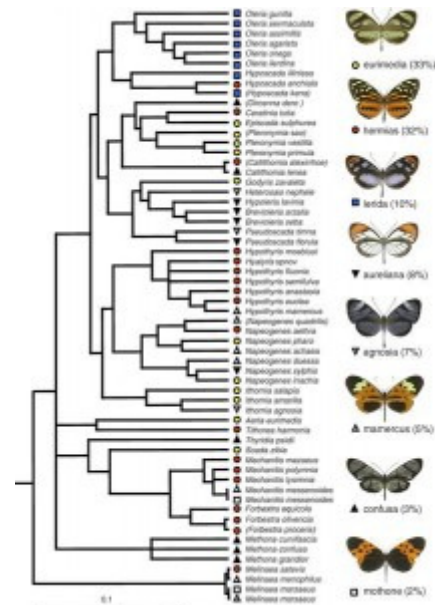




1. The correlation structure of interspecific data

2. Different scenarios of selection / drift

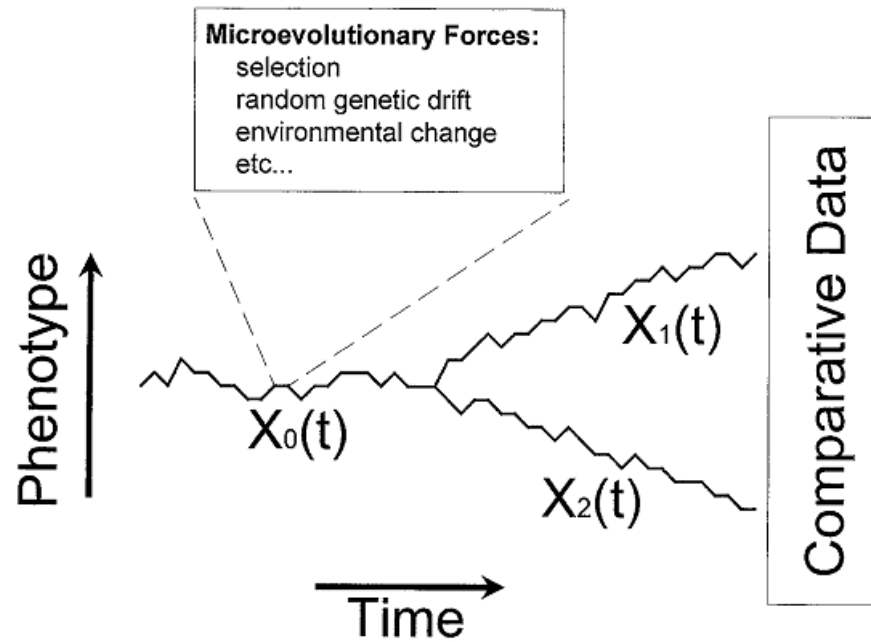
3. Change by mutation - directional selection



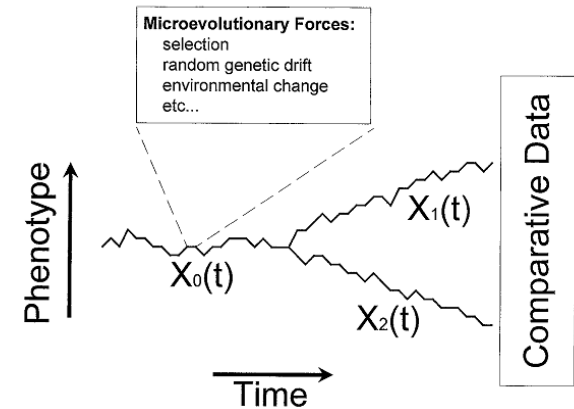
# 1. The correlation structure of interspecific data

Characterisation:

Markovian stochastic process evolving along a tree-like branching phylogeny



Species  $i$   
 Species  $j$   
 Most recent common ancestor  $v$



$$Cov[\underline{\mu}_i, \underline{\mu}_j] = Cov[E[\underline{\mu}_i | \mu_v], E[\underline{\mu}_j | \mu_v]] + E[Cov[\underline{\mu}_i, \underline{\mu}_j | \mu_v]]$$

$$\begin{aligned} E[Cov[\underline{\mu}_i, \underline{\mu}_j | \mu_v]] &= E[E[\underline{\mu}_i \underline{\mu}_j | \mu_v]] - E[E[\underline{\mu}_i | \mu_v] E[\underline{\mu}_j | \mu_v]] \\ &= E[\underline{\mu}_i \underline{\mu}_j] - E[E[\underline{\mu}_i | \mu_v] E[\underline{\mu}_j | \mu_v]] + E[\underline{\mu}_i] E[\underline{\mu}_j] - E[\underline{\mu}_i] E[\underline{\mu}_j] \\ &= Cov[\underline{\mu}_i, \underline{\mu}_j] - Cov[E[\underline{\mu}_i | \mu_v], E[\underline{\mu}_j | \mu_v]] \end{aligned}$$

When evolutionary changes after  $\mu_v$  are independent in  $i$  and  $j$ , then

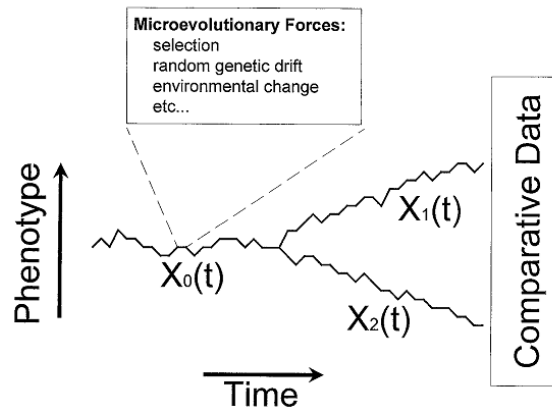
$$Cov[\underline{\mu}_i, \underline{\mu}_j | \mu_v] = 0$$

GAUSSIAN PROCESS (GRADUAL CHANGE)  
RENEWAL PROCESS (BURSTS OF CHANGE)

see appendix of Hansen and Martins (1996)

A diffusion process where the infinitesimal mean and variance are linear in the state variables and with suitable initial conditions, will produce collections of states of independently running processes which are MVN distributed.

The trait vectors of species on a tree can be shown to have MVN distributions, if the root phenotype has a MVN distribution.



## JUST DRIFT

The mean trait vector of a species changes as

$$\Delta \underline{\mu}(t) = \underline{\mu}(t+1) - \underline{\mu}(t)$$

With only drift, it changes according the distribution  $N\left(\mathbf{0}, \frac{\mathbf{G}(t)}{N_e^{(v)}}\right)$

if  $\mathbf{G}$  is assumed constant

$\underline{\mu}(t)$  changes according the distribution  $N\left(\underline{\mu}(0), \frac{\mathbf{G}}{N_e^{(v)}} t\right)$

The covariance between species becomes

$$\text{cov}(\underline{\mu}_i, \underline{\mu}_j) = \text{cov}(E[\underline{\mu}_i | \underline{\mu}_z], E[\underline{\mu}_j | \underline{\mu}_z]) = \frac{\mathbf{G}t_z}{N_e^{(v)}}$$

When there is an equilibrium between drift and mutation in finite populations:

$$\text{cov}(\underline{\mu}_i, \underline{\mu}_j) = \text{cov}(E[\underline{\mu}_i | \underline{\mu}_z], E[\underline{\mu}_j | \underline{\mu}_z]) = 2G_m t_z$$

Effective population size can be simplified away.

The covariance between species is proportional to the time they evolved as a single lineage, before the split.

! It is assumed that the variance at the root of the tree is zero.

## Random Genetic Drift

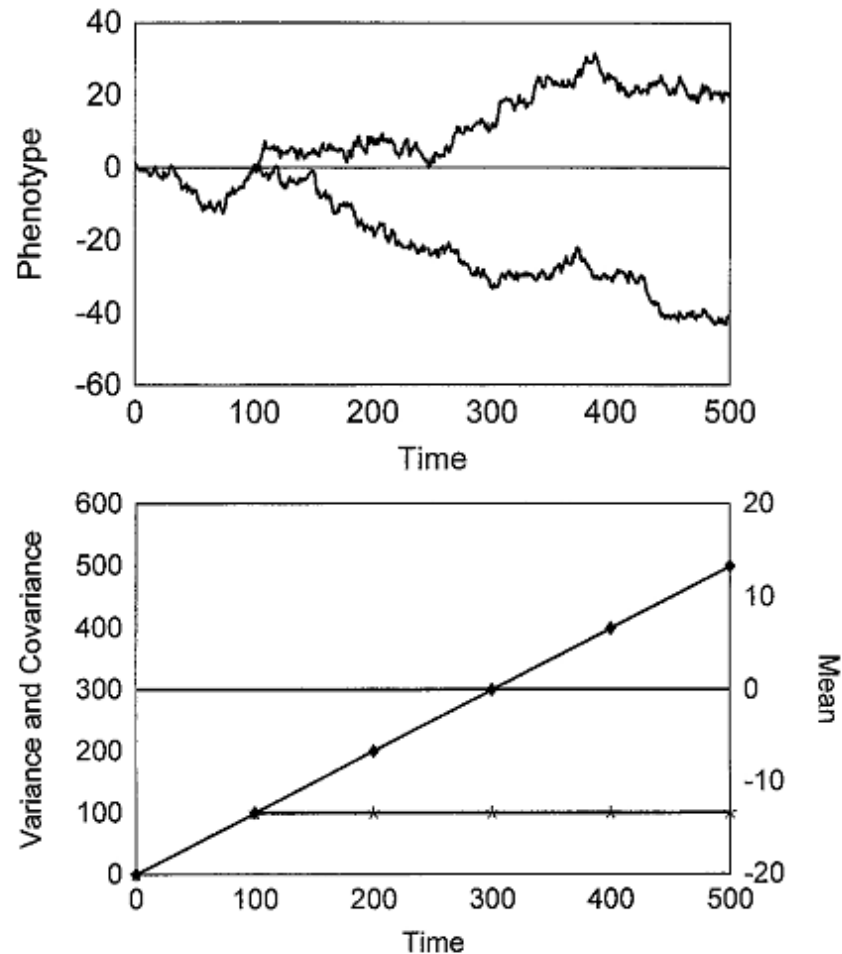


FIG. 3. An illustration of phenotypic change expected under a Brownian motion model of phenotypic evolution under random genetic drift. Brownian motion can also be used to describe phenotypic evolution under fluctuating, but on average undirected, directional selection. Diamonds show changes in the variance through phylogenetic time, asterisks denote changes in the covariance, and the solid line denotes shifts in the expectation of the phenotype.



## DIRECTIONAL SELECTION

A. Brownian motion with a trend  $G\beta$

(unfortunately called drift in diffusion language)

ignoring the change in  $G$  caused by selection

B. If the strength and direction of selection fluctuates

$\underline{\beta} = P^{-1}\underline{s}$  becomes a random variable with distribution  $N(\underline{\beta}, V_{\beta})$

A. The result is a diffusion process with a trend equal to  $G\beta$  and

$$\text{variance} \left( \frac{\mathbf{G}}{N_e^{(v)}} \right) t$$

We get

$$\text{cov}(\underline{\mu}_i, \underline{\mu}_j) = \text{cov}(E[\underline{\mu}_i | \mu_z], E[\underline{\mu}_j | \mu_z]) = \left( \frac{\mathbf{G}}{N_e^{(v)}} \right) t_z$$

B. The result is a diffusion process with a trend equal to  $\mathbf{G}\beta$  and

$$\text{variance} \left( \frac{\mathbf{G}}{N_e^{(v)}} + \mathbf{G}\mathbf{V}_\beta\mathbf{G} \right) t$$

We get

$$\text{cov}(\underline{\mu}_i, \underline{\mu}_j) = \text{cov}(E[\underline{\mu}_i | \underline{\mu}_z], E[\underline{\mu}_j | \underline{\mu}_z]) = \left( \frac{\mathbf{G}}{N_e^{(v)}} + \mathbf{G}\mathbf{V}_\beta\mathbf{G} \right) t_z$$

## Directional Selection

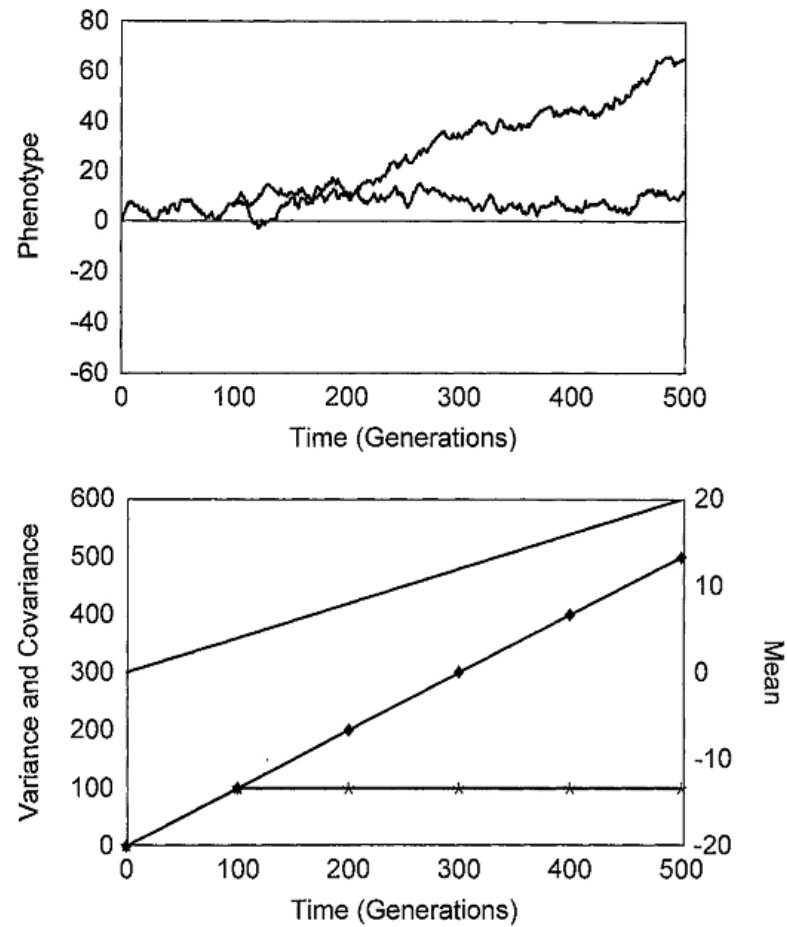


FIG. 4. An illustration of phenotypic change expected under a model of directional selection (Brownian motion with a trend). The random fluctuations can be due to random genetic drift or random fluctuations in the selection differential. Diamonds show changes in the variance through phylogenetic time, asterisks denote changes in the covariance, and the solid line denotes shifts in the expectation of the phenotype.

## STABILIZING SELECTION

According exponential function  $w$

*Weak selection  $W \ll P$*

the mean phenotype changes according  $-GW(\underline{\mu} - \theta)$

Ornstein Uhlenbeck process – rubber band process

$\underline{\mu}(t)$  changes according an ugly distribution;  $G$  is assumed constant

$$E[\underline{\mu}(t) | \underline{\mu}(z)] = \exp[-GWt]\underline{\mu}(z) + (\mathbf{I} - \exp[-(GW)^T t])\theta$$

The variance approaches an equilibrium

$$V(t) = (2N_e^{(v)}W)^{-1}$$

if the variance at the root is set at zero.

The correlation between species phenotypes becomes for a single trait  
and a stationary process

$$\text{corr}(\underline{\mu}_i, \underline{\mu}_j) = \exp(-Gwt_{i \leftrightarrow j})$$

The correlation between species averages decreases exponentially with  
phylogenetic distance

## Stabilizing Selection

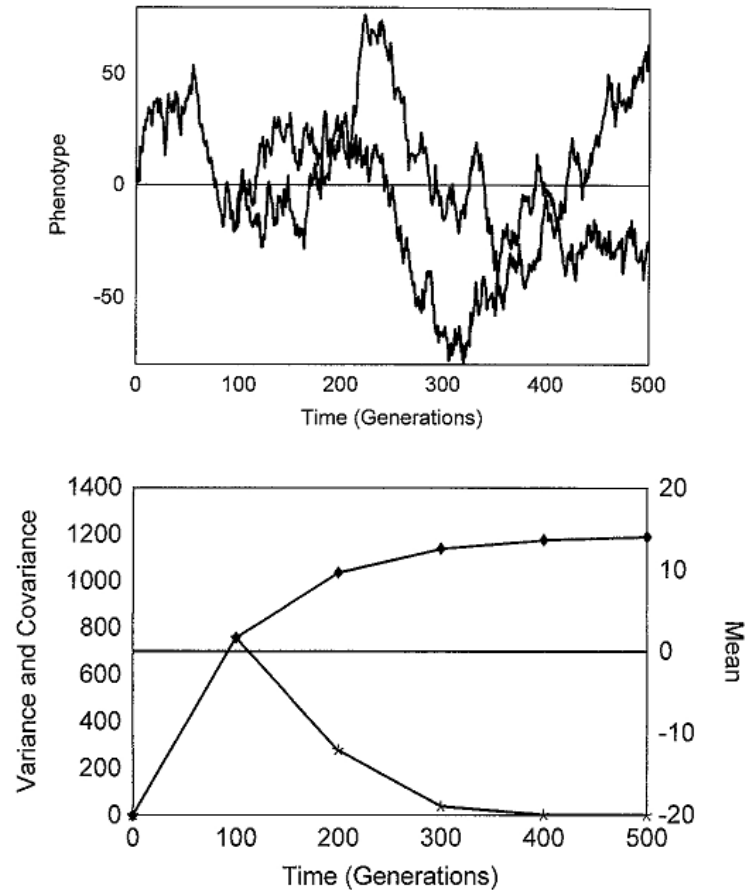


FIG. 5. An illustration of phenotypic change expected under stabilizing selection with random fluctuations due to random genetic drift or short scale fluctuations of the optimum (an Ornstein-Uhlenbeck process). In this illustration, the phenotype is pulled towards an (average) optimum of zero. Diamonds show changes in the variance through phylogenetic time, asterisks denote changes in the covariance, and the solid line denotes shifts in the expectation of the phenotype.

## WITH ENVIRONMENTAL CHANGE

Large jumps in optima: as if selection were directional  
The optimum fluctuates fast: exponential decrease in covariance between  
species with phylogenetic distance

## PUNCTUATED EQUILIBRIUM

Bursts of phenotypic evolution at random points in time.

A renewal counting process  
Counts the number of events until time  $t$



## Burst-like Change

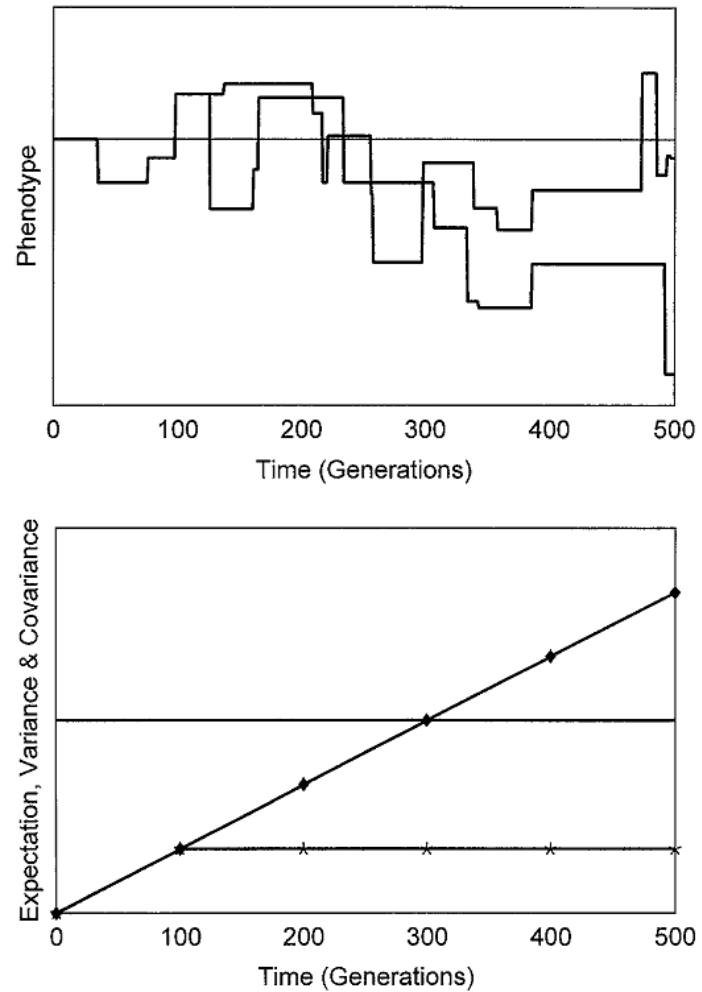
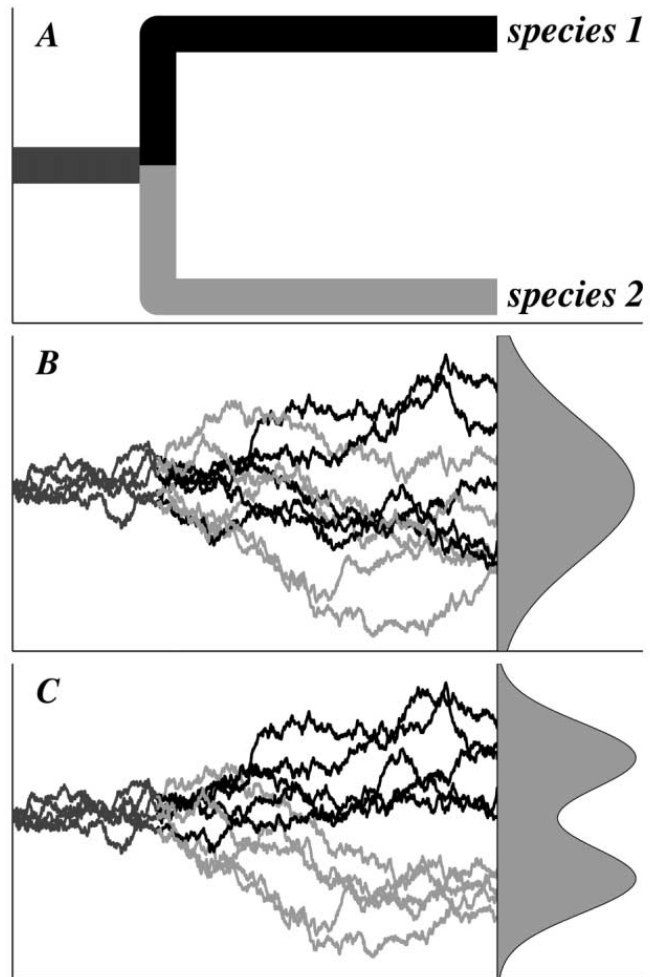
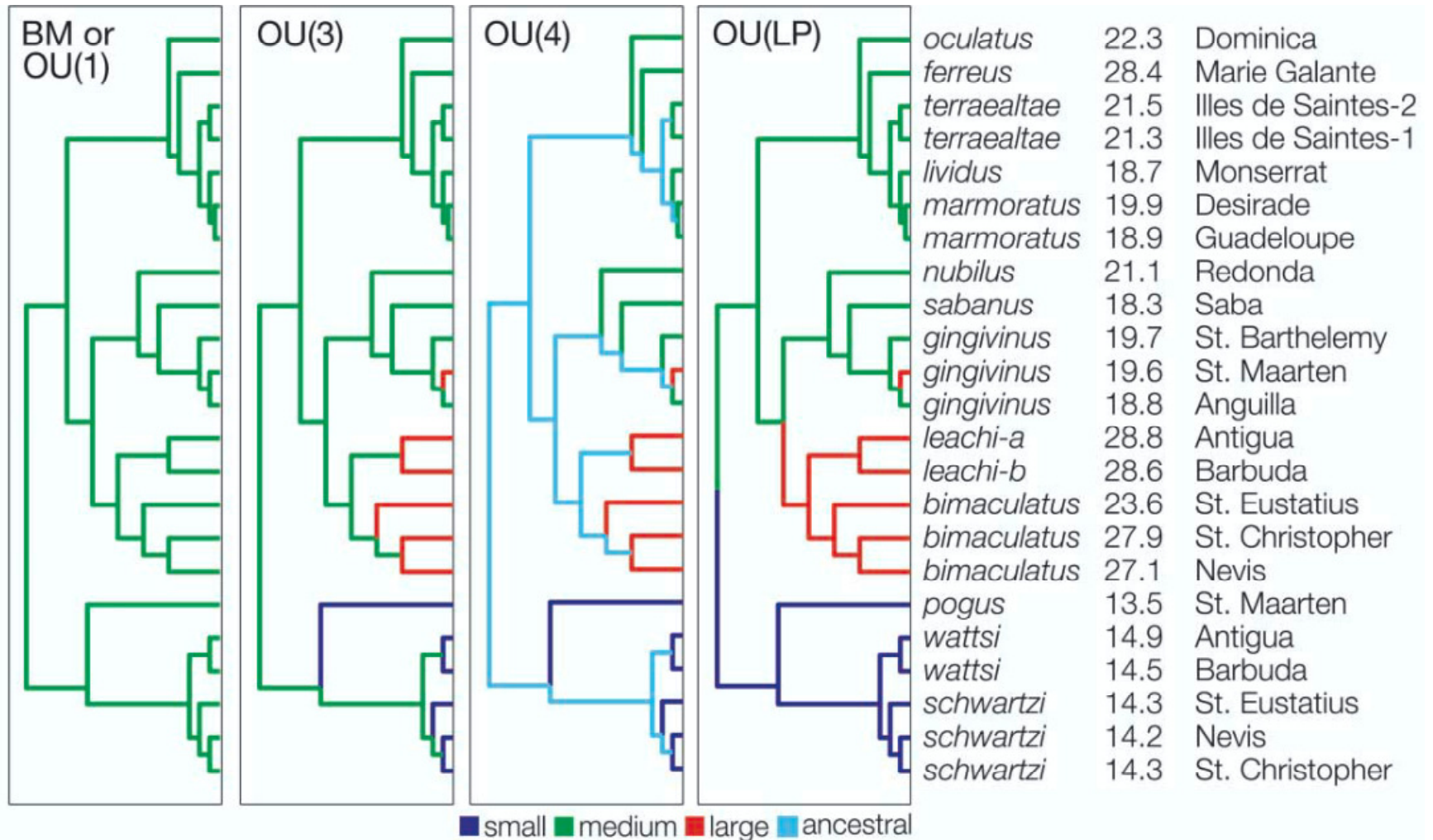


FIG. 6. An illustration of phenotypic change under a model of punctuated change occurring at random points in time. Although evolutionary change according to this model is quite different from evolutionary change under the Brownian motion model illustrated in Figure 3, changes in the means, variances and covariances of

We want to compare evolutionary models





alternative models for character displacement in *Anolis* (Butler and King 2004)

Table 1: Performance of alternative models for body size evolution in the character displacement study

	BM	OU(1)	OU(3)	OU(4)	OU(LP)
$-2 \log \mathcal{L}$	-34.66	-34.66	-40.21	-47.22	-49.69
AIC	-30.66	-26.66	-28.21	-33.22	-37.69
SIC	-28.39	-22.12	-21.40	-25.27	-30.88
LR		0	5.55	12.56	15.03
<i>P</i> value		1	.24	.028	.0046

Note: For each model, the likelihood values ( $-2 \log \mathcal{L}$ ), Akaike Information Criterion (AIC), likelihood ratio test value (LR), and associated *P* values are given. The LR tests were conducted for each model versus Brownian motion. Columns contain alternative evolutionary models. Model abbreviations are as follows: BM = Brownian motion, OU = Ornstein-Uhlenbeck with one (1), three (3), or four (4) optima or based on linear parsimony (LP) reconstruction of the colonization events (see text). For the OU(1) model, the best-fit  $\alpha = 0$ ; therefore, the OU(1) and BM models are identical.

## Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution

Marguerite A. Butler<sup>\*</sup> and Aaron A. King<sup>†</sup>

## A DIFFERENT DERIVATION

~ DIRECTIONAL SELECTION A.

Hill (1982a&b) found, for a completely additive genetic model and a constant selection differential  $s$  that the asymptotic response to selection becomes

$$\Delta\mu_{z,\infty} = 2N_e^{(v)}\mathbf{G}_m\mathbf{P}^{-1}\mathbf{s}$$

where  $N_e^{(v)}$  is the so-called variance effective population size, a scaled measure of true population size.

The instantaneous phenotypic change per generation coming from new mutations equals

$$\Delta\mu_z = \mathbf{G}_m\mathbf{P}^{-1}\mathbf{s}$$

## A DIFFERENT DERIVATION

~ DIRECTIONAL SELECTION A.

$$\Delta\mu_z = G_m P^{-1} s$$

This result can be incorporated in the comparative models discussed above. This hasn't happened yet and mutation is only assumed and discussed for the basic Brownian motion model.

It is a result halfway quantitative genetics and adaptive dynamics.

It bridges the different approaches and could act as a landmark for further developments.

## References

- Hansen, T. F. and E. P. Martins. 1996. Translating between microevolutionary process and macroevolutionary patterns: the correlation structure of interspecific data. *Evolution* 50:1404-1417.
- Hill, W. G. 1982. Predictions of response to artificial selection from new mutations. *Genetical Research* 40: 255-278.
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