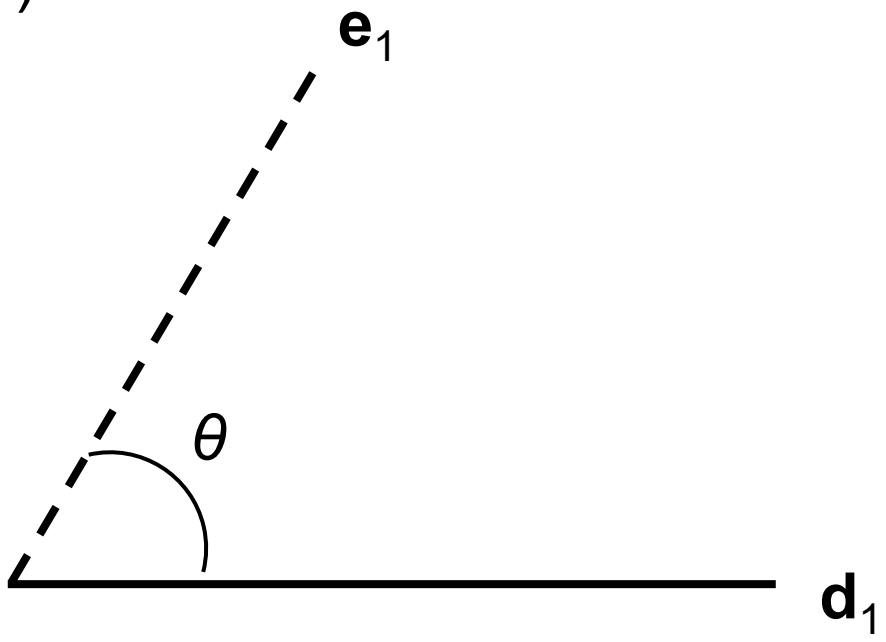


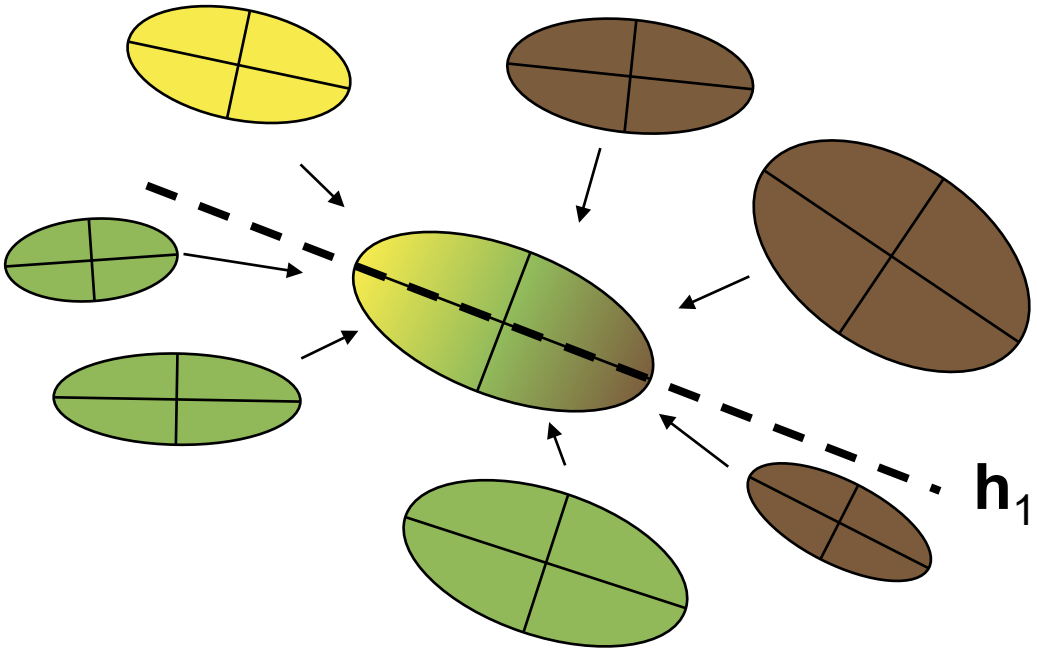
Aligned
$\theta < 36°$ ($P < 0.01$)





Not aligned
$\theta > 36°$ ($P > 0.01$)



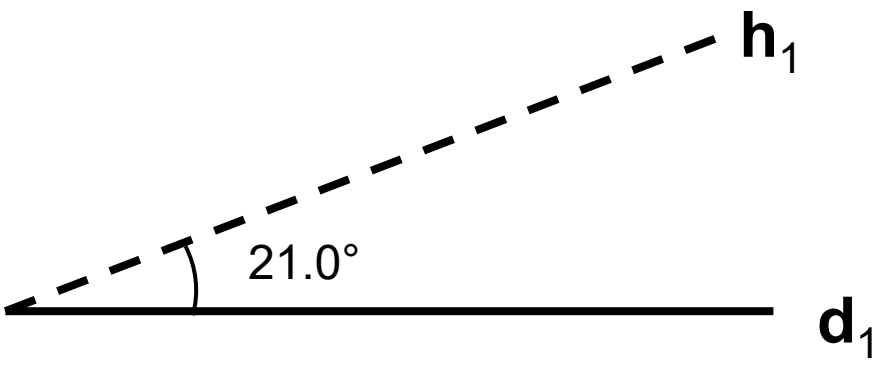


Common subspace analysis:
How are **G** matrices most similar?

	$\mathbf{h}_1$
avg % variance	52.8
jaw length	0.187
head width	0.139
pectoral	0.250
pelvis	0.197
humerus	0.500
ulna	0.491
femur	0.401
tibia	0.438

$\mathbf{h}_1$ explains 46 – 61% of variance within species

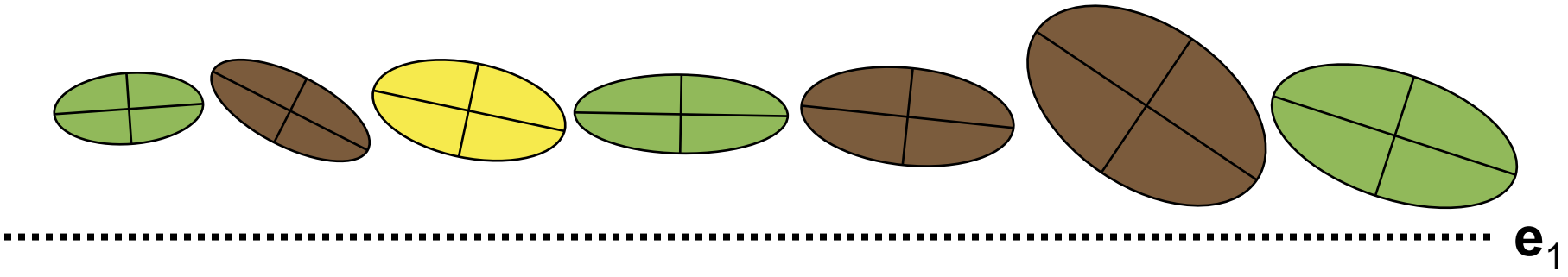
Similar to shared $\mathbf{g}_{max}$ (92% of $\mathbf{g}_{max}$)



	$\mathbf{d}_1$	$\mathbf{h}_1$
% variance	73.5	52.8
jaw length	0.017	0.187
head width	0.365	0.139
pectoral	0.140	0.250
pelvis	0.216	0.197
humerus	0.323	0.500
ulna	0.532	0.491
femur	0.373	0.401
tibia	0.522	0.438

Most divergence is aligned with $\mathbf{g}_{max}$

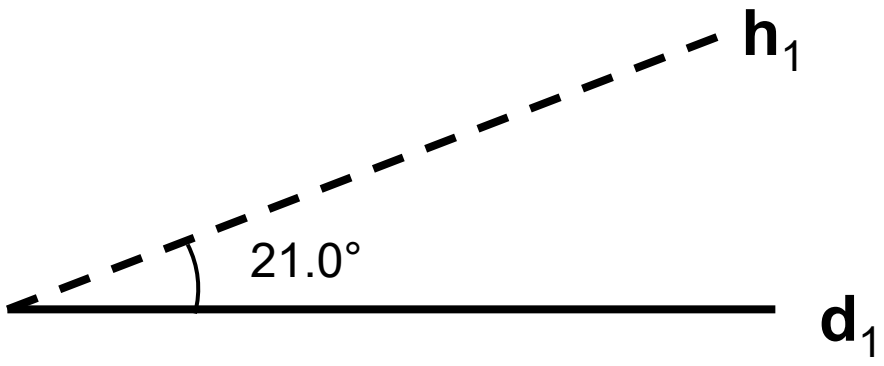
Tensor analysis:
How do **G** matrices differ the most?



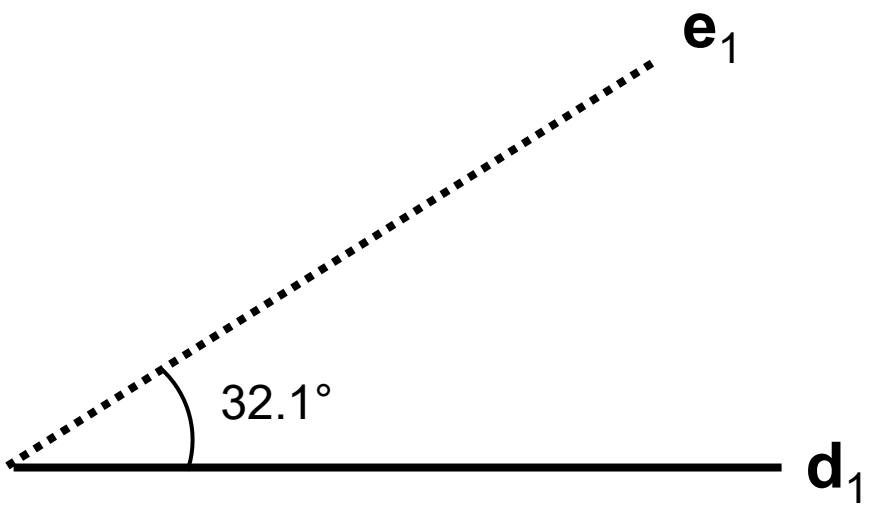
	$\mathbf{e}_1$
% variance	40.7
jaw length	-0.020
head width	0.006
pectoral	-0.104
pelvis	-0.019
humerus	0.459
ulna	0.411
femur	0.531
tibia	0.571

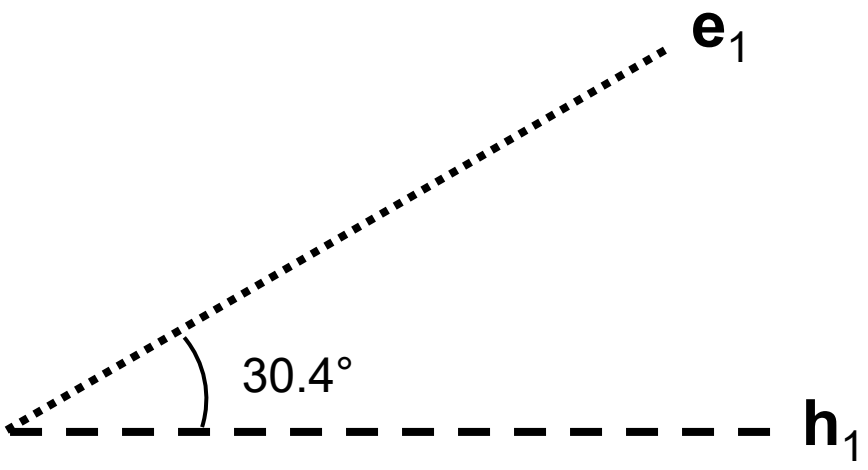
84% of variation among **G** matrices in 3 subspaces (“eigentensors”)

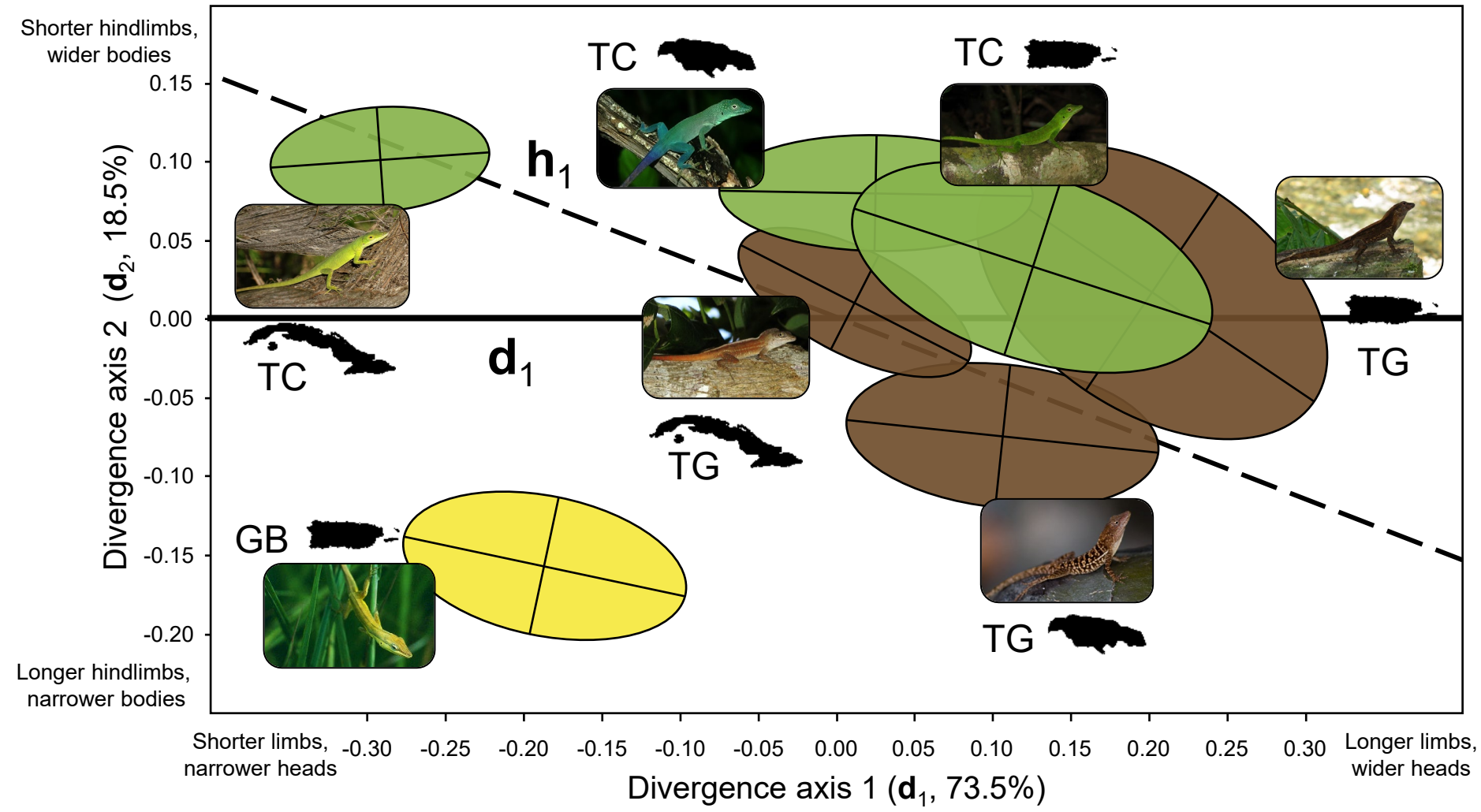
41% of variation explained by $\mathbf{e}_1$

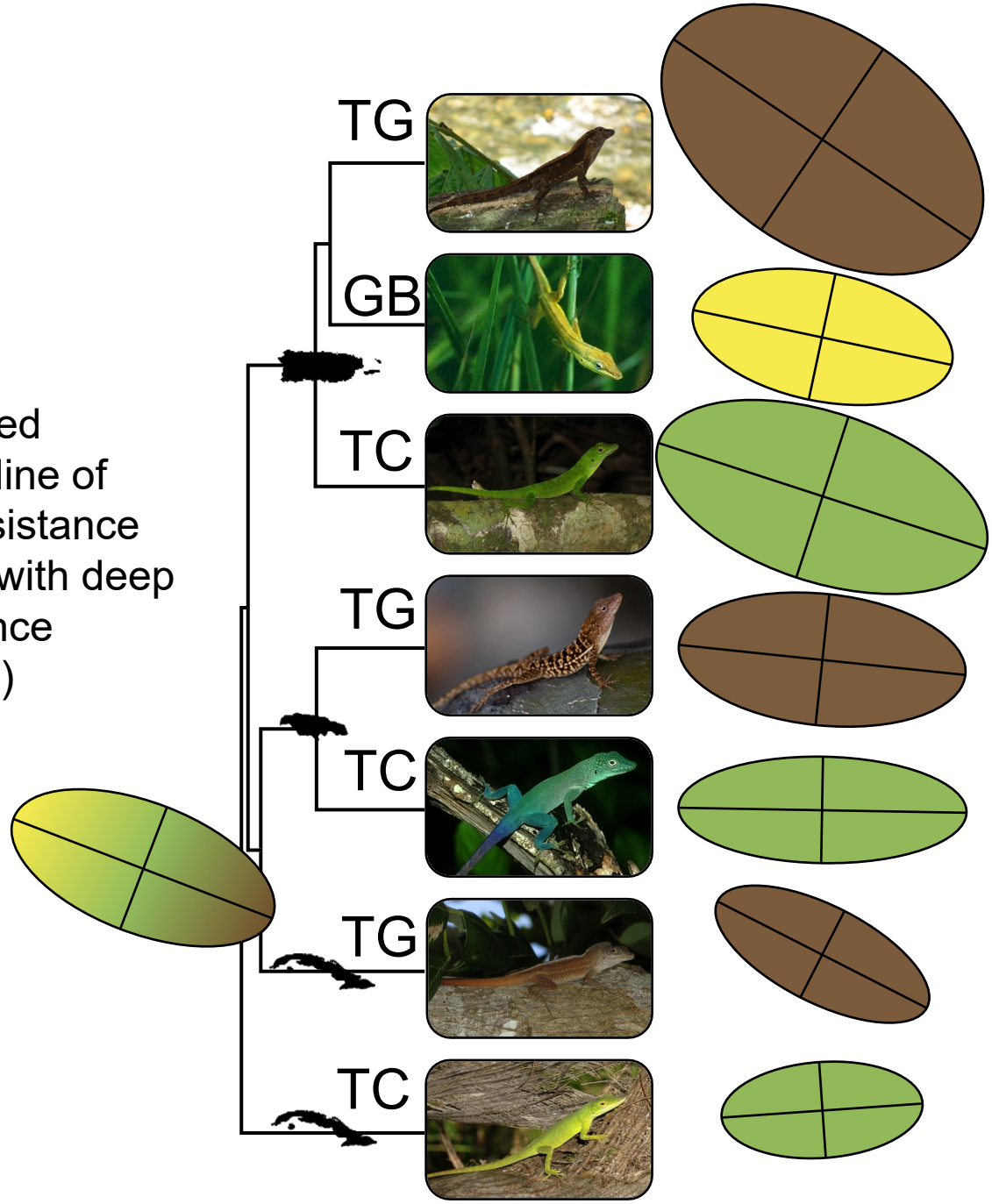


	d_1	h_1	e_1
% variance	73.5	52.8	40.7
jaw length	0.017	0.187	-0.020
head width	0.365	0.139	0.006
pectoral	0.140	0.250	-0.104
pelvis	0.216	0.197	-0.019
humerus	0.323	0.500	0.459
ulna	0.532	0.491	0.411
femur	0.373	0.401	0.531
tibia	0.522	0.438	0.571





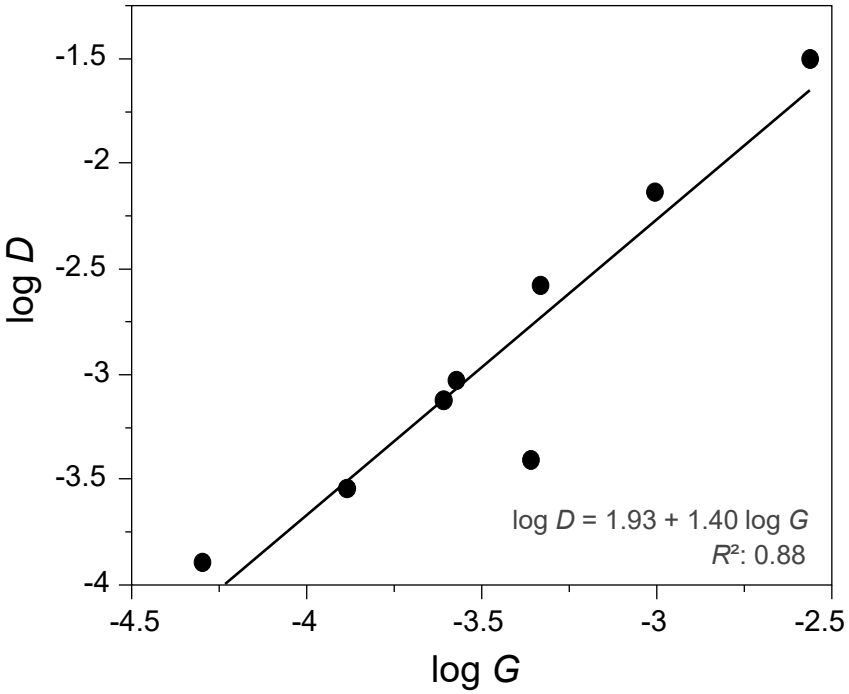

Shorter hindlimbs, wider bodies
Longer hindlimbs, narrower bodies
Divergence axis 2 (d2, 18.5%)
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
h1
d1
TC
TC
TC
TG
TG
TG
GB
Shorter limbs, narrower heads
-0.30
-0.25
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Longer limbs, wider heads
Divergence axis 1 (d1, 73.5%)

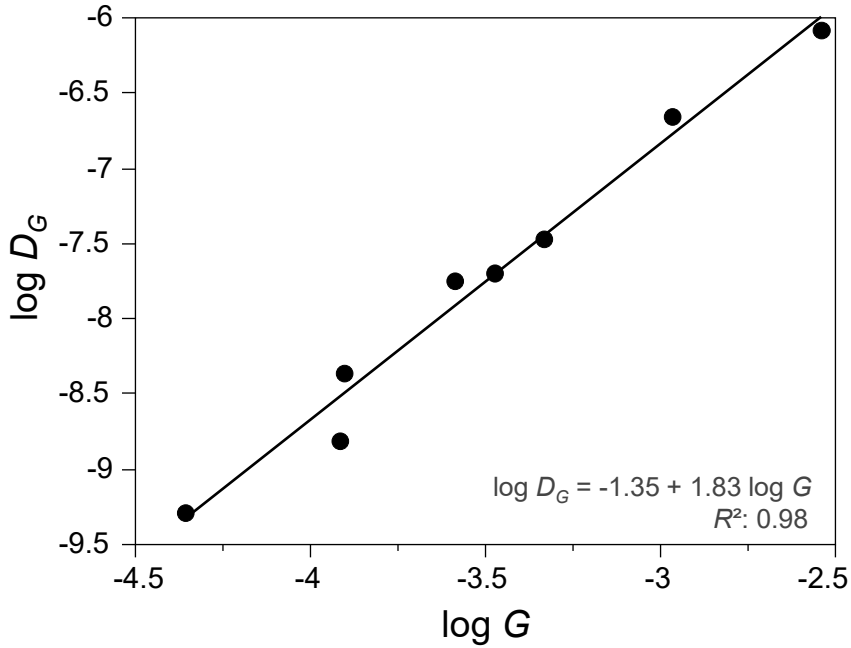


Deeply conserved genetic line of least resistance aligned with deep divergence (40+ my)

Triple alignment of divergence, $\mathbf{g}_{max}$, and change in **G**

Signature of constraint persists even as constraints evolve


-1.5
-2
-2.5
-3
-3.5
-4
log D
-4.5
-4
-3.5
-3
-2.5
log G
log D = 1.93 + 1.40 log G
R²: 0.88


-6
-6.5
-7
-7.5
-8
-8.5
-9
-9.5
log D_G
-4.5
-4
-3.5
-3
-2.5
log G
log D_G = -1.35 + 1.83 log G
R²: 0.98

Conclusions from *Anolis* work

General discussion