

1 **Running head:** INFERRING PHYLOGENIES FROM CONTINUOUS CHARACTERS

2 **Title:** Continuous Characters Outperform Binary Discrete Characters in Phylogenetic Inference

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8 **ABSTRACT**

9 The recent surge in enthusiasm for simultaneously inferring relationships from extinct and
10 extant species has reinvigorated interest in statistical approaches for modelling morphological
11 evolution. Current statistical methods use the Mk model to describe substitutions between
12 discrete character states. Although representing a significant step forward, the Mk model presents
13 challenges in biological interpretation, and its adequacy in modelling character evolution has not
14 been well explored. Another major hurdle toward increasing objectivity and reproducibility in
15 morphological phylogenetics is the often subjective process of character coding of discrete
16 characters. Assignment of discrete characters by different researchers can often yield discordant
17 phylogenetic hypotheses. One potential solution to issues may be the employment of continuous
18 measurements to infer phylogenies. Although not widely used in the inference of topology,
19 models describing the evolution of continuous characters have been well examined, and their
20 statistical behaviour is well understood. Also, continuous measurements avoid the substantial
21 ambiguity often associated with the assignment of discrete characters to states. I present a set of
22 simulations to determine whether use of continuous characters is a feasible alternative to discrete
23 for inferring phylogeny. I compare relative reconstruction accuracy by inferring phylogenies from
24 continuous characters simulated under unbounded Brownian motion and discrete characters
25 simulated under the Mk model of morphological evolution. These tests demonstrate significant
26 promise for continuous traits by demonstrating their higher overall accuracy as compared to
27 reconstruction from discrete characters under Mk. Continuous characters also perform reasonably
28 well in the presence of covariance between sites. This study provides the first step toward
29 recognition of the potential utility of continuous characters in phylogenetic inference through use
30 of Brownian motion and related Gaussian models.

31 **Keywords:** phylogenetics, morphology, paleontology, quantitative characters, Bayesian

32 The widespread development and adoption of statistical phylogenetic methods has
33 revolutionized disparate disciplines in evolutionary biology, epidemiology, and systematics.
34 Studies utilizing maximum-likelihood (ML) and Bayesian approaches have become the preferred
35 means to analyse molecular data, largely eclipsing parsimony and distance methods. Despite this,
36 approaches which draw inference from morphological data have remained comparatively
37 underdeveloped. As a result, non-statistical tree inference methods have continued to be
38 employed for the phylogenetic analysis of morphological characters. Nonetheless, several
39 landmark advances in the development of statistical morphological phylogenetic methods have
40 demonstrated the benefits of further developing this framework. This will be particularly
41 important in the near future as burgeoning approaches enabling the rapid collection of
42 morphological data, such as that of Chang and Alfaro (2015b,a), may begin to outstrip methods
43 through which to analyse them. This may significantly alter and enhance our view of the tree of
44 life, especially considering that the majority of macro-organisms, represented by fossil taxa, can
45 only be analysed from their morphology.

46 A critical contribution to statistical phylogenetic methods has been the Mk model to describe
47 discrete trait evolution (Lewis 2001). This is a version of the Jukes-Cantor model of nucleotide
48 substitution generalised to accommodate varying numbers of character states (Jukes and Cantor
49 1969). Extensions to this model accommodate for biased sampling of parsimony informative
50 characters (Lewis 2001), rate heterogeneity between sites (Wagner 2012), and asymmetric
51 transition rates (Wright *et al.* 2015). The deployment of this model has demonstrated the utility of
52 statistical approaches to morphological phylogenetics, both through their ability to better describe
53 uncertainty over non-statistical approaches, and to estimate branch lengths. This has enabled a
54 better understanding of much of the fossil tree of life (Dávalos *et al.* 2014; Pattinson *et al.* 2014;

55 Dembo *et al.* 2015). The unique ability of Mk to estimate morphological branch lengths has also
56 enabled the development of tip dating, methods, which combine morphological and molecular
57 data to co-estimate phylogeny between living and fossil data (Nylander *et al.* 2004; Ronquist
58 *et al.* 2012). Tip dating methods have been widely used since their introduction, and are
59 implemented in the BEAST (Bouckaert *et al.* 2014) and MrBayes (Ronquist and Huelsenbeck
60 2003) packages. These have shown the potential to more resolutely understand the timing of
61 species divergences and relationships between fossil and living taxa (Wiens *et al.* 2010; Wood
62 *et al.* 2012; Lee *et al.* 2013, 2014; Arcila *et al.* 2015). Overall, statistical approaches to
63 morphological phylogenetics appear to represent an improvement in accuracy compared to
64 cladistic methods, and are indispensable in their distinct ability to allow the estimation of branch
65 lengths and evolutionary rate. The benefits of a statistical total-evidence framework will only
66 become clearer as more data become available and improved methods are developed (Pennell and
67 Harmon 2013; Lee and Palci 2015).

68 Despite the great strides made through their development, discrete character models represent
69 an imperfect solution. Although Bayesian inference under Mk appears to outperform parsimony,
70 error increases at high evolutionary rates (Wright and Hillis 2014). Also, under many
71 circumstances, phylogenetic inference under the Mk model includes imprecision and uncertainty,
72 both in simulations (O'Reilly *et al.* 2016; Puttick *et al.* 2017) and empirical studies (Lee and
73 Worthy 2012; Dembo *et al.* 2015). Previous researchers have also expressed concerns over the
74 efficacy of model-based approaches in the presence of missing data (Livezey and Zusi 2007;
75 O'leary *et al.* 2013), although these have been largely assuaged (Wright and Hillis 2014).
76 Another potential issue is the lack of clarity in interpreting the Mk model biologically. Although
77 transition rates have a strong theoretical and empirical basis in population genetics, their

78 significance beyond serving as nuisance parameters is less straightforward when applied to
79 morphological data. Discrete morphological characters may not undergo change in a manner
80 analogous to nucleotides, whose change is better understood as a relatively consistent,
81 population-based process. This leaves ambiguity in the interpretation of Mk substitution rate, and
82 weakens biologists' ability to examine biological process from Mk rate estimation. Therefore, it
83 is unclear whether the slightly nebulous interpretations of evolutionary rate gleaned through
84 discrete morphological substitution models can be employed for major biological discoveries in
85 the same way as has been done with molecular data (e.g. Smith and Donoghue 2008; Bromham
86 2011). This is particularly important when considering the importance of branch lengths in the
87 total-evidence methods discussed above.

88 Aside from the model concerns discussed above, discrete characters themselves present a
89 non-trivial set of challenges to phylogenetics that are distinct from those possessed by molecular
90 data. Perhaps, foremost among these is disagreement between researchers in the categorisation,
91 ordering, and weighing of discrete character states (Farris 1990; Hauser and Presch 1991; Pleijel
92 1995; Wilkinson 1995). Despite extensive discussion among comparative biologists, the
93 interpretive nature of the process of character coding has continued to leave major palenotological
94 questions unresolved (Upchurch 1995; Wilson and Sereno 1998; Bloch and Boyer 2002; Kirk
95 *et al.* 2003). Character coding methods that increase the objectivity of discrete character
96 collection may represent an improvement to these issues (Thiele 1993; Wiens 2001), but it may
97 also be worthwhile to explore alternate sources of data for phylogenetic reconstruction.

98 Use of continuous characters may help to address some of the concerns with discrete traits
99 discussed above. They can be collected more objectively than qualitative observations and do not
100 require ordering of states. Their use in phylogenetic inference has been discussed among the

101 earliest advancements in statistical phylogenetics (Cavalli-Sforza and Edwards 1967; Felsenstein
102 1973), and their phylogenetic informativeness has been demonstrated empirically (Goloboff *et al.*
103 2006; Smith and Hendricks 2013). Still, the use of continuous characters for the inference of
104 phylogenetic topology has remained uncommon, with statistical methods for their use in
105 phylogenetics remaining relatively poorly examined.

106 Another potential benefit to inferring phylogeny from continuous characters is the wealth of
107 models developed in phylogenetic comparative methods to describe their evolution. Most
108 comparative models of continuous trait evolution belong to the Gaussian class, which are also
109 well utilized in disparate fields such as physics, economics, and engineering. In comparative
110 biology, they are used to describe stochastic Markovian movement through trait space along
111 continuous time. This class of models includes Brownian motion (BM) (Felsenstein 1973, 1985;
112 Gingerich 1993), Ornstein-Uhlenbeck (OU) (Hansen 1997; Butler and King 2004; Beaulieu *et al.*
113 2012), and Lèvy processes (Landis *et al.* 2013). Under BM, evolution is described as a random
114 walk, with phenotypic change being normally distributed with a mean displacement of zero, and
115 variance σ^2 . OU models expand upon this by introducing terms producing a stabilizing force
116 which stabilizes movement around an optimal trait value, while Lèvy processes contain terms
117 producing saltational jumps in character space, interspersed either by BM diffusion or stasis. Two
118 major benefits to Gaussian models in phylogenetics are their relatively straightforward
119 interpretability and the relative ease of deriving mathematical extensions to describe a range of
120 biological processes.

121 Given the existence of well understood and clearly interpretable models describing their
122 evolution, the use of continuous traits may offer several advantages over discrete characters in
123 phylogenetic inference. However, their behaviour is not well understood when applied to the

124 inference of phylogenetic topology, and so further investigation is needed. In addition, there are
125 potential hurdles to their efficacy. Possibly foremost among these is the widespread covariance
126 between continuous measurements that is expected through both genetic and morphometric
127 perspectives (Lynch *et al.* 1998; Uyeda *et al.* 2015; Adams and Felice 2014). Nevertheless, the
128 expected magnitude in covariance among continuous morphological measurements and the
129 robusticity of phylogenetic methods to this violation is not known. Furthermore, it is also
130 generally reasonable to expect evolutionary covariance between nucleotide sites, and
131 phylogenetic methods that do not accommodate for this are routinely applied to molecular data.

132 In this study, I carry out simulations to compare the relative performance of binary discrete
133 and continuous characters at reconstructing phylogenetic relationships. Simulations of continuous
134 characters were designed to reflect a range of scenarios that may influence accuracy including
135 overall evolutionary rate and matrix sizes. I also conduct inference on continuous traits that have
136 undergone correlated evolution, an important violation to single-rate BM thought to be
137 widespread in continuous character evolution.

138 **METHODS**

139 *Simulations*

140 I generated a set of 100 pure birth trees using the Phytools package (Revell 2012), each
141 containing ten taxa. All trees were ultrametric and generated with a total length of 1.0 for
142 consistency in parameter scaling for trait simulations (Fig. 1). These trees were used to simulate
143 continuous characters evolving along an unbounded BM process in the OUwie package (Beaulieu
144 and O'Meara 2012). This is a Markovian process in continuous time where the variance of the
145 process can increase infinitely through time. This differs from the BM σ^2 parameter, which gives
146 the variance in the amount of character displacement at each draw, effectively describing the

147 magnitude of the random BM walk or a rate of character displacement. To assess performance
148 across several biological scenarios, traits were simulated at σ^2 parameterizations of 0.05, 0.5, 1.0,
149 1.5, and 3. Since the process under which traits were simulated is unbounded, phylogenetic signal
150 is expected to remain consistent across rates (Revell *et al.* 2008), but different rates were chosen
151 to illustrate this consistency and to provide even comparison to discrete trait simulations. Discrete
152 characters were simulated in the Phytools package (Revell 2012) under an Mk model with
153 homogeneous transition probabilities. Traits were generated at transition rates 0.05, 0.5, 1.0, 1.5,
154 and 3. All character matrices were generated without rate heterogeneity, and with all invariable
155 sites (ie. no acquisition bias).

156 Matrices were generated at a length of 500 traits and subsampled to create smaller sets of 20
157 and 100 characters to reflect a range of sampling depths. These were chosen because many
158 published morphological matrices fall within this range. The subsampled matrix sizes were
159 chosen to represent reasonably sized paleontological datasets, while the 500 trait matrices were
160 tested to assess performance in complete abundance of data. While such large datasets are
161 uncommon in morphology, several studies have produced character matrices of this size, and for
162 continuous characters, it may be feasible to generate such large datasets from morphometric data.

163 Data were also generated under a correlated BM process to mimic inference in the presence of
164 multidimensionality. These datasets were constructed at covariance strengths of 0.1, 0.5, and 0.9
165 and covarying dimensions of 5 and 25 traits. These were chosen to represent situations where
166 traits range from being loosely to tightly correlated to each another, and where the number of
167 correlated dimensions is large to small. Although differing, these values were chosen to loosely
168 follow the scheme of Adams and Felice (2014).

169 *Estimation of Phylogenies and Reconstruction Accuracy*

170 I estimated Bayesian phylogenetic trees from continuous data under single rate BM in
171 RevBayes (Höhna *et al.* 2016). Tree likelihoods were computed from the phylogenetic
172 independent contrasts (Felsenstein 1985) using reduced maximum likelihood (REML) as
173 implemented in RevBayes. MCMC simulations were run for 150,000 generations. Trees were
174 inferred from discrete data in MrBayes version 3.2.6 (Ronquist and Huelsenbeck 2003),
175 simulating for 1,000,000 generations. Example configuration files for RevBayes and MrBayes
176 analyses are provided as supplementary data. Trees were summarized using TreeAnnotator
177 version 2.4.2 (Rambaut and Drummond 2013) to yield maximum clade credibility (MCC)
178 topologies. MCC trees maximize the posterior probability of each individual clade, summarizing
179 across all trees sampled during MCMC simulation. Once summarised, all trees were rescaled to
180 match inferred tree lengths to the true trees using Phyx (<https://github.com/FePhyFoFum/phyx>).

181 I assessed topological accuracy from simulated trait data using the symmetric
182 (Robinson-Foulds) distance measure (Robinson and Foulds 1981), giving the topological distance
183 between true trees and inferred trees. Symmetric distance is calculated as a count of the number
184 of shared and unshared partitions between compared trees. As such, the maximum symmetric
185 distance between two unrooted trees can be calculated as $2(N-3)$. These values were then scaled
186 to the total possible symmetric distance for interpretability. Additionally, I measured error in
187 branch length reconstruction using the branch length distance (BLD) measure of Kuhner and
188 Felsenstein, also referred to as Euclidean distance (Kuhner and Felsenstein 1994). This is
189 calculated as the sum of the vector representing the individual differences between the branch
190 lengths of all shared bipartitions. The scale of this value depends on the lengths of the trees under
191 comparison. If trees of different lengths are compared, BLD can be very high. However, in this
192 study, all trees are scaled to a root height of 1 to allow comparison of topological and internal

193 branch length reconstruction error. All distances were calculated using the DendroPy Python
194 package (Sukumaran and Holder 2010).

195 **RESULTS**

196 *Reconstruction from Independently Evolving Traits*

197 Reconstruction error is lower overall for trees estimated from continuous characters than from
198 binary discrete (Fig. 2a, Supp. Fig. 1a). For discrete characters, symmetric distance increases
199 significantly at high evolutionary rates, likely due to saturation and loss of phylogenetic signal.
200 Distance also increases in discrete characters when rate is very slow, due to lack of time for
201 phylogenetic signal to develop. This pattern is similar to that recovered by (Wright and Hillis
202 2014) in their test of Bayesian inference of Mk, which revealed highest topological error at very
203 low and high rates. As expected, continuous characters perform consistently across rates because
204 saturation cannot occur, even at very fast rates. Because of the differing sensitivities of each data
205 type to evolutionary rate, topological error should also be compared using the most favourable
206 rate class for discrete characters, 0.5 substitutions per million years (Fig. 2b, Supp. Fig. 1b).
207 Even at this rate, continuous reconstruction performs more consistently than discrete, with error
208 more tightly distributed around a slightly lower mean. It is possible that this occurs because of the
209 relative lack of informativeness of binary characters compared to continuous. The small state
210 space of the binary character model likely causes phylogenetic signal to become saturated more
211 quickly at fast rates, and develop too slowly at slow rates than multi-state characters. BM and Mk
212 appear to perform fairly similarly in reconstructing branch lengths (Fig. 2; Supp. Fig. 1). The
213 pattern across rates and matrix sizes are very similar between BLD and symmetric distances, with
214 the fastest rates producing the most error. This likely results from increased saturation at fast
215 rates, causing underestimation of hidden character changes.

216 Matrix size has a major impact on tree reconstruction accuracy. Estimations from both
217 discrete and continuous traits improve substantially at each increasing matrix size (Fig. 2).
218 Estimates from 20-character matrices possess fairly high error in both data types, with
219 approximately 1 in 5 bipartitions being incorrectly estimated from continuous characters, and 2 in
220 5 incorrectly being incorrectly estimated from discrete data. Increasing matrix size to 100 traits
221 improves accuracy significantly, with both data types estimating approximately 1 in 10
222 bipartitions incorrectly. Although at several rates, mean symmetric distance compared between
223 data types is close, continuous characters tend to be less widely distributed, and thus appear to
224 reconstruct trees with more consistent accuracy. When matrix size is increased to 500 characters,
225 both continuous and discrete characters are able to recover phylogeny with very high accuracy,
226 except for at very fast rates, where discrete characters estimate approximately half of all
227 bipartitions incorrectly on average.

228 *Simulation of Covarying Continuous Characters*

229 Tree inference under BM appears relatively robust to the violation of co-evolving continuous
230 characters. Although error is recognisably greater with strong covariance and many trait
231 dimensions, symmetric distance is remains close to values from uncorrelated traits at lower
232 covariance strengths and/or fewer trait dimensions (Fig. 3). When correlated traits are of low
233 dimensionality and covariance strength, reconstruction appears to be nearly as accurate as
234 uncorrelated traits, with all bipartitions estimated correctly on average. As covariance strength and
235 dimensionality are increased to intermediate values, topological error increases such that between
236 0 and 17% of bipartitions are estimated incorrectly, with a wider distribution than is present at the
237 lowest values. Accuracy is most diminished when covariance and dimensionality are strongest,
238 with most reconstructions estimating between 17-29% of bipartitions incorrectly. Although

239 statistical significance cannot be estimated for BLD and symmetric distance, estimation under
240 low to intermediate trait covariance appears at least qualitatively similar, albeit slightly worse, to
241 uncorrelated continuous and binary discrete characters. The decreases in accuracy observed can
242 likely be attributed to the decrease in total information content caused by covariance. This
243 reduces the effective amount of data from which to draw inference. This is reflected in the results,
244 with higher covariances and dimensionalities reconstructing trees with a similar magnitude of
245 error as is shown for the 100 character datasets.

246 **DISCUSSION**

247 These results suggest that, although imperfect, phylogenetic reconstruction from continuous
248 trait data may provide a reasonable supplement or alternative to inference from discrete
249 characters. Continuous characters appear to perform better in phylogenetic inference than binary
250 discrete overall. Their resilience to high evolutionary rate is expected, because continuous
251 characters evolving under an unbounded BM process will continue to increase in variance
252 through time. Therefore, such characters are able to retain phylogenetic information at high
253 evolutionary rates that may cause rampant saturation in discrete characters (Fig. 4). Although
254 bounded evolutionary models should experience diminished phylogenetic signal at high
255 evolutionary rates and/or long timescales in comparison, the larger amount of information
256 contained in continuous datasets may allow longer retention of signal. Further adding to this,
257 temporal variation in evolutionary regimes and model parameters can interact in complex ways,
258 sometimes extending the maintenance of phylogenetic signal through time (Revell *et al.* 2008).
259 Therefore, although real continuous characters are undoubtedly bounded in their evolution, the
260 added information contained in continuous character datasets may lessen the extent of saturation
261 relative to discrete. More empirical and simulation work is needed to better understand realistic

262 conditions for loss of signal in continuous traits.

263 The susceptibility of discrete characters to the loss of phylogenetic signal at high evolutionary
264 rates and deep timescales has long been recognised (Hillis and Huelsenbeck 1992; Yang 1998).
265 Although this effect is understood to affect molecular data, discrete morphological datasets may
266 possess increased susceptibility to this effect because of the frequent use of binary character
267 coding schemes. Discrete characters constrained to fewer states increases signal loss at high
268 evolutionary rates due to increased levels of homoplasy, saturation, and lower information content
269 overall (Donoghue and Ree 2000). This is ultimately a result of the fewer number of possible
270 evolutionary transitions in binary characters than those with larger state spaces. Although
271 continuous characters are expected to exhibit more severe loss of phylogenetic signal through
272 time in empirical datasets than the simulated examples generated in this study, the greater
273 information contained in continuous characters suggests the possibility that they are more
274 resilient to saturation than discrete characters.

275 Error in branch length estimation was fairly high with the 20-trait matrices, but decreased
276 substantially when matrix size was increased to 100 traits. Although BM and Mk achieve similar
277 accuracy in estimating branch lengths in this study, careful thought should continue to be applied
278 when relying upon Mk branch length estimates in the future. Branch length error may be higher
279 when inferring under Mk from empirical datasets, since many discrete morphological matrices
280 are constructed to include only parsimony informative characters. In these cases, characters are
281 expected to have undergone only single synapomorphic changes. Although this issue is addressed
282 through the ascertainment bias correction developed by (Lewis 2001), it is unclear how
283 meaningfully single character changes can inform evolutionary rates. This mode of change,
284 which may characterise much of discrete character evolution, differs from the population

285 dynamics of nucleotide substitution. This raises questions surrounding the interpretability of rates
286 estimated from discrete morphology. Molecular data matrices (ie. nucleotides and amino acids)
287 share ontologies between sites. And so, substitution rates estimated across sites are easily
288 interpretable. By contrast, discrete morphological character matrices differ in ontology between
289 sites, rendering substitution rates estimated across sites non-interpretable. One solution would be
290 to calculate per-site rates in morphology. However, the problem related to single state changes,
291 described above, makes this problematic. Continuous characters may be expected in many cases
292 to evolve at fairly consistent rates through time (Simpson 1944), lending an intuitive biological
293 interpretation to branch lengths estimated from continuous characters as the amount of character
294 displacement over time. This interpretation remains consistent even in cases where traits may not
295 evolve gradually or are bounded by physical limitations and/or attraction to selective optima, with
296 the only difference being in the parameters describing the process of character displacement. Of
297 course, this is stated cautiously, as further studies addressing the interpretability and adequacy of
298 both discrete and continuous trait models are needed.

299 Although continuous measurements may often follow covarying evolutionary trajectories in
300 nature, this appears to have a relatively minor impact on reconstruction. Accuracy was only
301 greatly lowered in the simultaneous presence of very high dimensionality and covariance
302 strength. Offering further support to the ability of continuous characters to reconstruct phylogeny
303 despite evolutionary covariance, Adams and Felice (2014) also report the presence of
304 phylogenetic information in multidimensional characters, even when the number of dimensions is
305 greater than the number of taxa. Despite these generally positive findings, it should be noted that
306 inference may be misled if sampling is significantly biased to include relatively small numbers
307 of strongly correlated measurements. In these cases, it would be beneficial to examine the

308 correlation structure and information content of the dataset to assess the amount of biased
309 redundancy in signal.

310 *Are Continuous Characters a Feasible Data Source for Phylogenetics?*

311 Use of continuous traits has the benefit of reducing subjectivity in the construction of data
312 matrices. While categorizing qualitative characters often requires subjective interpretation,
313 quantitative measurements can be taken without this source of human error. This would allow
314 biologists to assess uncertainty statistically instead of attributing discordance in tree estimates to
315 differences in opinion. Translation of morphological observations into data that can be analysed
316 can present serious complications in discrete characters. Steps such as the determination of
317 whether or not to order states, the total number of states chosen to describe characters, and the
318 assignment of character states states can vary greatly and often yield widely different results
319 (Hauser and Presch 1991; Pleijel 1995; Wilkinson 1995; Hawkins *et al.* 1997; Scotland and
320 Pennington 2000; Scotland *et al.* 2003). Continuous measurements avoid many of these issues
321 because they can be measured, by definition, objectively and quantitatively. In addition, they may
322 better describe variation than discrete characters. Several workers have suggested that the
323 majority of biological variation is fundamentally continuous (Thiele 1993; Rae 1998; Wiens
324 2001). Although continuous characters have long been employed in phylogenetic analysis, they
325 are generally artificially discretised, either using quantitative approaches, or through gross
326 categorisations such as 'large' and 'small. The major disadvantage to this approach is the loss of
327 valuable biological information. Several researchers have condemned with the use of continuous
328 characters in phylogenetics, arguing that intraspecies variation may be too great for clear
329 phylogenetic signal to exist (Pimentel and Riggins 1987; Chappill 1989). However, these
330 arguments have been largely undermined by studies demonstrating the phylogenetic

331 informativeness of continuous measurements (Goloboff *et al.* 2006; Smith and Hendricks 2013).

332 The expectation of correlated evolution between continuous characters has been a major
333 argument against their use in phylogenetic reconstruction in the past (Felsenstein 1985).
334 However, evolutionary covariance between sites is not a phenomenon that is restricted to
335 continuous morphological characters. Population genetic theory predicts tight covariance
336 between nucleotide sites under many conditions (e.g. Hill and Robertson 1968; Reich *et al.* 2001;
337 Palaisa *et al.* 2004; Schlenke and Begun 2004; McVean 2007). Such covariance also may be
338 expected to occur in discrete morphological characters in cases where traits are genetically linked.
339 While it is difficult to assess the relative magnitude of sitewise covariance between continuous,
340 discrete, and molecular data, examination of the correlation structure of traits may be more
341 straightforward in continuous characters using standard regression techniques. This would ease
342 the identification of biased and positively misleading signal among continuous characters,
343 enabling correction through common transformation approaches such as principal components
344 analyses or by weighting likelihood calculations by the amount of overall variance contributed by
345 covarying sets of characters.

346 The fundamentally continuous nature of many biological traits is supported by differential
347 gene expression and quantitative trait loci mapping studies, which demonstrate their quantitative
348 genetic basis (Andersson *et al.* 1994; Hunt *et al.* 1998; Frary *et al.* 2000; Valdar *et al.* 2006).
349 Nevertheless, there remain well known instances where traits are truly discrete. Studies in
350 evolutionary developmental biology have shown that many traits can be switched on or off in
351 response to single genes controlling genetic cascades (e.g. Wilkinson *et al.* 1989; Burke *et al.*
352 1995; Cohn and Tickle 1999). Such traits may be incorporated as separate partitions into
353 integrated analyses along with continuous measurements, using Mk or parsimony approaches.

354 Characters under the control of developmental expression pathways may also exhibit very deep
355 phylogenetic signal (De Rosa *et al.* 1999; Cook *et al.* 2001). Thus, such integrated analyses may
356 enable the construction of large phylogenies from morphology by use of datasets containing
357 phylogenetic signal at multiple taxonomic levels.

358 Accuracy in both character types increases with dataset size, but continuous characters
359 outperform discrete at each matrix length. Practically, the performance disparity between the two
360 may be most important when analysing small datasets, when error is highest for both character
361 types. Use of continuous characters may help in paleontological studies. Since paleontologists
362 are often restricted to analysing small datasets, use of continuous characters may improve
363 confidence and resolution of phylogeny by increasing the information content of character
364 matrices. Although many paleontological datasets many never achieve sufficient size to resolve
365 relationships with high confidence, use of continuous characters may increase the efficiency of
366 data use. Also, the measurement of continuous characters may be easier to automate than
367 recognition of discrete characters. This would enable the collection of large datasets that are
368 impractical to assemble manually. Improved ability to infer phylogeny among fossil taxa would
369 also benefit molecular phylogenetics because the incorporation of fossils into total evidence
370 matrices can improve both inference of molecular dates and alleviate long branch attraction
371 (Huelsenbeck 1991; Wiens 2005; Ronquist *et al.* 2012). These findings should urge
372 paleontologists to consider data collection schemes that give greater consideration to continuous
373 measurements. Overall, this may improve efficiency in the use of hard-won paleontological data
374 by maximizing the amount of information gleaned from specimens.

375 Moving forward, several extensions to Gaussian models should be explored for application to
376 phylogenetic inference. For example, further work is needed to determine the extent and

377 distribution of rate heterogeneity between sites in continuous alignments. Since its presence has
378 been well documented in molecular and discrete morphological data, it is likely that such rate
379 heterogeneity is present in continuous measurements, and should be accommodated in empirical
380 studies. Since traits can evolve under a broad range of processes, the fit of alternative models of
381 continuous character evolution to empirical data and their adequacy in describing variation among
382 them should also be examined.

383 *Is Mk a reasonable model for discrete character evolution?*

384 Although Mk and its extensions have been increasingly adopted in morphological
385 phylogenetics, it is unclear whether it provides a reasonable approximation of the evolutionary
386 process. Although there are explicit theoretical links between Markovian substitution models and
387 population genetic processes (Jukes and Cantor 1969), such theory does not exist in morphology.
388 In addition, morphological evolution might be intuitively expected to evolve in a fashion more
389 idiosyncratic to individual taxa and traits. Parsimony accounts for this idiosyncrasy, being
390 mathematically equivalent to the no common mechanisms (NCM) model which treats each
391 character individually (Tuffley and Steel 1997), while Mk approaches do not. There have been
392 extensions to Mk that address several of the most egregious model violations, but fundamental
393 issues remain concerning the applicability of substitution processes to morphological character
394 change. In particular, the difficulty of interpreting rates of character change in empirical datasets,
395 discussed above, begs deeper discussion of the application of branch lengths estimated under Mk
396 to larger biological questions. This is especially important in total-evidence tip dating methods
397 employing Mk, as poor branch length estimates may weaken the ability to infer branching times.
398 Although presenting a unique set of challenges, the use of continuous characters may mitigate
399 some of these issues through the more straightforward interpretability of models describing their

400 change. Nonetheless, further work is needed to address the relative adequacy of discrete and
401 continuous trait models in describing the evolution of phenotypic data. These questions will be of
402 critical importance moving forward as advances in morphological data and new fossil discoveries
403 usher in an age of unprecedented discovery in morphological phylogenetics.

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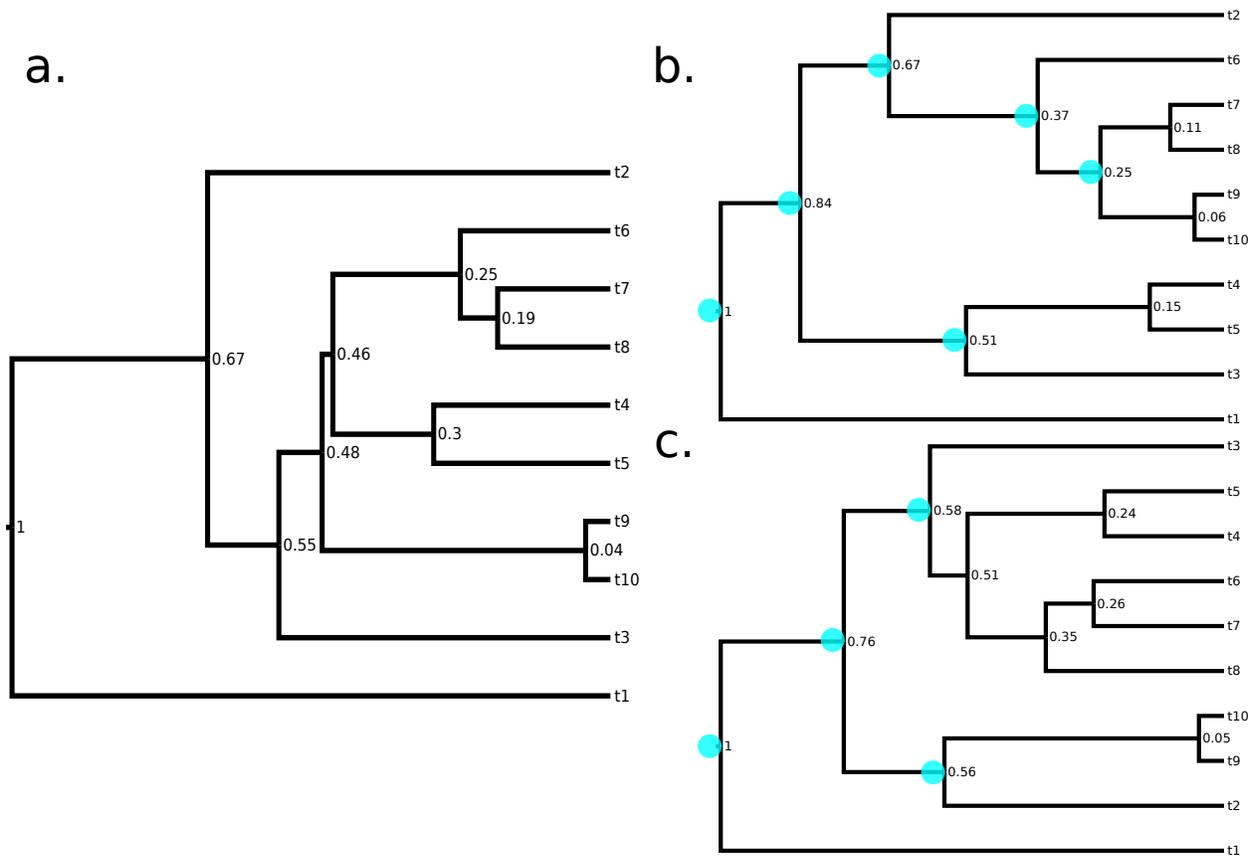


Figure 1: **a.** Exemplar true simulated tree. **b.** Tree inferred from 20 discrete characters simulated under Mk from true tree. **c.** Tree inferred from 20 continuous characters simulated under Brownian motion. Node labels correspond to node heights. Blue dots represent bipartitions not present in the true tree.

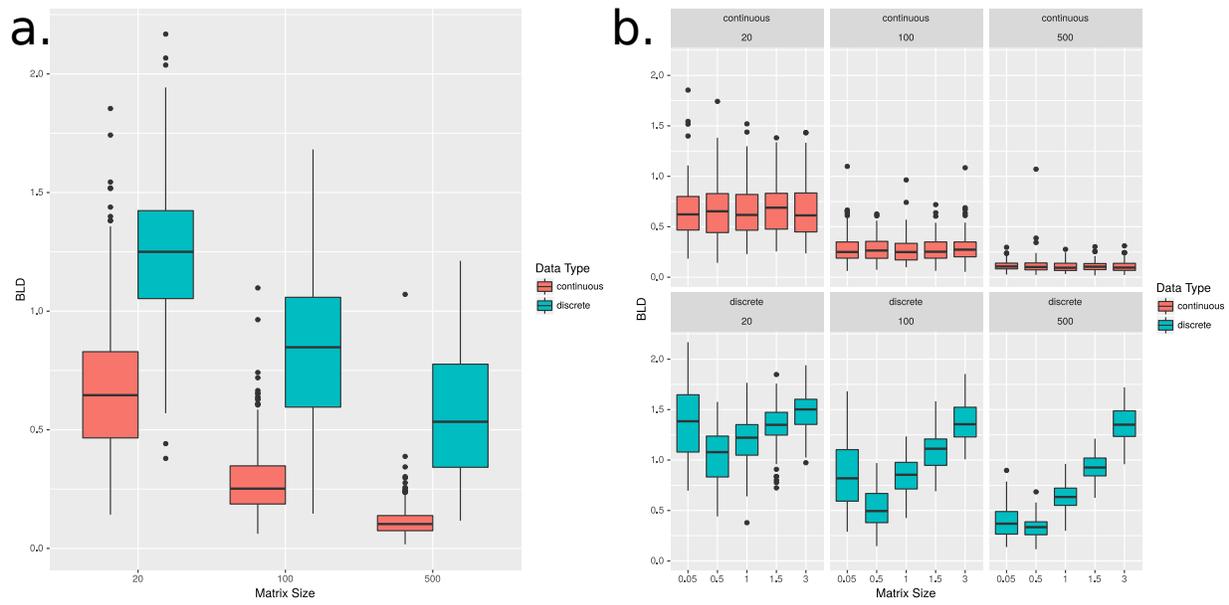


Figure 2: Branch length distance (BLD) across trees estimated from independently evolving continuous characters. **a.** BLD averaged across all rates except for the highest rate category, which resulted in the highest error when inferring under Mk. **b.** BLD across all matrix sizes and rates.

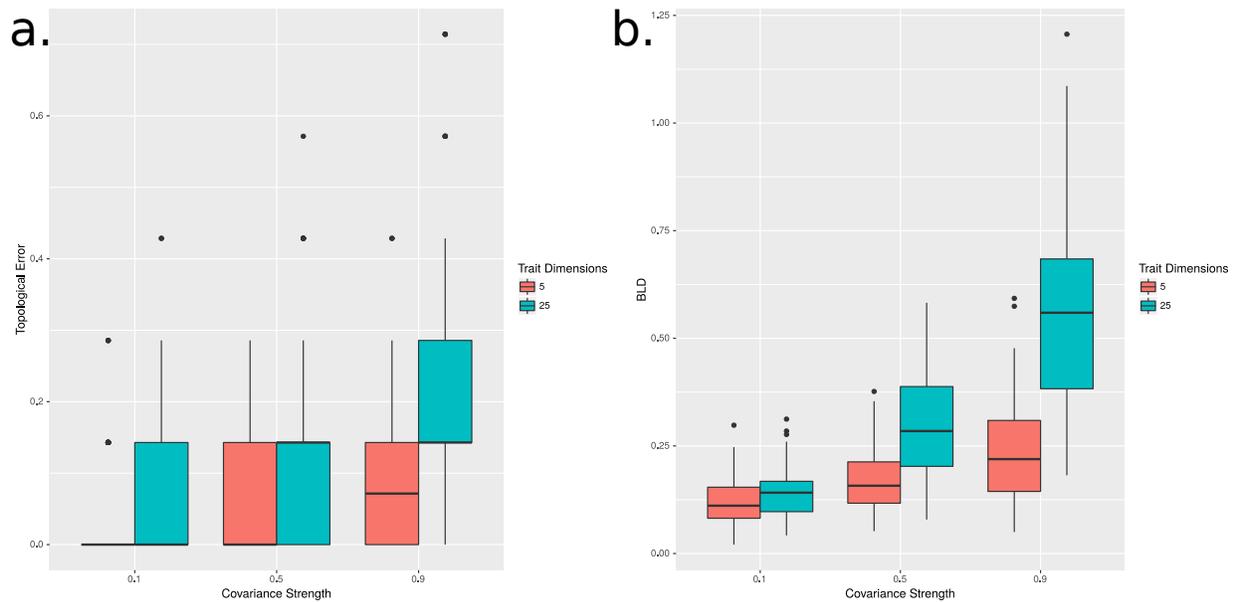


Figure 3: a. Topological error, calculated as proportion of maximum symmetric distance across trees estimated from covarying continuous characters. **b.** Branch length distance (BLD) across trees estimated from covarying continuous characters. Dimensions refers to the number of traits within covarying blocks. Covariance strength refers to the strength of the correlation between covarying characters, with 1 describing perfect correlation.

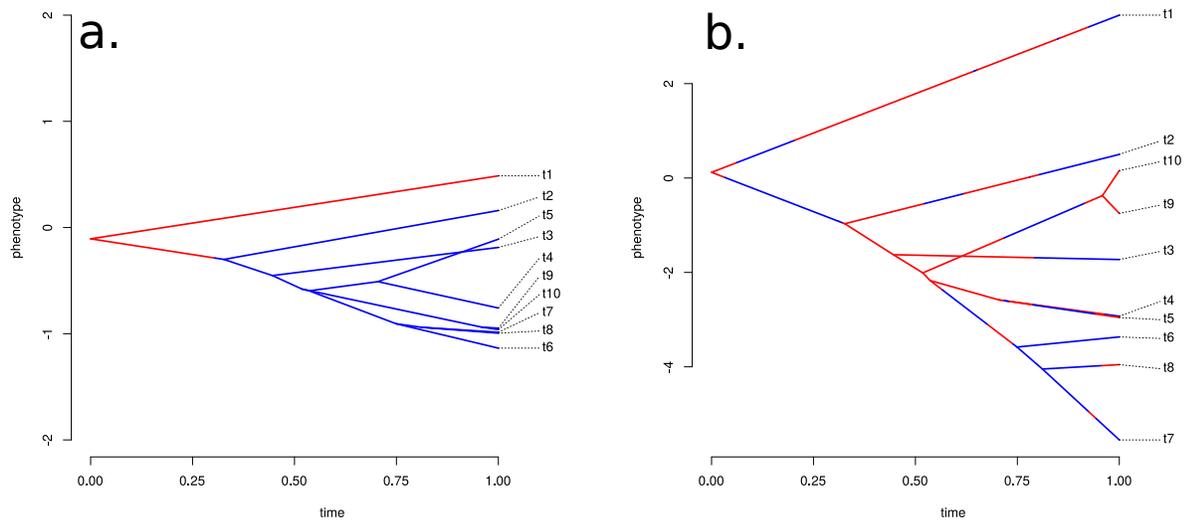


Figure 4: Discrete and continuous characters simulated **a.** at slow evolutionary rate and **b.** fast evolutionary rate. Y axis represents continuous phenotype. Changes in colour represent changes in discrete character state. Note how continuous characters retain phylogenetic signal at fast rates, while discrete characters saturate.

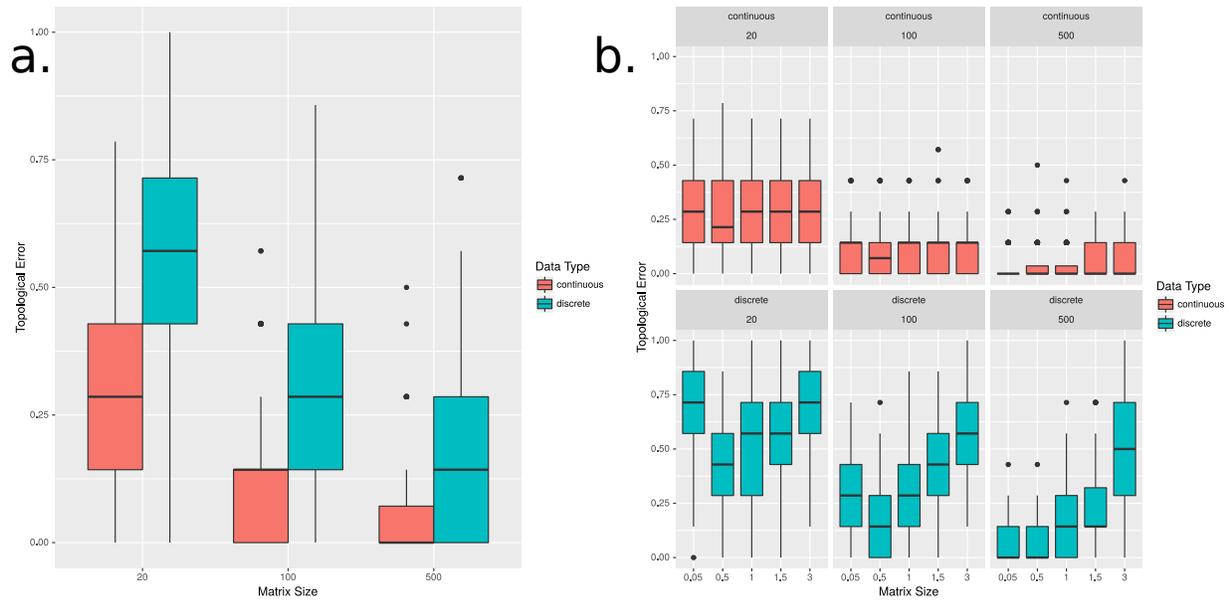


Figure S1: Topological error calculated as the proportion of maximum symmetric distance across trees estimated from independently evolving continuous characters. **a.** Error averaged across all rates except for the highest rate category, which resulted in the highest error when inferring under Mk. **b.** Error across all matrix sizes and rates.