

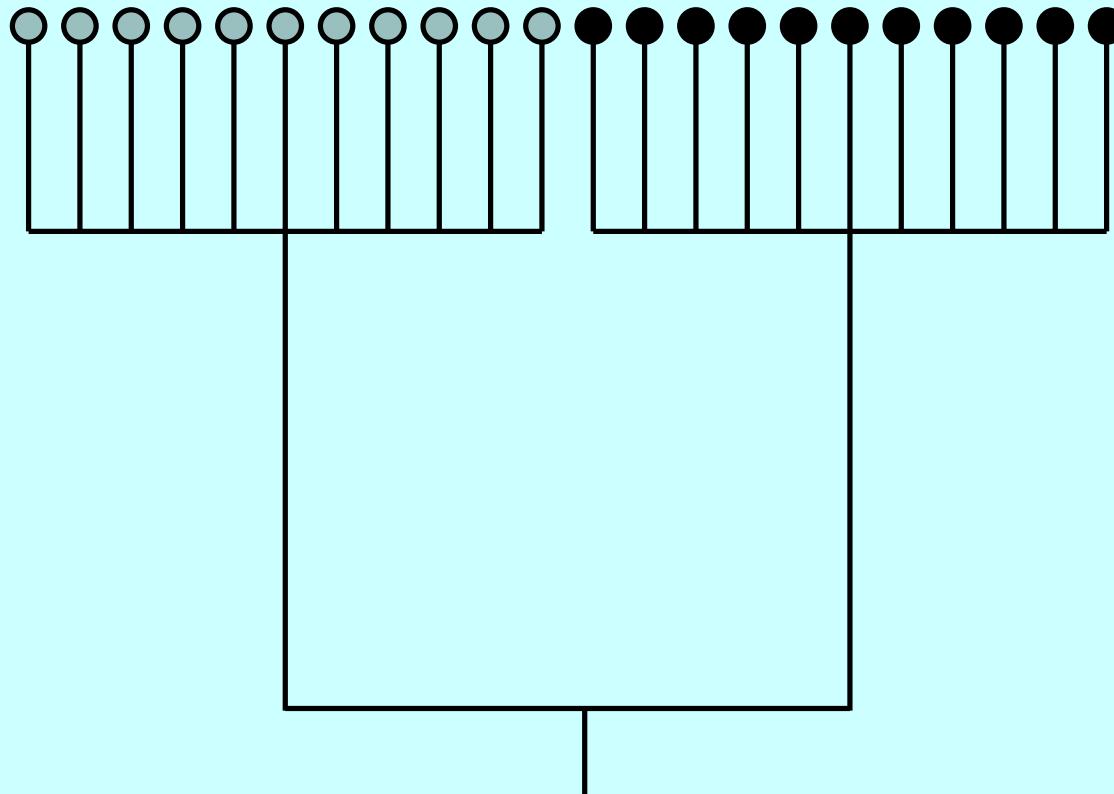
# **Comparative method and phylogenies**

7 August 2014.

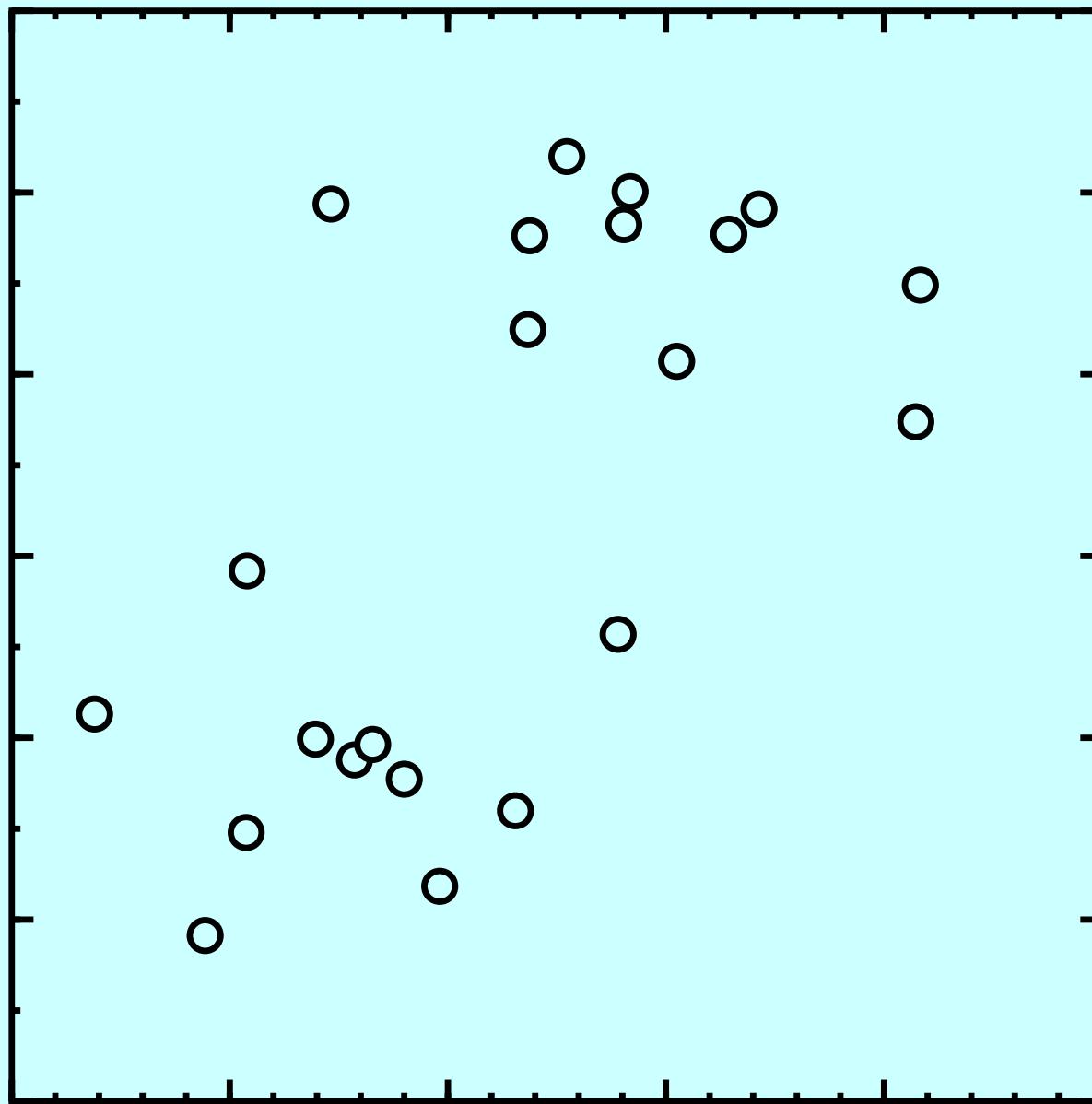
Joe Felsenstein

NIMBioS Tutorial on Evolutionary Quantitative Genetics

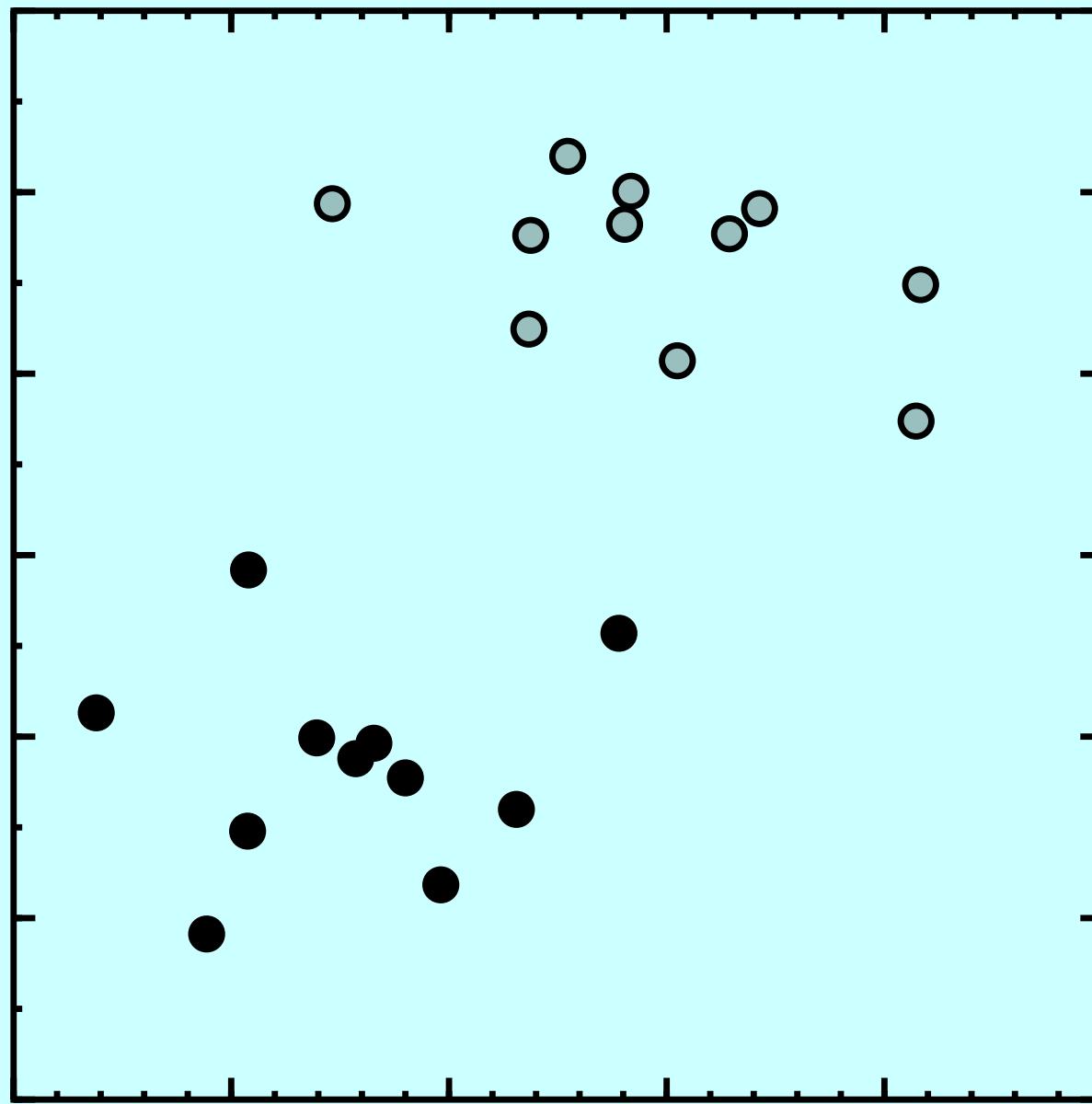
## A simple case to show effects of phylogeny



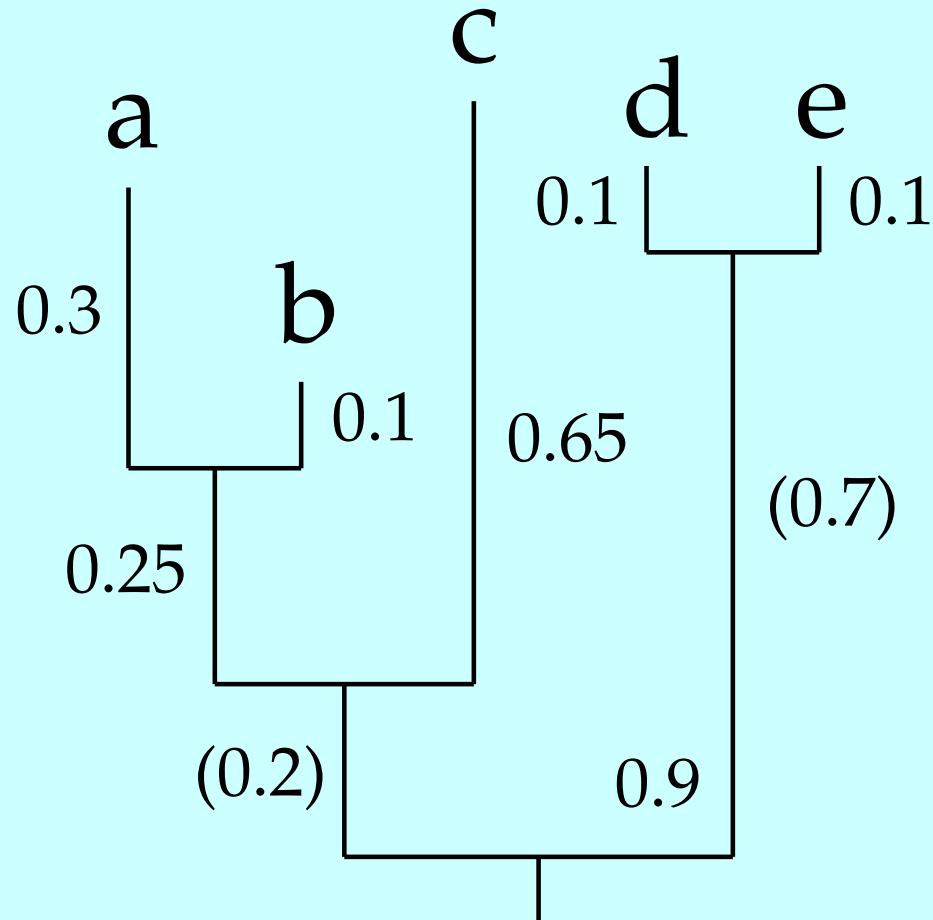
**Two uncorrelated characters evolving on that tree**



## Identifying the two clades



## A tree on which we are to observe two characters



## Contrasts on that tree

Contrast

Variance  
proportional  
to

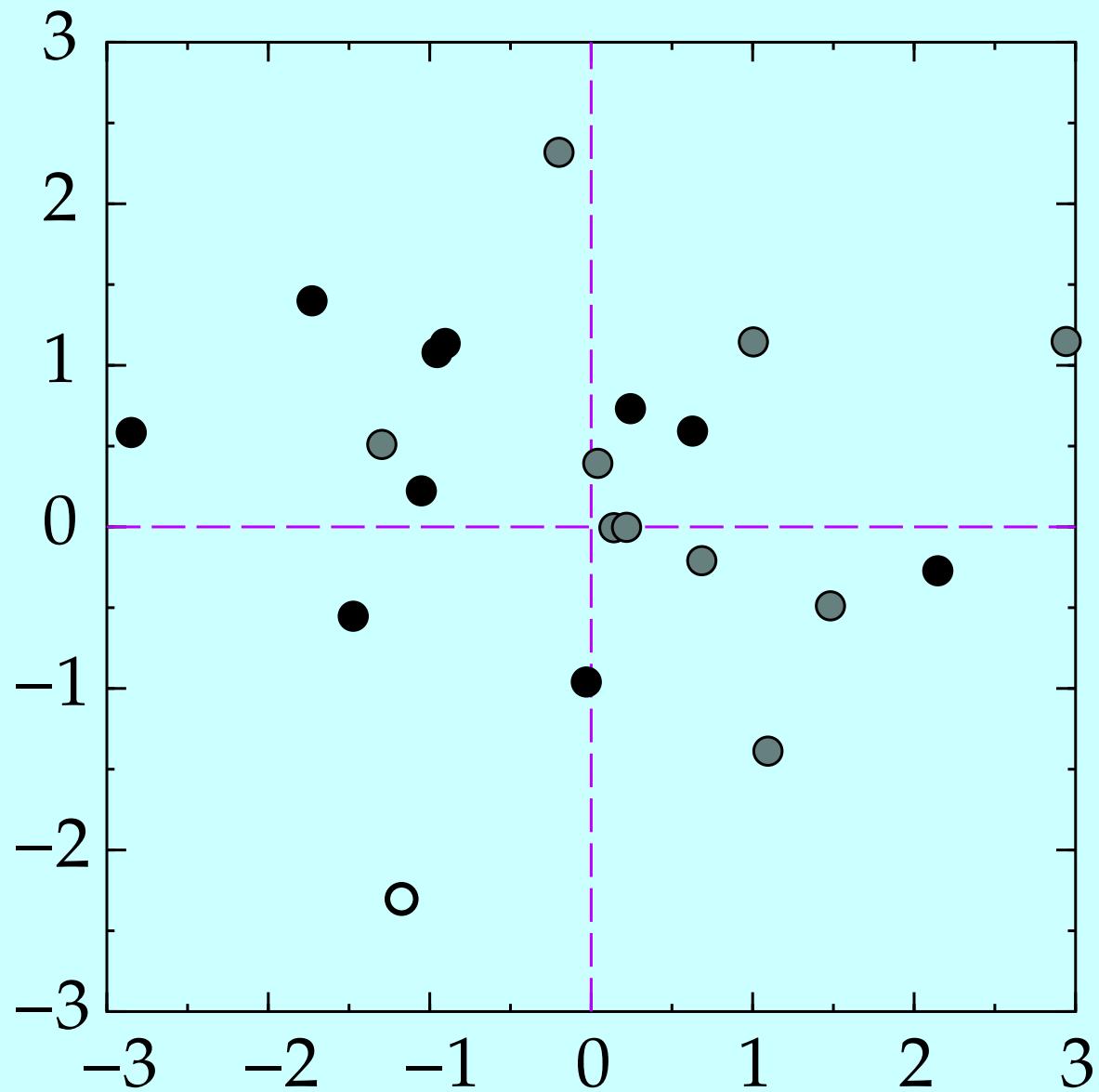
$$y_1 = x_a - x_b \quad 0.4$$

$$y_2 = \frac{1}{4} x_a + \frac{3}{4} x_b - x_c \quad 0.975$$

$$y_3 = \quad \quad \quad x_d - x_e \quad 0.2$$

$$y_4 = \frac{1}{6} x_a + \frac{1}{2} x_b + \frac{1}{3} x_c - \frac{1}{2} x_d - \frac{1}{2} x_e \quad 1.11666$$

## Contrasts for the 20-species two-clade example



## The algebra

If  $\mathbf{T}$  is the covariances of  $n$  tips on the tree, and  $\mathbf{V}$  is the (unknown) covariances of the Brownian motion of the  $p$  characters, the log-likelihood of a set of characters (stacked as a vector)  $\mathbf{x}$  is

$$\ln L = -(np/2) \ln(2\pi) - (1/2) \ln |\mathbf{T} \otimes \mathbf{V}| - (1/2)(\mathbf{x} - \boldsymbol{\mu})^t (\mathbf{T} \otimes \mathbf{V})^{-1} (\mathbf{x} - \boldsymbol{\mu})$$

If  $\mathbf{C}$  is an  $(n - 1) \times n$  set of contrasts, each orthogonal to the grand mean, such that  $\mathbf{C}\mathbf{C}^t$  is an  $n - 1$ -dimensional identity matrix, then taking the density of the transformed data  $\mathbf{y} = \mathbf{C} \mathbf{x}$ , this has expectation vector  $\mathbf{0}$ :

$$\ln L = K - (1/2) \ln |\mathbf{I}_{n-1} \otimes \mathbf{V}| - (1/2)\mathbf{y}^t (\mathbf{I}_{(n-1)} \otimes \mathbf{V})^{-1} \mathbf{y}$$

(where  $K$  collects the constant stuff, including the  $\ln(v_1 + v_2)$ ) Jacobian term.

## ... simplifying ...

This can also be expressed as

$$\ln L = K - ((n-1)/2) \ln |\mathbf{V}| - (1/2) \text{tr} (\mathbf{S}\mathbf{V})^{-1}$$

where

$$\mathbf{S} = \sum_i \mathbf{y}^{(i)} \left( \mathbf{y}^{(i)} \right)^t$$

is the  $p \times p$  sum of squares matrix of characters across contrasts.  
Inferring the Brownian motion phylogenetic covariances by maximum likelihood we find that

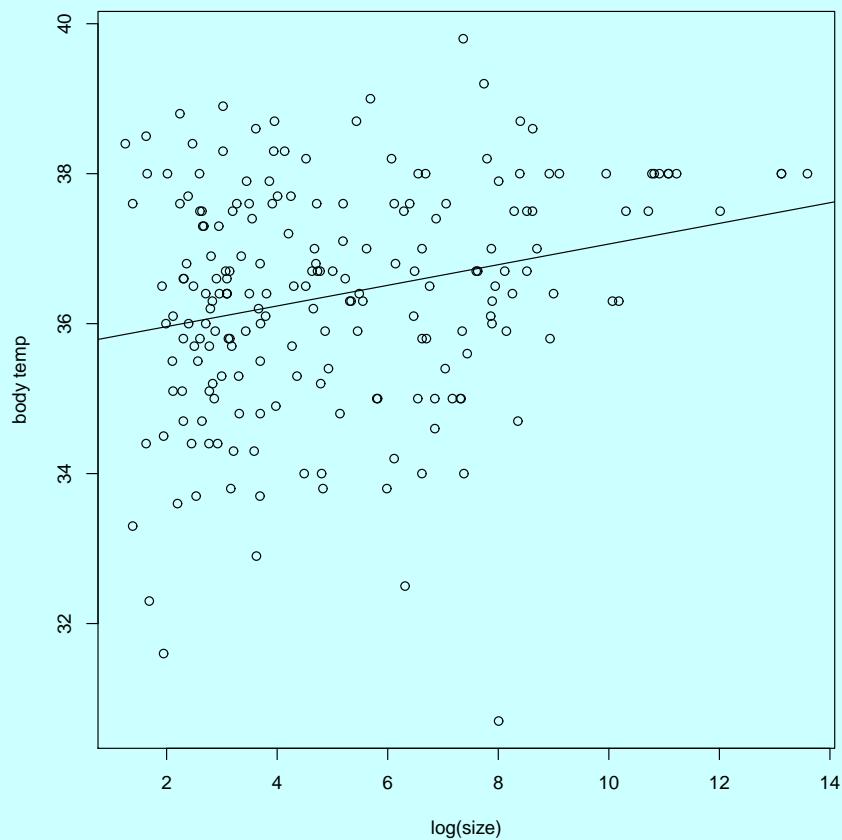
$$\widehat{\mathbf{V}} = \mathbf{S}/(n-1)$$

which leads to

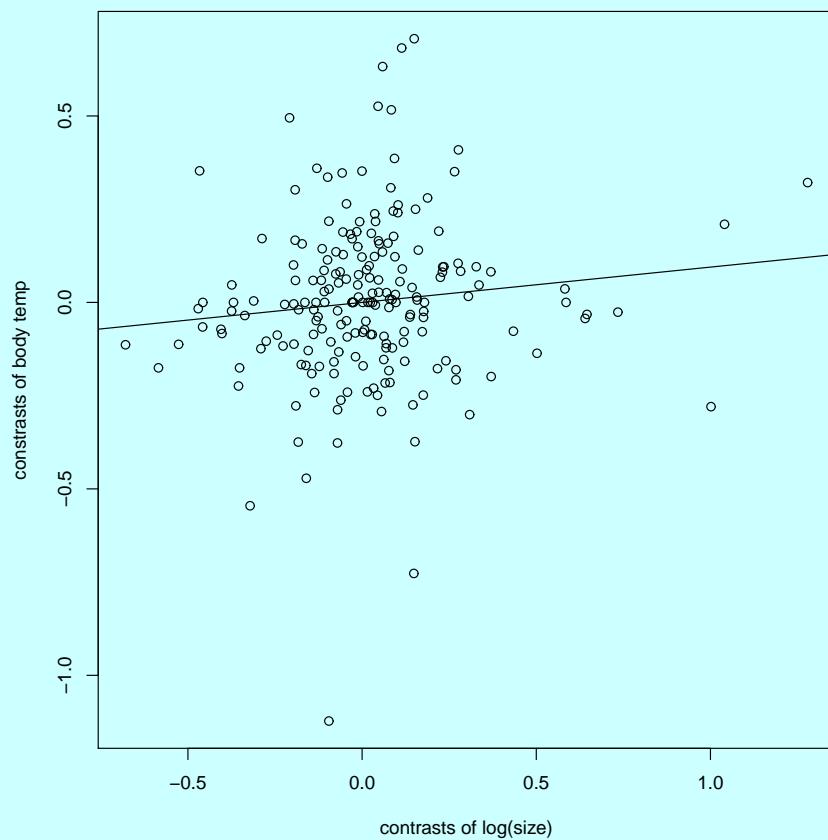
$$\ln L = K' - ((n-1)/2) \ln |\widehat{\mathbf{V}}|$$

## An example: Riek and Geiser, 2013

Alexander Riek and Fritz Geiser. 2013. Allometry of thermal variables in mammals: consequences of body size and phylogeny. *Biological Reviews* 88 (3): 564-572.



body temperature vs. log(body size)  
( $P$  for slope  $\neq 0$  is 0.000375)



contrasts vs. contrasts  
( $P$  for slope  $\neq 0$  is 0.116)

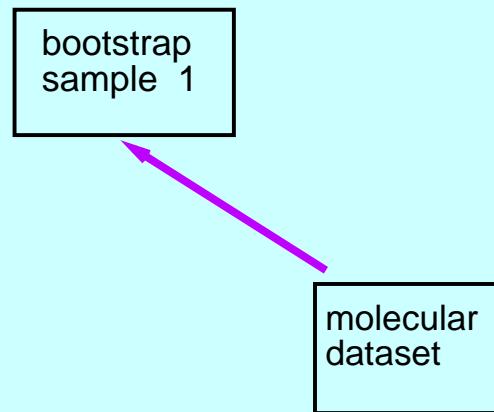
# When the tree is noisy: Propagating bootstrap sampling

morphological  
data

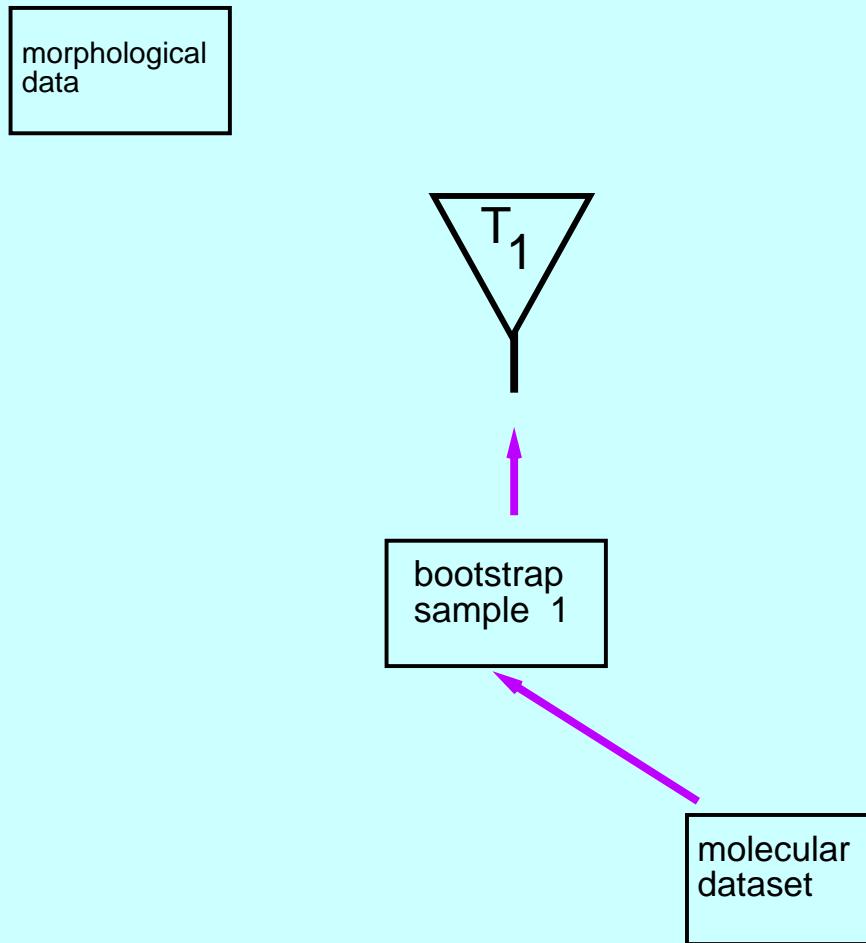
molecular  
dataset

# Propagating bootstrap sampling

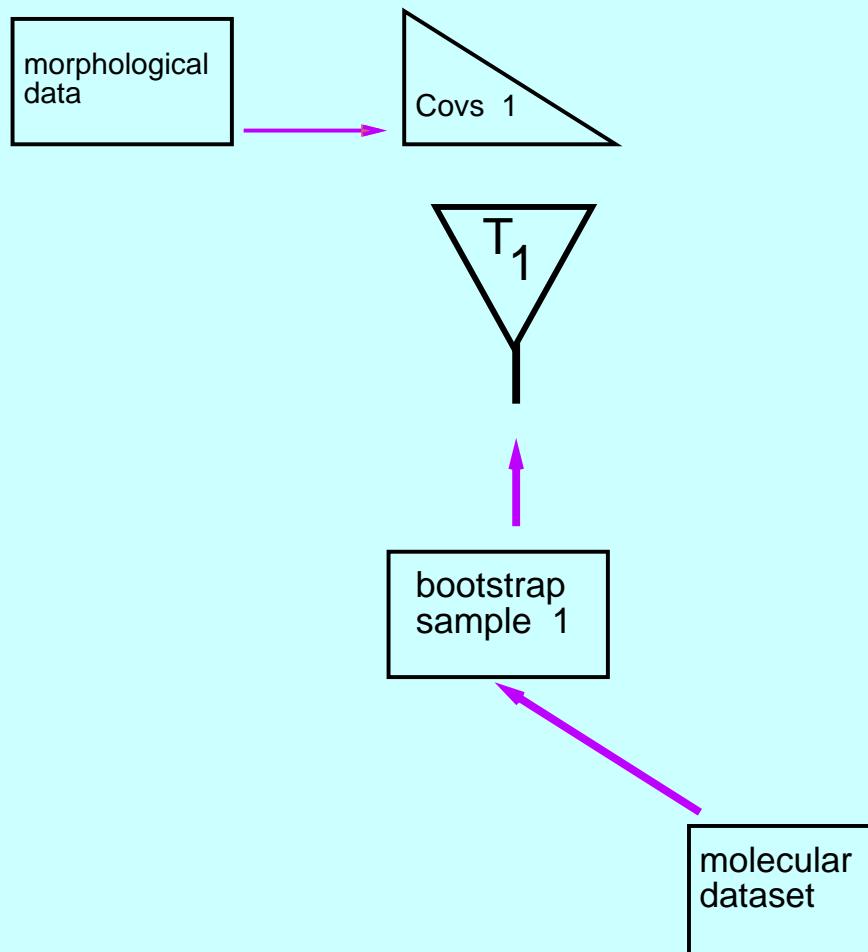
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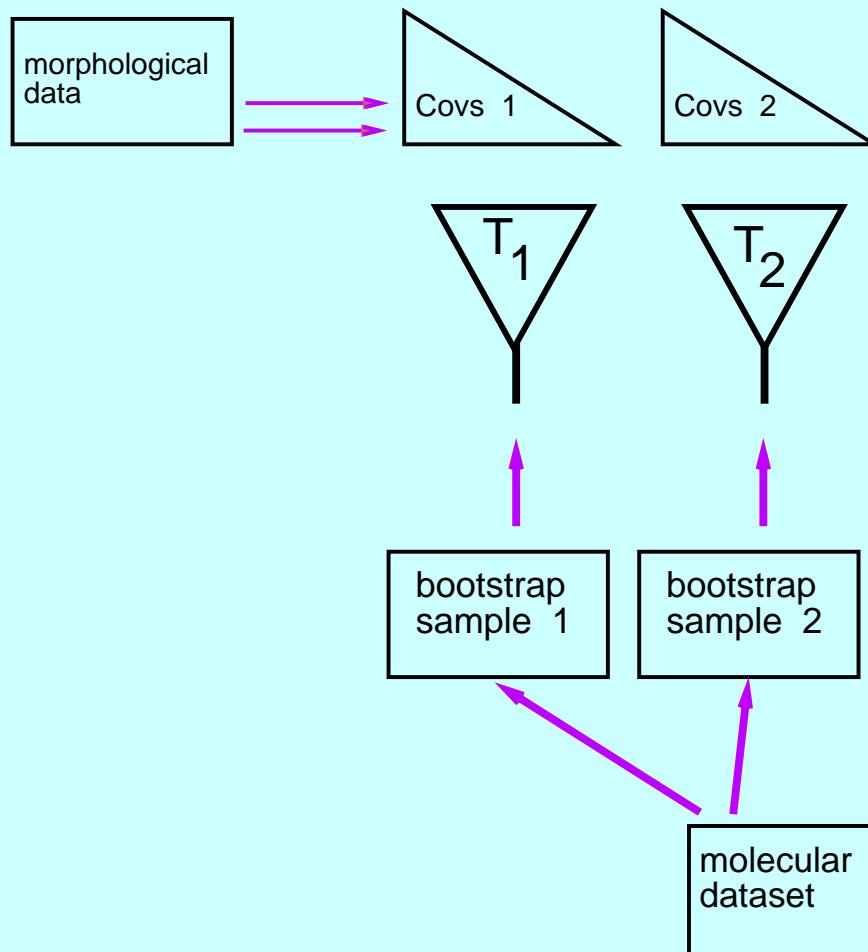
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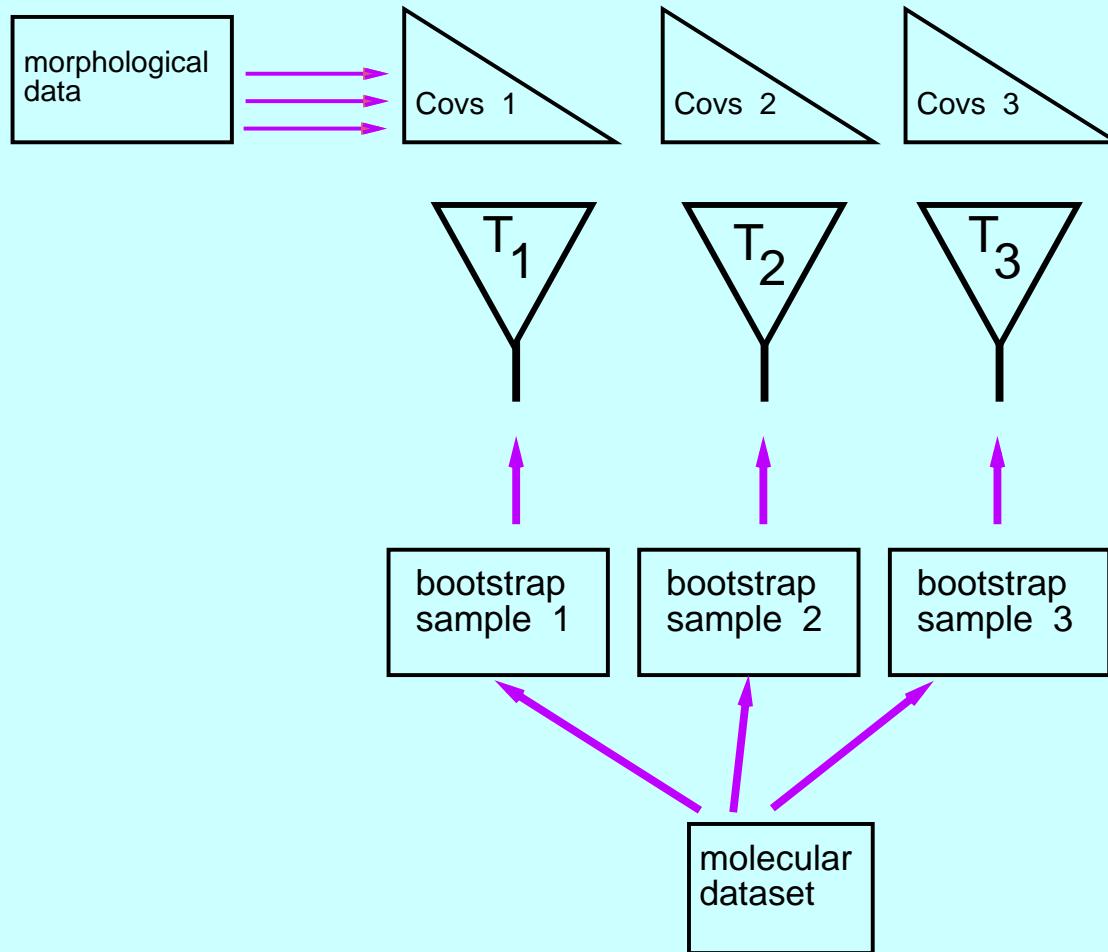
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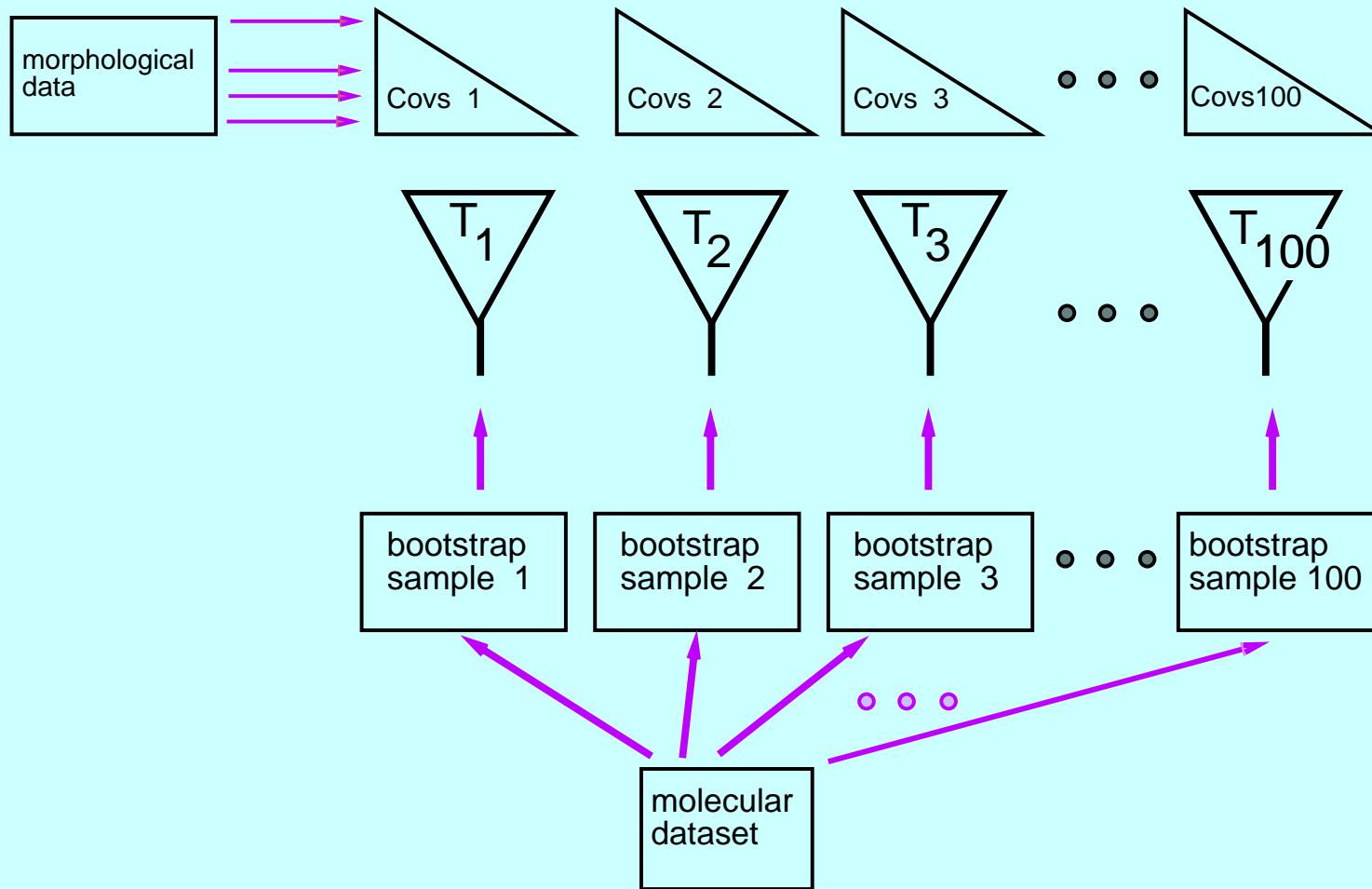
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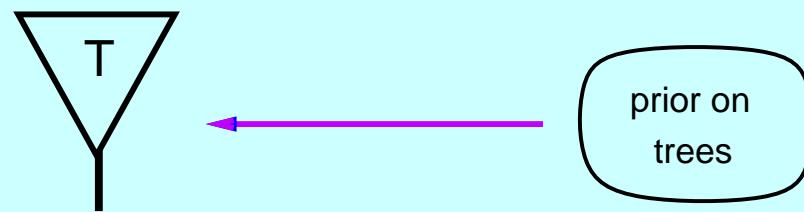
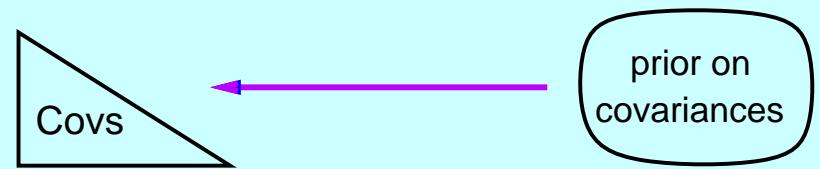
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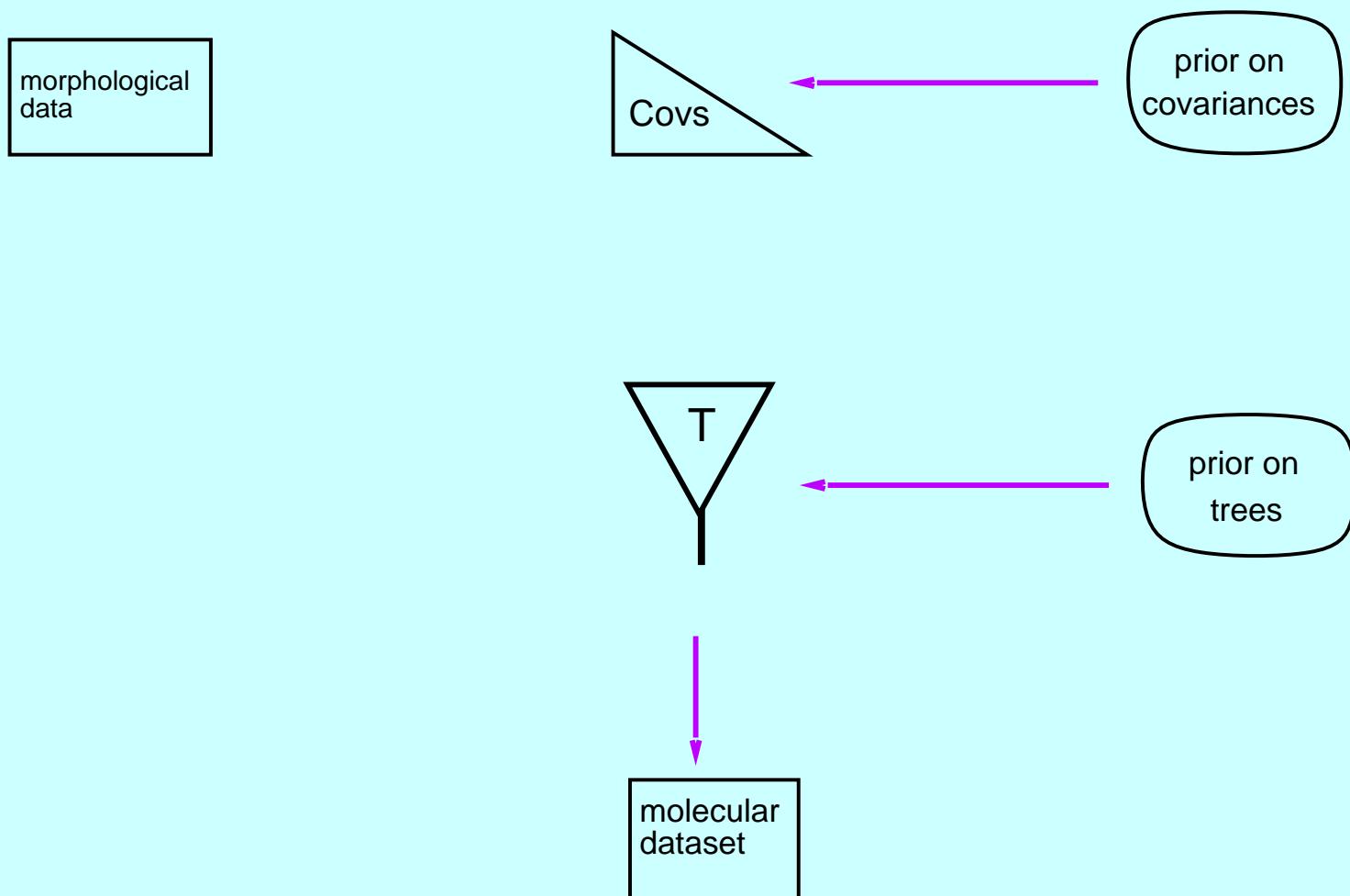
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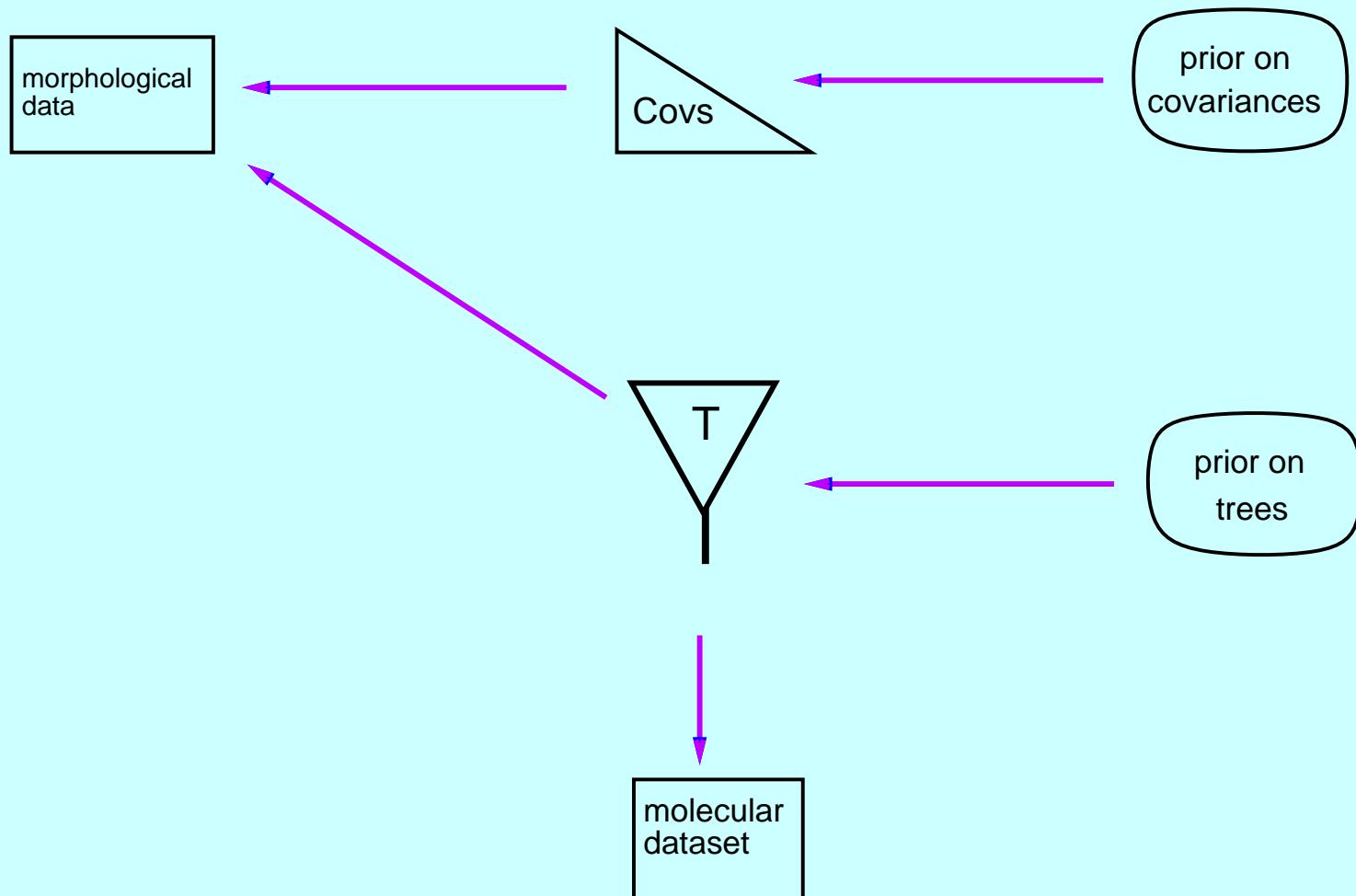
# A Bayesian model



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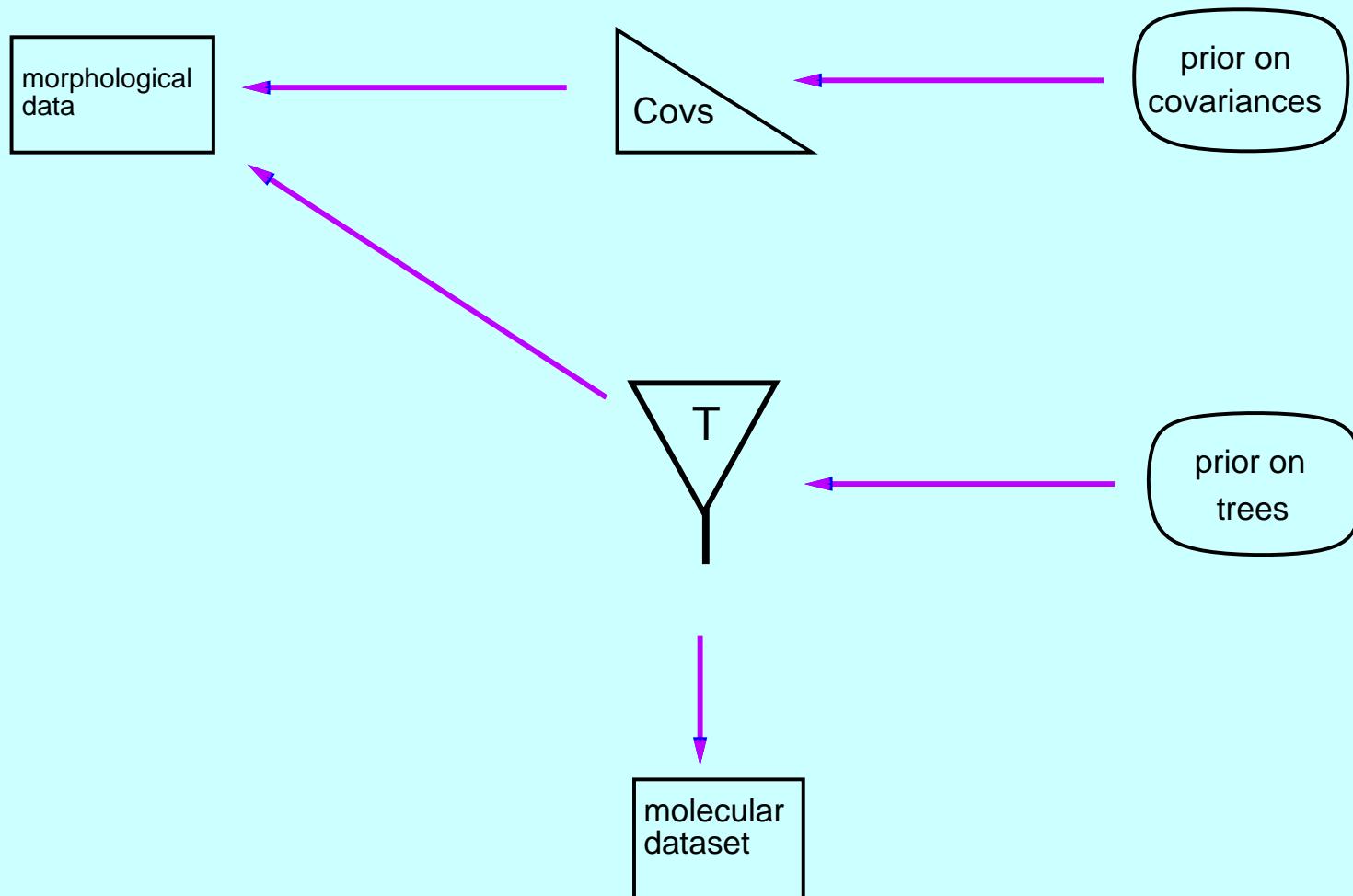


# A Bayesian model

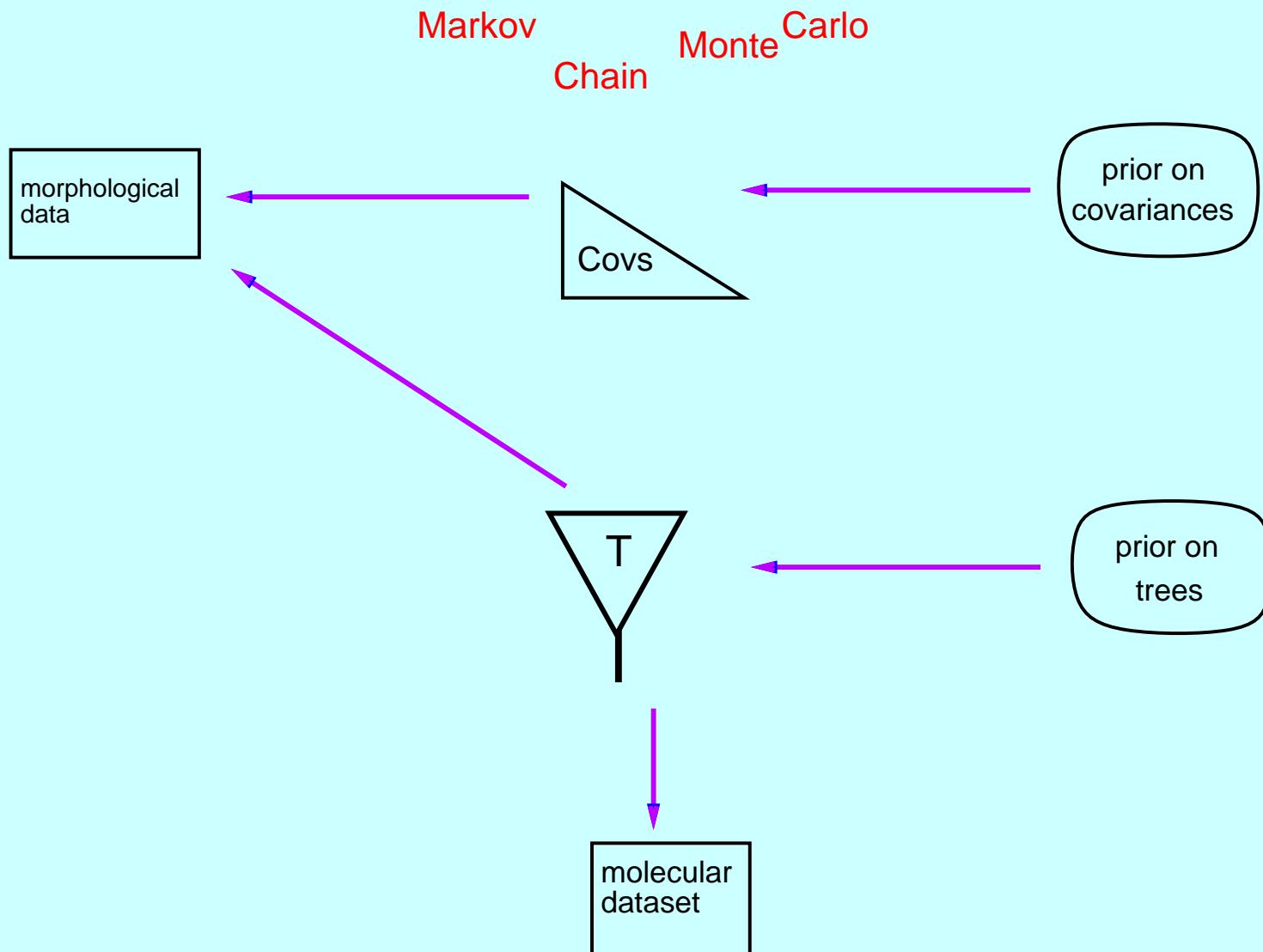


# Bayesian MCMC

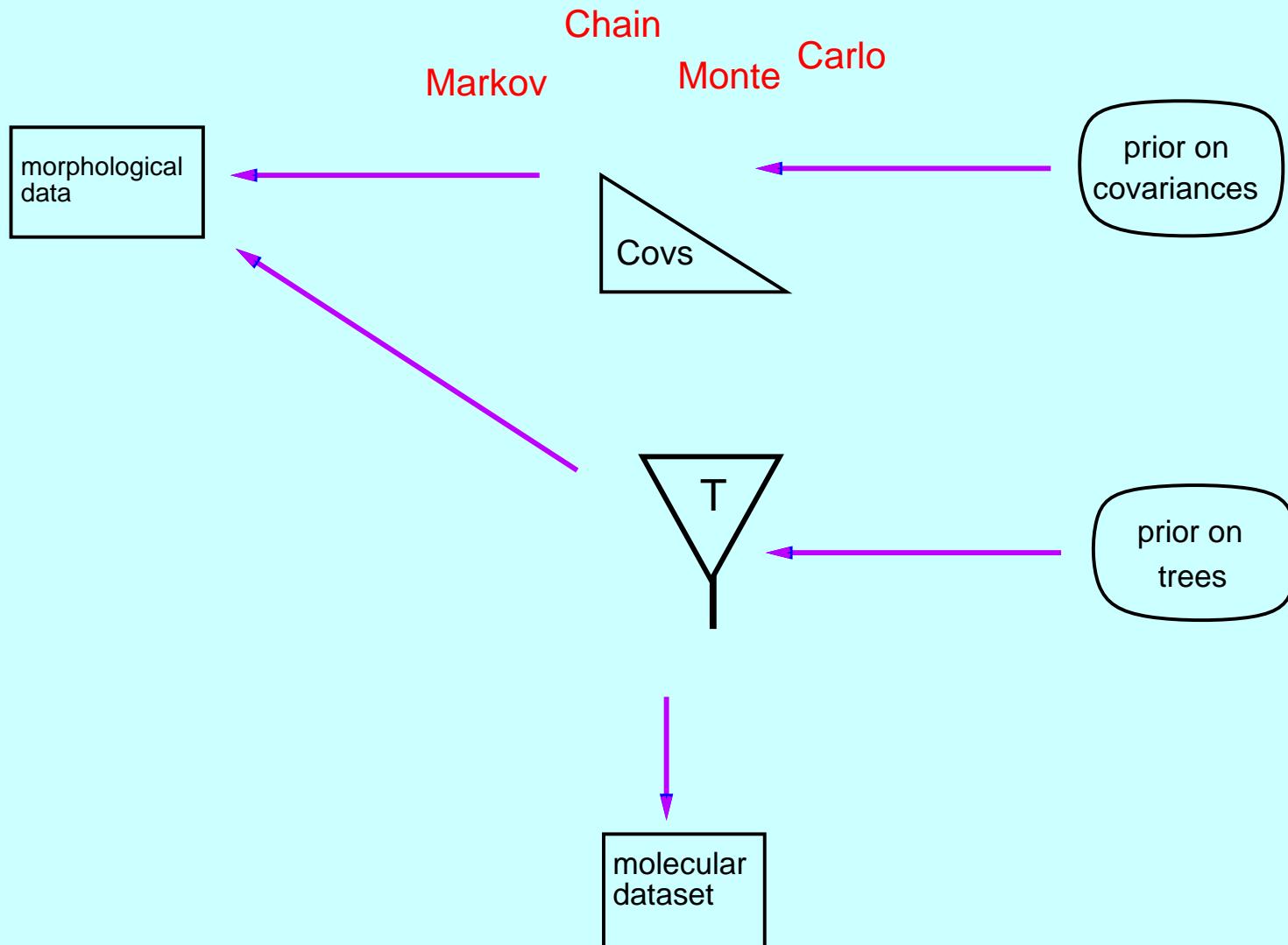
## Markov Chain Monte Carlo



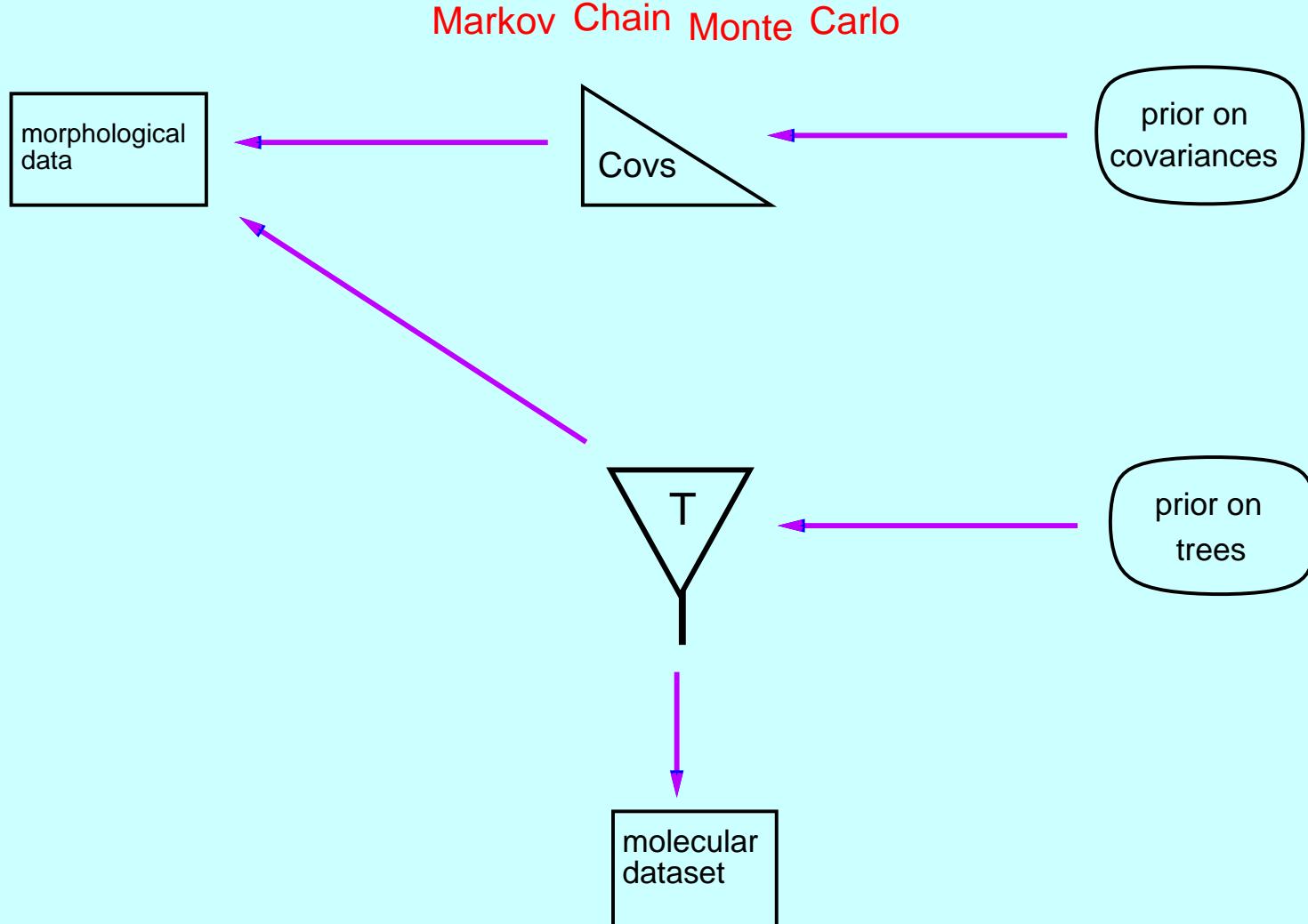
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- Might be able to assume environment does Brownian motion and infer covariances.

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- Expanding to more characters just adds new parameters to estimate

## References for phylogenetic comparative methods

- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**: 1–5. [Introduces the contrasts method]
- Felsenstein, J. 1988. Phylogenies and quantitative characters. *Annual Review of Ecology and Systematics* [Suggests using bootstrapping to correct comparative methods for uncertainty about the phylogeny] **19**: 445–471.
- Harvey, P. H. and M. D. Pagel. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford. [The major book introducing statistical phylogenetic comparative methods]
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London, Series B* **326**: 119–157. [Using generalized least squares to evaluate the likelihood for Brownian Motion phylogenies and do comparative methods analysis, without the contrasts methods. In the simplest case, is exactly equivalent to the contrasts method. Discusses ways of coping with unresolved parts of the phylogeny and with varying evolutionary rates.]

## References, continued

Ricklefs, R. E. and J. M. Starck. 1996. Applications of phylogenetically independent contrasts: A mixed progress report. *Oikos* 77: 167–172.

[Pointing out that small sample size within species is a problem for comparative methods]

Ives, A. R., P. E. Midford, and T. Garland. 2007. Within-species variation and measurement error in phylogenetic comparative methods. *Systematic Biology* 56: 252-270. [Taking small sample size into account when we know the within-species phenotypic covariances]

Hansen, T. F., and K. Bartoszek. 2012. Interpreting the evolutionary regression: the interplay between observational and biological errors in phylogenetic comparative studies. *Systematic Biology* 61(3): 413 – 425.

Felsenstein, J. 2008 Comparative methods with sampling error and within-species variation: contrasts revisited and revised. *American Naturalist* 171: 713–725. [Inferring both between-species evolutionary covariances and within-species phenotypic variation]

Felsenstein, J. 2004. *Inferring Phylogenies*. Sinauer Associates, Sunderland, Massachusetts. **Mentions this model and also sample size issues in contrasts method.**