A general comparative phylogenetic framework for coevolving traits and coevolving lineages

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Introduction	Leading ideas in phenotypic evolution	General framework	Biologically informed models	Conclusion
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## How do phenotypes evolve over macroevolutionary timescale ?

Adressing biological questions with phylogenetic comparative models

- 1. Parameter inference
  - Tempo of evolution
  - Differential lability of traits
  - Correlation of traits
- 2. Evolutionary history inference
  - Ancestral state inference
  - Tree inference
- 3. Model comparison
  - Which processes are driving phenotypic evolution over long time-scales ?



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Short background on phylogenetic comparative models Continuous traits following a Stochastic Differential Equation

$$dX_t^{(i)} = \psi(\theta - X_t^{(i)})dt + \sigma dB_t^{(i)}$$



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Some tra	its seem unconstrained			
Brownian mc	odel			

- Some traits do not confer any adaptive advantage/disadvantage over long time-scale.
- > They are supposed to evolve following a "phenotypic drift".

$$dX_t^{(i)} = \sigma dB_t^{(i)}$$



Time

Example 1 : body mass

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Abiotic c Ornstein-Uhl	conditions determine an o	optimal trait va	alue	
•	Some traits confer an adaptiv	ve advantage arou	ınd a given value.	

They evolve with a balance between the strength of selection and random noise.

$$dX_t^{(i)} = \psi( heta - X_t^{(i)})dt + \sigma dB_t^{(i)}$$



Time

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Biotic interactions impose constraints on phenotypic evolution Nuismer and Harmon, Ecology Letters, 2014

- S < 0: competition leads to trait repulsion.
- S > 0: mimicry confers a selective advantage.

$$dX_{t}^{(i)} = S\left(\frac{1}{n}\sum_{j=1}^{n}X_{t}^{(j)} - X_{t}^{(i)}\right)dt + \sigma dB_{t}^{(i)}$$

Example 3 : Müllerian mimicry in the Heliconius genus





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A genera	al framework			

$$\begin{cases} dX_t = (a(t) - AX_t)dt + \Gamma(t)dW_t \\ X(0) = X_0 \end{cases}$$

Code	Equation on a living lineage k	а	А	Г
BM	$dX_t^{(k)} = \sigma dW_t^{(k)}$	0	0	$\sigma I$
OU	$dX_t^{(k)} = \psi( heta - X_t^{(k)})dt + \sigma dW_t^{(k)}$	$\psi \theta V$	$\psi$ I	$\sigma I$
PM	$dX_t^{(k)} = \psi( heta - X_t^{(k)})dt$	$\psi \theta V$	$(\psi + S)I - \frac{S}{n}U$	$\sigma I$
	$+S\left(rac{1}{n_t}\sum_{l=1}^{n_t}X_t^{(l)}-X_t^{(k)} ight)dt+\sigma dW_t^{(k)}$			
EB	$dX_t^{(k)} = \sigma_0 e^{-\frac{1}{2}rt} dW_t^{(k)}$	0	0	$\sigma_0 e^{-\frac{1}{2}rt}I$
DD	$dX_t^{(k)} = \sigma_0 e^{-rn_t} dW_t^{(k)}$	0	0	$\sigma_0 e^{-rn_t} I$

Illustration : Ornstein-Uhlenbeck process

$$d\begin{pmatrix} X_t^{(1)} \\ X_t^{(2)} \\ \vdots \\ X_t^{(n)} \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} \psi\theta \\ \psi\theta \\ \vdots \\ \vdots \\ \psi\theta \end{pmatrix} - \begin{pmatrix} \psi & 0 & \cdots & 0 \\ 0 & \psi & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & \psi \end{pmatrix} \begin{pmatrix} X_t^{(1)} \\ X_t^{(2)} \\ \vdots \\ X_t^{(n)} \end{pmatrix} dt + \begin{pmatrix} \sigma & 0 & \cdots & 0 \\ 0 & \sigma & \ddots & \vdots \\ 0 & \sigma & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & \sigma \end{pmatrix} d\begin{pmatrix} B_t^{(1)} \\ B_t^{(2)} \\ \vdots \\ B_t^{(n)} \end{pmatrix}$$

One formula to rule them all

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Likelihood Turnkey codes	d computation s available on github			

- Fix the parameter set *p* of the models.
- $X_T$  at present time is Gaussian with computable mean  $m_p$  and variance  $\Sigma_p$ .
- > A numerical algorithm derives this distribution for any model.

```
getTipDistribution(model1, parameters)
getDataLikelihood(model1, traitValues, parameters)
```



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Using the Turnkey code	e likelihood s available on github			

traitValues <- simulateTipData(model1, parameters)</pre>

Sp. A	Sp. B	Sp. C	Sp. D
10.2	8.4	6.9	4.8

inferredParameters <- fitTipData(model1, traitValues)

$m_0$	$v_0$	lpha	$\theta$	$\sigma$
1	0	-1	0	2.2

AlCweights <- modelSelection(c(model1, model2, model3), traitValues)

AIC <sub>model1</sub>	$AIC_{model2}$	$AIC_{model3}$
4.2	0	6.7

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Adding bi	ogeography knowledge f Systematic Biology, 2016	to the model		

 Trait evolution is driven by biotic interactions within separated communities.

$$A = \begin{pmatrix} \frac{25}{3} & \frac{-5}{23} & \frac{-5}{3} & 0 & 0\\ \frac{-5}{3} & \frac{25}{3} & \frac{-5}{3} & 0 & 0\\ \frac{-5}{3} & \frac{-5}{3} & \frac{25}{3} & 0 & 0\\ 0 & 0 & 0 & \frac{5}{2} & \frac{-5}{2}\\ 0 & 0 & 0 & \frac{-5}{2} & \frac{5}{2} \end{pmatrix}$$



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Strengths of competition in different settings Work in progress, Jonathan Drury							
Which factors are associated to the strongest influence of other lineages ?							

- ▶ In different geographic areas : islands, climatic regions, ...
- Depending on other factors : diet, dispersal ability, ...





- Coevolution with predation, parasitism or mutualism, should drive a signature on phenotypic data.
- Could we use this signature to infer past interactions between lineages ?

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Take-hom	e message			

- 1. Existence of this framework to build biologically informed models of trait evolution.
- 2. Easy computation of the likelihood, turnkey codes available.
- 3. Paves the way to new questions regarding phenotypic macroevolution.

Thank you for your attention ! And many thanks to workmates for helpful discussions on this topic



 ${\sf Codes \ freely \ available \ on \ the \ Github \ repository \ of \ the \ RPANDA \ package \ : \ https://github.com/hmorlon/PANDA \ repository \ of \ the \ repository \ of \ the \ repository \ rep$ 

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