

Phylogenetic non-independence in rates of trait evolution

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1 **Phylogenetic non-independence in rates of**
2 **trait evolution**

3

4 **RUNNING HEAD:** Phylogenetic non-independence in rates

5

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13

14 **ABSTRACT**

15 Statistical non-independence of species' biological traits is recognized in most traits under
16 selection. Yet, whether or not the evolutionary rates of such biological traits are statistically
17 non-independent remains to be tested. Here we test the hypothesis that phenotypic
18 evolutionary rates are non-independent, i.e. contain phylogenetic signal, using empirical rates
19 of evolution in three separate traits: body mass in mammals; beak shape in birds; and bite force
20 in amniotes. Specifically, we test whether rates are non-independent throughout the
21 evolutionary history of each tree. We find evidence for phylogenetic signal in evolutionary rates
22 in all three case studies. While phylogenetic signal diminishes deeper in time, this is reflective
23 of statistical power owing to small sample and effect sizes. When effect size is large, e.g., owing
24 to the presence of fossil tips, we detect high phylogenetic signals even in deeper time slices.
25 Thus, we recommend that rates be treated as being non-independent throughout the
26 evolutionary history of the group of organisms under study, and any summaries or analyses of
27 rates through time – including associations of rates with traits – need account for the undesired
28 effects of shared ancestry.

29

30 **KEY WORDS:** evolutionary rates; trait evolution; phylogeny; phylogenetic comparative
31 methods; phylogenetic signal

32

33

34 Descent with modification [1] is of fundamental importance to evolution and is recognized in
35 most traits under selection. Through evolutionary time, trait values will be more similar in
36 closely related species compared to distantly related species, since the variance of trait values
37 will be proportional to the divergence in evolutionary time [2]. This equates to shared ancestry,
38 i.e. phylogeny. The degree to which shared ancestry affects biological traits can thus be
39 described by the proportion of variance in trait data across a comparative sample of species
40 that can be explained by phylogenetic relations, or phylogenetic signal – e.g., K [3] or λ [4]. This
41 has statistical implications, i.e., phylogenetic non-independence.

42 While acknowledgement of phylogenetic non-independence in phenotypic trait data has
43 become common in comparative studies [5], it is not so for the rates of evolution (how fast
44 organisms' characteristics evolve). As rates are often used as proxies for adaptations [6, 7], it is
45 of immense importance that we understand their statistical properties, in particular,
46 phylogenetic non-independence. However, we have not been able to identify any study in the
47 literature that explicitly tests for phylogenetic signal in phenotypic evolutionary rates aside
48 from rare instances in which this was implied [8].

49 Here, we test whether evolutionary rates contain phylogenetic signal using three
50 empirical case studies: body mass in mammals [9]; beak shape in birds [10]; and bite force in
51 terrestrial amniotes (ESM). Our basic premise is that if phylogenetic signal is detected in rates,
52 then rates evolve along the branches of a phylogenetic tree in proportion to the passage of
53 time and that closely related species are more similar in rates than distantly related species.
54 Naturally, this necessitates a non-homogenous distribution of rates across the branches of the
55 tree – i.e., variable-rates of phenotypic trait evolution [8, 11-14].

56

57 **MATERIALS AND METHODS**

58 We obtained 100 sets of phenotypic evolutionary rates and the associated time-calibrated
59 phylogenetic trees (time-trees) from the authors of the three case studies (ESM). As we would
60 expect rates along all branches of a phylogenetic tree to be affected by shared ancestry, not
61 just the tips, we tested for phylogenetic signal in rates along both terminal and internal
62 branches, by time-slicing the phylogenetic tree. We time-sliced the three time-trees at 1-Myr
63 intervals for the mammals and birds (167 and 109 time slices respectively), and at 5-Myr
64 intervals for amniotes (65 time slices) (see ESM for details). The latter interval was chosen for
65 amniotes owing to their much longer evolutionary history (approx. 350 Myr) compared to
66 mammals and birds. For each time-sliced tree, we matched the terminal branches to the
67 corresponding branches in the complete time-tree (Fig S1). We then assigned the
68 corresponding rates to those terminal branches on the time-sliced tree as tip trait values. We
69 fitted a maximum likelihood (ML) phylogenetic generalized least squares (GLS) model in
70 BayesTraits V3 to estimate phylogenetic signal λ in rates at the tips for each time-slice (GLS $_{\lambda}$).
71 We tested GLS $_{\lambda}$ against the null model in which λ is fixed to 0 (GLS $_{\lambda=0}$) as the likelihood ratio
72 (LR $_{\lambda}$) between GLS $_{\lambda}$ and GLS $_{\lambda=0}$ and determined significance using the χ^2 distribution (df=1).
73 When λ was significant in >95% of the sample in any given time slice, we determined that
74 phylogenetic signal was present in that time slice. We also compared the significance of an
75 alternative model in which λ is fixed to 1 (GLS $_{\lambda=1}$). The root estimate α of a GLS $_{\lambda=0}$ model is the
76 equivalent of estimating the non-phylogenetic mean rate, while GLS $_{\lambda}$ and GLS $_{\lambda=1}$ estimate the
77 phylogenetically corrected mean rates.

78

79

80 **RESULTS**

81 Overall, phylogenetic signal at the tips of the complete time trees are high (body mass in
82 mammals, median $\lambda = 0.926$; beaks in birds, median $\lambda = 0.729$; and bite force in amniotes, $\lambda =$
83 1), providing evidence for strong effects of shared ancestry in rates of phenotypic trait
84 evolution along the terminal branches. Phylogenetic signal in rates are generally high and
85 significant in at least 95% of the sample in younger time slices – younger than: 48 Myr ago
86 (mammals); 45 Myr ago (birds); and 30 Myr ago (amniotes) (Fig. 1; ESM). Phylogenetic signal
87 depreciates (drops in strength and significance) rapidly in deeper time slices (Fig. 1; ESM). Fixing
88 λ to 1 ($GLS_{\lambda=1}$) result in qualitatively similar patterns across time slices compared to when λ is
89 estimated (GLS_{λ}) (Fig. 1), but depreciation of λ start at younger time slices compared to GLS_{λ}
90 (Fig. 1).

91

92 **DISCUSSION**

93 Through our time-sliced GLS models on three datasets, we demonstrate that evolutionary rates
94 of phenotypic traits are indeed phylogenetically non-independent – λ is significant and high,
95 both along the terminal and internal branches (Fig. 1). Crucially, although λ ceases to be
96 significant in deeper time slices in all trees tested (Fig. 1), this reduction in phylogenetic signal
97 most likely depends on two aspects of the rates in the focal time slice: 1) number of tips [15]
98 and 2) rate heterogeneity (ESM). Both reflect issues of statistical power with the former
99 concerning sample size (as determined through simulations; ESM) and the latter effect size (as

100 evident from the effects of fossil tips; Fig 1C; ESM). Incidentally, un-sampled tips of any sort
101 (not just fossils) will likely increase rate heterogeneity should they be sampled. Additionally,
102 information contained at the tips of an ultrametric tree (e.g., trait values) is expected to be lost
103 progressively deeper in the tree (proportional to the phylogenetic variance-covariance
104 structure) as subsequent evolution towards the tips overprints ancestral information – this is an
105 issue plaguing phylogenetic comparative methods in general. Furthermore, since rates are
106 estimated from the phylogeny using models with constant rate evolution as the underlying
107 process of evolution, the resulting rates would inevitably contain phylogenetic signal. Whether
108 this is true or not, this does not alter (rather it reinforces) our argument that inferred rates
109 contain phylogenetic signal (regardless of the reason) and crucially that all downstream
110 summaries and analyses of rates thus must account for phylogenetic non-independence. Thus,
111 we argue that it is safest to assume that phylogenetic signal will be present and strong in
112 deeper time slices [8].

113 An important implication here is that as rates will be statistically non-independent at
114 various time intervals throughout the history of the clade of interest, patterns gleaned from
115 simple summaries (e.g., interval means) of rates-through-time (RTT) can potentially be
116 misleading. Simple RTT plots are prevalent in recent literature [e.g., 10, 16, 17-21], the profiles
117 of which routinely interpreted at face value, with peaks and troughs representing periods of
118 bursts and declines in rates [16, 17, 19]. However, accounting for phylogenetic non-
119 independence by assuming strong phylogenetic signal uniformly across all time slices [8] – i.e.
120 phylogenetic mean α from our $GLS_{\lambda=1}$ models across time slices – results in phylo-RTT profiles
121 that are often different from those of non-phylogenetic RTT (Fig. 2). Thus, non-phylogenetic

122 RTT profiles cannot be taken at face value without knowledge of phylogenetic signal through
123 time. More crucially, this implies that statistical analyses of rates need also account for
124 phylogenetic non-independence. Testing hypotheses of external influences (ecological or
125 environmental) on rates of evolution would require the application of appropriate phylogenetic
126 statistical methods – e.g. phylogenetic regression models [14, 22]. Not doing so will run the risk
127 of resulting in misleading statistical results [2, 5].

128 As phenotypic evolutionary rates have been interpreted as reflecting the intensity of
129 natural selection [6, 14], that they contain phylogenetic signal implies that ancestors and
130 descendants as well as closely related species either: 1) share intrinsic mechanisms for selection
131 responsiveness (e.g., genetic predisposition); 2) share similar levels of extrinsic selection
132 pressures (e.g., similar ecological niches, environments, etc); or 3) both. Two (or more) species
133 descended from a parent species would be expected to start their respective independent
134 evolution with the same level of intrinsic responsiveness as well as extrinsic selection pressures,
135 and thus at the phenotypic evolutionary rate, of the parent species. The daughter species then
136 would be subject to independent genetic mutations and selection pressures depending on their
137 respective environments.

138 However, this is not to say that descendent rates are rigidly constrained by ancestry;
139 exceptional rate shifts along individual branches are widely observed in many traits across
140 various groups of organisms [8, 9, 11, 14, 23]. Such exceptional rate shifts can often be orders
141 of magnitude greater than the background rate and occur instantaneously (with respect to
142 geological time) such that the effects of ancestry may be marginal.

143 In conclusion, our analyses demonstrate that rates of phenotypic evolution estimated
144 from phylogenetic trees using models of trait evolution are statistically non-independent (most
145 likely owing to shared ancestry), across the tips and through time – we posit that our results are
146 conservative with phylogenetic signal actually being more prevalent. Thus, we recommend that
147 phylogenetic non-independence be accounted for in summaries and analyses of evolutionary
148 rates through time, using appropriate phylogenetic comparative methods.

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221

222 **AUTHOR CONTRIBUTIONS:**

223 All authors made substantial contributions to conception and design, acquisition of data,
224 analysis and interpretation of data; drafted and revised the article critically for important
225 intellectual content; made final approval of the version to be published; and made agreements
226 to be accountable for all aspects of the work in ensuring that questions related to the accuracy
227 or integrity of any part of the work are appropriately investigated and resolved.

228

229 **DATA ACCESSIBILITY:**

230 Supporting data are made available through the Open Science Framework
231 (https://osf.io/pn4ma/?view_only=2de49c7ad61944ed97c373783a7d1956)[24], and described
232 in ESM.

233

234 **COMPETING INTERESTS:**

235 The authors declare no competing interests.

236 **FIGURE LEGENDS**

237 **Figure 1. Phylogenetic signal in rates of trait evolution through time.**

238 Phylogenetic signal (λ) was estimated across time sliced phylogenetic trees (top row) in three
239 independent data sets: A, mammalian body mass; B, avian beak shape; and C, amniote bite
240 force. Faint lines represent each of the 100 samples with the bold line representing the median
241 λ . The percentage of the sample in which LR_λ (likelihood ratio between GLS_λ and $GLS_{\lambda=0}$) was
242 significant is shown for each time slice (second row). Further, the fit of $GLS_{\lambda=1}$ is shown as the
243 percentage of the sample in which $LR_{\lambda=1}$ (likelihood ratio between $GLS_{\lambda=1}$ and $GLS_{\lambda=0}$) was
244 significant for each time slice (third row). Red dashed line represents the 95% threshold. Blue
245 dashed line (top) represents the time slice for the 95% threshold as determined through
246 simulations (Fig. S3). The relationship between the percentage of significant λ and N_{Tips} (bottom
247 row) shows a clear drop off in the percentage from 95% of the sample (red box).

248

249 **Figure 2. Mean evolutionary rates through time compared to phylogenetically corrected**

250 **mean rates.** Simple mean values of evolutionary rates at each time slice across the three
251 datasets (A, mammalian body mass; B, avian beak shape; C, amniote bite force) show distinctive
252 patterns of rates through time. However, these patterns are far less prominent in
253 phylogenetically corrected mean rates (α) through time. α are the phylogenetic root estimates
254 of the $GLS_{\lambda=1}$ model. Faint lines represent each MCMC run while the bold line shows the median
255 value for each time slice.

256