



Deposited via The University of Sheffield.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/167370/>

Version: Accepted Version

Article:

Cooney, C.R. and Thomas, G.H. (2021) Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nature Ecology & Evolution*, 5 (1). pp. 101-110.

<https://doi.org/10.1038/s41559-020-01321-y>

This is a post-peer-review, pre-copyedit version of an article published in *Nature Ecology and Evolution*. The final authenticated version is available online at:

<https://doi.org/10.1038/s41559-020-01321-y>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

1 **Heterogeneous relationships between rates of speciation and**
2 **body size evolution across vertebrate clades**

3
4 **Christopher R. Cooney^{1*} & Gavin H. Thomas¹**

5
6 *¹Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield*
7 *S10 2TN, UK.*

8
9 ***Author for correspondence:** c.cooney@sheffield.ac.uk

10
11 **Article type:** Article

12 **Running head:** Trait rates and speciation rates

13 **Number of words in abstract:** 163

14 **Total number of words in main text:** 3591 + 2708 in Methods

15 **Number of figures:** 5 (10 in Extended Data)

16 **Number of tables:** 0

17 **Number of references:** 94

18
19 **Author contributions:** C.R.C., G.H.T conceived and designed the research. C.R.C
20 collected data and conducted the analyses. C.R.C., G.H.T. wrote the manuscript.

21
22 **Data availability:** All data used in the study is sourced from publicly assessible sources.
23 Compiled datasets are available as Supplementary Data.

24
25 **Code availability:** R code is available [https://github.com/christophercooney/Cor-](https://github.com/christophercooney/Cor-STRATES)
26 [STRATES](https://github.com/christophercooney/Cor-STRATES).

27
28 **Competing interests statement:** None of the authors have competing financial or non-
29 financial interests.

30
31

32 **ABSTRACT**

33 Several theories predict that rates of phenotypic evolution should be related to the rate at which new
34 lineages arise. However, drawing general conclusions regarding the coupling between these
35 fundamental evolutionary rates has been difficult, due to the inconsistent nature of previous results
36 combined with uncertainty over the most appropriate methodology with which to investigate such
37 relationships. Here we propose and compare the performance of several different approaches for
38 testing associations between lineage-specific rates of speciation and phenotypic evolution using
39 phylogenetic data. We then use the best-performing method to test relationships between rates of
40 speciation and body size evolution in five major vertebrate clades (amphibians, birds, mammals,
41 ray-finned fish, squamate reptiles) at two phylogenetic scales. Our results provide support for the
42 longstanding view that rates of speciation and morphological evolution are generally positively
43 related at broad macroevolutionary scales, but they also reveal a substantial degree of
44 heterogeneity in the strength and direction of these associations at finer scales across the
45 vertebrate tree of life.

46

47

48 INTRODUCTION

49 The rate at which new species arise and at which phenotypic traits evolve are two fundamental
50 evolutionary rates^{1,2}, that, together, are thought to explain major patterns in the distribution of
51 species richness and phenotypic diversity across the tree of life³⁻⁶. It has long been suspected that
52 rates of speciation and phenotypic evolution may be correlated at macroevolutionary scales^{1,7,8}. On
53 the one hand, several long-standing evolutionary theories predict a positive coupling between these
54 rates. Such theories include the concept of punctuated equilibrium⁹ and the versatility hypothesis¹⁰⁻
55 ¹², where in the latter, increased phenotypic ‘evolvability’ promotes elevated rates of speciation by
56 allowing diversifying lineages to utilise a broader spectrum of available resources. Similarly, a
57 positive coupling between rates of lineage splitting and phenotypic (ecological) divergence is a
58 fundamental component of adaptive radiation theory¹³, and rapid phenotypic differentiation has
59 been identified as an important feature of many celebrated evolutionary radiations (e.g. Hawaiian
60 honeycreepers¹⁴, Galapagos finches¹⁵, cichlid fishes¹⁶, *Anolis* lizards¹⁷).

61 On the other hand, there is growing evidence from a range of taxa that lineage diversification
62 often proceeds without substantial phenotypic evolution, challenging the notion that phenotypic
63 differentiation is a requirement for the origin and build-up of species diversity in evolutionary
64 radiations¹⁸⁻²². For instance, studies integrating both ecological and evolutionary information have
65 documented several examples of ‘non-adaptive radiation’ in a range taxa including snails,
66 salamanders, birds, lizards and plants¹⁸ in which lineage diversification has seemingly proceeded
67 with minimal ecological divergence. Examples such as these are at odds with the notion of a
68 general coupling between speciation and phenotypic divergence, and therefore challenge the
69 expectation for widespread positive relationships between rates of speciation and phenotypic
70 evolution at macroevolutionary scales.

71 To date, several studies have attempted to resolve these issues by testing for associations
72 between per-lineage rates of speciation and phenotypic evolution estimated using phylogenetic
73 data. However, such tests have found mixed results²³⁻³⁶, ranging from strong positive associations
74 between speciation and phenotypic evolution in some groups (e.g. ray-finned fishes²⁴) to no
75 relationship in others (e.g. birds³⁶), making broad conclusions difficult to draw. A further
76 complicating factor is that previous studies have addressed these questions using a range of
77 different methodologies, making it difficult to assess whether the signal of inconsistent relationships
78 across groups is real, or at least partly caused by methodological differences between studies.
79 Indeed, as yet there has been no direct assessment of the relative strengths and weaknesses of
80 different approaches for testing associations between speciation and phenotypic rates derived from
81 phylogenetic data.

82 Here we address these issues in two ways. First, we use simulated datasets to conduct a
83 systematic assessment of the accuracy and performance of different approaches for testing
84 correlations between phylogenetic rates of speciation and trait evolution under a range of simulated

85 conditions. In particular, we focus on assessing the potential for trait measurement error to mislead
86 such tests, as this issue has previously been shown to cause biases in models of trait evolution³⁷⁻³⁹
87 that could negatively impact tests of the relationship between speciation and trait evolution⁴⁰.
88 Second, using the best-performing approach, which we refer to as the Correlated Speciation and
89 Trait Rates Simulation (Cor-STRATES) framework, we test longstanding hypotheses for the
90 relationship between rates of speciation and morphological (body size) evolution in five major
91 vertebrate taxa (amphibians, birds, mammals, ray-finned fish, squamate reptiles). Together these
92 clades encompass >63,000 species spanning over 450 million years of evolutionary history, and in
93 each case we examine relationships at both the whole-clade level and between major subclades
94 within each group. This two-scale approach, combined with the application of a single robust
95 methodological framework throughout, provides insight into the relationship between two
96 fundamental macroevolutionary rates across a major section of the tree of life.

97

98 **RESULTS**

99 **Performance of evolutionary rate models.** We tested the accuracy and performance of two
100 methods for estimating per-lineage speciation rates (BAMM⁴¹, DR⁴) and four methods for estimating
101 per-lineage rates of trait evolution (BAMM²⁴, BayesTraits⁵, StableTraits⁴², mvBM⁴³). For speciation
102 rates, we found that BAMM consistently outperformed DR for all but the smallest tree sizes (50 tips),
103 generating speciation rate estimates that were more accurate, less biased and more strongly
104 correlated with true (i.e. simulated) rates (Extended Data Figure 1). This was the case regardless of
105 whether we compared BAMM speciation rates across all branches in the tree or for terminal
106 branches (i.e. tips) only (Extended Data Figure 1). For trait rates, we found that BAMM and
107 BayesTraits outperformed StableTraits and mvBM, providing more accurate (absolute) rate
108 estimates that were considerably more strongly correlated with true rates, particularly in larger trees
109 (100-500 tips; Extended Data Figure 1). Based on these results, we focused our subsequent
110 performance analyses on speciation rates estimated by BAMM (λ_{BAMM}) and trait rates estimated by
111 either BAMM (σ^2_{BAMM}) or BayesTraits (σ^2_{BT}).

112

113 **Testing associations between rates of speciation and trait evolution.** We used simulated 250-
114 tip datasets exhibiting positive, negative, and no coupling between rates to test the performance of
115 four different approaches for inferring the correct association between rates of speciation and trait
116 evolution (Figure 1 and Extended Data Figure 2). The best performing approach (simulation + tree-
117 rescaling) consisted of an initial tree-scaling step using Pagel's lambda⁴⁴ to adjust for the extent of
118 phylogenetic signal in the trait data, followed by a simulation-based significance test whereby the
119 observed correlation between rates is compared to a null distribution of correlations generated by
120 evolutionary simulation (Figure 2). This approach had good power to detect both positive and
121 negative associations between speciation and trait rates, regardless of whether trait rates were

122 estimated with BayesTraits (Figure 1) or BAMM (Extended Data Figure 2). Importantly, Type I error
123 (false discovery) rates remained consistently low (~5%), even in the presence of considerable trait
124 measurement error. The same outcomes were not observed for the three other approaches we
125 investigated (PGLS only, PGLS + tree-rescaling, simulation only), which exhibited reduced
126 statistical power and/or unacceptably high Type I error rates, particularly with measurement error in
127 trait values (Figure 1 and Extended Data Figure 2).

128 Focusing on this best-performing approach, which we refer to as the Cor-STRATES
129 framework (Figure 2), we found that comparing per-branch rates across all branches in the tree and
130 at the tips only showed similar performance, whereas a weighted-averaging approach incorporating
131 information from deeper branches but weighted towards the tips slightly underperformed relative to
132 the other two approaches (Extended Data Figures 2 and 3). We also found that in the context of
133 testing for relationships with speciation rates, trait rates derived from BayesTraits (σ^2_{BT}) (Figure 1)
134 generally lead to better performance than trait rates derived from BAMM (σ^2_{BAMM}) (Extended Data
135 Figure 2). A further comparison of effect sizes showed that BayesTraits rates generally gave larger
136 average effect sizes than BAMM rates, particularly in scenarios involving negative associations
137 between rates (Extended Data Figure 3). Although the differences in performance between
138 BayesTraits and BAMM are marginal, we therefore conducted all subsequent analyses using trait
139 rates derived from BayesTraits (σ^2_{BT}). However, we acknowledge that alternative scenarios not
140 considered here may favour alternative frameworks.

141 Further testing using the Cor-STRATES framework showed that the power to detect
142 significant associations between rates unsurprisingly depends on tree size and simulated correlation
143 strength (Extended Data Figure 4), ranging from low power (~0.1) in small datasets (50 tips) to very
144 high power (~1.0) in large datasets (500 tips) simulated with strong correlations between rates (see
145 Methods). These results also showed that trait measurement error reduced the power to detect
146 significant associations between speciation and trait rates, but that this reduction disproportionately
147 affects the detection of negative relationships relative to positive ones (Extended Data Figure 4).
148 Importantly, Type I error rates remained acceptably low (~5%) at all tree sizes, irrespective of the
149 level of measurement error in trait values.

150 We also investigated the impact of incomplete species sampling and non-zero turnover
151 (relative extinction) rates on test performance. Predictably, we found that the power to detect
152 significant associations fell as the proportion of missing species increased (Extended Data Figure
153 5), but only declined to very low levels under the most extreme combinations of trait measurement
154 error and sampling incompleteness (i.e. 75% of species missing from a 250-tip tree). For turnover,
155 we found that when trait measurement error was absent, non-zero relative extinction rates had
156 relatively little impact on the power to detect either positive or negative associations between rates
157 (Extended Data Figure 6). In fact, we found that power marginally increased under these scenarios
158 relative to base levels (Extended Data Figure 6), which may reflect to some extent relatively unusual

159 shape of trees generated assuming increasingly high rates lineage turnover. In scenarios involving
160 trait measurement error, however, we found that lineage turnover disproportionately reduced the
161 power to detect negative associations between rates, particularly under very high turnover levels
162 (0.9), whereas the power to detect positive associations was relatively unaffected (Extended Data
163 Figure 6). Lineage turnover had no effect on Type I error rates, however, which remained
164 acceptably low in all cases.

165

166 **Relationships between speciation and body size evolution in vertebrates.** We used the Cor-
167 STRATES framework (Figure 2) to test the coupling between rates of speciation and body size
168 evolution in five major vertebrate groups: amphibians (sampled / total richness = 3,193 / 7,238
169 spp.), birds (6,670 / 9,993 spp.), ray-finned fish (10,868 / 31,516 spp.), mammals (4,095 / 5,561
170 spp.) and squamate reptiles (5,398 / 9,755 spp.) (Supplementary Data 1). Comparing speciation
171 rates estimated by BAMM (λ_{BAMM}) to body size rates estimated by BayesTraits (σ_{BT}^2) (Figure 3), our
172 tests revealed consistently positive relationships between rates of speciation and body size
173 evolution across the five groups that were significantly more extreme than expected based on null
174 simulations (Figure 4). The strength of the association between rates varied between groups,
175 however, ranging from an effect size (observed ρ – simulated ρ) of 0.15 [95% CI: 0.06, 0.24] in birds
176 to 0.47 [95% CI: 0.39, 0.57] in squamates (Extended Data Figure 7). These results correspond to
177 correlations based on tip rates, but tests based on rate variation across all branches in the tree gave
178 similar results (Extended Data Figure 7).

179 To further investigate the extent of among-clade variability in the coupling between
180 speciation and body size evolution, we also tested relationships separately for major subclades
181 within each of the five groups. Focusing largely on recognised subclades (usually orders or families)
182 containing >100 species with trait data and for which satisfactory convergence of rate models could
183 be achieved ($n = 65$ clades), we found that relationships between speciation and trait rates varied
184 considerably between subclades (Figure 5; Extended Data Figure 8), despite overarching positive
185 relationships. For example, focusing on results based on tip rates, effect sizes for individual
186 subclades ranged from 0.69 [95% CI: 0.19, 1.10] in shorebirds (Order: Charadriiformes) to -0.56
187 [95% CI: -0.97, -0.17] in toads (Family: Bufonidae). Results were generally similar when tests were
188 conducted using rates extracted from all branches in the tree (Figure 5). Overall, 15 out of the 65
189 subclades exhibited significant associations between rates of speciation and body size evolution in
190 at least one of the comparisons, representing 13 positive associations and 2 negative associations
191 (Supplementary Data 2).

192 Using Bayesian phylogenetic mixed models, we found that variation in effect size scores
193 across individual subclades was largely unrelated to differences in crown age (Myr), total species
194 richness, sampling proportion, the degree of phylogenetic signal in body size values and the
195 variance in per-branch rate estimates within clades. Specifically, we found some limited evidence

196 that absolute effect size was related to species richness and the extent of within-clade variance in
197 speciation rates (i.e. stronger relationships in more species-rich clades and those with greater
198 variance in speciation rates), but these relationships were weak and highly inconsistent across
199 datasets (Extended Data Figure 9).

200

201 **DISCUSSION**

202 Here we have developed an approach for testing associations between rates of speciation and
203 phenotypic evolution using phylogenetic data – the Cor-STRATES framework – and used it to
204 robustly test longstanding theories concerning the coupling between rates of speciation and
205 morphological evolution at macroevolutionary scales. Focusing on the relationships between
206 speciation rates and rates of body size evolution, we found strong evidence that these fundamental
207 evolutionary rates are positively correlated in five major vertebrate clades (amphibians, birds
208 mammals, ray-finned fish, squamate reptiles). Analysing these relationships at a finer phylogenetic
209 scale (i.e. among subclades within the five main groups) revealed evidence for more extensive
210 variation in the coupling between speciation and body size evolution, but where significant
211 relationships were inferred, most clades (13 out of 15) exhibited positive associations.

212 These results have several important implications. First, as we found significant positive
213 associations between rates in each of the five groups tested, our results suggest that a positive
214 coupling between speciation and morphological evolution represents a general feature of vertebrate
215 evolution. Previous studies investigating these relationships at a similar phylogenetic scale in select
216 vertebrate groups have reached mixed conclusions (e.g. birds^{26,36}, mammals^{5,35}). As a result, broad
217 insights concerning the nature of the relationships between speciation rates and rates of
218 morphological evolution in these groups and in vertebrates more generally remained difficult to
219 draw. Our results, based on the application of a consistent methodological framework to each of the
220 five groups, bolster support for the existence of positive relationships between evolutionary rates in
221 these taxa, in line with the idea that positive correlations between rates speciation and
222 morphological evolution have played an important role in shaping the vast majority of vertebrate
223 diversity²⁴.

224 Several explanations have been proposed to explain positive correlations between rates of
225 speciation and morphological evolution at macroevolutionary scales. For instance, adaptive
226 radiation theory predicts a co-incidence between the evolution of ecological diversity and rapid
227 lineage splitting, as lineages rapidly ecologically differentiate to fill unoccupied niche space¹³. These
228 ideas are closely related to the notion of morphological evolvability or ‘versatility’ promoting
229 accelerated speciation rates, in the sense that enhanced rates of morphological change facilitates
230 rapid species accumulation by allowing lineages to diversify to utilise a broader spectrum of
231 available resources^{10,11}. Similarly, mechanisms associated with the more traditional concept of
232 punctuated equilibrium (i.e. phenotypic change concentrated largely at speciation events) also

233 predict a general positive coupling between speciation rates and rates of morphological evolution,
234 albeit with the opposite direction of causality (i.e. the speciation process itself drives rapid
235 morphological change⁹). Separating these alternative interpretations based on correlations between
236 evolutionary rates remains difficult⁴⁵, but irrespective of the underlying mechanism, broad positive
237 relationships between rates of speciation and body size evolution imply a central role for
238 morphological evolution in facilitating diversification in evolutionary radiations²⁴.

239 However, an important additional feature of our results is that despite these overarching
240 relationships, there appears to be considerable variation in the strength of coupling between rates of
241 speciation and body size evolution both within and between vertebrate radiations. For instance, at
242 the whole-clade level, we found a much tighter relationship between rates of speciation and body
243 size evolution in squamate reptiles than in the other four groups. Counter-intuitively, the relatively
244 strong whole-clade correlation in squamates is not reflected by within-clade trends, that are
245 significantly positive for only one clade (Colubridae). This indicates that rates of speciation and trait
246 evolution may often be decoupled, or show idiosyncratic trends, at comparatively fine phylogenetic
247 scales but that clade-specific factors could simultaneously drive changes in rates of both speciation
248 and trait evolution at broader scale. Indeed, at finer phylogenetic scales, our subclade analyses
249 revealed considerable variation in the coupling between rates of speciation and body size evolution
250 between major subclades within each of the five radiations. At least some of this variation in effect
251 strength between clades (particularly at the subclade level) may simply reflect variation in statistical
252 power relating to clade size (see Extended Data Figure 4) or species sampling (see Extended Data
253 Figure 5), and other issues connected to the extent of 'arbitrariness' with which the taxonomic units
254 we study are defined (i.e. Simpson's paradox^{46,47}). However, at least some of this variation may be
255 indicative of differences in the relative importance of particular speciation processes driving
256 speciation among taxa. For instance, we found strong positive associations between rates of
257 speciation and body size evolution in several subclades in which it has been argued that size
258 differentiation has played a major role in facilitating species diversification [e.g. cichliform fish^{48,49}
259 (Cichliformes), bats^{50,51} (Chiroptera), colubrid snakes⁵² (Colubridae) and shorebirds⁵³
260 (Charadriiformes)].

261 In contrast, we identified a small number of clades – namely, toads (Bufonidae) and lacertid
262 lizards (Lacertidae) – in which speciation rates were negatively (i.e. inversely) related to rates
263 morphological evolution, in line with previous results implying a strong connection between lineage
264 splitting and relative morphological stasis in these groups⁵⁴⁻⁵⁷. The existence of 'inverted'
265 relationships between speciation and morphological rates such as these are intriguing, because
266 they suggest that the processes driving speciation in these groups are deterministically different to
267 the processes dominating in other subclades and over broader phylogenetic and temporal scales
268 more generally. In particular, negative associations between speciation rates and rates of body size
269 evolution are consistent with diversification via so-called 'non-adaptive radiation', in which lineage

270 splitting is primarily driven by factors such as geographic isolation and/or mating differentiation, with
271 little morphological or ecological differentiation among taxa^{18-20,22}. However, it may be that
272 diversification in ecomorphological traits other than body size have been important in facilitating
273 speciation in these groups (see below). Nonetheless, this heterogeneity between subclades can
274 also help to explain the generally ‘noisy’ positive relationships between speciation rates and rates of
275 body size evolution when viewed at broader phylogenetic scales (i.e. Figure 3).

276 It is important to note that these conclusions are subject to other potential caveats. For
277 instance, our approach does not bypass general issues concerning our ability to accurately estimate
278 evolutionary rates (speciation and trait evolution). Indeed, such rates are intrinsically difficult to
279 estimate based on phylogenetic data alone, particularly over deep timescales⁵⁸ and when rate shifts
280 involves slow-downs rather than speed-ups in rate⁵⁹. It is therefore likely that such issues weaken
281 our ability to detect tight couplings between evolutionary rates. However, our performance analyses
282 allowed us to select rate modelling frameworks with the highest degree of accuracy among those
283 that we were able to test, and by predominately focusing on tip rates (i.e. the most recent branches
284 of the phylogeny), our approach should maximise our ability to infer accurate relationships between
285 evolutionary rates. More generally, although our analyses allowed us to identify a seemingly robust
286 framework for testing correlations between speciation and phenotypic rates, future analyses may
287 wish to refine our general workflow (Figure 2) by factoring in more powerful rate models and/or
288 more precise information concerning potential sources of error, as the necessary methods and data
289 become available. In particular, we note that our current approach does not explicitly account for
290 lineage-specific variation in trait measurement error, nor other potentially important sources of bias,
291 such as systematic error in phylogenetic branch lengths, which has the potential to bias estimates of
292 both speciation and trait rates. Finally, our own performance analyses clearly show that it is
293 generally harder to detect negative associations between rates of speciation and trait evolution than
294 positive ones – particularly in situations with considerable trait measurement error, reduced species
295 sampling and/or high relative extinction. Thus, negative associations between speciation and
296 morphological evolution may be more common than our results imply and so may be more
297 widespread in nature than currently recognized.

298 Furthermore, it is worth noting that the coupling between rates of speciation and phenotypic
299 evolution may also depend on the identity of the particular trait(s) being studied. Here we focus on
300 body size, under the assumption that evolutionary changes in size (or lack thereof) are informative
301 about the processes driving speciation in these lineages. Body size is strongly correlated with many
302 important aspects of organismal biology (e.g. habitat, life history, trophic position⁶⁰) and divergence
303 in body size has been linked to ecological differentiation and reproductive isolation in a variety
304 vertebrate lineages^{15,21,61}. However, in many cases speciation may depend more strongly on
305 divergence in traits other than body size, that are more closely connected to ecological
306 differentiation and/or reproductive isolation among lineages. For example, it is possible that

307 divergence in ecomorphological traits such body shape or environmental niche traits such as
308 climate or habitat type are characterised by contrasting relationships with speciation rates than we
309 find here for body size. Likewise, studying traits more directly relevant to mate choice and species
310 recognition (e.g. sexual signalling traits^{62,63}) may also provide more direct insight into the role of
311 reproductive isolation in determining variation in speciation rates at macroevolutionary scales⁶⁴.

312 Overall, our results in relation to body size evolution support longstanding predictions for a
313 consistent positive coupling between rates of speciation and morphological divergence at broad
314 macroevolutionary scales^{1,2,7}. At the same time, however, they reveal evidence for considerable
315 variability in the association between these evolutionary rates in different parts of the vertebrate
316 radiation, consistent with the general idea that the relative importance of processes driving
317 speciation – such as adaptive and non-adaptive radiation – varies across the tree of life¹⁸. Our multi-
318 predictor models of subclade effect sizes suggested that this variation in the coupling between rates
319 is unrelated to both clade age and species richness, as may be expected if macroevolutionary rates
320 change in concert over time⁶⁵ or if factors such as branch length error simultaneously bias estimates
321 of clade age and speciation and phenotypic rates within clades⁶⁶. Thus, the ‘predictability’ of clade-
322 specific relationships between speciation and phenotypic evolution remains to be determined, but
323 factors such as ecological opportunity^{13,67}, sexual selection^{22,68} and dispersal ability^{69,70} may
324 deterministically increase the potential for positive and negative rate-relationships, respectively.
325 Nonetheless, our study sheds light on the association between rates of speciation and
326 morphological evolution at broad phylogenetic scales and provides a promising framework for
327 testing relationships between speciation and phenotypic evolution using phylogenetic data.

328

329 **METHODS**

330 **Rates of speciation.** We investigated the performance of two different approaches for inferring
331 variation in per-lineage rates of speciation: BAMM⁴¹ (version 2.5.0) and DR⁴. BAMM uses a
332 Bayesian model-based approach to estimate speciation (and extinction) rates across the tree, under
333 the assumption that phylogenetic diversification dynamics can be approximated by a set of discrete
334 rate regimes. In contrast, the DR statistic is a model-free tip rate metric that incorporates information
335 on the number of splitting events and internode distances along a root-to-tip path of a phylogeny
336 (weighted toward the present) to provide a measure of recent lineage-specific speciation rate⁷¹. We
337 focused on these two approaches because they are capable of providing lineage-specific speciation
338 rate estimates and in the case of DR have been shown to outperform other related approaches (e.g.
339 the node density metric⁷²). We did not explore the performance of ClaDS⁷³, another recently
340 developed model-based method, because we found that it was computational unfeasible to fit this
341 model to either our simulated or empirical datasets. We acknowledge however that the ClaDS
342 method can outperform both DR and (more marginally) BAMM in accurately reconstructing

343 simulated patterns of speciation rate variation across phylogenies in some diversification
344 scenarios⁷³.

345 To fit BAMM diversification models to our datasets (simulated and empirical), we used
346 default priors generated by the 'setBAMMpriors' function in BAMMtools⁷⁴. The only exception to this
347 was that in all cases we set the 'expectedNumberOfShifts' prior to be proportional to the number of
348 tips in the phylogeny. We adjusted MCMC run length according to tree size, using iteration lengths
349 of 2 million (250 tips or less) or 5 million (500 tips) for simulated datasets, and 20 million (<500 tips),
350 50 million (500-1000 tips) or 100 million (>1000 tips) for empirical vertebrate datasets (see below).
351 For analyses based on simulated datasets we took 2,000 samples from the posterior, and for
352 vertebrate analyses we took 10,000 samples. Runs were checked for satisfactory convergence and
353 in all cases we discarded the first 20% of sampled iterations as burn-in. Mean per-branch speciation
354 rates were estimated using the 'getMeanBranchLengthTree' function in BAMMtools, and DR values
355 were estimate using the equations provided in ref. ⁴.

356

357 **Rates of trait evolution.** We investigated the performance of four different approaches for
358 reconstructing patterns of trait rate heterogeneity, each of which have been used to infer per-lineage
359 rates of trait evolution in empirical datasets: (i) BAMM²⁴, (ii) the BayesTraits (version 3) variable
360 rates model⁵, (iii) the StableTraits model⁴², (iv) the 'mvBM' method⁴³ implemented in the R package
361 'evomap'. BAMM and BayesTraits both use Bayesian model-based approaches to estimate shifts in
362 rates of evolution across a phylogeny, though the manner in which rate shifts are modelled differs
363 between the methods. Specifically, BAMM models discrete shifts for a node and all of its
364 descendants and allows rates to vary through time. BayesTraits also models discrete shifts for a
365 node and all of its descendants and also explicitly allows discrete shifts on single internal branches,
366 but does not model temporal rate variation (see ref. ⁷⁵ for a more comprehensive overview). In
367 contrast, StableTraits and mvBM are primarily geared toward ancestral states inference but
368 estimates of per-lineage evolutionary rate emerge as a consequence of the inferred pattern of trait
369 change between ancestral and descendent nodes in the tree. StableTraits draws increments in
370 evolving characters from a heavy-tailed stable distribution so that trait evolution is modelled as a
371 mixture of background gradual change interspersed with occasional large jumps⁴². Finally, mvBM is
372 a method that deterministically calculates branch-specific rates of evolution and uses those
373 estimates to parameterize a multivariate BM which is then used to infer ancestral trait values.
374 Collectively these four methods are used extensively to study phylogenetic patterns of trait evolution
375 [e.g. refs. ^{3,5,24,32,76-78}], yet their relative performance and accuracy for correctly inferring rate
376 heterogeneity across phylogenies has not been systematically assessed (though see ref. ⁷⁵).

377 To fit BAMM trait models we used the same approach as we used for estimating speciation
378 rates (see above). We used the same MCMC run settings to fit the BayesTraits variable rates
379 model, using default priors in all cases. StableTraits models were run for 1 million iterations

380 (sampling every 500 iterations), which was sufficient to achieve model convergence in all cases. As
381 above, for BAMM we estimated mean per-branch evolutionary rates using the
382 'getMeanBranchLengthTree' function in BAMMtools. For the other models, we calculated per-
383 branch estimates of evolutionary rate by dividing output tree branch lengths (which are set
384 proportion to the estimated degree of evolutionary change on each branch) by the corresponding
385 branch lengths of the time-calibrated input tree^{3,79}.

386

387 **Simulating patterns of trait rate-dependent speciation.** We evaluated the ability of various
388 approaches to infer true relationships between speciation rates and trait rates (see below) by
389 assessing their performance on trees simulated using ClaDS⁷³. The ClaDS model considers a birth-
390 death diversification process in which diversification rates (speciation and extinction) are inherited
391 along lineages but change stochastically at speciation events, shifting to new values drawn from a
392 specified distribution centred on ancestral values. As mentioned above, this approach performs well
393 at inferring both small and large changes in diversification rates⁷³, and for our purposes provides a
394 useful approach for simulating phylogenies exhibiting patterns of speciation rate heterogeneity. We
395 used the 'sim_ClaDS' function in RPANDA⁸⁰ to simulate phylogenetic trees of different sizes under
396 the default ClaDS model in which new speciation rates are drawn from a lognormal distribution with
397 mean = $\alpha \cdot \lambda$ and variance = σ^2 , where λ is the ancestral speciation rate and α is a trend parameter.
398 We simulated trees with 50, 150, 250 and 500 tips (100 trees in each case) using the following
399 parameters $\lambda_0 = 0.1$, $\sigma = 0.175$, $\alpha = 1$, $\epsilon = 0$, where λ_0 is the initial speciation rate and ϵ is the
400 turnover (extinction/speciation) rate (i.e. extinction rate = 0). We also simulated an additional set of
401 250-tip trees with low ($\epsilon = 0.1$) and high ($\epsilon = 0.9$) turnover rates to allow us to assess the impact of
402 extinction on model performance.

403 For each simulated tree we extracted values for the realised speciation rate of each branch
404 and used these values to calculate branch-specific trait rates that were positively, negatively or
405 uncorrelated with speciation rates. For scenarios involving correlated rates, we generated branch
406 trait rates that were strongly ($r = \pm 1$) or more weakly ($r = \pm 0.5$) associated with speciation rates. We
407 note, however, that due to the stochastic nature of the trait simulations (see below), the realised
408 correlation between speciation and trait rate heterogeneity in our simulated datasets is always lower
409 than implied by the strength of the correlation between branch rates in the generating model (see
410 Extended Data Figure 10 for estimates of realised correlation strengths). For uncorrelated
411 scenarios, we used two different approaches to generate uncorrelated trait rates: first we simply
412 constrained trait rates to be constant across the tree, and second we generated variable trait rates
413 across the tree that were random with respect to speciation rates. This allowed us to explore the
414 impact of two different forms of uncorrelated trait rates on model performance (i.e. constant and
415 variable rates). To generate trait values based on these patterns of rate heterogeneity, we simulated
416 trait values using a Brownian motion model applied to the appropriate rate-scaled trees^{75,81}. While

417 this approach does not constitute a formal process-based simulation procedure, whereby trait rates
418 are directly linked to speciation rates, it is capable of generating patterns consistent with a process
419 of trait rate-dependent speciation.

420 Finally, to explore the impact of trait measurement error on the inference of speciation rate-
421 trait rate correlations, for each set of simulated trait values described above, we generated two
422 additional sets of tip values representing average measurement error of 1% and 10% of the
423 standard deviation of the original set of trait values.

424

425 **Testing the accuracy of evolutionary rate models.** To investigate the relative performance of our
426 focal rate models, we applied each model to a subset of our simulated trees and compared the
427 accuracy of the resulting rate estimates to the true (i.e. generating) values. Specifically, we fit the
428 two speciation rate (BAMM and DR) and four trait rate methods (BAMM, BayesTraits, StableTraits,
429 mvBM) to simulated datasets with 50, 150, 250 and 500 tips (without extinction and measurement
430 error; $n = 100$ trees in each case). We then assessed accuracy using two measures of error (mean
431 absolute error and mean proportional error; for equations see ref. ⁷¹) and by calculating the
432 correlation (Pearson's r) between true and estimated rates.

433

434 **Exploring alternative rate summary statistics.** We explored three different approaches for
435 summarising rate heterogeneity that differ in the extent to which they incorporate information from
436 deeper branches. First, we compared per-branch speciation and trait rates across all branches in
437 the tree. Second, we compared per-branch rate variation among terminal branches (tips) only.
438 Finally, we examined the performance a recently-developed metric for summarising rate variation at
439 the tips of the tree. This metric, called TR by Cooney *et al.* [ref. ⁶³], uses a weighted-averaging
440 approach to summarise rate variation from the full root-to-tip path for each tip, while weighting
441 values towards variation at the tips of the tree. The input for this approach is a tree with branch
442 lengths in units of (mean) evolutionary rate, therefore it can be used to summarise variation in both
443 trait and speciation rates, using mean rate trees as input in each case. We compared the
444 performance of these three summary approaches (i.e. all branches, tips only and weighted-average)
445 for detecting relationships between rates of speciation and trait evolution from phylogenetic trees.

446

447 **Significance tests.** We compared the performance of two distinct approaches for inferring the
448 significance of associations between speciation and trait rates: (i) phylogenetic generalised least-
449 squares (PGLS) regression and (ii) a simulation-based test where the observed correlation between
450 rates is compared to a null set of correlations generated by simulation. PGLS models were fit using
451 the 'phylolm' function in phylolm⁸², assuming an optimised lambda model for the error structure. For
452 the simulation-based test, we simulated sets of trait values ($n = 100$ or 200 for simulated and
453 vertebrate datasets, respectively) based on a Brownian motion (BM) null model, utilising the

454 diffusion rate (σ^2) parameter from a maximum likelihood fit of the BM model to the observed trait
455 data. We then re-estimated trait rates for each null dataset, using run lengths of 500,000 (250 tips or
456 less) or 1,250,000 (500 tips) for simulated datasets, and 2 million (<500 tips), 5 million (500-1000
457 tips) or 10 million (>1000 tips) for empirical vertebrate datasets, taking 1,000 (simulated datasets) or
458 2,000 (vertebrate datasets) posterior samples in each case. We then compared mean trait rates for
459 each null simulation to observed speciation rates and used the resulting distribution of correlation
460 coefficients to compute a two-tailed P value for the observed correlation coefficient⁸³. We used
461 Spearman's rank correlation (ρ) to measure the association between rates because the distribution
462 of estimated speciation and/or trait rates is often highly non-normal, even after log-transformation,
463 which makes applying parametric statistics such as Pearson's r problematic.

464 In combination with these two approaches, we also explored the impact of controlling for the
465 observed level of phylogenetic signal in the trait data prior to estimating trait rates, by first rescaling
466 the empirical phylogeny by the estimated value of Pagel's lambda⁴⁴. Measurement error and other
467 sources of non-phylogenetic trait variation (e.g. intra-specific variation) can generate biases in
468 estimates of trait evolutionary rates, particularly for short branches⁸⁴, potentially leading to spurious
469 correlations between trait rate metrics and speciation⁴⁰. However, rescaling branch lengths by an
470 appropriate value of lambda (estimated using the empirical time tree and the trait data) prior to
471 estimating trait rates may account for (or at least mitigate) this bias, and in turn reduce the potential
472 for spurious correlations between rates. We therefore combined this tree-rescaling step with each of
473 the significance tests described above to generate four distinct approaches for testing the
474 association between speciation and trait evolution: (i) PGLS only, (ii) PGLS + tree-rescaling, (iii)
475 simulation only, (iv) simulation + tree-rescaling. (Note: the tree-rescaling is only used in relation to
476 rates of trait evolution; speciation rates are always calculated using the original, time-calibrated
477 phylogeny; see Figure 1).

478

479 **Performance tests.** We assessed the ability of different approaches to detect the correct
480 association between rates of speciation and trait evolution by applying each method to simulated
481 datasets of 250-tip trees generated assuming positive, negative and no correlation between rates,
482 and with varying degrees of trait measurement error (0%, 1%, 10%). For each scenario, we counted
483 the proportion of times (out of 100) a given method inferred a significant ($P < 0.05$) association
484 between rates. Following this initial assessment, we then applied the best-performing method
485 (simulation + tree-rescaling; see Results) to a broader range of simulated scenarios to explore
486 changes in power and false discovery rates associated with varying tree sizes, sampling
487 proportions, and extinction (turnover) rates.

488

489 **Vertebrate analyses.** We investigated relationships between rates of speciation and body size
490 evolution in five vertebrate clades with good data on body size and phylogeny: amphibians, birds,

491 mammals, ray-finned fish and squamate reptiles. Phylogenetic data came from recent, time-
492 calibrated molecular phylogenies for each group^{4,6,85-87}. Because the evolutionary rates models we
493 use are computationally expensive to fit (particularly to large phylogenies), our analyses are based
494 on a maximum clade credibility (MCC) tree for each group, generated in each case using the
495 'maxCladeCred' function in phangorn⁸⁸ and based on 1,000 trees sampled at random from the
496 posterior distribution. To ensure reliable estimates of evolutionary rates⁸⁴, our analyses only include
497 species placed in phylogenies using genetic data. For speciation rate analyses using BAMM, we
498 included information on the proportion of sampled species in each analysis compared to the
499 corresponding taxonomy associated with each phylogeny (for values see Extended Data Figure 7
500 and Supplementary Data 2). Body size information for each group was compiled from various
501 sources: for birds⁸⁹ and mammals⁸⁶ we used estimates of species' mean body mass (g), whereas
502 for amphibians^{90,91}, fish⁹² and squamates⁹³ we used estimates of species' maximum length (mm).
503 Size maxima are good proxies of body size in species with indeterminate growth⁹³, as in common in
504 amphibians, fish and reptiles, and despite downsides related to comparability among species with
505 different body plans, we focused on length measurements for these groups as they are by far the
506 most readily available data in the literature. In each case, size values were log₁₀-transformed prior
507 to rate model fitting. The full size dataset is provided in Supplementary Data 1.

508 We performed two sets of analyses on our vertebrate datasets using the best-performing
509 method identified by our performance analyses (simulation + tree-scaling). First, we tested the
510 association between rates of speciation and body size evolution at the whole-clade level. Second,
511 we assessed the extent of intra-group variation in speciation rate-body size rate relationships by
512 running separate analyses on subclades within each group that contained 100 or more sampled
513 species. In most cases, these subclades corresponded to recognised taxonomic units within each
514 group (e.g. orders, families), with the exception of a small number of fish taxa that have recently
515 been found to be non-monophyletic⁶ (see Supplementary Data 1 for clade designations). In each
516 case, effect sizes describing the strength and direction of the inferred relationship were was
517 calculated as either $\rho_{\text{obs}} - \text{mean}(\rho_{\text{null}})$ giving the unstandardised effect size, or $\rho_{\text{obs}} - \text{mean}(\rho_{\text{null}}) /$
518 $\text{sd}(\rho_{\text{null}})$ giving the standardised effect size.

519 Finally, we tested whether variation in subclade effect size estimates was related to
520 differences in among clades in taxonomic richness and/or crown age (Myr; extracted from MCC
521 trees), whilst also controlling for differences in sampling rates, the degree of phylogenetic signal in
522 body size values, and the extent of within-clade variance in speciation and body size rate estimates,
523 measured as the coefficient of variation (CV) for log-normal data:

$$CV = \sqrt{e^{\sigma^2} - 1}$$

524 , where σ^2 is the variance of per-branch rate estimates. To do this, we ran multi-predictor Bayesian
525 phylogenetic mixed-models using the MCMCglmm⁹⁴ R package and the backbone tree illustrated in

526 Figure 3. We used uninformative priors and included as random effects both the phylogenetic co-
527 variance matrix and a variable denoting whether mass or length estimates were used to test the
528 relationship between body size and speciation rates. Models were run with the following settings:
529 nitt = 1,100,000, burnin = 100,000, thin = 200 and all models showed suitable convergence.
530

531 **ACKNOWLEDGEMENTS.** We thank Joseph Brown, Angela Chira, Yichen He, Emma Hughes
532 and Jonathon Kennedy for helpful discussion, and Matthew Pennell and Daniel Rabosky for
533 constructive comments on the manuscript. This work was funded by the European Research
534 Council (grant number 615709 Project 'ToLERates'), and by a Leverhulme Early Career Fellowship
535 to CRC (ECF-2018-101) and a Royal Society University Research Fellowship to GHT (UF120016
536 and URF\R\180006).
537
538

539 **REFERENCES**

- 540 1 Simpson, G. G. *The major features of evolution*. (Columbia University Press, 1953).
- 541 2 Simpson, G. G. *Tempo and mode in evolution*. (Columbia University Press, 1944).
- 542 3 Cooney, C. R. *et al.* Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature*
543 **542**, 344-347, (2017).
- 544 4 Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds
545 in space and time. *Nature* **491**, 444-448, (2012).
- 546 5 Venditti, C., Meade, A. & Pagel, M. Multiple routes to mammalian diversity. *Nature* **479**,
547 393-396, (2011).
- 548 6 Rabosky, D. L. *et al.* An inverse latitudinal gradient in speciation rate for marine fishes.
549 *Nature* **559**, 392-395, (2018).
- 550 7 Stanley, S. M. *Macroevolution: pattern and process*. (Freeman, 1979).
- 551 8 Reznick, D. N. & Ricklefs, R. E. Darwin's bridge between microevolution and macroevolution.
552 *Nature* **457**, 837-842, (2009).
- 553 9 Gould, S. J. & Eldredge, N. Punctuated equilibria: the tempo and mode of evolution
554 reconsidered. *Paleobiology* **3**, 115-151, (1977).
- 555 10 Vermeij, G. J. Biological versatility and earth history. *Proc. Natl. Acad. Sci. U.S.A.* **70**, 1936-
556 1938, (1973).
- 557 11 Vermeij, G. J. Adaptation, versatility, and evolution. *Systematic Zoology* **22**, 466-477, (1973).
- 558 12 Liem, K. F. Biological versatility, evolution, and food resource exploitation in African cichlid
559 fishes. *Am. Zool.* **15**, 427-454, (1975).
- 560 13 Schluter, D. *The ecology of adaptive radiation*. (Oxford University Press, 2000).
- 561 14 Lovette, I. J., Bermingham, E. & Ricklefs, R. E. Clade-specific morphological diversification
562 and adaptive radiation in Hawaiian songbirds. *Proc. R. Soc. London Ser. B* **269**, 37-42, (2002).
- 563 15 Grant, P. R. & Grant, B. R. *How and why species multiply: the radiation of Darwin's finches*.
564 (Princeton University Press, 2008).
- 565 16 Danely, P. D. & Kocher, T. D. Speciation in rapidly diverging systems: lessons from Lake
566 Malawi. *Mol. Ecol.* **10**, 1075-1086, (2001).
- 567 17 Losos, J. B. *et al.* Niche lability in the evolution of a Caribbean lizard community. *Nature* **424**,
568 542-545, (2003).
- 569 18 Czekanski-Moir, J. E. & Rundell, R. J. The ecology of nonecological speciation and
570 nonadaptive radiations. *Trends Ecol. Evol.* **34**, 400-415, (2019).
- 571 19 Rundell, R. J. & Price, T. D. Adaptive radiation, nonadaptive radiation, ecological speciation
572 and nonecological speciation. *Trends Ecol. Evol.* **24**, 394-399, (2009).
- 573 20 Svensson, E. I. Non-ecological speciation, niche conservatism and thermal adaptation: how
574 are they connected? *Organisms Diversity & Evolution* **12**, 229-240, (2012).
- 575 21 Wollenberg Valero, K. C. *et al.* Patterns, mechanisms and genetics of speciation in reptiles
576 and amphibians. *Genes* **10**, 646, (2019).
- 577 22 Mendelson, T. C., Martin, M. D. & Flaxman, S. M. Mutation-order divergence by sexual
578 selection: diversification of sexual signals in similar environments as a first step in
579 speciation. *Ecol. Lett.* **17**, 1053-1066, (2014).
- 580 23 Rabosky, D. L. & Adams, D. C. Rates of morphological evolution are correlated with species
581 richness in salamanders. *Evolution* **66**, 1807-1818, (2012).
- 582 24 Rabosky, D. L. *et al.* Rates of speciation and morphological evolution are correlated across
583 the largest vertebrate radiation. *Nature communications* **4**, 1958, (2013).
- 584 25 Gomes, A. C. R., Sorenson, M. D. & Cardoso, G. C. Speciation is associated with changing
585 ornamentation rather than stronger sexual selection. *Evolution* **70**, 2823-2838, (2016).

- 586 26 Ricklefs, R. E. Cladogenesis and morphological diversification in passerine birds. *Nature* **430**,
587 338-341, (2004).
- 588 27 Title, P. O. & Burns, K. J. Rates of climatic niche evolution are correlated with species
589 richness in a large and ecologically diverse radiation of songbirds. *Ecol. Lett.* **18**, 433-440,
590 (2015).
- 591 28 Cooney, C. R., Seddon, N. & Tobias, J. A. Widespread correlations between climatic niche
592 evolution and species diversification in birds. *J. Anim. Ecol.* **85**, 869-878, (2016).
- 593 29 Cardoso, G. C. & Mota, P. G. Speciation evolution of coloration in the genus *Carduelis*.
594 *Evolution* **62**, 753-762, (2008).
- 595 30 Mason, N. A. *et al.* Song evolution, speciation, and vocal learning in passerine birds.
596 *Evolution* **71**, 786-796, (2017).
- 597 31 Igea, J., Miller, E. F., Papadopoulos, A. S. T. & Tanentzap, A. J. Seed size and its rate of
598 evolution correlate with species diversification across angiosperms. *PLoS Biol.* **15**, e2002792,
599 (2017).
- 600 32 Puttick, M. N., Clark, J. & Donoghue, P. C. J. Size is not everything: rates of genome size
601 evolution, not C-value, correlate with speciation in angiosperms. *Proc. R. Soc. London Ser. B*
602 **282**, 20152289, (2015).
- 603 33 Cantalapiedra, J. L., Prado, J. L., Hernandez Fernández, M. & Alberdi, M. T. Decoupled
604 ecomorphological evolution and diversification in Neogene-Quaternary horses. *Science* **355**,
605 627-630, (2017).
- 606 34 Lee, M. S. Y., Sanders, K. L., King, B. & Palci, A. Diversification rates and phenotypic evolution
607 in venomous snakes (Elapidae). *Royal Society Open Science* **3**, 150277, (2016).
- 608 35 Monroe, Melanie J. & Bokma, F. Do speciation rates drive rates of body size evolution in
609 mammals? *Am. Nat.* **174**, 912-918, (2009).
- 610 36 Crouch, N. M. A. & Ricklefs, R. E. Speciation rate is independent of the rate of evolution of
611 morphological size, shape, and absolute morphological specialization in a large clade of
612 birds. *Am. Nat.* **193**, E78-E91, (2019).
- 613 37 Cooper, N., Thomas, G. H., Venditti, C., Meade, A. & Freckleton, R. P. A cautionary note on
614 the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biol. J. Linn. Soc.* **118**,
615 64-77, (2016).
- 616 38 Silvestro, D., Kostikova, A., Litsios, G., Pearman, P. B. & Salamin, N. Measurement errors
617 should always be incorporated in phylogenetic comparative analysis. *Methods in Ecology*
618 *and Evolution* **6**, 340-346, (2015).
- 619 39 Ho, L. S. T. & Ané, C. Intrinsic inference difficulties for trait evolution with Ornstein-
620 Uhlenbeck models. *Methods in Ecology and Evolution* **5**, 1133-1146, (2014).
- 621 40 Pennell, M. W., Harmon, L. J. & Uyeda, J. C. Is there room for punctuated equilibrium in
622 macroevolution? *Trends Ecol. Evol.* **25**, 23-32, (2014).
- 623 41 Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-dependence
624 on phylogenetic trees. *PLoS one* **9**, e89543, (2014).
- 625 42 Elliot, M. G. & Mooers, A. Ø. Inferring ancestral states without assuming neutrality or
626 gradualism using a stable model of continuous character evolution. *BMC Evol. Biol.* **14**, 226,
627 (2014).
- 628 43 Smaers, J. B., Mongle, C. S. & Kandler, A. A multiple variance Brownian motion framework
629 for estimating variable rates and inferring ancestral states. *Biol. J. Linn. Soc.* **118**, 78-94,
630 (2016).
- 631 44 Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877-884,
632 (1999).

633 45 Rabosky, D. L. Positive correlation between diversification rates and phenotypic evolvability
634 can mimic punctuated equilibrium on molecular phylogenies. *Evolution* **66**, 2622-2627,
635 (2012).

636 46 Simpson, E. H. The interpretation of interaction in contingency tables. *Journal of the Royal*
637 *Statistical Society B* **13**, 238-241, (1951).

638 47 Pearl, J. Comment: Understanding Simpson's paradox. *American Statistician* **68**, 8-13,
639 (2014).

640 48 Romanuk, T. N., Hayward, A. & Hutchings, J. A. Trophic level scales positively with body size
641 in fishes. *Global Ecol. Biogeogr.* **20**, 231-240, (2011).

642 49 Steele, S. E. & López-Fernández, H. Body size diversity and frequency distributions of
643 Neotropical cichlid fishes (Cichliformes: Cichlidae: Cichlinae). *PloS one* **9**, e106336, (2014).

644 50 Murillo-García, O. & De la vega, M. Divergence, convergence and phenotypic diversity of
645 neotropical frugivorous bats. *Diversity* **10**, 100, (2018).

646 51 Morales, A. E., Ruedi, M., Field, K. & Carstens, B. C. Diversification rates have no effect on
647 the convergent evolution of foraging strategies in the most speciose genus of bats, *Myotis*.
648 *Evolution* **73**, 2263-2280, (2019).

649 52 Rodríguez-Robles, J. A. Molecular systematics of New World lampropeltine snakes
650 (Colubridae): implications for biogeography and evolution of food habits. *Biol. J. Linn. Soc.*
651 **68**, 355-385, (1999).

652 53 Weir, J. T. & Mursleen, S. Diversity-dependent cladogenesis and trait evolution in the
653 adaptive radiation of the auks (Aves: Alcidae). *Evolution* **67**, 403-416, (2013).

654 54 Moen, D. S., Irschick, D. J. & Wiens, J. J. Evolutionary conservatism and convergence both
655 lead to striking similarity in ecology, morphology and performance across continents in
656 frogs. *Proc. R. Soc. London Ser. B* **280**, 20132156, (2013).

657 55 Ahmadzadeh, F. *et al.* Cryptic speciation patterns in Iranian rock lizards uncovered by
658 integrative taxonomy. *PloS one* **8**, e80563, (2013).

659 56 Gabriot, M., Lopez, P. & Martin, J. Differences in chemical sexual signals may promote
660 reproductive isolation and cryptic speciation between Iberian wall lizard populations.
661 *International journal of evolutionary biology* **2012**, 698520, (2012).

662 57 Hipsley, C. A., Miles, D. B. & Müller, J. Morphological disparity opposes latitudinal diversity
663 gradient in lacertid lizards. *Biol. Lett.* **10**, 20140101, (2014).

664 58 Louca, S. & Pennell, M. W. Extant timetrees are consistent with a myriad of diversification
665 histories. *Nature* **580**, 502-505, (2020).

666 59 Liow, L. H., Quental, T. B. & Marshall, C. R. When can decreasing diversification rates be
667 detected with molecular phylogenies and the fossil record? *Syst. Biol.* **59**, 646-659, (2010).

668 60 Brown, J. H. *Macroecology*. (University of Chicago Press, 1995).

669 61 Schluter, D. Ecology and the origin of species. *Trends Ecol. Evol.* **16**, 372-380, (2001).

670 62 Arnegard, M. E. *et al.* Sexual signal evolution outpaces ecological divergence during electric
671 fish species radiation. *Am. Nat.* **176**, 335-356, (2010).

672 63 Cooney, C. R. *et al.* Sexual selection predicts the rate and direction of colour divergence in a
673 large avian radiation. *Nature communications* **10**, 1773, (2019).

674 64 Rabosky, D. L. Reproductive isolation and the causes of speciation rate variation in nature.
675 *Biol. J. Linn. Soc.* **118**, 13-25, (2016).

676 65 Henao Diaz, L. F., Harmon, L. J., Sugawara, M. T. C., Miller, E. T. & Pennell, M. W.
677 Macroevolutionary diversification rates show time dependency. *Proc. Natl. Acad. Sci. U.S.A.*
678 **116**, 7403-7408, (2019).

679 66 Shafir, A., Azouri, D., Goldberg, E. E. & Mayrose, I. Heterogeneity in the rate of molecular
680 sequence evolution substantially impacts the accuracy of detecting shifts in diversification
681 rates. *Evolution* **74**, 1620-1639, (2020).

682 67 Losos, J. B. Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am.*
683 *Nat.* **175**, 623-639, (2010).

684 68 Price, T. Sexual selection and natural selection in bird speciation. *Philos. Trans. R. Soc.*
685 *London Ser. B* **353**, 251-260, (1998).

686 69 Salisbury, C. L., Seddon, N., Cooney, C. R. & Tobias, J. A. The latitudinal gradient in dispersal
687 constraints: ecological specialisation drives diversification in tropical birds. *Ecol. Lett.* **15**,
688 847-855, (2012).

689 70 Moyle, R. G., Filardi, C. E., Smith, C. E. & Diamond, J. Explosive Pleistocene diversification
690 and hemispheric expansion of a "great speciator". *Proc. Natl. Acad. Sci. U.S.A.* **106**, 1863-
691 1868, (2009).

692 71 Title, P. O. & Rabosky, D. L. Tip rates, phylogenies and diversification: what are we
693 estimating, and how good are the estimates? *Methods in Ecology and Evolution* **10**, 821-834,
694 (2019).

695 72 Freckleton, R. P., Phillimore, A. B. & Pagel, M. Relating traits to diversification: a simple test.
696 *Am. Nat.* **172**, 102-115, (2008).

697 73 Maliet, O., Hartig, F. & Morlon, H. A model with many small shifts for estimating species-
698 specific diversification rates. *Nature Ecology & Evolution* **3**, 1086-1092, (2019).

699 74 Rabosky, D. L. *et al.* BAMMtools: an R package for the analysis of evolutionary dynamics on
700 phylogenetic trees. *Methods in Ecology and Evolution* **5**, 701-707, (2014).

701 75 Chira, A. M. & Thomas, G. H. The impact of rate heterogeneity on inference of phylogenetic
702 models of trait evolution. *J. Evol. Biol.* **29**, 2502-2518, (2016).

703 76 Zelditch, M. L., Ye, J., Mitchell, J. S. & Swiderski, D. L. Rare ecomorphological convergence on
704 a complex adaptive landscape: body size and diet mediate evolution of jaw shape in
705 squirrels (Sciuridae). *Evolution* **71**, 633-649, (2017).

706 77 Pimiento, C., Cantalapiedra, J. L., Shimada, K., Field, D. J. & Smaers, J. B. Evolutionary
707 pathways toward gigantism in sharks and rays. *Evolution* **73**, 588-599, (2019).

708 78 Gómez-Robles, A., Smaers, J. B., Holloway, R. L., Polly, P. D. & Wood, B. A. Brain
709 enlargement and dental reduction were not linked in hominin evolution. *Proc. Natl. Acad.*
710 *Sci. U.S.A.* **114**, 468-473, (2017).

711 79 Chira, A. M. *et al.* Correlates of rate heterogeneity in avian ecomorphological traits. *Ecol.*
712 *Lett.* **21**, 1505-1514, (2018).

713 80 Morlon, H. *et al.* RPANDA: an R package for macroevolutionary analyses on phylogenetic
714 trees. *Methods in Ecology and Evolution* **7**, 589-597, (2016).

715 81 Pennell, M. W., FitzJohn, R. G., Cornwell, W. K. & Harmon, L. J. Model adequacy and the
716 macroevolution of angiosperm functional traits. *Am. Nat.* **186**, E33-E50, (2015).

717 82 Ho, L. S. T. & Ané, C. A linear-time algorithm for Gaussian and non-Gaussian trait evolution
718 models. *Syst. Biol.* **63**, 397-408, (2014).

719 83 Harvey, M. G. & Rabosky, D. L. Continuous traits and speciation rates: alternatives to state-
720 dependent diversification models. *Methods in Ecology and Evolution* **9**, 984-993, (2018).

721 84 Rabosky, D. L. No substitute for real data: a cautionary note on the use of phylogenies from
722 birth-death polytomy resolvers for downstream comparative analyses. *Evolution* **69**, 3207-
723 3216, (2015).

724 85 Jetz, W. & Pyron, R. A. The interplay of past diversification and evolutionary isolation with
725 present imperilment across the amphibian tree of life. *Nat Ecol Evol* **2**, 850-858, (2018).

726 86 Faurby, S. *et al.* PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. *Ecology*
727 **99**, 2626, (2018).

728 87 Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W. & Pyron, R. A. Fully-sampled phylogenies
729 of squamates reveal evolutionary patterns in threat status. *Biol. Conserv.* **204**, 23-31, (2016).

730 88 Schliep, K. P. phangorn: phylogenetic analysis in R. *Bioinformatics* **27**, 592-593, (2011).

731 89 Wilman, H. *et al.* EltonTraits 1.0: species-level foraging attributes of the world's birds and
732 mammals. *Ecology* **95**, 2027, (2014).

733 90 Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C. & Costa, G. C. AmphiBIO, a
734 global database for amphibian ecological traits. *Scientific Data* **4**, 170123, (2017).

735 91 Amado, T. F., Bidau, C. J. & Olalla-Tárraga, M. Á. Geographic variation of body size in New
736 World anurans: energy and water in a balance. *Ecography* **42**, 456-466, (2018).

737 92 Froese, R. & Pauly, D. www.fishbase.org (accessed 27/02/2019).

738 93 Feldman, A., Sabath, N., Pyron, R. A., Mayrose, I. & Meiri, S. Body sizes and diversification
739 rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecol. Biogeogr.* **25**, 187-197,
740 (2016).

741 94 Hadfield, J. D. MCMC methods for multi-response generalised linear mixed models: the
742 MCMCglmm R package. *Journal of Statistical Software* **33**, 1-22, (2010).

743

744

745 **FIGURE LEGENDS**

746

747 **Figure 1. Comparison of the performance of different approaches for testing correlations**
748 **between rates of speciation and trait evolution.** Results are based on simulated datasets of 250-
749 tip trees ($n = 100$) assuming strong correlations between rates (columns 1 and 2), with speciation
750 rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits (σ^2_{BT}). See
751 *Methods* for details of the simulation procedure, rate metrics and significance tests used. The grey
752 shaded area indicates false discovery (Type I error) rates of <5%.

753

754 **Figure 2. The Correlated Speciation and Trait Rates Simulation (Cor-STRATES) framework.**
755 This schematic provides an overview of the steps involved in the best-performing approach
756 investigated in this study for testing relationships between rates of speciation and trait evolution
757 using phylogenetic data. See text for full details.

758

759 **Figure 3. Phylogenetic patterns of evolutionary rate heterogeneity for five vertebrate clades.**
760 For each group, mean per-branch rates of speciation (λ_{BAMM} , left) and body size evolution (σ^2_{BT} ,
761 right) are shown. Dark colours correspond to slow rates, light colours correspond to fast rates.

762

763 **Figure 4. The relationship between rates of speciation and body size evolution for five**
764 **vertebrate groups. a-e,** Scatterplots (left column) show the relationship between log-transformed
765 tip rates of speciation (λ_{BAMM}) and body size evolution (σ^2_{BT}) in each group. Histograms (right
766 column) show the correlation coefficient for the observed relationship (arrow) in relation to a null
767 distribution of correlation coefficients calculated from 200 simulated datasets. NB: outlier points ($n =$
768 6) with extremely small relative trait rate values have been omitted from the scatterplot in **c**. The
769 trend lines for the scatterplots are based on ordinary least-squares regression and are indicative
770 only.

771

772 **Figure 5. Heterogeneity in the relationship between rates of speciation and body size**
773 **evolution among major vertebrate subclades.** Plot shows the distribution of mean effect sizes
774 (points) and 95% confidence intervals (lines) for the relationship between rates of speciation (λ_{BAMM})
775 and body size evolution (σ^2_{BT}) within subclades of five vertebrate groups. Tests were performed
776 using rate comparisons among tips only or across all branches in the tree. Filled points indicate
777 cases in which the relationship between rates is statistically significant ($P < 0.05$) based on
778 comparisons to simulated datasets ($n = 200$). Figures in parentheses following clade names
779 indicate taxonomic species richness and the proportion of those taxa included in the trait rates
780 analysis. Asterisks indicate clades exhibiting significant associations in either or both analyses.

781

782 **Extended Data Figure 1. The performance of different phylogenetic approaches for**
783 **estimating rates of speciation (λ) and trait evolution (σ^2).** Plots show the error, bias and
784 correlation of estimated rates of speciation (**c**) and trait evolution (**b-c**) compared to true (i.e.
785 simulated) values. In **b**, results are based on comparing rates across all branches of the tree,
786 whereas in **c**, results are based on comparing tip rates only. Results are based on fitting models to
787 100 simulated tree and trait datasets, each with 250 tips. Boxplots show the median value (thick
788 line) and 0.25-0.75 (box) and 0.05-0.95 (whiskers) quantile ranges. BT, BayesTraits; ST,
789 StableTraits.

790

791 **Extended Data Figure 2. Comparison of the performance of different approaches for testing**
792 **correlations between rates of speciation and trait evolution.** Results are based on simulated
793 datasets of 250-tip trees ($n = 100$) assuming strong correlations between rates (columns 1 and 2),
794 with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates also estimated using BAMM
795 (σ^2_{BAMM}). See *Methods* for details of the simulation procedure, rate metrics and significance tests
796 used. The grey shaded area indicates false discovery (Type I error) rates of <5%.

797

798 **Extended Data Figure 3. Comparison of mean standardised effect sizes derived from the**
799 **'simulation + rescale' approach using alternate rate metrics.** Speciation rates are estimated
800 using BAMM (λ_{BAMM}) and trait rates are estimated using either BayesTraits (σ^2_{BT}) or BAMM (σ^2_{BAMM}).
801 Results are based on applying the 'tree-transformation + simulation' method to datasets of 250-tip
802 trees ($n = 100$) generated assuming strong correlations between rates (columns 1 and 2).

803

804 **Extended Data Figure 4. Comparison of the performance of the 'simulation + rescale'**
805 **approach with varying tree size and simulated correlation strength.** Results are based on
806 simulated datasets of 100 trees, with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates
807 estimated using BayesTraits (σ^2_{BT}). For the scenarios involving correlated rates, solid and dashed
808 lines correspond to strong ($r = \pm 1$) and weaker ($r = \pm 0.5$) simulated correlation strengths,
809 respectively. (Note: realised correlation strengths associated with these scenarios are lower than
810 implied by the generating values; see Extended Data Figure 10). The grey shaded area indicates
811 false discovery (Type I error) rates of <5%. ME, measurement error.

812

813 **Extended Data Figure 5. Comparison of the performance of the 'simulation + rescale'**
814 **approach with decreasing sampling proportions.** Results are based on simulated datasets of
815 250-tip trees ($n = 100$) assuming strong correlations between rates (columns 1 and 2), with
816 speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits (σ^2_{BT}).
817 The grey shaded area indicates false discovery (Type I error) rates of <5%. ME, measurement
818 error.

819

820 **Extended Data Figure 6. Comparison of the performance of the ‘simulation + rescale’**
821 **approach with increasing relative extinction (turnover) rates.** Results are based on simulated
822 datasets of 250-tip trees ($n = 100$) assuming strong correlations between rates (columns 1 and 2),
823 with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits
824 (σ^2_{BT}). The grey shaded area indicates false discovery (Type I error) rates of <5%. ME,
825 measurement error.

826

827 **Extended Data Figure 7. Results for tests of the relationship between rates of speciation and**
828 **body size evolution within five vertebrate taxa.** Results are based on speciation rates estimated
829 using BAMM (λ_{BAMM}) and body size rates estimated using BayesTraits (σ^2_{BT}). N = total species
830 richness; N_{samp} = number of species sampled in rate analyses; phy. sig. = body size phylogenetic
831 signal (Pagel’s lambda); ρ_{obs} = observed correlation coefficient (Spearman’s ρ); ρ_{null} = null
832 correlation coefficients derived from null simulations ($n = 200$); SES = standardised effect size.

833

834 **Extended Data Figure 8. Relationships between rates of speciation and body size evolution**
835 **in vertebrate subclades.** Plots show the relationship between log-transformed tip rates of
836 speciation (λ_{BAMM}) and body size evolution (σ^2_{BT}) in each clade. Colours reflect the five vertebrate
837 groups (birds = blue, mammals = red, amphibians = green, squamates = purple, fish = orange).
838 Inset numbers give the mean effect size for each relationship, with significant ($P < 0.05$)
839 associations marked with an asterisk and highlighted in bold.

840

841 **Extended Data Figure 9. Multipredictor models of effect sizes measuring the strength of the**
842 **association between rates of speciation and body size evolution in vertebrate subclades.**
843 Results are based on speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated
844 using BayesTraits (σ^2_{BT}). All predictor variables were standardised (mean = 0, sd = 1) prior to
845 analysis. SE = standard error. *, $P_{\text{MCMC}} < 0.05$.

846

847 **Extended Data Figure 10. Mean (sd) correlation coefficients (Pearson’s r) for the realised**
848 **relationship between simulated rates of speciation and trait evolution.** Realised rates of trait
849 evolution are inferred by calculating the squared-trait distance between known simulated ancestral
850 and descendent nodes in the tree, divided by phylogenetic branch length (i.e. time). Note: Pearson’s
851 r values in the table header refer to the correlation strength between speciation and trait rates used
852 in the stochastic model used to generate trait values. $n = 100$ trees in each case.

853

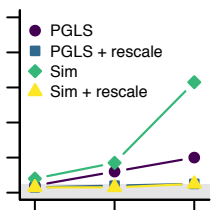
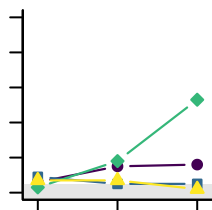
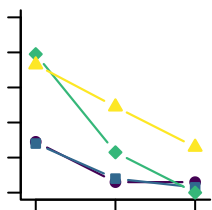
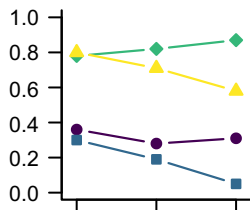
854

Positive correlation

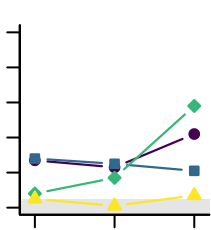
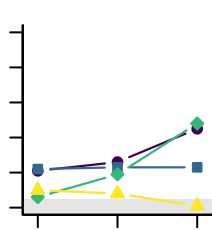
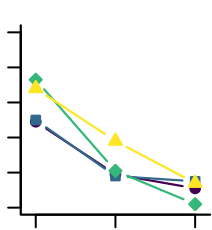
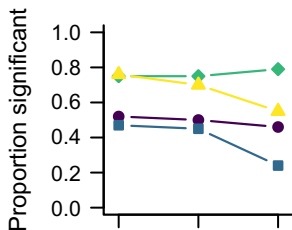
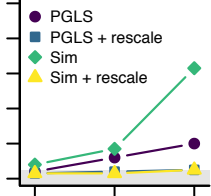
Negative correlation

No correlation (constant rates)

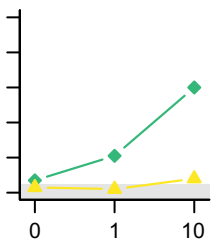
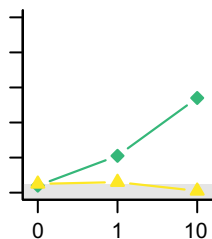
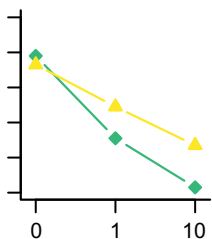
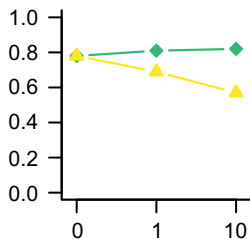
No correlation (variable rates)



Tips only



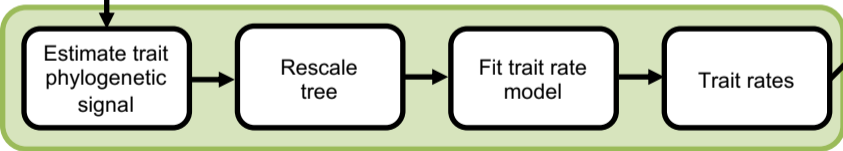
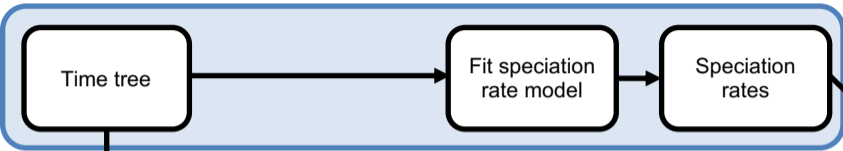
Weighted average



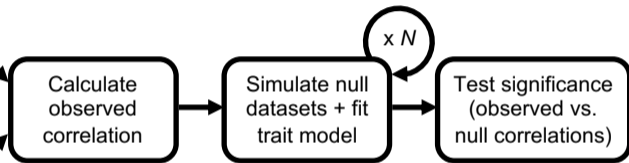
All branches

Trait measurement error (%)

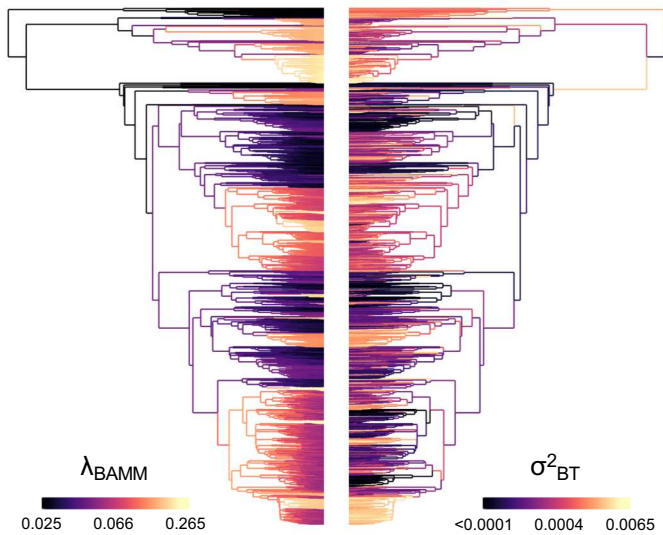
Speciation rates



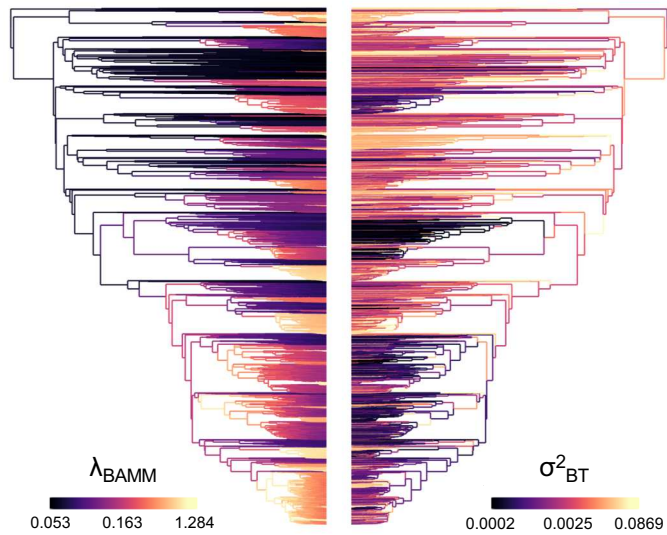
Trait rates



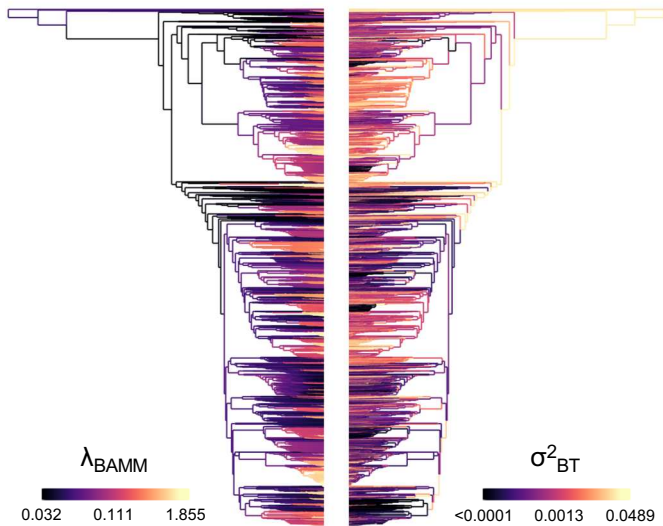
Amphibians



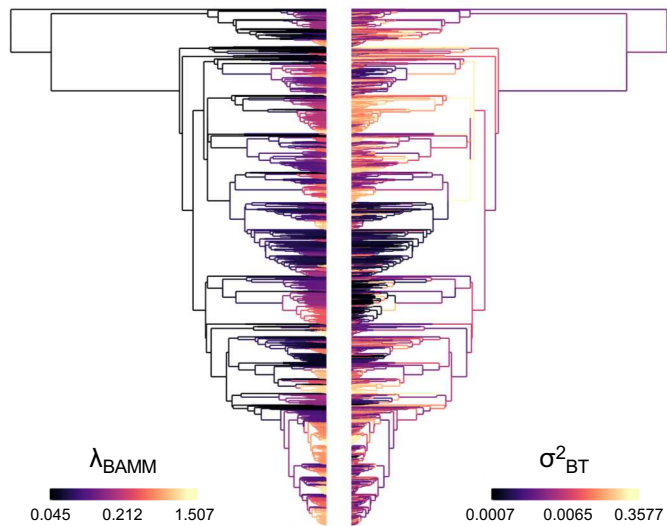
Birds



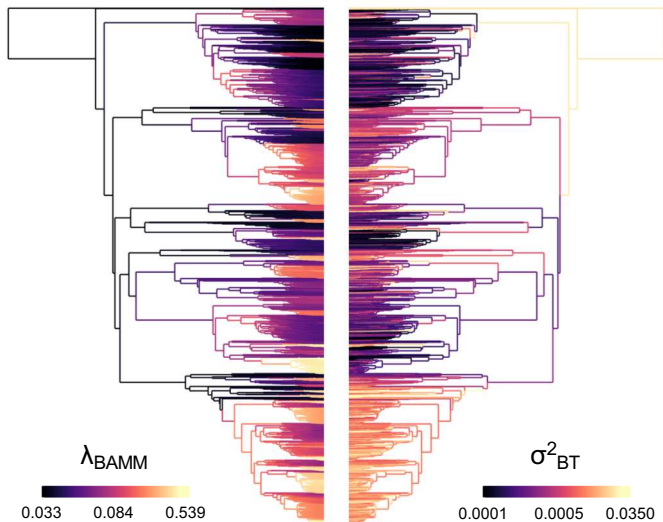
Fish

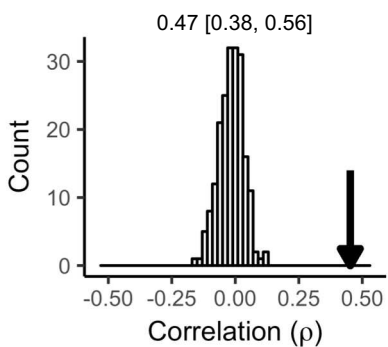
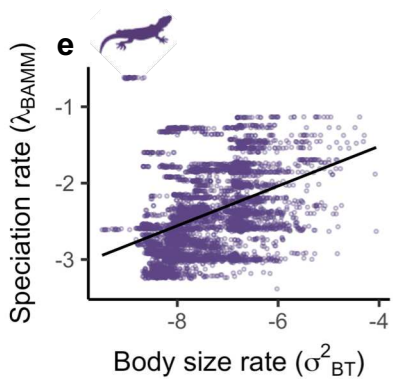
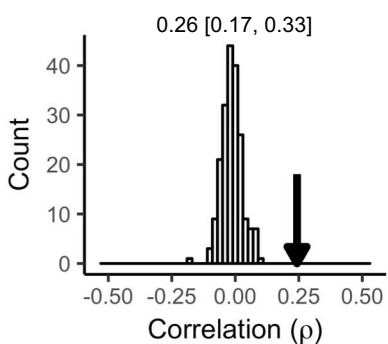
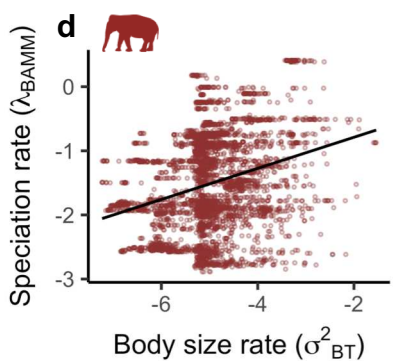
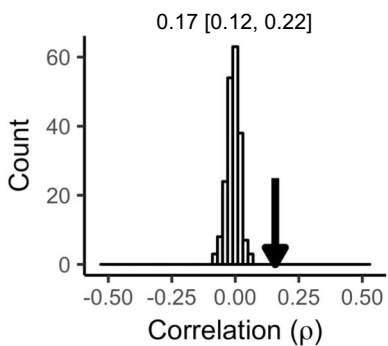
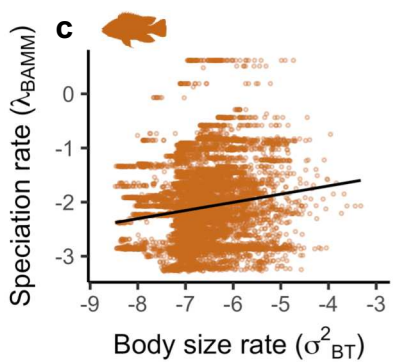
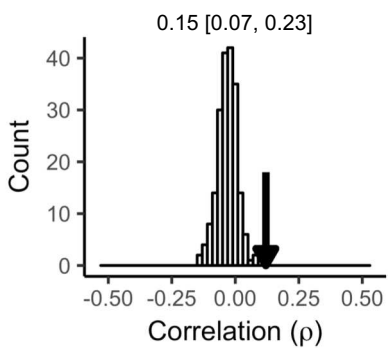
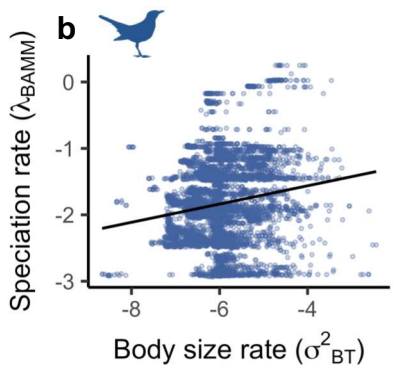
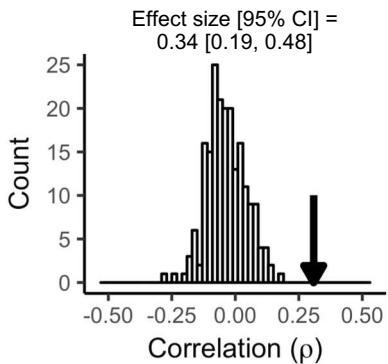
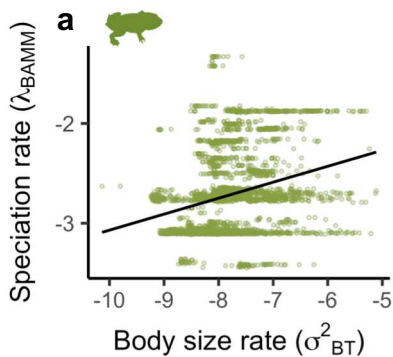


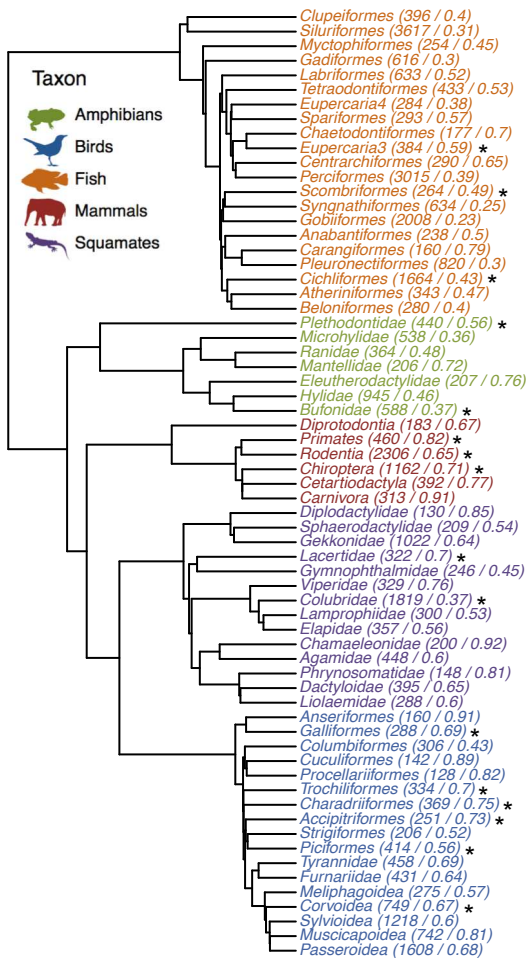
Mammals



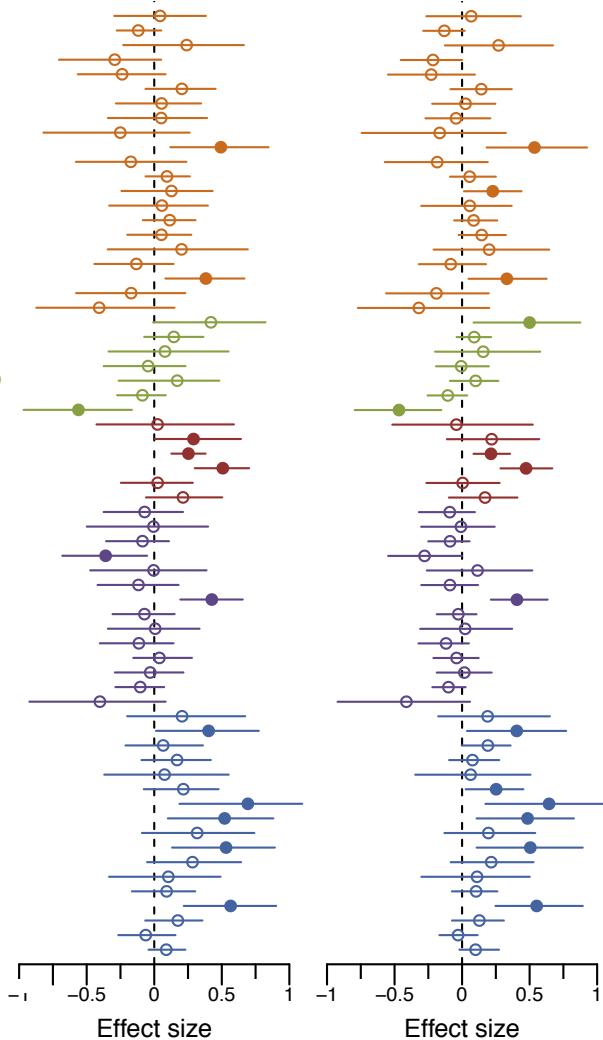
Squamates



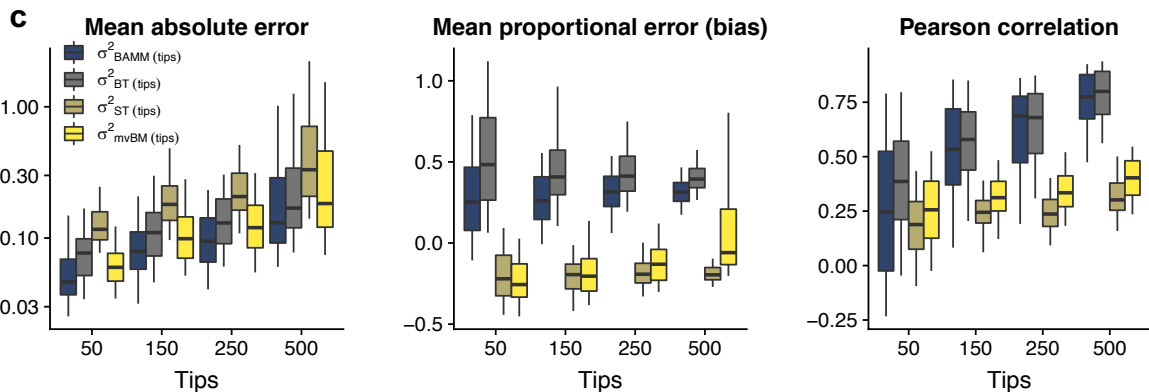
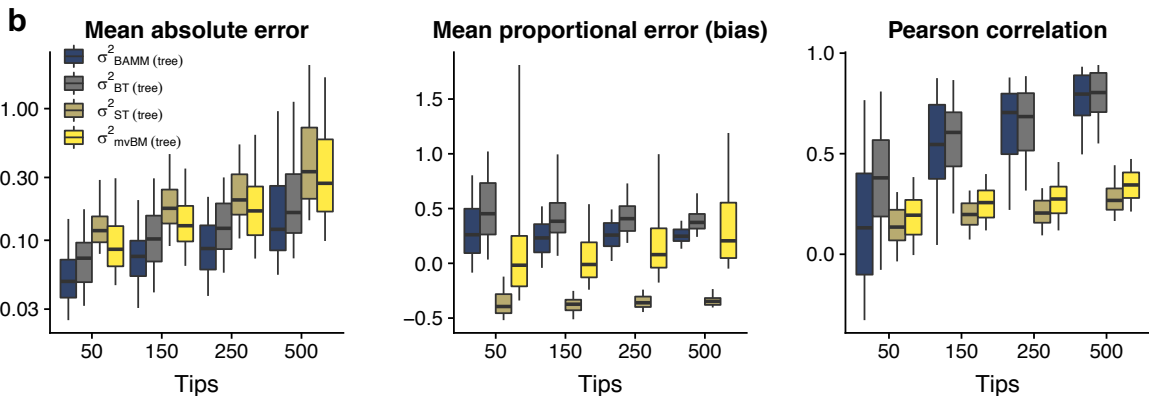
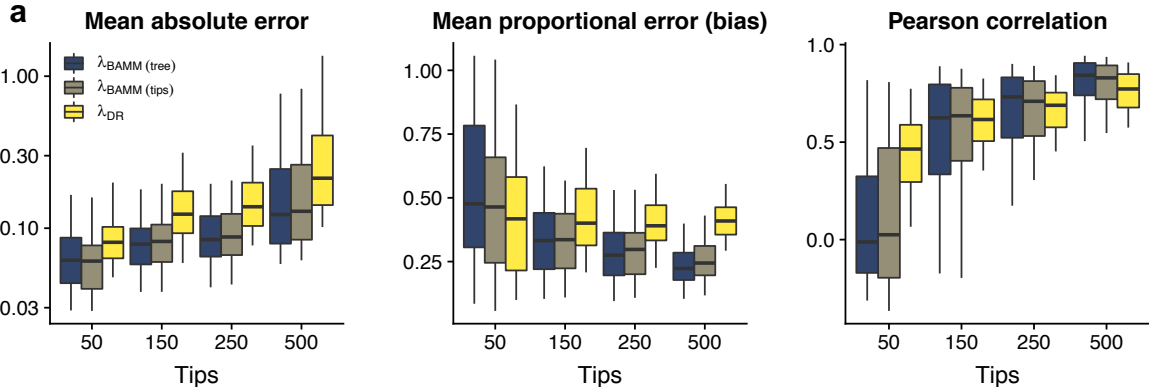


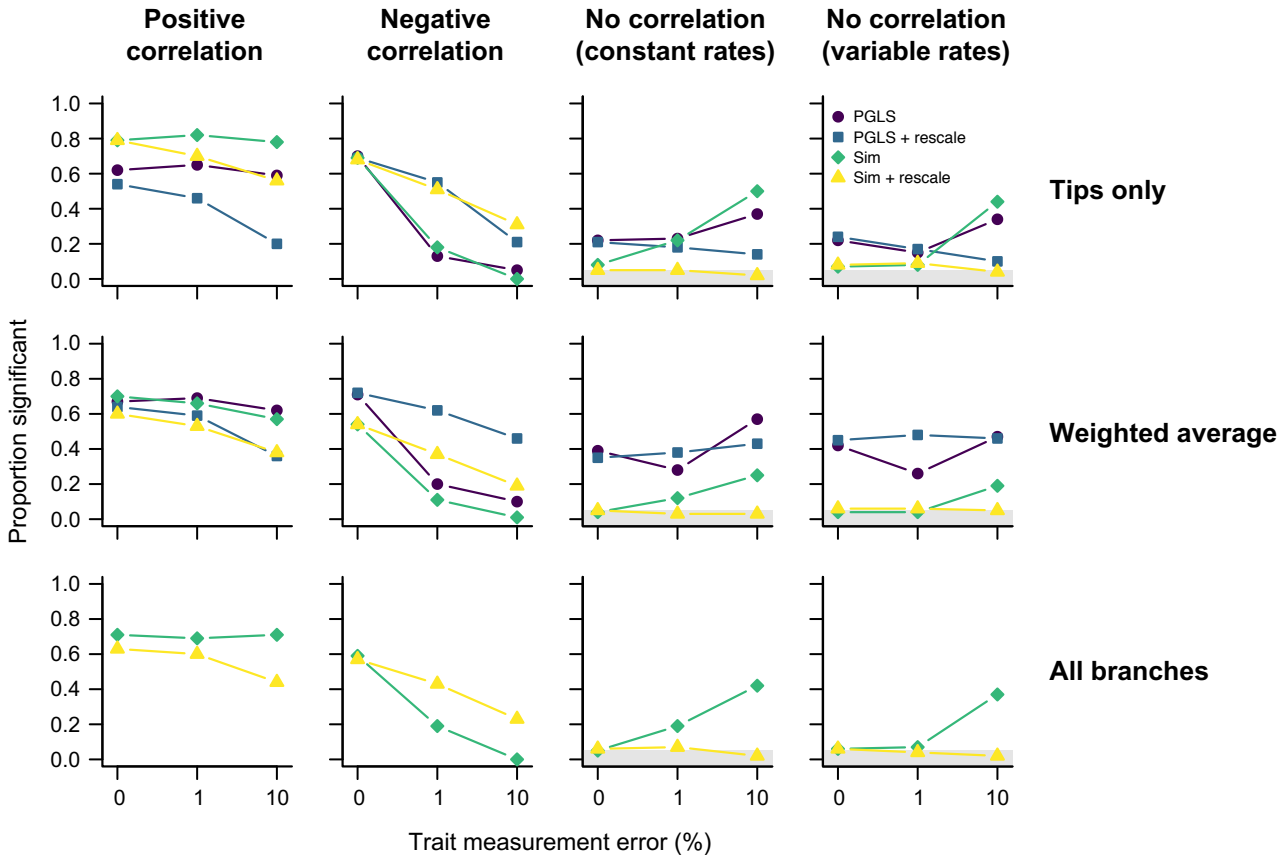


Tips only



All branches



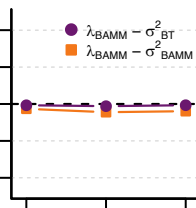
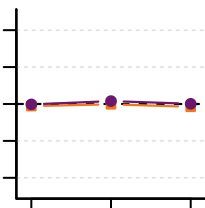
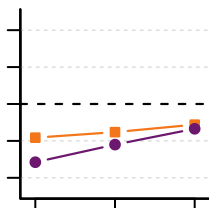
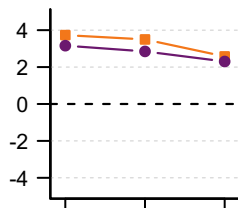


Positive correlation

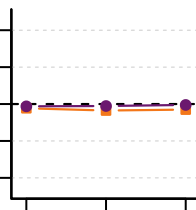
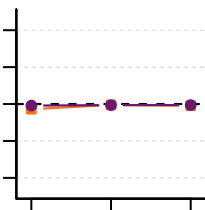
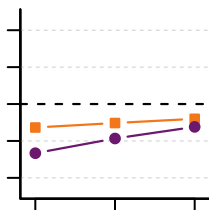
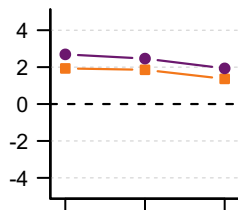
Negative correlation

No correlation (constant rates)

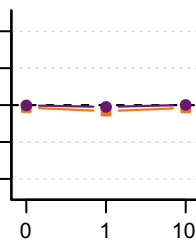
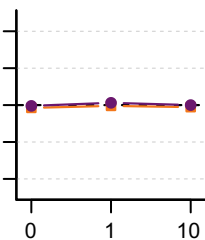
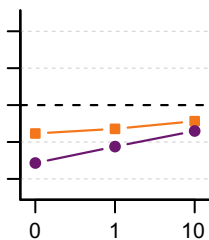
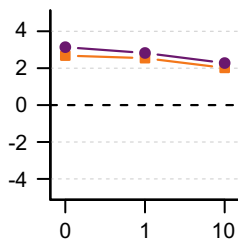
No correlation (variable rates)



Tips only



Weighted average



All branches

Standardised effect size

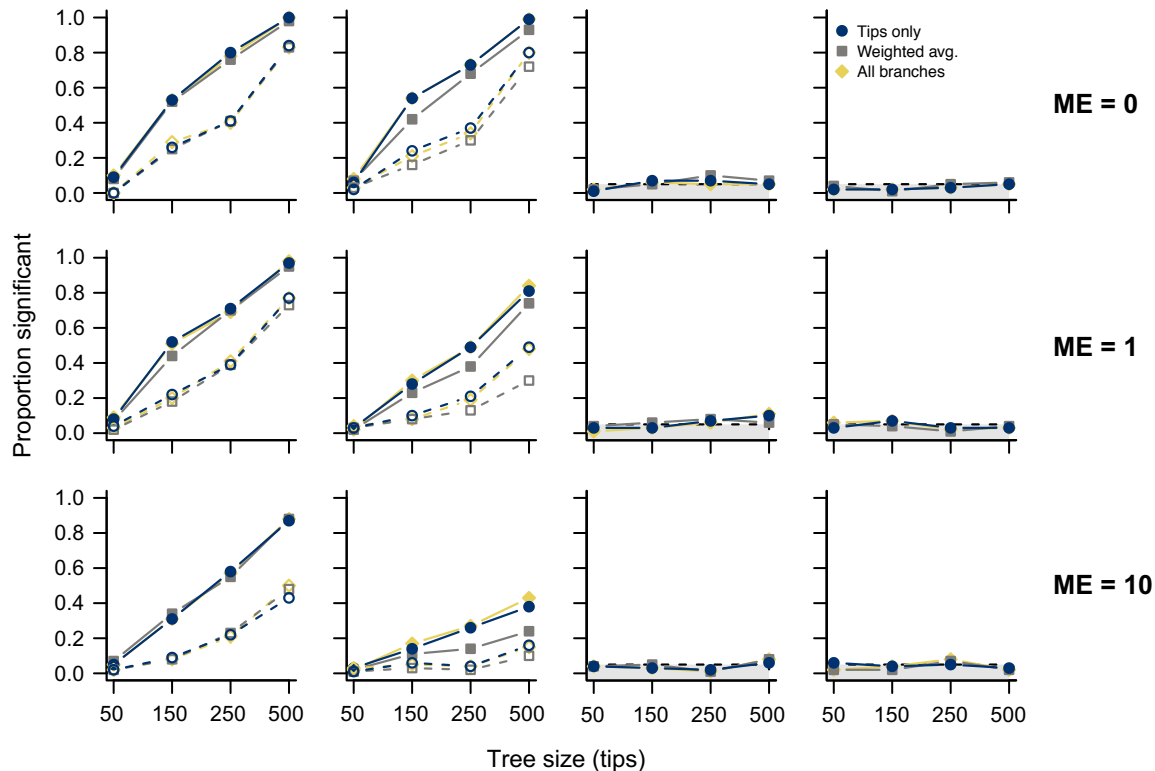
Trait measurement error (%)

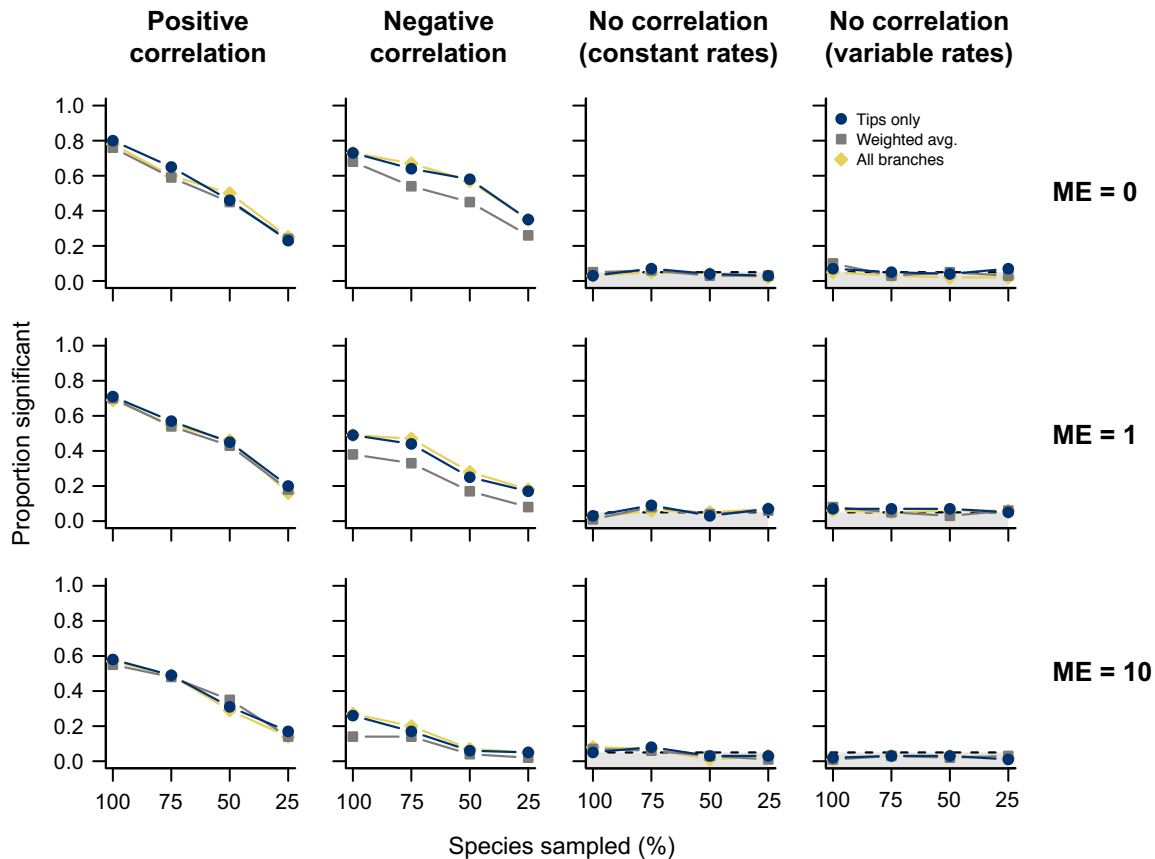
Positive correlation

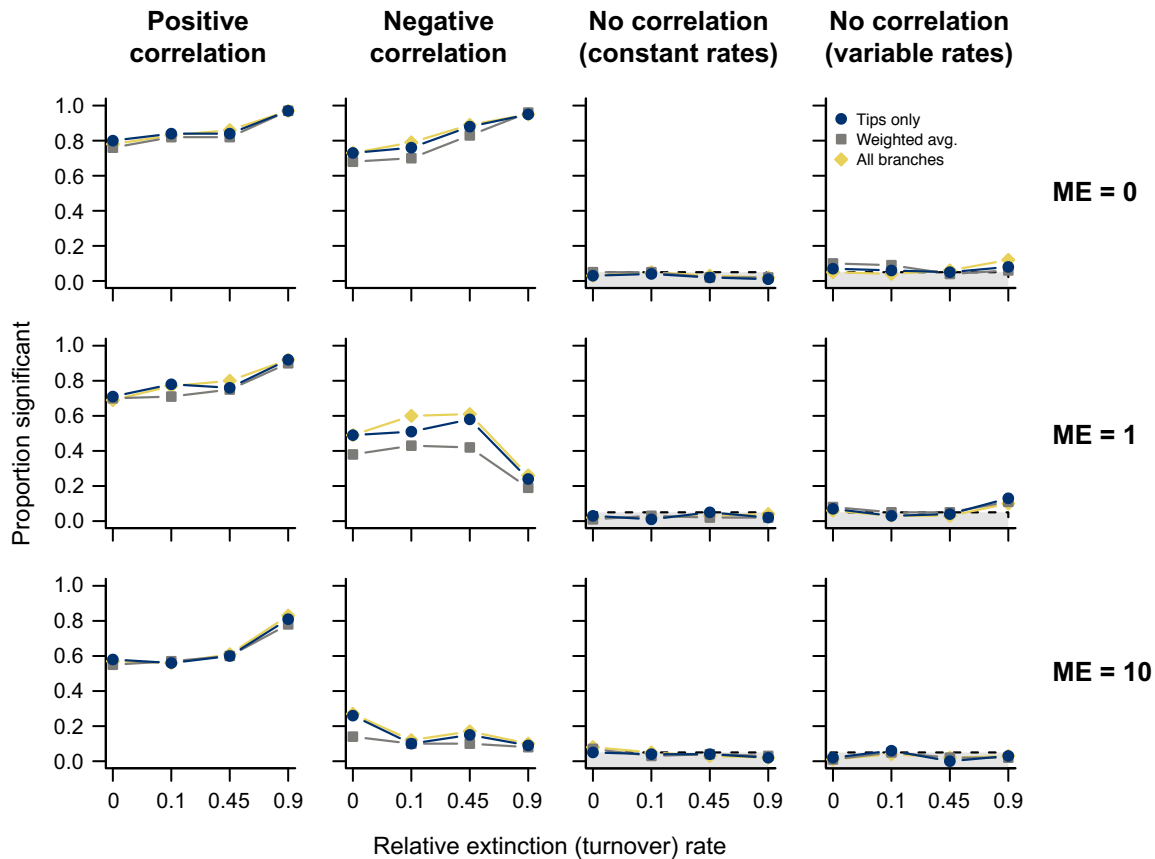
Negative correlation

No correlation (constant rates)

No correlation (variable rates)

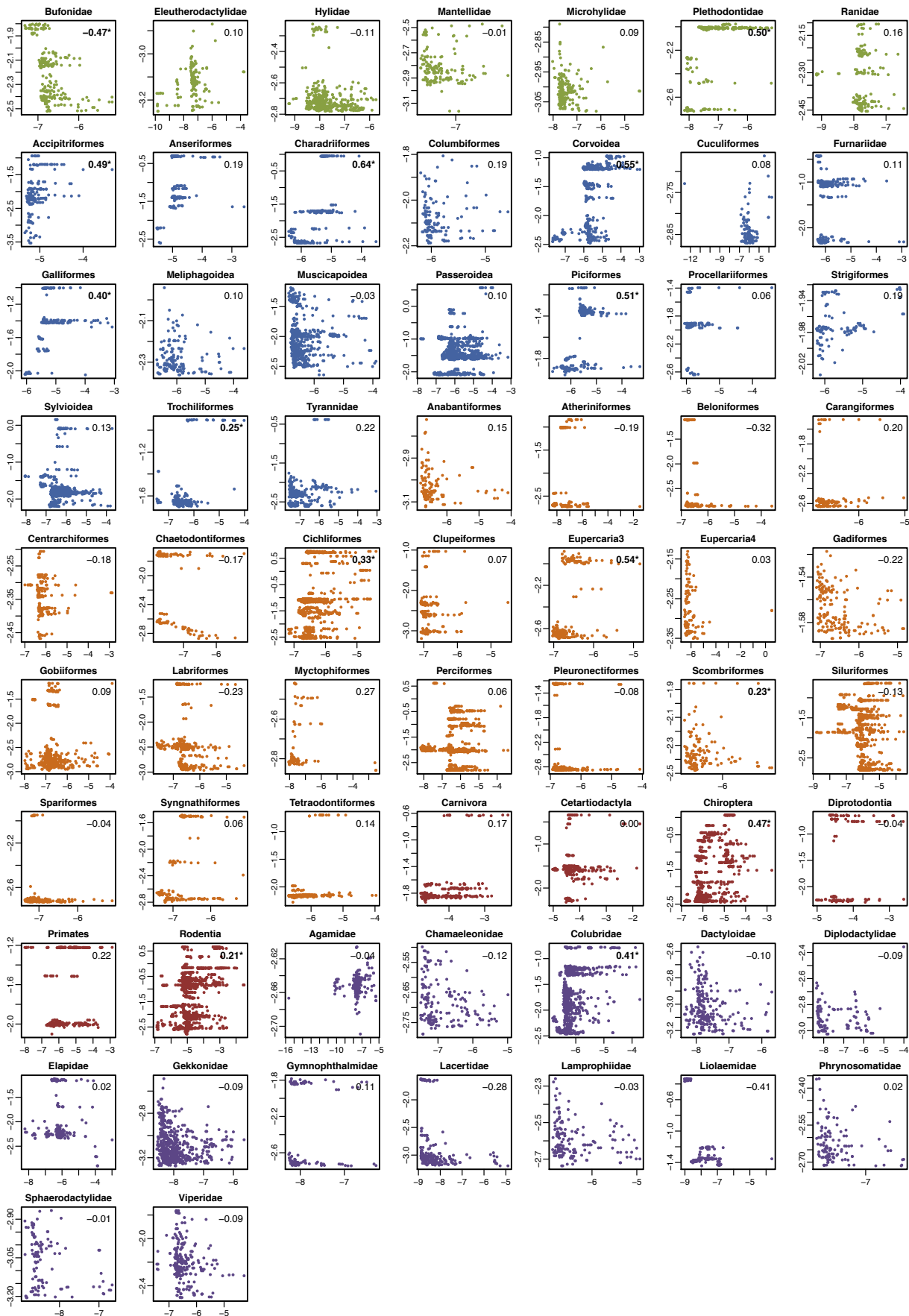






Taxon	<i>N</i>	<i>N_{samp}</i>	<i>Phy. sig.</i>	Dataset	ρ_{obs}	ρ_{null} [95% CI]	Effect size [95% CI]	SES	<i>P</i>
Amphibians	7238	3193	0.96	Tips only	0.309	-0.035 [-0.175, 0.119]	0.343 [0.190, 0.483]	4.515	<0.01
				All branches	0.301	-0.010 [-0.144, 0.133]	0.311 [0.168, 0.445]	4.198	<0.01
Birds	9993	6670	0.98	Tips only	0.120	-0.030 [-0.112, 0.047]	0.150 [0.074, 0.232]	3.826	0.02
				All branches	0.108	-0.005 [-0.092, 0.071]	0.113 [0.037, 0.200]	2.845	0.02
Fish	31516	10868	0.96	Tips only	0.157	-0.008 [-0.062, 0.041]	0.166 [0.116, 0.219]	6.553	<0.01
				All branches	0.171	0.022 [-0.027, 0.068]	0.148 [0.102, 0.198]	6.189	<0.01
Mammals	5561	4095	0.99	Tips only	0.243	-0.014 [-0.084, 0.077]	0.257 [0.166, 0.327]	6.306	<0.01
				All branches	0.253	0.029 [-0.037, 0.108]	0.224 [0.145, 0.291]	5.867	<0.01
Squamates	9755	5398	0.96	Tips only	0.453	-0.016 [-0.112, 0.068]	0.468 [0.384, 0.564]	9.758	<0.01
				All branches	0.453	0.007 [-0.098, 0.078]	0.447 [0.376, 0.552]	9.533	<0.01

Speciation rate (λ_{BMM})



Body size rate (σ^2_{BT})

Term	Tips only		All branches	
	Estimate [95% CI]	P_{MCMC}	Estimate [95% CI]	P_{MCMC}
<i>Effect size</i>				
(Intercept)	0.109 [-1.378, 1.822]	0.590	0.182 [-1.386, 1.572]	0.562
Crown age	0.037 [-0.037, 0.114]	0.347	0.016 [-0.051, 0.094]	0.662
Clade richness	0.044 [-0.032, 0.119]	0.264	0.031 [-0.041, 0.104]	0.398
Sampling proportion	0.034 [-0.048, 0.123]	0.411	0.018 [-0.062, 0.097]	0.644
Trait phylogenetic signal	-0.047 [-0.113, 0.023]	0.164	-0.051 [-0.115, 0.011]	0.116
Speciation rate variation	0.005 [-0.065, 0.071]	0.883	0.006 [-0.059, 0.069]	0.849
Body size rate variation	-0.014 [-0.076, 0.037]	0.631	-0.031 [-0.086, 0.026]	0.267
<i>Absolute effect size</i>				
(Intercept)	0.164 [-0.370, 0.697]	0.167	0.206 [-0.536, 0.748]	0.174
Crown age	0.000 [-0.052, 0.056]	0.996	-0.005 [-0.055, 0.049]	0.852
Clade richness	0.000 [-0.053, 0.057]	0.995	0.001 [-0.055, 0.056]	0.973
Sampling proportion	0.001 [-0.060, 0.060]	0.992	-0.007 [-0.067, 0.052]	0.834
Trait phylogenetic signal	0.003 [-0.048, 0.053]	0.916	-0.014 [-0.064, 0.032]	0.570
Speciation rate variation	0.059 [0.009, 0.111]	0.024*	0.042 [-0.005, 0.090]	0.084
Body size rate variation	0.000 [-0.043, 0.043]	0.989	-0.010 [-0.049, 0.032]	0.630
<i>Standardised effect size</i>				
(Intercept)	-0.736 [-8.420, 9.610]	0.515	2.908 [-7.752, 11.083]	0.508
Crown age	0.126 [-0.280, 0.563]	0.549	-0.020 [-0.491, 0.428]	0.946
Clade richness	0.372 [-0.062, 0.818]	0.097	0.235 [-0.214, 0.725]	0.319
Sampling proportion	0.151 [-0.306, 0.640]	0.532	-0.017 [-0.538, 0.482]	0.950
Trait phylogenetic signal	-0.195 [-0.579, 0.186]	0.327	-0.279 [-0.676, 0.159]	0.188
Speciation rate variation	0.110 [-0.268, 0.493]	0.577	0.089 [-0.309, 0.508]	0.656
Body size rate variation	-0.023 [-0.378, 0.291]	0.895	-0.144 [-0.488, 0.212]	0.419
<i>Absolute standardised effect size</i>				
(Intercept)	1.113 [-0.073, 2.720]	0.061	1.215 [-0.009, 2.822]	0.049*
Crown age	-0.048 [-0.328, 0.210]	0.734	-0.116 [-0.407, 0.163]	0.421
Clade richness	0.400 [0.114, 0.705]	0.010*	0.372 [0.056, 0.664]	0.016*
Sampling proportion	0.133 [-0.165, 0.464]	0.390	0.044 [-0.284, 0.386]	0.787
Trait phylogenetic signal	0.065 [-0.186, 0.321]	0.620	-0.001 [-0.270, 0.251]	0.987
Speciation rate variation	0.254 [-0.002, 0.511]	0.058	0.093 [-0.176, 0.349]	0.477
Body size rate variation	0.017 [-0.191, 0.249]	0.882	-0.041 [-0.285, 0.188]	0.733

Scenario	Tree size (tips)	$r = \pm 1$	$r = \pm 0.5$	$r = 0$
Positive correlation	50	0.19 (0.12)	0.08 (0.10)	-
	150	0.24 (0.08)	0.11 (0.06)	-
	250	0.26 (0.08)	0.14 (0.06)	-
	500	0.35 (0.10)	0.16 (0.05)	-
Negative correlation	50	-0.18 (0.12)	-0.10 (0.10)	-
	150	-0.24 (0.08)	-0.12 (0.06)	-
	250	-0.26 (0.08)	-0.13 (0.06)	-
	500	-0.34 (0.10)	-0.16 (0.05)	-
No correlation (variable rates)	50	-	-	0.01 (0.10)
	150	-	-	0.00 (0.05)
	250	-	-	0.00 (0.04)
	500	-	-	0.00 (0.03)
No correlation (constant rates)	50	-	-	-0.01 (0.11)
	150	-	-	0.00 (0.06)
	250	-	-	0.00 (0.04)
	500	-	-	0.00 (0.03)