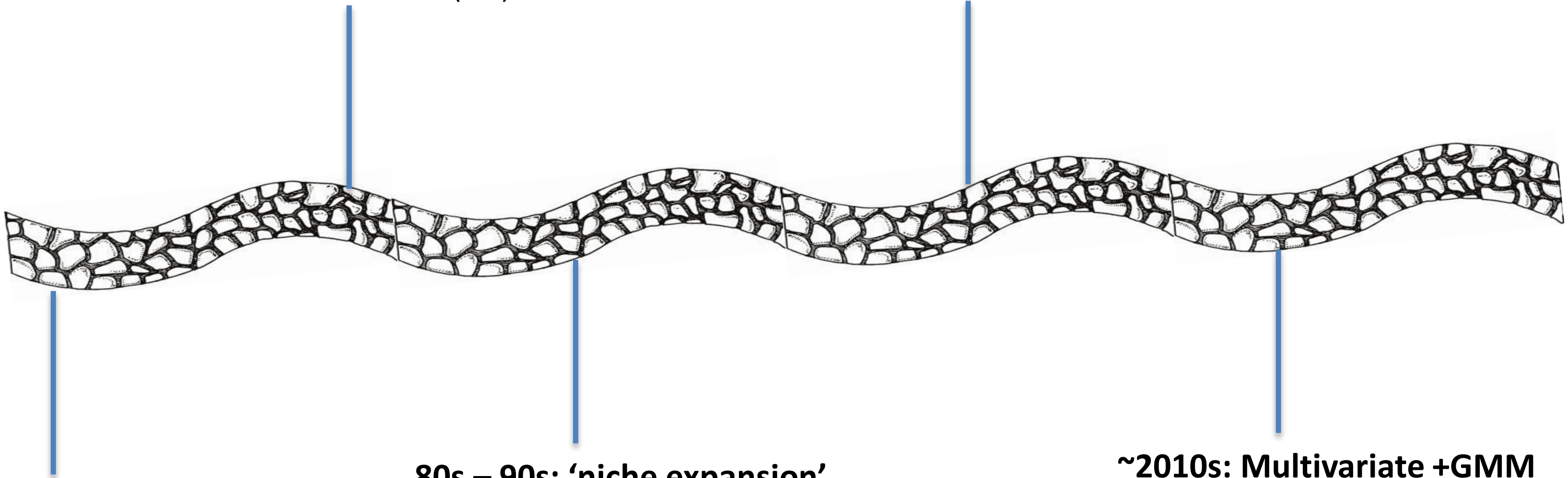
Phylogenetic Comparative Methods for Multivariate Data

The (Incomplete) Road to Comparative Methods



70s – early 80s: early attempts

Nested ANOVA

Phylogenetic autocorrelation

1985: The Breakthrough

Phylogenetic Independent Contrasts (PIC)

80s – 90s: ‘niche expansion’

PGLS

Phylogenetic signal (λ, *K*)

Phylogenetic ANOVA

Evolutionary models (BM1, OU1, ACDC, λ)

Diversity plots (LTT & DTT)

Diversification rates

Discrete trait change models

2000s: Maturation phase

Synthesis: PIC, PGLS, Phylo-transform

Complex model comparison (BM1, BMM, OU1, OMM)

Bayesian methods

Parameter-shift methods (e.g., MEDUSA, BAMM)

Discrete diversification associations (BiSSe family)

~2010s: Multivariate +GMM

Present day: PCMs: A diverse toolkit for evaluating evolutionary hypotheses

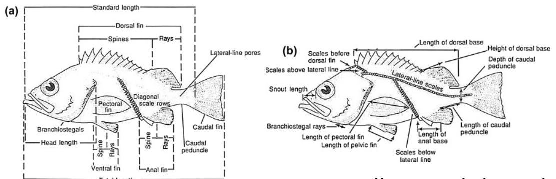
The (Incomplete) Road to Geometric Morphometrics

Morphological quantification has advanced dramatically*

Rank-Order

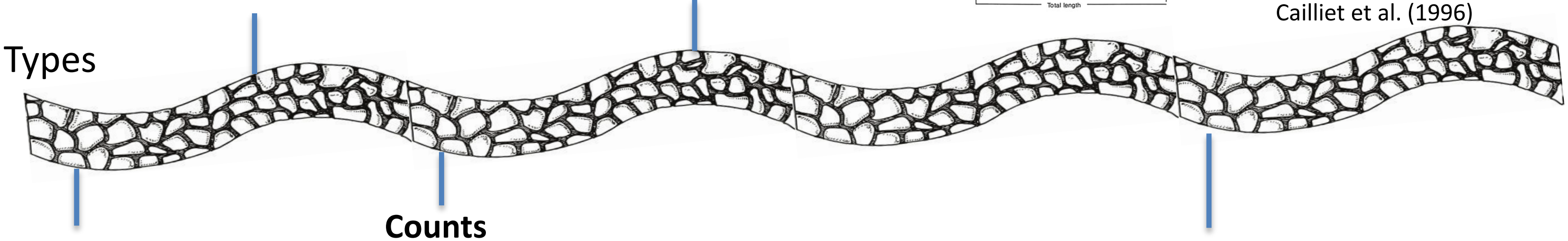
A>B>C

Linear Distances
(multivariate morphometrics)

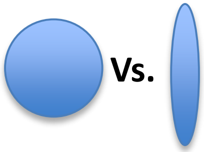


Cailliet et al. (1996)

Data Types

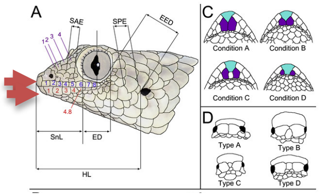


Categories



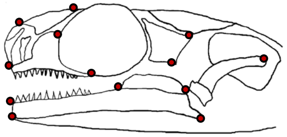
Vs.

Counts

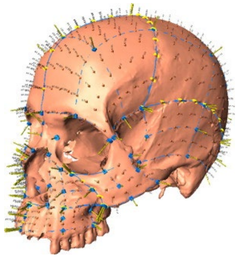


Scherz et al.
(2017)

Landmarks, curves, surfaces
(geometric morphometrics)



Adams & Rohlf (2000)



Friess 2010

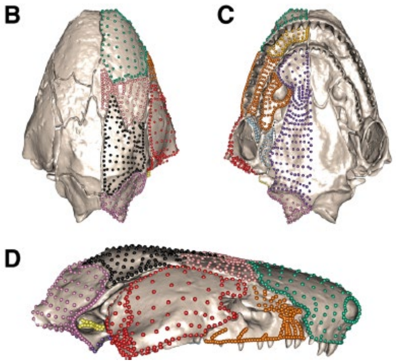
GMM provides greater biological realism, but…

- -greater data complexity
- -requires new mathematical theory
- -analytical and statistical challenges

*See historical treatments in: Reyment, 1996; Bookstein 1998, Adams et al. 2013; Bookstein 2014, 2018, 2019, among others

High-Dimensional Data

GMM (+ new technology) leads to ever-complex & HD datasets

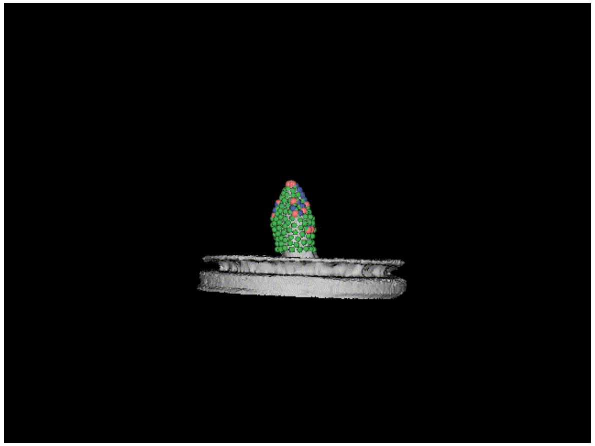


Bardua et al. 2019

1469 landmarks =
4407 variables

From this …

Obtain this

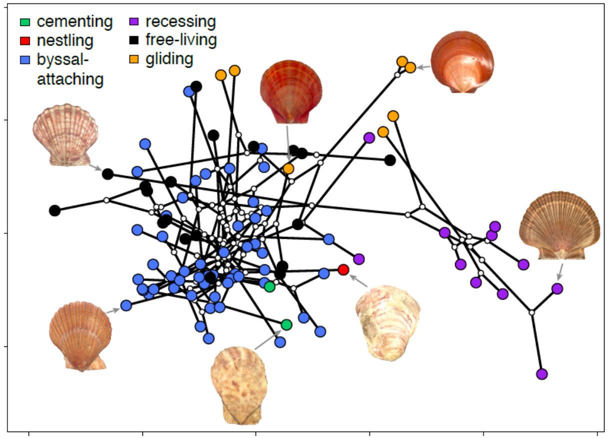


How do we handle such phenotypes with statistical rigor?

Phylogenetic Comparative Methods

PCMs *condition* the data on the phylogeny during the analysis

Empirical Goal: Evaluate evolutionary hypotheses while accounting for (phylogenetic) non-independence



Sherratt, Alejandrino, Kraemer, Serb, & Adams (2016)

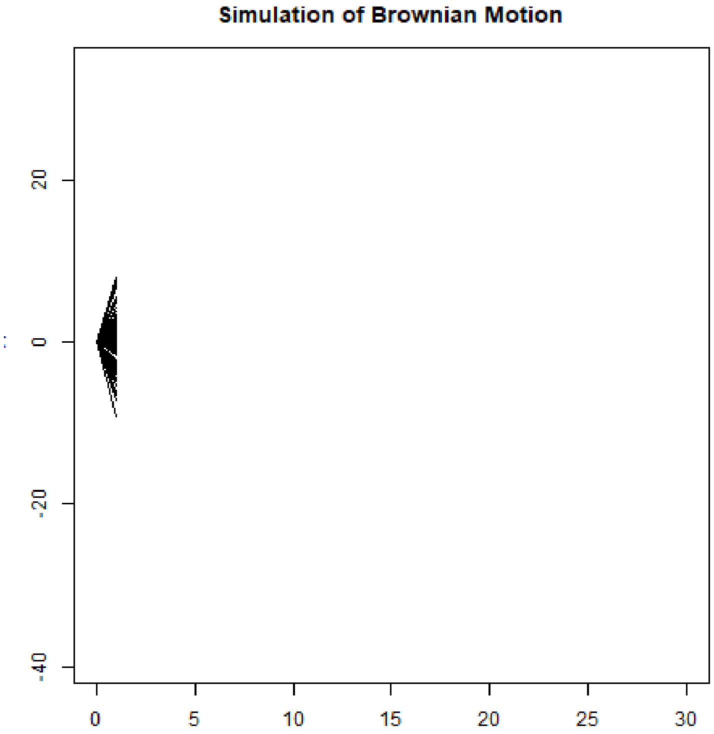
Requires an evolutionary model of how trait variation is expected to accumulate

Testing Patterns: Brownian Motion

Brownian motion (BM): a *null model* of trait change

Trait changes are independent from time step to time step

Results in: $\Delta\mu=0$, but $\sigma^2 \uparrow \propto$ time

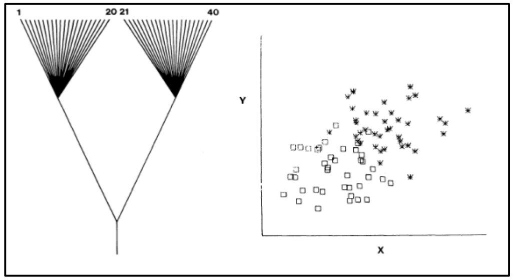


Side-note: this is the continuous-trait model equivalent of the Markov process, and is intimately related to Gaussian theory and the normal distribution

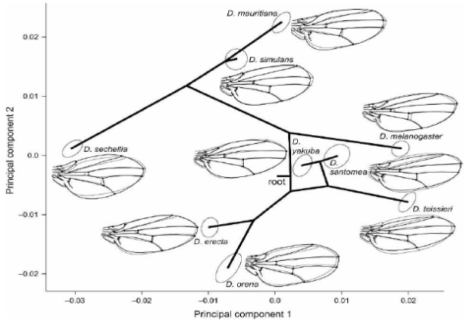
Felsenstein (1973; 1985)

The PCM Toolkit

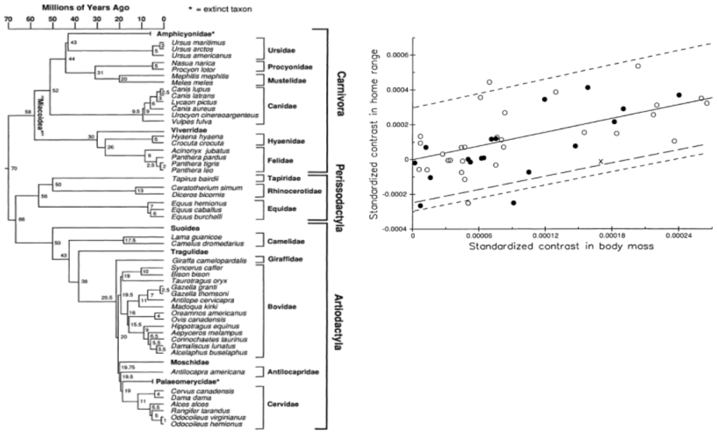
Phylogenetic Signal



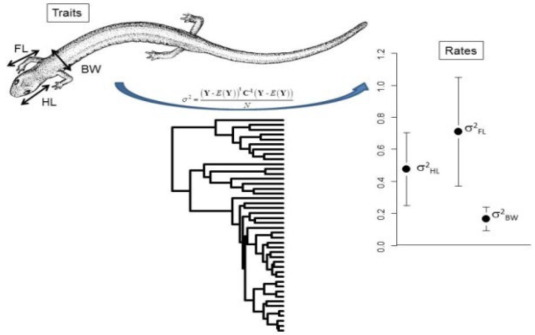
Phylomorphospace



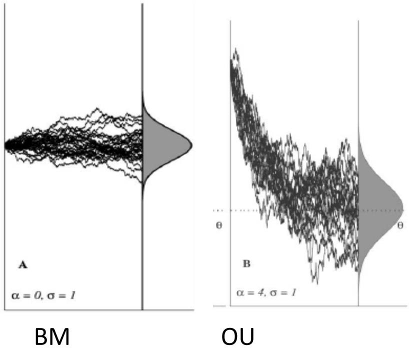
Phylogenetic Regression (PIC & PGLS)



Evolutionary Rates



Evolutionary Models



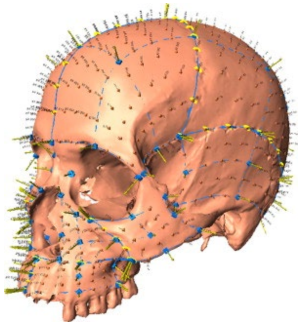
All are derived from the general PCM model (PGLS)

The General PCM Model

The primary statistical model of PCM: GLS (generalized least squares)

$$\mathbf{Y} = \mathbf{X}\widehat{\boldsymbol{\beta}} + \mathbf{E}$$

Continuous Response Data



Friess 2010

shape

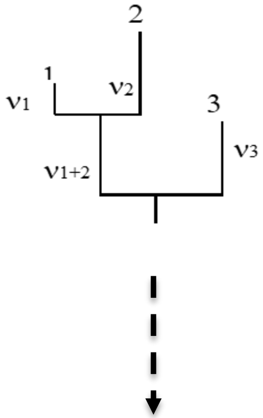
The Design

$$\begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 1 \\ 1 & 1 \\ 1 & 1 \\ 1 & 1 \end{bmatrix}$$

Island vs. Mainland

region

Error: $\mathcal{N}(0, \mathbf{V})$
(as described by phylogeny)

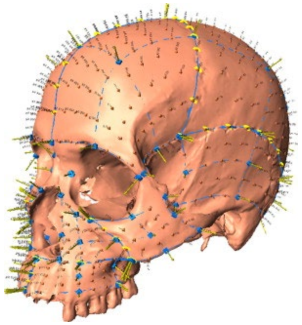


$$\mathbf{V}=\mathbf{R}\otimes\begin{pmatrix} v_1+v_{1+2} & v_{1+2} & 0 \\ v_{1+2} & v_2+v_{1+2} & 0 \\ 0 & 0 & v_3 \end{pmatrix}$$

*$\mathbf{V}$ can have other formulations for alternative evolutionary models

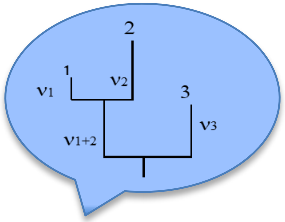
GMM-PCM Merger: Challenges

Shape ~ Region | phylogeny



Friess 2010

$$= \begin{bmatrix}1 & 0\\1 & 0\\1 & 0\\1 & 0\\1 & 1\\1 & 1\\1 & 1\\1 & 1\end{bmatrix} * \beta + \varepsilon$$



This GMM/PCM approach requires that one:

1: Condition multivariate data on phylogeny & fit model parameters

2: Obtain robust summary statistics

3: Evaluate significance and effect sizes in reliable manner

These were rather significant analytical challenges to overcome!

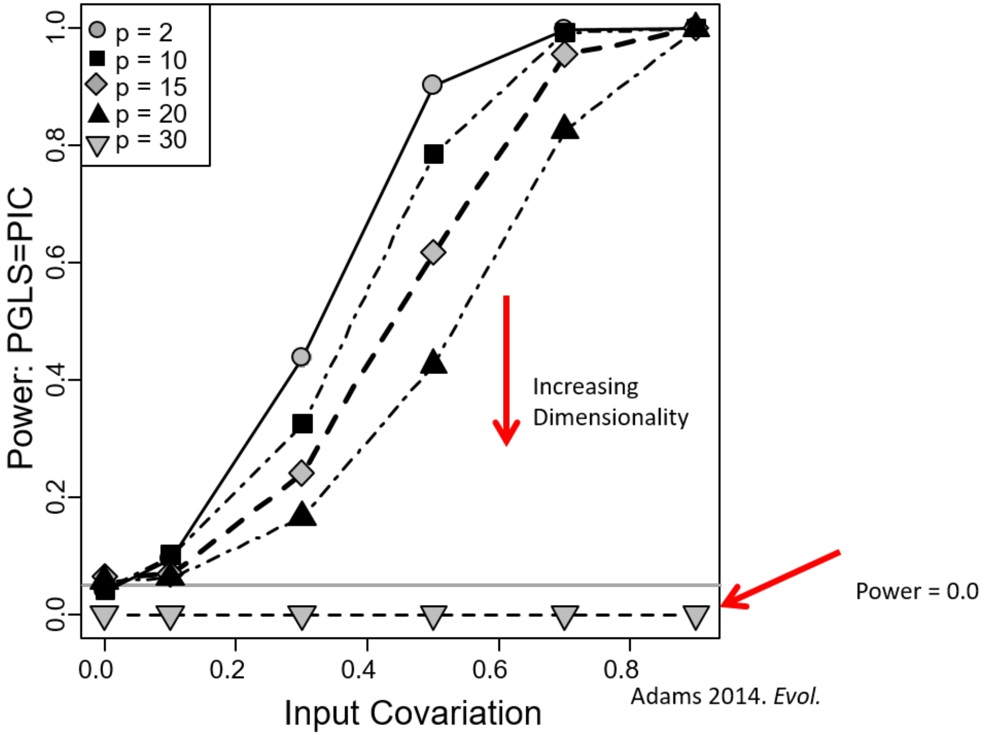
Why is There a Problem?

Why not just ‘scale up’ standard PCMs for GM-data?

Example: phylogenetic regression

$$\mathbf{Y} = \mathbf{X}\hat{\boldsymbol{\beta}} + \mathbf{E} \qquad \mathbf{E} \sim \mathcal{N}(0, \mathbf{V})$$

Power decreases as *p*-dimensions increases



Increasing Dimensionality

Power = 0.0

Adams 2014. *Evol.*

Why does this happen?

Adams (2014)
Adams and Collyer (2018)

The Curse of Parametric Hypothesis Testing

Standard PCMs are rooted in likelihood-based statistical theory

$$\log L = \log\left[\frac{\exp\left(-0.5\left(\mathbf{Y}-E(\mathbf{Y})\right)^{t}\mathbf{V}^{-1}\left(\mathbf{Y}-E(\mathbf{Y})\right)\right)}{\sqrt{(2\pi)^{np}|\mathbf{V}|}}\right]$$

Lots of math here!

$\log L = \frac{\dots}{\sqrt{\dots+|\mathbf{V}|}}$ The problem? As $|\mathbf{V}| \rightarrow \mathbf{0}$ as $\boldsymbol{p} \rightarrow \boldsymbol{n}$

Translation: divide by zero!

We need another solution for highly multivariate data!

See: Adams (2014), (2015)
Adams and Collyer (2018a), (2018b); Adams and Collyer (2019)

Multivariate PCMs: The Solution

Forgo standard ML and parametric approaches for statistical evaluation, and use robust methods

New GMM/PCM Approach:

1: Condition data on phylogeny & fit model parameters
2: Obtain robust summary measures (avoid $|\mathbf{V}| = 0$)
3: Evaluate significance and effect sizes *NOT* using log*L*

See: Adams (2014a), (2014b) (2014c)
Adams and Collyer (2015), (2018a), (2018b); Adams and Collyer (2019)

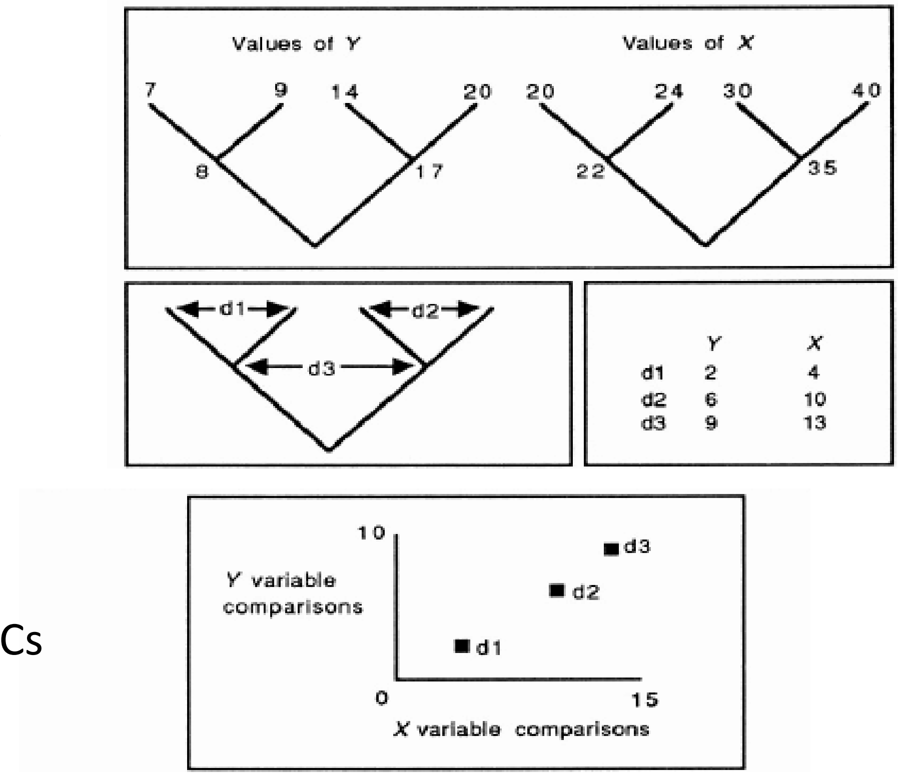
I: Conditioning on Phylogeny

Three equivalent algebraic implementations

1: Phylogenetically Independent Contrasts

Calculate PICs

Analysis of PICs



	Y	X
d1	2	4
d2	6	10
d3	9	13

From Harvey & Pagel (1991)

$$\hat{\boldsymbol{\beta}} = \left(\mathbf{X}_{pic}^{t}\mathbf{X}_{pic}\right)^{-1}\mathbf{X}_{pic}^{t}\mathbf{Y}_{pic}$$

Felsenstein (1985)

See: Garland and Ives (2000)
Rohlf (2006); Blomberg et al (2012); Adams (2014a)

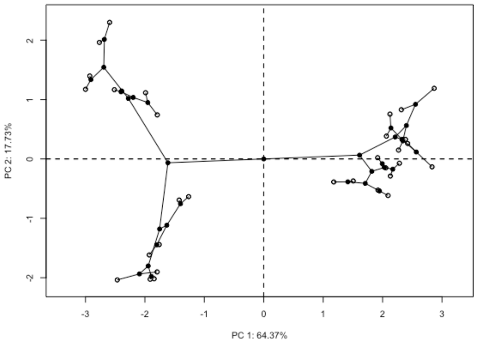
I: Conditioning on Phylogeny

Three equivalent algebraic implementations

2: Phylogenetic (GLS) Regression ($\mathbf{Y} = \mathbf{X}\widehat{\boldsymbol{\beta}} \mid \boldsymbol{phy}$)

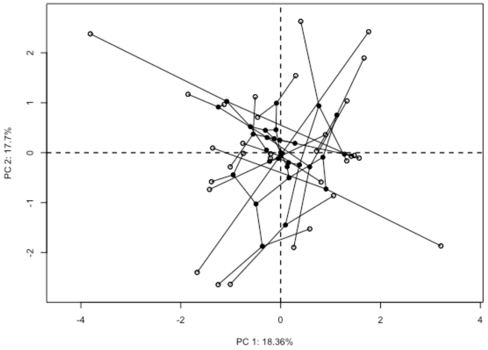
Accounts for phylogeny during analysis

Before



$$\widehat{\boldsymbol{\beta}} = \left(\mathbf{X}^t\mathbf{V}^{-1}\mathbf{X}\right)^{-1}\mathbf{X}^t\mathbf{V}^{-1}\mathbf{Y}$$

After:
E_{resid} independent of phylogeny



Images from Collyer & Adams (2021)

Grafen (1989)

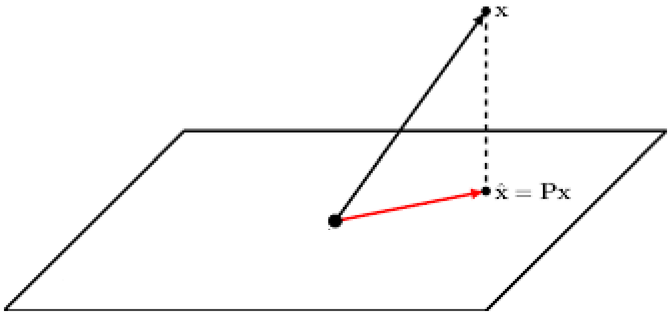
See: Garland and Ives (2000)
Rohlf (2006); Blomberg et al (2012); Adams (2014a)

I: Conditioning on Phylogeny

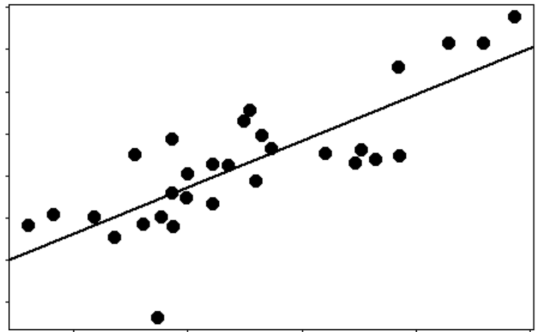
Three equivalent algebraic implementations

3: Phylogenetic Transformation (GLS→OLS)

Project data to phylogenetically-transformed space



Analysis of **Py** vs. **Px**



$$\widehat{\boldsymbol{\beta}} = \left(\widetilde{\mathbf{X}}^{t}\ \widetilde{\mathbf{X}}\right)^{-1}\widetilde{\mathbf{X}}^{t}\ \widetilde{\mathbf{Y}}$$

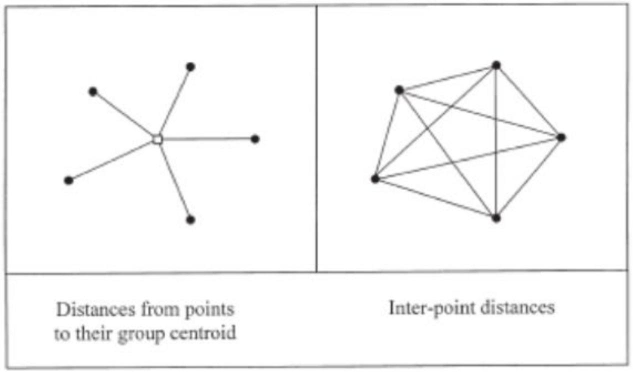
We utilize this procedure!

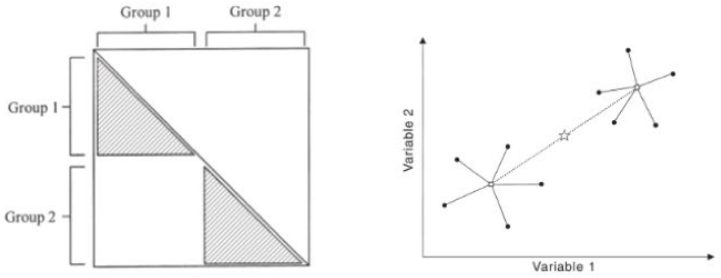
Garland and Ives (2000)
Adams (2014)

See: Garland and Ives (2000)
Rohlf (2006); Blomberg et al (2012); Adams (2014a)

II: Robust Summary Statistics

Leverage geometry to obtain robust summary statistics





Same group: $e_{ij}=1$

Different group: $e_{ij}=0$

Images from Anderson (2001)

See: Gower (1966); Goodall (1991); Anderson (2001)

One way: Sums-of-squares from object distances*

Avoids $|\mathbf{V}| = 0$, but still obtains: SS, MS, F, R^2, etc.

*Note: approach also used for Goodall's F-test

See: Adams (2014a), (2014b) (2014c)
Adams and Collyer (2015), (2018a), (2018b); Adams and Collyer (2019)

III: Residual Randomization

Significance testing via RRPP (Residual Randomization in Permutation Procedures)

Full

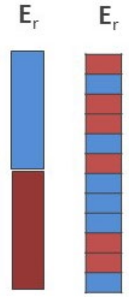
$\mathbf{Y} = \mathbf{X1} + \mathbf{X2} + \mathbf{E}_f$

Reduced

$\mathbf{Y} = \mathbf{X1} + \mathbf{E}_r$

1: Fit models

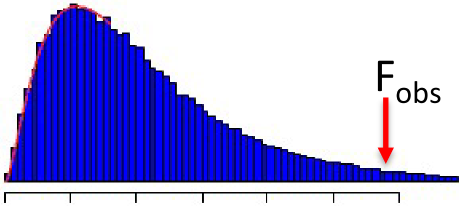
obtain β, and summary stats, SS, MS, R^2, F



2: Permute $\mathbf{E_R}$ (residuals of $\mathbf{Y}$)

obtain pseudo-values: $\boldsymbol{y} = \widehat{\mathbf{Y}} + \mathbf{E}_r^*$

3: Fit model with $\boldsymbol{y}$, repeat



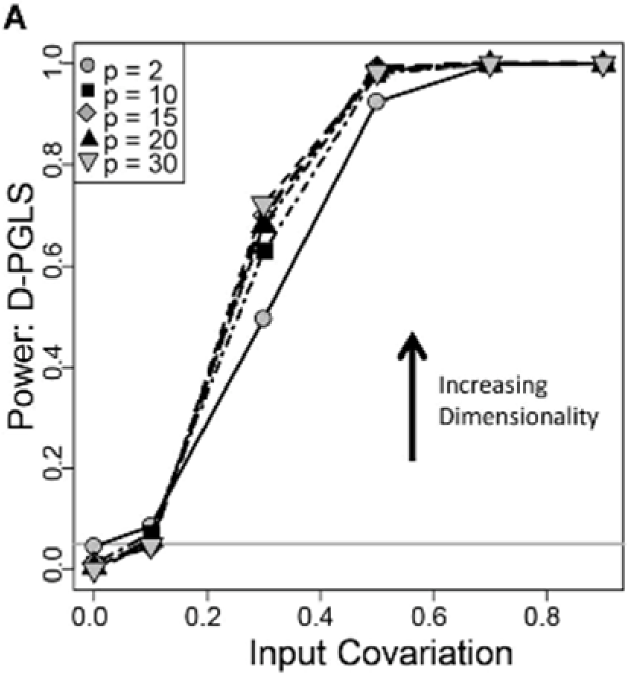
4: Effect size: $z = \dfrac{\left(\log(F) - \mu_{\log(F_r)}\right)}{\sigma_{\log(F_r)}}$

*Note: Proper permutation requires identifying correct exchangeable units (Commanges 2003: Adams and Collyer 2018a,b).

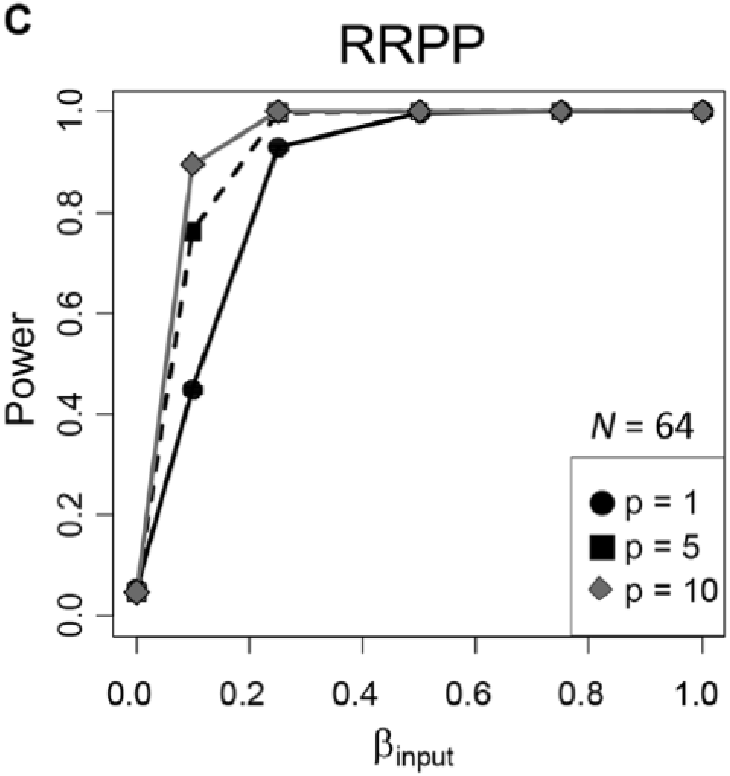
Collyer, Sekora, Adams (2015)
Adams & Collyer. (2016)
Adams & Collyer. (2018a); (2018b)

RRPP and Power

Breaks Rao's paradox



Adams 2014. *Evolution*

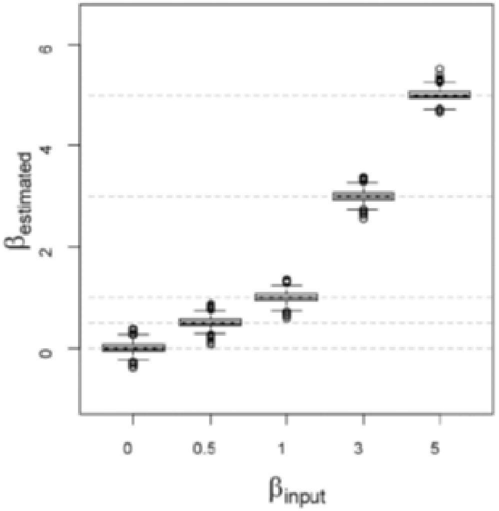


Adams and Collyer 2018. *Evolution*

Displays appropriate type I error and high power

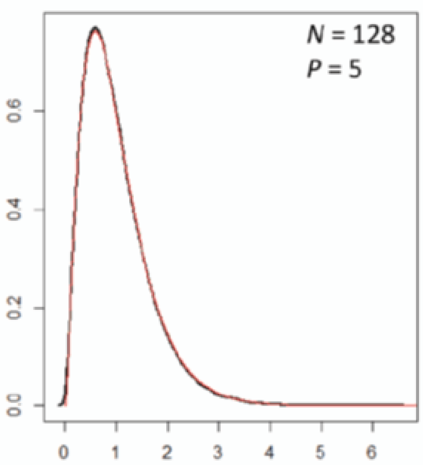
RRPP Properties

RRPP sampling distribution matches theory (but extends to p>>N)



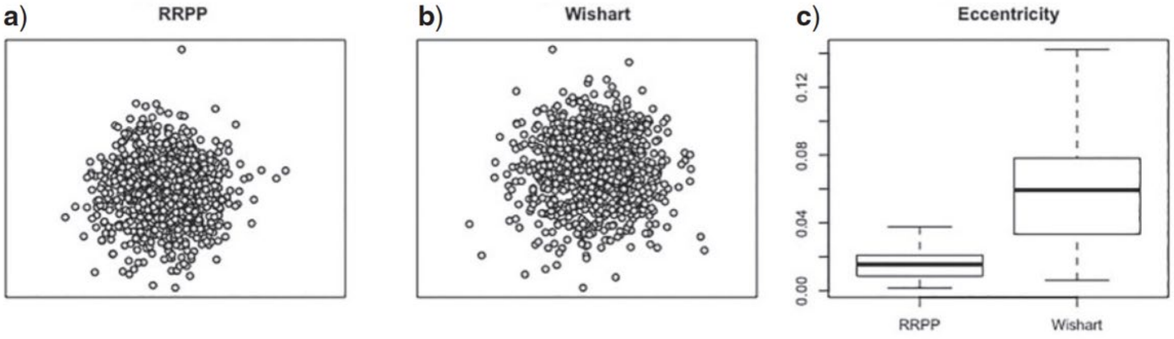
Correct parameter estimates

Adams and Collyer (2018a)



Empirical sampling distribution matches theory

Adams and Collyer (2018a)



Estimated covariance matrices equivalent to sampling a Wishart distribution

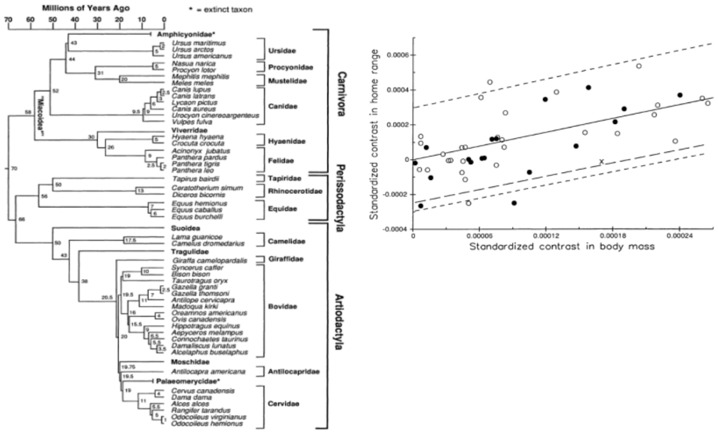
Adams and Collyer (2018b)

Conclusion: RRPP provides analytics for multivariate PCMs (and other applications)

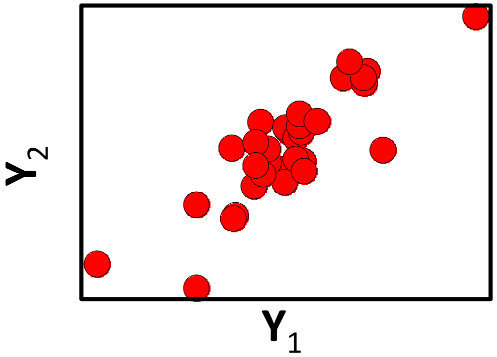
Summary: PCM-GMM Merger

Phylo-transform + RRPP enables multivariate PCMs

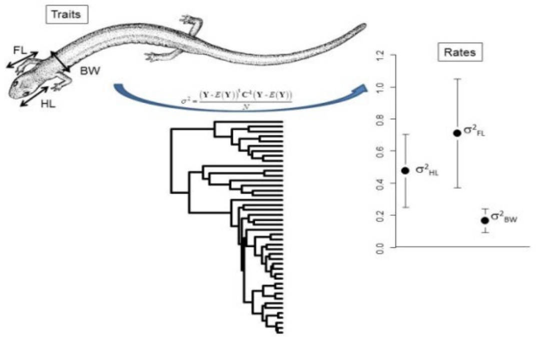
1: PGLS: Phylogenetic ANOVA/Regression



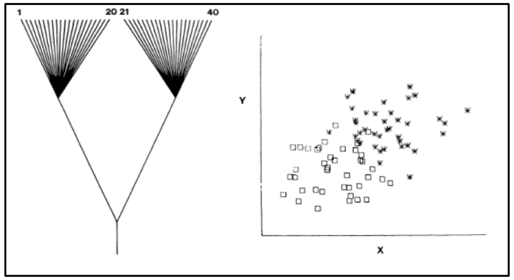
2: Phylogenetic PLS
(evolutionary covariation
of 2 *SETS* of variables)



3: Net Evolutionary Rates


Traits
FL
BW
HL
$\sigma^2 = \frac{(\mathbf{Y}-E(\mathbf{Y}))^T \mathbf{C}^{-1}(\mathbf{Y}-E(\mathbf{Y}))}{N}$
Rates
1.2
1.0
0.8
0.6
0.4
0.2
0.0
σ^2_{FL}
σ^2_{HL}
σ^2_{BW}

4: Phylogenetic Signal



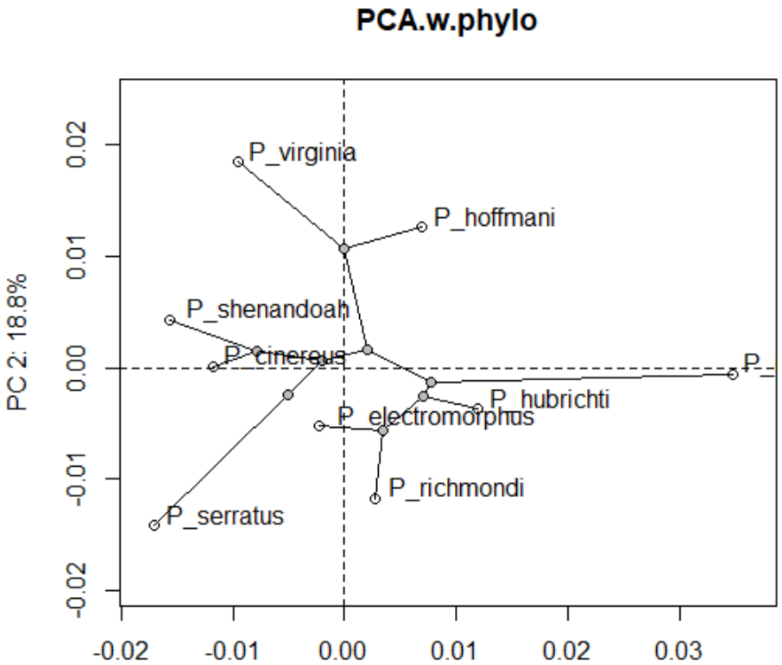
This facilitates investigations of the macroevolution of shape and other complex phenotypes

Adams (2014a), 2014b), (2014c)
Adams & Felice (2104)
Adams and Collyer (2015);
Denton and Adams (2015)
Adams and Collyer (2018a), (2018b), (2019)
Collyer, Baken, Adams (2022)

How to Visualize Evolutionary Patterns?

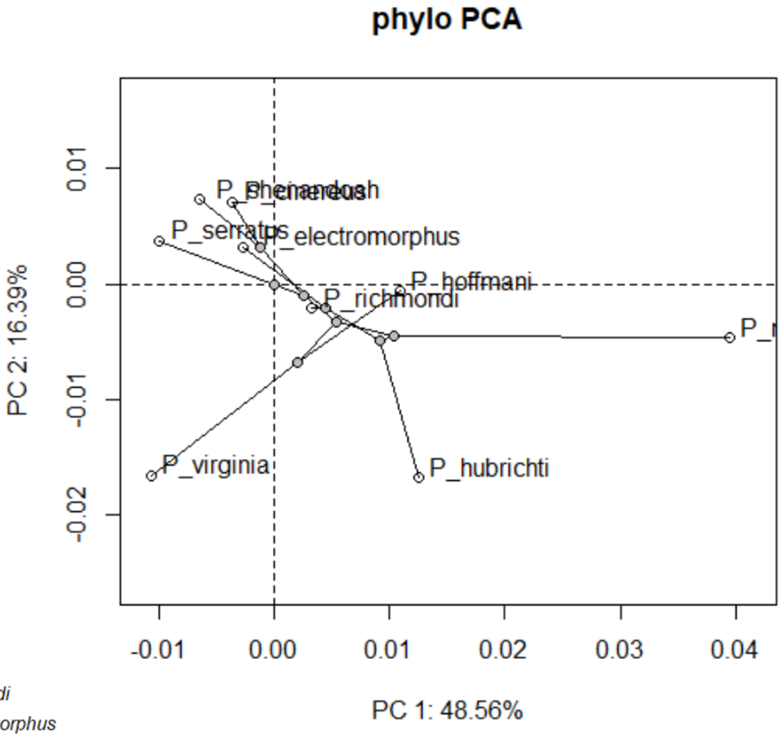
Phylomorphospace (PCA)

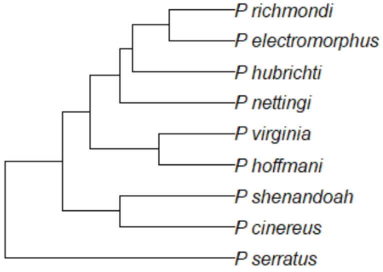
Align data to directions of maximal variation



Phylogenetic PCA (pPCA)

Align data to directions *independent* of phylogenetic signal (1st dimension)

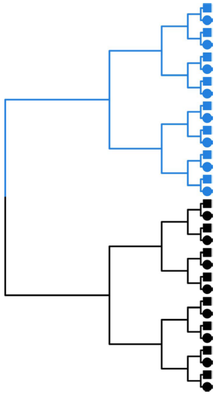


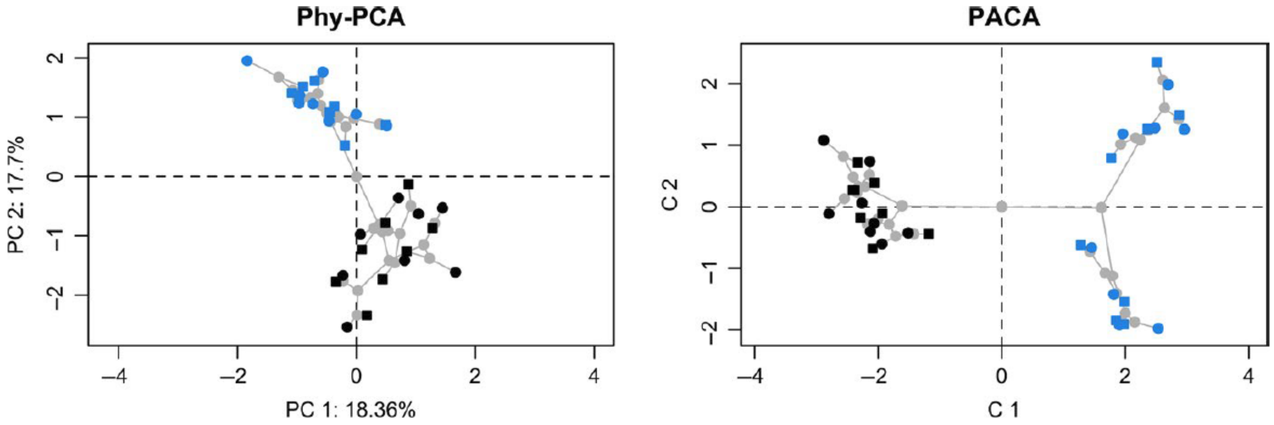


Interpretation can be challenging (e.g., with mixed ecological and phylogenetic signal)

Phylogenetically Aligned Components: PACA

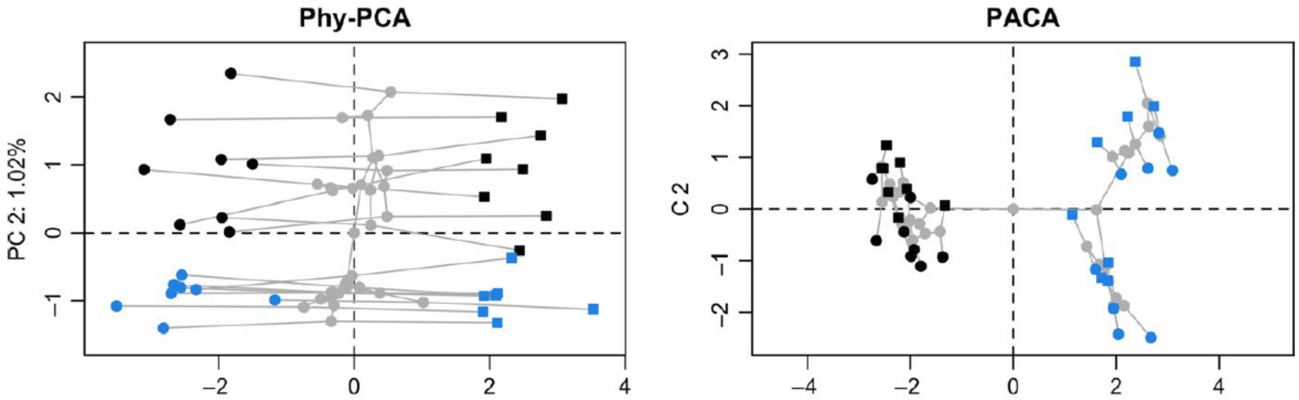
Align data to directions that maximize phylogenetic signal





Data

$\mathbf{P}_{\mathrm{BM}} + \mathbf{R}_{\mathrm{noise}}$



Data

$\mathbf{P}_{\mathrm{BM}} + \mathbf{E}_{\mathrm{ecol}} + \mathbf{R}_{\mathrm{noise}}$

PACA reveals phylogenetic trends in data irrespective of other signals!

Collyer and Adams (2021)

Phylogenetic 'Correlation' (PLS)

Account for phylogeny during PLS correlation

-PLS of evolutionary covariance (rate) matrix

$$\mathbf{R} = \frac{\left(\mathbf{Y} - E\left(\mathbf{Y}\right)\right)^{\mathbf{t}} \mathbf{C}^{-1} \left(\mathbf{Y} - E\left(\mathbf{Y}\right)\right)}{N - 1}$$

$$\mathbf{R}_{12} = \mathbf{U}_{\mathbf{R}1} \mathbf{D} \mathbf{V}_{\mathbf{R}2}^{t}$$

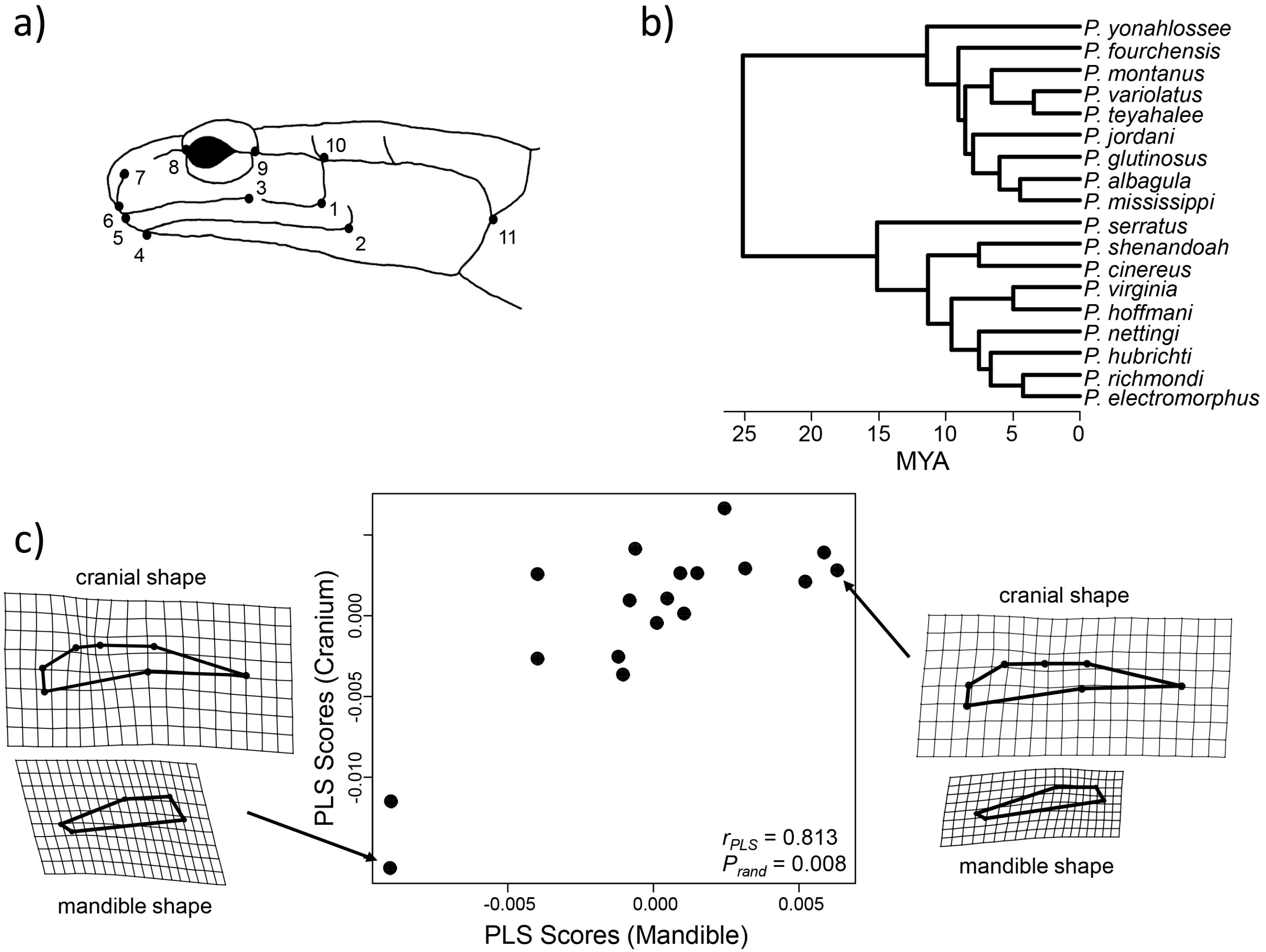
-Equivalently found from PLS of **PY** (phylo-transformed data)

-Significance found from permutation of phylo-transformed data

Adams and Felice 2014. *PloS One.*
Adams and Collyer. 2018. *Syst. Biol.*

Phylogenetic PLS: Example

PLS of cranium vs. mandible in *Plethodon*



Adams and Felice 2014. *PloS One.*

Phylogenetic Signal

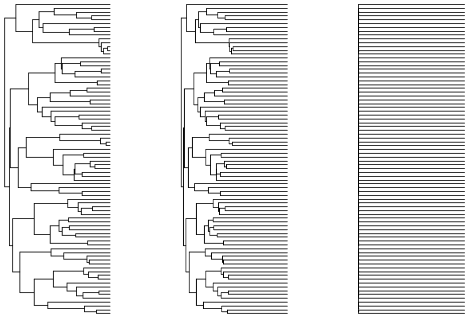
The degree to which phenotypic similarity associates with phylogenetic relatedness

-Blomberg's K: one measure (Adams, 2014 generalized to multivariate)

$$K = \frac{\left(\mathbf{Y} - E(\mathbf{Y})\right)^{\mathbf{t}}\left(\mathbf{Y} - E(\mathbf{Y})\right)}{\left(\mathbf{Y} - E(\mathbf{Y})\right)^{\mathbf{t}}\mathbf{C}^{-1}\left(\mathbf{Y} - E(\mathbf{Y})\right)} \Bigg/ \frac{tr(\mathbf{C}) - N(\mathbf{1}^{\mathbf{t}}\mathbf{C}^{-1}\mathbf{1})^{-1}}{N-1}$$

- Pagel's λ: a branch-length transformation during logL fitting

$$\log L = \log\left[\frac{\exp\left(-0.5\left(\mathbf{Y} - E(\mathbf{Y})\right)^{t}\mathbf{V}^{\boldsymbol{\lambda}-1}\left(\mathbf{Y} - E(\mathbf{Y})\right)\right)}{\sqrt{(2\pi)^{Np} \times |\mathbf{V}^{\boldsymbol{\lambda}}|}}\right]$$



Original (λ=1) λ = 0.5 λ = 0 (star)

Phylogenetic Signal

Both K and λ are related to a permutation-based Z-score, which can be used to compare the strength of signal across datasets

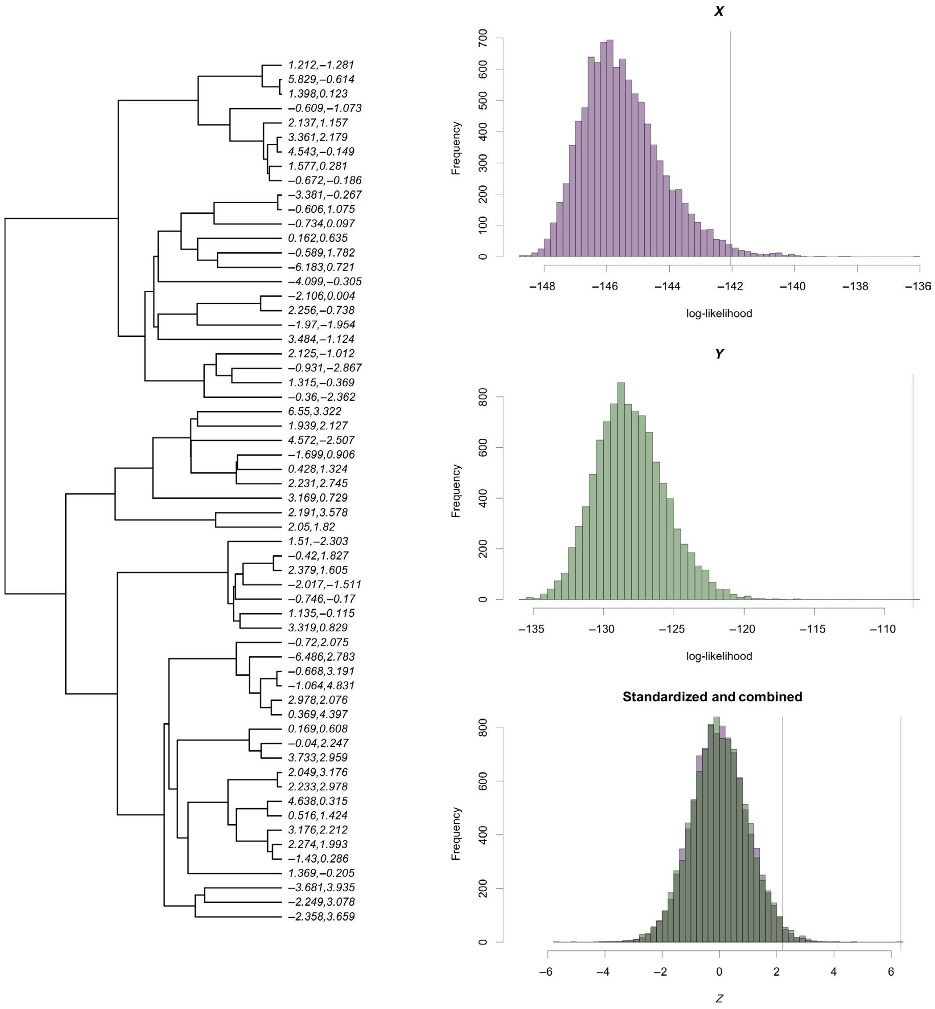


FIGURE 1 Plot of phylogenetic tree with x, y values, plus frequency histograms for the RRPP log-likelihood values for two variables, X and Y. Vertical lines indicate observed values. In the last panel, histograms have been combined for standardized values

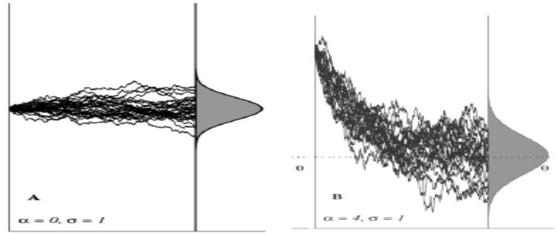
Collyer, Baken, Adams (2022). *MEE*.

Comparing Evolutionary Models

What evolutionary model best describes trait variation?

-Fit data to phylogeny under differing evolutionary models

Evolutionary Models



BM OU

Butler and King 2004

Model comparisons of:

1: Evolutionary rates (and covariances): BM1, BMM, etc.

2: Evolutionary ‘modes’: BM, OU1, OUM, etc.

Methods for multivariate data:

1: $logL_{Mult}$ (Revell and Harmon, 2008; Clavel et al. 2015)

2: σ^2_{mult} (Adams, 2014; Denton and Adams, 2015)

3: $\Sigma \log L_{indiv}$ (Ingram & Mahler, 2013; Grundler and Rabosky, 2014; Moen et al. 2016)

4: PCL (Goolsby, 2016)

Comparing Evolutionary Models: $\log L_{mult}$

Evolutionary rate for a trait σ^2: Phylogenetically-standardized variance

-Estimated from data and phylogeny under Brownian motion (see Felsenstein 1973)

$$\sigma^2 = \frac{(\mathbf{Y} - E(\mathbf{Y}))^t \mathbf{C}^{-1} (\mathbf{Y} - E(\mathbf{Y}))}{N}$$

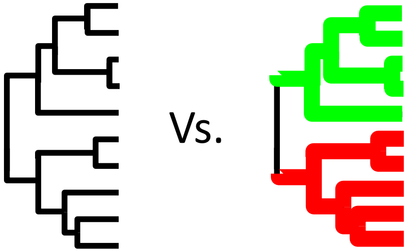
Felsenstein 1973. *Am J. Hum. Gen.*

$$\mathbf{R} = \begin{bmatrix} \sigma_1^2 & & \\ \sigma_{21} & \sigma_2^2 & \\ \sigma_{31} & \sigma_{32} & \sigma_3^2 \end{bmatrix}$$

Revell & Harmon 2008. *Ev. Ecol. Res.*

Is there evidence for multiple evolutionary rates on the phylogeny?

1: Define 'regimes' for models (BM1, BMM, etc.)

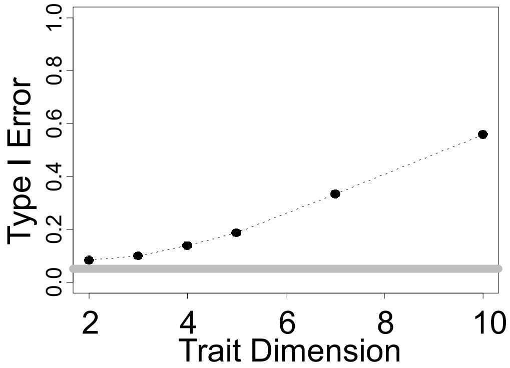


2: Estimate σ^2 (**R** multivariate) and $\log L_{mult}$

3: Compare log*L* (<u>LRT tests, AIC, phylogenetic simulation, etc</u>).

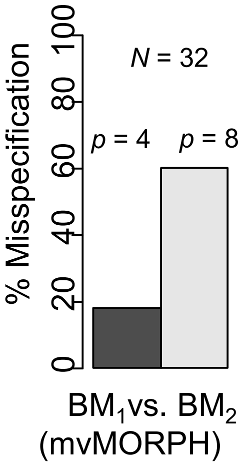
logL$_{mult}$: Problems

Type I error of LRT ↑ with p (not useful for high-dimensional data)



Adams 2014b. *Syst. Biol.*

Embodiment of 'curse of dimensionality'



BM1-simulations (N=32, p=8)

Adams and Collyer 2018. *Syst. Biol.*

logL$_{Mult}$ cannot be computed when p≥N

For multi-dimensional traits, should have a single rate, not a matrix

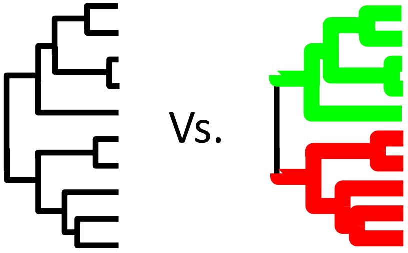
<u>LRT based on the logL$_{mult}$ not a general solution for high-D data</u>

Adams. 2014b. *Syst. Biol.*
Adams and Collyer 2018. *Syst. Biol.*
Adams and Collyer, 2019. *Ann. Rev. Ecol. Evol. Syst.*

Pairwise Composite Likelihood

Pairwise composite likelihood (PCL) as an alternative to $\mathrm{logL}_{\mathrm{mult}}$

1: Define ‘regimes’ for models (BM1, BMM, etc.)



2:Fit H_0 and H_1 for **PAIRS** of variables; obtain $\mathrm{log}L_{pair}$

3: Sum across $\mathrm{logL}_{\mathrm{pair}}$ for overall fit: $\Sigma \mathrm{log}L_{\mathrm{pair}}$

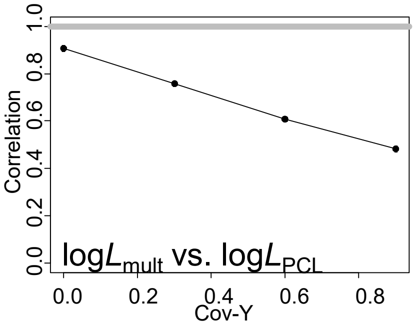
4: Simulate data under H_0 and compare

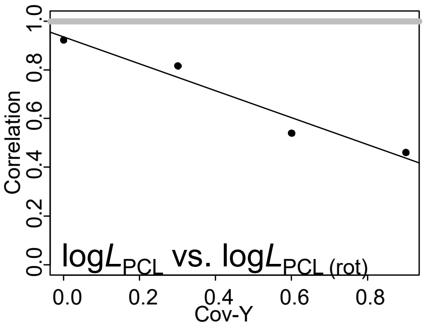
Goolsby 2016. *Syst. Biol.*

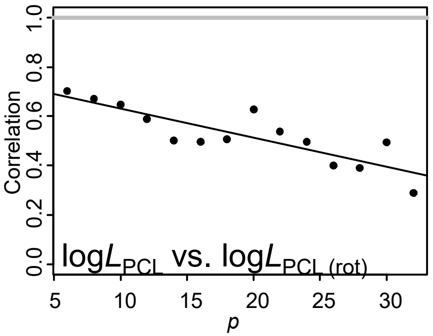
Pairwise Composite Likelihood: Problems

Pairwise composite likelihood to compare BM1 vs. BMM

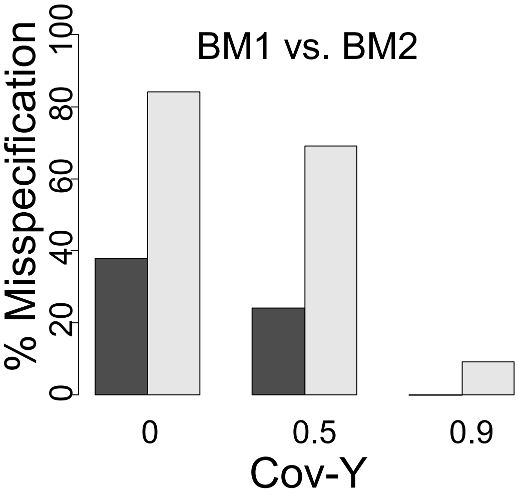
- Sensitive to *ALL* aspects of multivariate metric spaces







- Arbitrary results
  - Orientation-dependent
  - Cov-Y dependent



Data simulated under BM2
(N=32, p=8) with known
difference in $\mathbf{R}_1$ vs $\mathbf{R}_2$

- PCL **NOT** useful for comparing evolutionary rates

Adams and Collyer 2018. *Syst. Biol.*

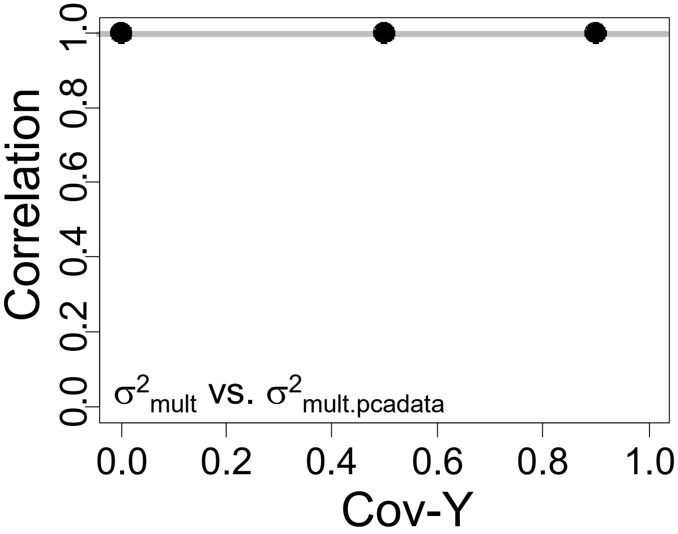
Generalize σ^2 for multidimensional data: **net evolutionary rates**

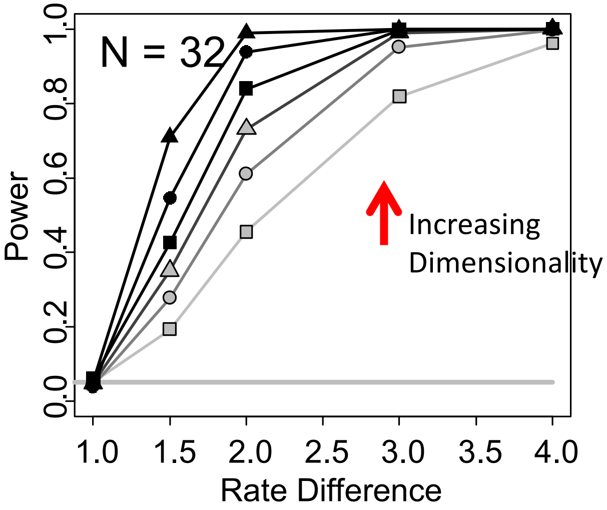
- Define 'regimes' for models (BM1, BMM)
- Phylogenetic transform of data
- Estimate σ^2_{mult} for BM1, BMM
- Permute (or simulate), repeat

$$\boxed{\sigma^2_{mult} = \frac{\mathbf{PD}^t_{\mathbf{U},0}\mathbf{PD}_{\mathbf{U},0}}{N}}$$

Adams 2014a. *Syst. Biol.*
Denton and Adams. 2015. *Evol.*

- Method rotation-invariant, and appropriate Type I error/power





- σ^2_{mult} **<u>IS</u>** useful for comparing multivariate evolutionary rates!

Adams and Collyer 2018. *Syst. Biol.*

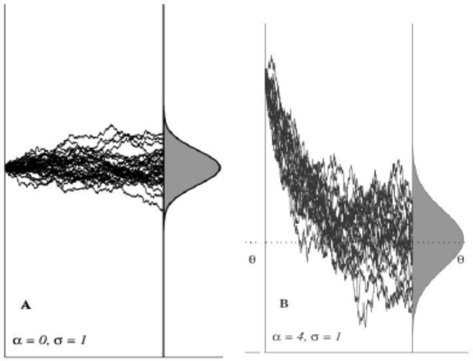
Complex Model Comparisons

Evolutionary models go beyond Brownian motion

-BM, OU, EB, ACDC, etc.

-Fit data to phylogeny under differing evolutionary models

Evolutionary Models



BM OU Butler and King 2004

Methods for multivariate data:

1: $logL_{Mult}$ (Clavel et al. 2015: extending Revell & Harmon, 2008)

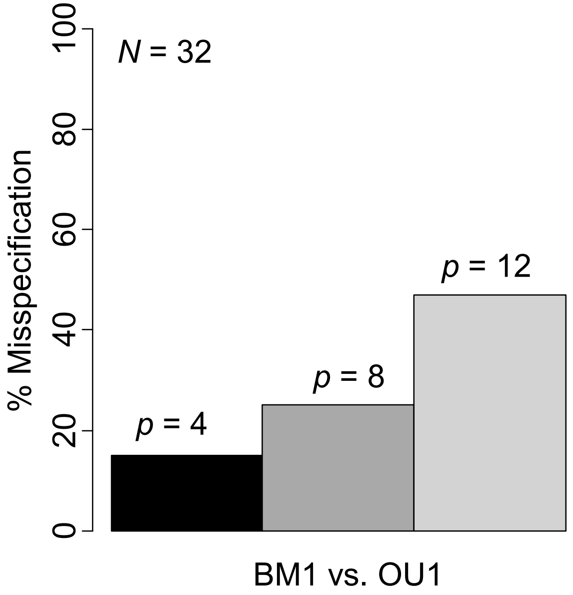
2: $\Sigma \mathrm{log}L_{\mathrm{indiv}}$ (Ingram & Mahler, 2013; Grundler and Rabosky, 2014; Moen et al. 2016)

3: PCL (Goolsby, 2016)

logL$_{mult}$: Problems

1: logL$_{mult}$ (various implementations)

AIC: Model misspecification ↑ with *p* (not useful for high-dimensional data)



BM1-simulations
(N=32)

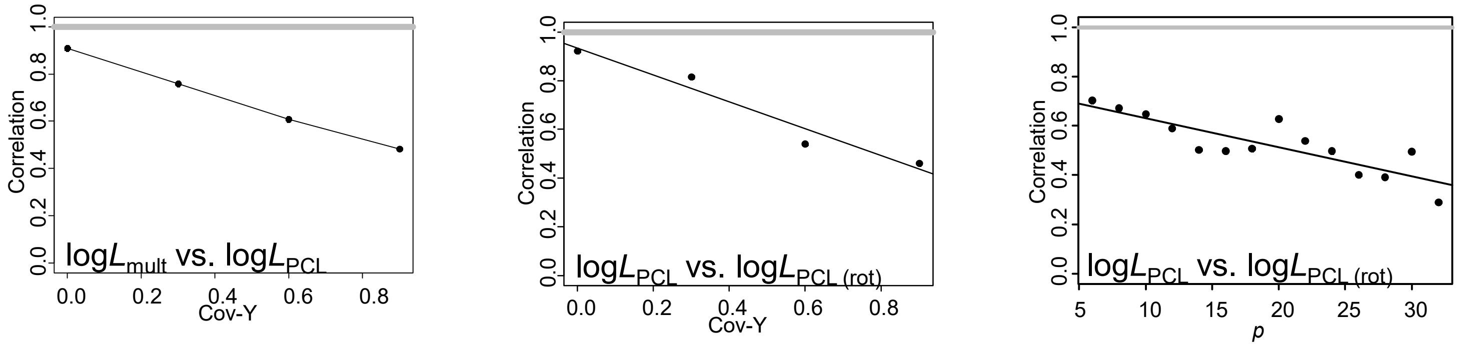
<u>AIC from logL$_{Mult}$ not general solution for model comparisons with high-D data</u>

Adams and Collyer 2018. *Syst. Biol.*
Adams and Collyer, 2019. *Ann. Rev. Ecol. Evol. Syst.*

PCL: Problems and Consequences

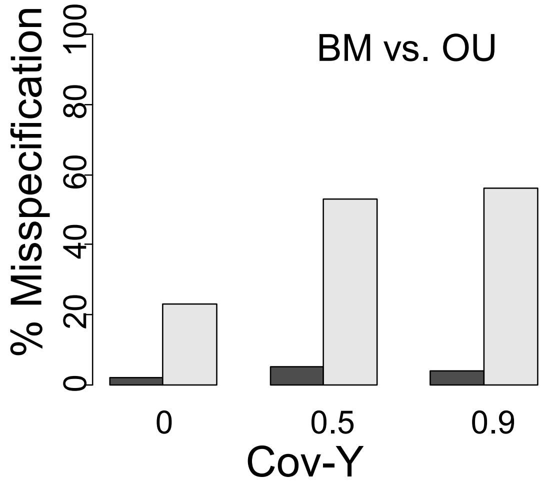
2: PCL

- Sensitive to *ALL* aspects of multivariate metric spaces



BM-simulations (p=8) on a 32 species phylogeny
(mean of 100 simulations per scenario)

- High misspecification and arbitrary results



Data simulated under BM1
(N=32, p=8)

- PCL **NOT** useful

Adams and Collyer 2018. *Syst. Biol.*
Adams and Collyer, 2019. *Ann. Rev. Ecol. Evol. Syst.*

$\Sigma \log L_{indiv}$: Surface-like Methods

3: Evaluate multivariate space dimension by dimension

- Assume trait independence
- Fit evolutionary models separately (on PPC_1, PPC_2, etc.)
- Obtain $\Sigma \log L$ and corresponding AIC to infer best model

(Ingram and Mahler, 2013; Grundler and Rabosky, 2014; Moen et al. 2016)

Mathematical Problems:

- Individual PCs misspecify model
  - EB preferred on lower PCs even for BM data (Uyeda et al. 2015)
- Dimensions not independent evolutionarily (mis-application of Edward's likelihood theorem)
  - Independence when **R** (NOT **S!**) is diagonal
  - ONLY occurs under BM for PPCA
  - For all other models, dimensions evolutionarily correlated
  - Thus, $\Sigma \log L \neq \log L_{Mult}$

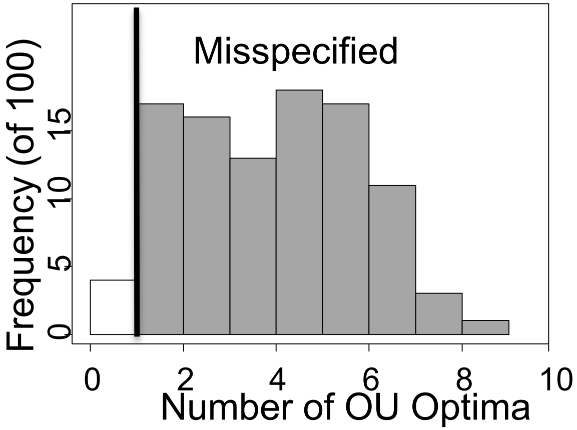
Adams and Collyer 2018. *Syst. Biol.*

$\Sigma \log L_{indiv}$ Consequences

Consequence: $\Sigma \log_{ind}$ greatly supports overly complex models

Example: Simulate datasets under BM, infer best model

- 2 or more inferred OU optima = misspecification



Data simulated under BM1
(N=32, p=8)

Result: > 95% model misspecification!

-NOTE: Comparing observed pattern to set of simulated outcomes post-hoc is not informative,
as one cannot distinguish the 'true' pattern in the observed from the pattern generated by method

Conclusion: $\Sigma \log_{ind}$ methods not reliable

Adams and Collyer 2018. *Syst. Biol.*

Conclusions and Future Directions

Multivariate PCM not trivial

-Algebraic generalizations appropriate mathematically

-Useful for hypotheses of:

1: Phylogenetic signal (K_{mult})
2: ANOVA/regression (D-PGLS)
3: Correlation (PPLS)
4: Net evolutionary rates (σ^2_{mult})

Analysis Type	$logL_{Mult}$	$\Sigma logL$	PCL	MultG
Phylogenetic Signal	-	-	-	Yes (K_{mult})
Phylogenetic ANOVA	-	-	NO	Yes (D-PGLS)
Phylogenetic Regression	-	-	NO	Yes (D-PGLS)
Phylogenetic Covariation (blocks of variables)	-	-	NO	Yes (P-PLS)
Comparing Evolutionary Models: BM1 vs BMM	Limited (when N>>>p)	-	NO	Yes (net rate only)
Comparing Evolutionary Models: BM1 vs BMM vs OU1 vs OUM	No	No	No	-

Current limitation: Brownian motion only

Adams and Collyer 2018. *Syst. Biol.*
Adams and Collyer, 2019. *Ann. Rev. Ecol. Evol. Syst.*

Conclusions and Future Directions

Multivariate PCM not trivial

-Evolutionary model comparisons remain a challenge

Analysis Type	**$\log L_{Mult}$**	**$\Sigma \log L$**	**PCL**	**MultG**
Phylogenetic Signal	-	-	-	Yes (K_{mult})
Phylogenetic ANOVA	-	-	NO	Yes (D-PGLS)
Phylogenetic Regression	-	-	NO	Yes (D-PGLS)
Phylogenetic Covariation (blocks of variables)	-	-	NO	Yes (P-PLS)
Comparing Evolutionary Models: **BM1 vs BMM**	Limited (when N>>>p)	-	NO	Yes (net rate only)
Comparing Evolutionary Models: **BM1 vs BMM vs OU1 vs OUM**	No	No	No	-

Multivariate Ornstein-Uhlenbeck models a particular challenge

We lack a robust multivariate method for evolutionary model comparisons!

Adams and Collyer 2018. *Syst. Biol.*
Adams and Collyer, 2019. *Ann. Rev. Ecol. Evol. Syst.*