



*Citation for published version:*

Puttick, MN, Ingram, T, Clarke, M & Thomas, GH 2020, 'MOTMOT: Models of trait macroevolution on trees (an update)', *Methods in Ecology and Evolution*, vol. 11, no. 3, pp. 464-471. <https://doi.org/10.1111/2041-210X.13343>

*DOI:*

[10.1111/2041-210X.13343](https://doi.org/10.1111/2041-210X.13343)

*Publication date:*

2020

*Document Version*

Peer reviewed version

[Link to publication](#)

This is the peer reviewed version of the following article: Puttick, MN, Ingram, T, Clarke, M, Thomas, GH. MOTMOT: Models of trait macroevolution on trees (an update). *Methods Ecol Evol.* 2020; 11: 464– 471, which has been published in final form at <https://doi.org/10.1111/2041-210X.13343>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

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# MOTMOT: models of trait macroevolution on trees (an update)

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## Abstract

1. The disparity in species' traits arises through variation in the tempo and mode of evolution over time and between lineages. Understanding these patterns is a core goal in evolutionary biology.

2. Here we present the comprehensively updated R package `MOTMOT: Models Of Trait Macroevolution On Trees` that contains methods to fit and test models of continuous trait evolution on phylogenies of extant and extinct species.

3. `MOTMOT` provides functions to investigate a range of evolutionary hypotheses, including flexible approaches to investigate heterogeneous rates and modes of evolution, models of trait change under interspecific competition, and patterns of trait change across significant evolutionary transitions such as mass extinctions. We introduce and test novel algorithms of heterogeneous tempo and mode of evolution that allow for phylogeny-wide shifts in evolution at specific times on a tree. We use these new `MOTMOT` functions to highlight an exceptionally high rate of mammalian body mass evolution for 10 million years following the Cretaceous-Palaeogene mass extinction.

4. These methods provide biologists and palaeontologists with the tools to analyse continuous trait data on phylogenies, including large trees of up to thousands of species.

**Keywords:** phylogenetic comparative methods, phylogenetics, maximum likelihood, macroevolution, R CRAN **Contact:** [marknputtick@gmail.com](mailto:marknputtick@gmail.com)

## 25 **1. INTRODUCTION**

26 Phylogenies provide a framework on which we can understand macroevolutionary  
27 trait change. For comparative studies, phylogenies are necessary to both account for  
28 statistical non-independence of taxa (Felsenstein, 1985; Grafen, 1989), and to act as a  
29 framework on which to model the tempo and mode of evolution (Simpson, 1944).  
30 Researchers have developed numerous methods to model the tempo and mode of evolution,  
31 particularly tree-transformation models for continuous traits based on Brownian motion (BM)  
32 (Hansen, 1997; Pagel, 1997, 1999; Blomberg, Jr, & Ives, 2003; Harmon et al., 2010;  
33 Eastman, Alfaro, Joyce, Hipp, & Harmon, 2011; Ingram, 2011; Venditti, Meade, & Pagel,  
34 2011; Thomas & Freckleton, 2012). Thomas and Freckleton (2012) introduced the R package  
35 MOTMOT to estimate parameters for many phylogenetic comparative methods, alongside  
36 novel approaches to analyse heterogeneous rates of continuous trait evolution on  
37 phylogenies. Here we update MOTMOT to flexible hypothesis testing by including novel  
38 methods and functions previously only available as stand-alone code, alongside all its  
39 original functions.

40

## 41 **2 DESCRIPTION**

### 42 **2.1 Overview**

43 We summarise the models of trait evolution and other functions introduced to the new  
44 release of MOTMOT in Table 1. Many of the methods available in MOTMOT have been  
45 described in detail elsewhere (see references in Table 1), and we provide a MOTMOT vignette  
46 with R code. Below we describe and assess the performance of a novel method to detect  
47 temporal shifts in tempo and mode of trait evolution and use these methods to study  
48 morphological evolution in Mammaliaformes using data from Slater (2013).

49            Nearly all methods in the package are usable with non-ultrametric phylogenies  
50 containing fossils, except the OU model in `transformPhylo.MCMC`. The  
51 `transformPhylo.ML` OU model is suitable for use with non-ultrametric trees (Slater,  
52 2014). Uncertainty in trait values (Silvestro, Kostikova, Litsios, Pearman, & Salamin, 2015)  
53 is incorporated using the *meserr* argument that takes a vector of trait errors. Finally, users can  
54 simulate data, including export of node states, for the majority of models using  
55 `transformPhylo.sim` to test model fit and adequacy.

## 56 **2.2 timeSlice and modeSlice models**

57            Many phylogenetic rate heterogeneous algorithms allow for rate variation on branches  
58 and lineages. Some rate-heterogeneous methods test for the presence of rate variation through  
59 time or among lineages but not specific rate changes for the whole tree at a certain time. The  
60 new *timeSlice* algorithm in `transformPhylo.ML` models changes in Brownian rates at  
61 certain times, similar to approaches introduced by Slater (2013). Previous models only  
62 allowed a single shift at a fixed time, these are extended as *timeSlice* allows users to set one  
63 or more shift time(s) of rate change. When users supply no split time, *timeSlice* will search  
64 multiple potential shift times and identify the time point with the highest likelihood using a  
65 stepwise approach similar to the *medusa* and *traitMedusa* approaches (Alfaro et al., 2009;  
66 Thomas & Freckleton, 2012). In the first iteration, the function tests all shift points, identifies  
67 and fixes the shift point leading to the highest likelihood one-shift model, then searches for  
68 the shift point leading to the highest likelihood two-shift model. The algorithm optimises the  
69 rate scalars for each time bin in each model, and sequentially fixes the best fitting shift time  
70 from each iteration for consequent searches. Finally, a comparison is made between BM, one  
71 shift, and the user defined *nth* model using  $AIC_c$ .

72            Unless stated, we summarise the output of the *timeSlice* model using the stepwise  
73 approach discussed above, but we note it is also possible to summarise outputs using a model

74 averaging approach. For each iteration (i.e, a model with  $n$  shifts; it is not possible to  
75 compare a  $n$  and  $n + 1$  shift model in this way), the model averaging summarises the relative  
76 fit of all shift positions based on their Akaike weights; and returns the weighted average rates  
77 through time.

78 We have also incorporated the new *modeSlice* model in `transformPhylo.ML`.  
79 *modeSlice* incorporates and extends the methods of Slater (2013) by allowing for multiple  
80 shifts in various modes of evolution (BM, OU, EB, and Kappa) at different times in the  
81 phylogeny's history. *modeSlice* is flexible as users can input multiple rate shift times with  
82 different combinations of modes. Furthermore, time bins with a BM mode can optionally  
83 vary in rate compared to the background variance (*rate.var* argument), and users can include  
84 a rate scalar alongside EB modes.

### 85 **2.3 Simulations with extant and fossil data**

86 On extant trees, the power and accuracy of the *timeSlice* algorithm (Figure 1)  
87 increases when shifts are more recent, in trees with more tips, and with larger differences in  
88 rates (see Supporting Information). On ultrametric trees, the number of branches decreases  
89 exponentially with age, so our results indicate *timeSlice* is more accurate with larger trees or  
90 trees including fossils.

### 91 **2.4 Simulations with fossil data**

92 The addition of fossils increases the power and accuracy of parameter estimation  
93 under *timeSlice*. We simulated data under the *timeSlice* model using the total-evidence  
94 Mammaliaformes tree (211 taxa, 153 extant) from Slater (2013) with rate shifts (2x,3x,5x  
95 background rate) at 233, 177, 122, 65, and 10 Ma. We repeated these simulations on an  
96 extant-only, Mammalia tree.

97 Correct support for the *timeSlice* model over BM is high for the Mammaliaformes  
98 tree: for rate shifts 3x background and above, with shifts at 122 Ma or younger, there is 95%

99 correct *timeSlice* support (Supplementary Figure S2). The higher power and accuracy of the  
100 *timeSlice* model at 65 Ma compared to 10 Ma is likely a consequence of the lack of time for  
101 trait variance to accrue or the absence of fossils in the 10 Ma–present bin.

102 Accuracy and precision for the *timeSlice* model is higher for the fossil  
103 Mammaliaformes analyses compared to the extant-only analyses (Supplementary Figure S3-  
104 4). The median error of rate estimates across all simulations is 0.63 for total-evidence  
105 analyses compared to 0.97 for the extant-only analyses. No *timeSlice* model produces an  
106 estimate of zero rates for any time bin on the fossil Mammaliaformes tree, only on the extant-  
107 only phylogeny (median 3.35% of models). When rates increase following a shift, there is  
108 strong support for the correct *timeSlice* model on the Mammaliaformes tree (median 66.1%  
109 correct support across analyses, >95% for some shifts) (Figure S5).

110 As a test of potential erroneous modelling of *timeSlice* process, we compared the fit of  
111 single process OU and EB models on the Mammaliaforms and Mammalia trees with  
112 *timeSlice* simulated data. In the Mammaliaformes tree the *timeSlice* pattern of high early rates  
113 results in increased support for an EB model compared to the Mammalia tree (Figure S5).  
114 This bias towards EB model support over *timeSlice* for *timeSlice* generated data occurs as  
115 both models describe a process in which high rates decrease through time. When simulations  
116 have higher rate differences between high ancient rate and subsequent lower rate, *timeSlice*  
117 models are more accurate.

118 This erroneous OU support on the extant tree (median 18.8% across all analyses) is  
119 likely a consequence of the OU model lengthening recent and reducing ancient branch  
120 lengths, mimicking simulated parameters (Cooper, Thomas, Venditti, Meade, & Freckleton,  
121 2015). This bias is apparent on the extant-only tree as the root-to-tip distance is equal for all  
122 taxa (Supplementary Figure S5).

123

## 124 2.5 Cretaceous-Palaeogene shifts in evolution

125 We analysed rates of morphological evolution in extinct and extant Mammaliaformes  
 126 using data from Slater (2013) using *timeSlice*. Slater showed a high Cenozoic rate of body  
 127 mass evolution in Mammaliaformes that resulted from an OU to BM shift in mode at the  
 128 Cretaceous-Palaeogene boundary (K-Pg) 66 Ma. Here, we analyse these data using  
 129 MOTMOT functions; after testing a number of hypothesis-based and exploratory models we  
 130 find best relative support for an increase in mammalian body mass evolution in the 10 million  
 131 years following the K-Pg mass extinction.

132 We extracted the mean mammal body mass and error measurement from the Slater  
 133 (2013) dataset, and then matched these data to the phylogeny using `sortTraitData`  
 134 (Figure 2a).

```
135 > data(mammals)
136 > attach(mammals)
137 > trait.phy <- sortTraitData(phy = mammal.phy,
138   y = as.matrix(mammal.mass), data.name = c("mean", "sem"),
139   log.trait = FALSE)
140 > phy <- trait.phy$phy
141 > y <- as.matrix(trait.phy$trait[, 1])
142 > errors <- as.numeric(trait.phy$trait[, 2])
143
```

144 With these body mass and error data data, we tested the relative fit of BM, OU, and  
 145 Early Burst using `transformPhylo`. As with Slater's K-Pg Shift model, estimated  
 146 Cenozoic rates are higher than Mesozoic rates, but *timeSlice* is not supported over BM as  
 147 shown by the *ModelFit* output the function `timeSliceSummary` (Table 2; Figure 2b).

```
148 > time.slice.66.model <- transformPhylo.ML(y = y, phy = phy,
149   Model = "timeSlice", splitTime = 66, meserr = errors)
150 > plot.timeSlice.ML(time.slice.66.model, phylo.plot = FALSE)
151 [c("ModelFit", "Rates")]
152
153 $ModelFit
154 [1] "BM"
155 $Rates
156 lnL          AIC          AICc          sigma.sq.1  anc.state.1
157 -466.62552164  937.25104327  937.30873558  0.09924604  4.28252379
158
```

159           However, we found support for a low background Mesozoic rate that accelerated  
 160 between 66-56 Ma (9.5x background) before reducing to a lower rate (56-0 Ma, 1.34x)  
 161 (Figure 2b).

```
162 > time.slice.66.model.multi <- transformPhylo.ML(y = y,
163   phy = phy, model = "timeSlice", splitTime = c(66, 56),
164   meserr = errors)
165 > plot.timeSlice.ML(time.slice.66.model.multi,
166   show.tip.label = FALSE, edge.col = "white", edge.width = 1,
167   cex = 1.3)[c("ModelFit", "Rates")]
168 [1] "split 1"
169
170 $Rates
171      lnL      AIC      AICc  sigma.sq.1
172 anc.state.1      rates1
173 -460.0902328  930.1804656  930.4731485    0.3589563
174  4.2811433    0.1785373
175      rates2      rates3  time.split1  time.split2
176  1.6957191    0.2400284    66.0000000    56.0000000
177
```

178           Here we fit a more naïve model that searches for all shifts in 1 Ma increments from 50  
 179 million years after the root age to 20 million years before the present. The best relative fit of  
 180 these models as judged by AIC<sub>c</sub> shows an ancient rate acceleration commencing 170 million  
 181 years ago. The two-shift model is not supported, and the single shift model has a poor relative  
 182 fit (Figure 2c).

```
183
184 > time.slice.66.model_naive <- transformPhylo.ML(y = y,
185   phy = phy, model = "timeSlice", nSplits = 2,
186   boundaryAge = c(50, 20), meserr = errors, testAge = 1)
187 > model.averaged.out <-
188 plot.timeSlice.ML(time.slice.66.model_naive, model.average =
189 TRUE)
190
```



191 We compared this *timeSlice* model to shifts in modes using the approach of Slater  
 192 (2013), now implemented in the *modeSlice* algorithm in `transformPhylo.ML`. The  
 193 ‘release and radiate’ model (Mesozoic OU shifts to BM at K-Pg) has a superior relative fit  
 194 compared to the *timeSlice* models, but we find a superior fit for a *modeSlice* model with low  
 195 Mesozoic rates (OU model) that accelerated to a high post-K-Pg rate (BM, rate scalar =  
 196 3.73), before shifting back to OU at 56 Ma (Table 2). The relative support for these models is  
 197 shown in Figure 2d.

198

```

199 > release.model <- transformPhylo.ML(y = y, phy = phy,
200   model = "modeslice", mode.order = c("ou", "bm"),
201   splitTime = 66, meserr = errors)
202 > release.radiate.model <- transformPhylo.ML(y = y, phy = phy,
203   Model = "modeslice", mode.order = c("ou", "bm"),
204   splitTime = 66, meserr = errors, rate.var = TRUE)
205 > release.radiate.recapture.model <- transformPhylo.ML(y = y,
206   Phy = phy, model = "modeslice",
207   mode.order = c("ou", "bm", "ou"), splitTime = c(66, 56),
208   meserr = errors, rate.var = TRUE)
209 $MaximumLikelihood
210 [1] -453.9791
211 $brownianVariance
212 [1] 0.1395728
213 $root.state
214 [1] 4.259928
215 $mode.1.ou
216       alpha          LCI          UCI
217 [1,] 0.02158316 0.01138688 0.03497292
218 $mode.2.bm
219       BM.rate          LCI          UCI
220 [1,] 4.69979 1.667876 10.93732
221 $mode.3.ou
222       alpha          LCI          UCI
223 [1,] 0.01343794 0.003040442 0.02588539
224 $AIC
225 [1] 917.9582
226 $AICc
227 [1] 918.2509
228
229

```

230 A high post-K-Pg rate of body mass evolution is congruent with data from the fossil  
 231 record (Alroy, 1999; Raia et al., 2013), and may represent an evolutionary ‘release’ following

232 the extinction of non-avian dinosaurs at the end of Cenozoic (Slater, 2013). Although body  
233 size evolution may be a poor proxy for functional traits such as dental characteristics, the  
234 high rates of evolution for mammals in the earliest Cenozoic may be indicative of clades  
235 movements into high level niches (Slater et al., 2019). Our new modelling framework, that  
236 allows flexibility in the estimation of the time, tempo, and mode of trait evolution, therefore  
237 provides new insight into body size evolution in the Mammaliaformes. More generally, we  
238 expect this approach to add potentially important nuance to our understanding of phenotypic  
239 macroevolutionary trends.

240

#### 241 **ADDITIONAL INFORMATION**

242

243 The package `motmot` is available on CRAN and can also be installed directly from GitHub  
244 ([github.com/PuttickMacroevolution/motmot](https://github.com/PuttickMacroevolution/motmot)). There is a full explanation of all functions and  
245 arguments as part of the R documentation, and a comprehensive vignette of the package is  
246 available online ([github.com/PuttickMacroevolution/motmot](https://github.com/PuttickMacroevolution/motmot)).

247

#### 248 **CONCLUSIONS**

249 `MOTMOT` provides a range of functions to analyse continuous trait evolution, with the main  
250 extensions summarised here. More details can be found in the package documentation and  
251 vignette available on CRAN.

252

#### 253 **AUTHOR CONTRIBUTIONS**

254 MNP and GHT conceived the ideas and designed methodology; code was written by MNP,  
255 GHT, MC, and TI. MNP analysed the data; MNP led the writing of the manuscript. All  
256 authors contributed critically to the drafts and gave final approval for publication.

257

258 **ACKNOWLEDGEMENTS**

259 We thank two anonymous reviewers and Lee Hsiang Liow for help and comments that  
260 improved the manuscript. MNP thanks the Royal Commission for the Exhibition of 1851 for  
261 funding.

262

263 **DATA AVAILABILITY**

264 The R MOTMOT package is available on CRAN ([https://cran.r-](https://cran.r-project.org/web/packages/motmot/index.html)  
265 [project.org/web/packages/motmot/index.html](https://cran.r-project.org/web/packages/motmot/index.html)) and the Mammaliaformes data can be accessed  
266 directly from the package. The code to generate simulations and analyses Mammaliaformes  
267 body mass evolution is available at Figshare (doi: 10.6084/m9.figshare.11337050).

268

269 **REFERENCES**

- 270 Alfaro, M. E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D. L., ... Harmon, L. J.  
271 (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed  
272 vertebrates. *Proceedings of the National Academy of Sciences*, **106**, 13410–13414.
- 273 Allen, B. J., Stubbs, T. L., Benton, M. J., & Puttick, M. N. (2018). Archosauromorph extinction  
274 selectivity during the Triassic-Jurassic mass extinction. *Palaeontology*, **62**, 1–14.
- 275 Alroy, J. (1999). The fossil record of North American mammals: evidence for a Paleocene  
276 evolutionary radiation. *Systematic Biology*, **48**, 107–118.
- 277 Blomberg, S. P., Jr, T. G., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative  
278 data: behavioral traits more labile. *Evolution*, **57**, 717–745.
- 279 Clarke, M., Thomas, G. H., & Freckleton, R. P. (2017). Trait evolution in adaptive radiations:  
280 Modeling and measuring interspecific competition on phylogenies. *The American*  
281 *Naturalist*, **189**, 121–137.
- 282 Cooper, N., Thomas, G. H., Venditti, C., Meade, A., & Freckleton, R. P. (2015). A cautionary

- 283 note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biological*  
284 *Journal of the Linnean Society*. **118**, 65-77.
- 285 Eastman, J. M., Alfaro, M. E., Joyce, P., Hipp, A. L., & Harmon, L. J. (2011). A Novel  
286 comparative method for identifying shifts in the rate of character evolution on trees.  
287 *Evolution*, **65**, 3578–3589.
- 288 Felsenstein, J. (1973). Maximum-likelihood estimation of evolutionary trees from  
289 continuous characters. *American Journal of Human Genetics*, **25**, 471–492.
- 290 Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*,  
291 **125**, 1-15.
- 292 Freckleton, R. P. (2012). Fast likelihood calculations for comparative analyses. *Methods in*  
293 *Ecology and Evolution*, **3**, 940–947.
- 294 Grafen. (1989). The Phylogenetic Regression. *Philosophical Transactions of the Royal*  
295 *Society of London, Series B*, **326**, 119–157.
- 296 Hansen, T. F. (1997). Stabilizing selection and the comparative analysis of adaptation.  
297 *Evolution*, **51**, 1341–1351.
- 298 Harmon, L. J., Losos, J. B., Jonathan Davies, T., Gillespie, R. G., Gittleman, J. L., Bryan  
299 Jennings, W., ... Mooers, A. T. (2010). Early bursts of body size and shape evolution are  
300 rare in comparative data. *Evolution*, **64**, 2385–2396.
- 301 Ingram, T. (2011). Speciation along a depth gradient in a marine adaptive radiation.  
302 *Proceedings of the Royal Society B: Biological Sciences*, **278**, 613–618.
- 303 Ingram, T., Harrison, A., Mahler, D. L., Castañeda, M. D. R., Glor, R. E., Herrel, A., ... Losos, J.  
304 B. (2016). Comparative tests of the role of dewlap size in Anolis lizard speciation.  
305 *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20162199.
- 306 Pagel, M. (1997). Inferring evolutionary processes from phylogenies. *Zoologica Scripta*, **26**,

307 331–348.

308 Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–  
309 884.

310 Pagel, M. (2002). Modelling the evolution of continuously varying characters on  
311 phylogenetic trees. In N. Macleod & P. L. Forey (Eds.), *Morphology, Shape and*  
312 *Phylogeny* (pp. 269–286). London: CRC Press.

313 Puttick, M. N. (2018). Mixed evidence for early bursts of morphological evolution in extant  
314 clades. *Journal of Evolutionary Biology*, **31**, 502–515

315 Puttick, M. N., Kriwet, J., Wen, W., Hu, S., Thomas, G. H., & Benton, M. J. (2017). Body length  
316 of bony fishes was not a selective factor during the biggest mass extinction of all time.  
317 *Palaeontology*, **60**, 727–741.

318 Raia, P., Carotenuto, F., Passaro, F., Piras, P., Fulgione, D., Werdelin, L., ... Fortelius, M.  
319 (2013). Rapid action in the Palaeogene, the relationship between phenotypic and  
320 taxonomic diversification in Coenozoic mammals. *Proceedings. Biological Sciences / The*  
321 *Royal Society*, **280**, 20122244.

322 Silvestro, D., Kostikova, A., Litsios, G., Pearman, P. B., & Salamin, N. (2015). Measurement  
323 Errors Should Always Be Incorporated in Phylogenetic Comparative Analysis. *Methods*  
324 *in Ecology and Evolution*, **6**, 340–346.

325 Simpson, G. (1944). *Tempo and mode in evolution*. Columbia University Press.

326 Slater, G. J. (2013). Phylogenetic evidence for a shift in the mode of mammalian body size  
327 evolution at the Cretaceous-Palaeogene boundary. *Methods in Ecology and Evolution*,  
328 **4**, 734–744.

329 Slater, G. J. (2014). Correction to ‘Phylogenetic evidence for a shift in the mode of  
330 mammalian body size evolution at the Cretaceous-Palaeogene boundary’, and a note

- 331 on fitting macroevolutionary models to comparative paleontological data sets.
- 332 *Methods in Ecology and Evolution*, **5**, 714–718.
- 333 Thomas, G. H., & Freckleton, R. P. (2012). MOTMOT: Models of trait macroevolution on
- 334 trees. *Methods in Ecology and Evolution*, **3**, 145–151.
- 335 Venditti, C., Meade, A., & Pagel, M. (2011). Multiple routes to mammalian diversity. *Nature*,
- 336 **479**, 393–396.
- 337

338 **Table 1.** A summary of the new and main functions included in MOTMOT. Multiple  
 339 traits can be analysed in models marked by an asterisk (\*).

New models		
Model	Description	Function(s)
<b>timeSlice*</b>	Identifies shifts in the tree-wide rate of evolution at discrete times. <i>timeSlice</i> takes user-supplied split times or the function searches and finds the highest-likelihood shift time(s). The function <code>timeSliceSummary</code> can summarise, plot, and calculate model averaging for <i>timeSlice</i> outputs.	<code>transformPhylo.ML</code> <code>timeSliceSummary</code>
<b>modeSlice*</b>	Estimates models with shifts in the tree-wide mode of evolution at specified times. Modes can shift between BM, Early Burst (EB), OU, and Kappa models. The BM modes can optionally have different rates (specified using the <i>rate.var</i> argument), and a rate scalar can be set to the EB model.	<code>transformPhylo.ML</code>
<b>nested modes*</b>	Calculates parameters for a shift from a Brownian motion to a different evolutionary mode ( $\lambda$ , $\delta$ , $\kappa$ , OU, ACDC, or $\phi$ ) within a subclade of a phylogeny (Puttick, 2018).	<code>transformPhylo.ML</code>
<b>character displacement</b>	Simulation of data under BM and trait change under intra-specific competition (Clarke, Thomas, & Freckleton, 2017).	<code>chr.disp.param</code> <code>chr.disp.lrt</code>
<b>Bayesian estimation of parameters*</b>	Bayesian MCMC estimation of $\lambda$ , $\delta$ , $\kappa$ , OU, ACDC, or $\phi$ models.	<code>transformPhylo.MCMC</code> <code>mcmc.plot</code>
<b><math>\phi</math> and multi-<math>\phi</math>*</b>	Estimation of the relative contributions of separational and gradual evolution to trait evolution; fit as a whole-tree process ( $\phi$ ) or with different values estimated in subclades (multi- $\phi$ ) (Ingram, 2011; Ingram et al., 2016).	<code>transformPhylo.ML</code> <code>traformPhylo.MCMC</code>
<b>Pagel's <math>\lambda</math>*</b>	Measure of phylogenetic signal, can be estimated simultaneously alongside $\delta$ , $\kappa$ , OU, ACDC, and $\phi$ models (Pagel, 1997, 1999).	<code>transformPhylo.ML</code> <code>transformPhylo.MCMC</code>
<b>Phylogenetic Generalised Least Squares (PGLS)</b>	Phylogenetic regression model with continuous traits estimated using contrasts, faster than using variance-covariance matrices (Felsenstein, 1973, 1985; Grafen, 1989; Freckleton, 2012).	<code>pic.pgls</code>
<b>Acceleration-</b>	Exponential change in evolutionary rate	<code>transformPhylo.ML</code>

<b>Deceleration (ACDC) / Early Burst*</b>	through time. If the <i>upperBound</i> argument is set to zero, ACDC becomes the Early Burst model (Blomberg et al., 2003; Harmon et al., 2010)	<code>transformPhylo.MCMC</code>
<b>trend*</b>	Time-dependent change in character values; only applicable for non-ultrametric trees (Pagel, 2002)	<code>transformPhylo.ML</code>
<b>utility functions</b>	Functions to facilitate analyses of trait selectivity of mass extinction in the fossil record (Puttick et al., 2017; Allen, Stubbs, Benton, & Puttick, 2018). Also functions to add fossils to ultrametric phylogenies.	<code>contemporaryPhy</code> <code>addFossilToPhy</code>

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342 **Table 2.** Modes of evolution fit to Mammaliaformes body mass evolution used to investigate  
 343 a shift in evolution at the Cretaceous-Palaeogene boundary 66 Ma. The *modeSlice* model  
 344 with best relative fit is shown in **bold**. The table summarises the `MOTMOT` function used for  
 345 each analysis, the estimated parameters with 95% confidence intervals in brackets, *n*  
 346 parameters, and  $AIC_c$ , and  $AIC_c$  weights.

Model	MOTMOT function	estimated parameters	<i>n</i>	$AIC_c$	$AIC_c$ Weights
Brownian motion	<code>transformPhylo.ML(y = y, phy = phy, model = "BM")</code>	$\sigma^2$ 0.0992 $\mu$ 4.2825	2	937.3087	6.81e-05
Ornstein-Uhlenbeck	<code>transformPhylo.ML(y = y, phy = phy, model = "OU")</code>	$\sigma^2$ 0.1022 $\mu$ 4.4433 $\alpha$ 5.976e-4 (1e-8, 0.006)	3	939.3174	2.50e-05
Early Burst	<code>transformPhylo.ML(y = y, phy = phy, model = "OU", upperBound = -1e-6)</code>	$\sigma^2$ 0.0967 $\mu$ 4.2825 $a$ -1e-06 (-0.002, -1e-06)	3	938.3214	4.11e-05
split at K-Pg (66 Ma)	<code>transformPhylo.ML(y = y, phy = phy, model = "timeSlice", splitTime = 66)</code>	$\sigma^2$ 0.2938 $\mu$ 4.2823 Pre-Kg rate: 1 (0.611, 1.679) Post-K-Pg rate: 1.33 (0.776, 2.23)	4	937.3087	6.81e-05
<i>timeSlice</i> with split at K-Pg (66 Ma) and 56 Ma	<code>transformPhylo.ML(y = y, phy = phy, model = "timeSlice", splitTime = c(66, 56))</code>	$\sigma^2$ 0.3590 $\mu$ 4.2811 Pre-Kg rate: 1 (0.650, 1.59) 66-53 Ma rate: 9.50 (3.59, 21.53) 53-0 Ma rate: 1.34 (0.859, 2.09)	5	930.4731	2.08e-03
<i>timeSlice</i> naïve search for two best-fitting shifts between 215-20 myrs in 1 myr increment.	<code>time.slice.66.model_naive &lt;- transformPhylo.ML(y = y, phy = phy, model = "timeSlice", nSplits = 2, boundaryAge = c(50, 20), meserr = errors, testAge = 1)</code>	One split: 171 Ma $\sigma^2$ 0.2979 $\mu$ 4.3561 Pre-171 Ma rate: 1 (0.413, 2.677) 171-0 Ma rate: 4.8589 (2.1035, 11.4792)	4	930.6699	1.88e-03
'Release' model OU to BM shift at K-	<code>transformPhylo.ML(y = y, phy = phy, model = "modeslice", mode.order = c("ou", "bm"), splitTime = 66)</code>	$\sigma^2$ 0.1145 $\mu$ 4.4345 $\alpha$ 0.015 (0.007, 0.0258)	3	925.7641	0.0219

Pg					
'Release and Radiate' (Slater model) OU to BM plus rate shift at K-Pg	transformPhylo.ML(y = y, phy = phy, model = "modeslice", mode.order = c("ou", "bm"), splitTime = c(66), rate.var = TRUE)	$\sigma^2$ 0.2146 $\mu$ 4.2652 $\alpha$ 0.0291 (0.0173, 0.0449) BM rate: 0.4629 (0.2785, 0.7607)	4	924.7107	0.0371
<b><i>modeSlice</i></b> <b>pre-K-Pg</b> <b>OU</b> <b>66-56 Ma</b> <b>BM with</b> <b>rate shift</b> <b>56-0 Ma</b> <b>OU</b>	<b>transformPhylo.ML(y = y, phy = phy, model = "modeslice", mode.order = c("ou", "bm", "ou"), splitTime = c(66, 56), rate.var = TRUE)</b>	<b><math>\sigma^2</math> 0.140</b> <b><math>\mu</math> 4.2599</b> <b>OU (root-66 Ma): <math>\alpha</math></b> <b>0.0216 (0.0114, 0.0350)</b> <b>BM rate (66-56 Ma):</b> <b>4.670 (1.6679, 10.9373)</b> <b><math>\alpha</math> 0.0134 (0.0030,</b> <b>0.0259)</b>	<b>5</b>	<b>918.2509</b>	<b>0.937</b>

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349 **Figure 1.** Relative support for the *timeSlice* model (light blue) and BM (dark blue) from fully  
350 simulated data. Data were generated under BM or with one shift to a rate higher or lower rate  
351 (scalar=2,3,5x background) and at various ages (0.1, 0.25, 0.5, 0.75, 0.9). 1000 replicates  
352 were generated on trees with 50, 100, and 500 tips with 1000 replicates. Model power of  
353 *timeSlice* increases with larger shift magnitudes, tree size, and when shifts are closer to the  
354 present.

355

356 **Figure 2. Analysis of mammal body mass evolution during the pass 250 million years.**

357 The output from `sortTraitData` showing the relative body mass for tips on the  
358 phylogeny (a). The estimated rates of evolution for shifts in body mass evolution at 66 and 53  
359 Ma from the *timeSlice* model in `transformPhylo.ML` with branches scaled to rates and  
360 these same rate estimates and associated CIs plotted through time using  
361 `timeSliceSummary` (b). The model-average rate estimates from a naïve *timeSlice* search  
362 with two shifts identified as the best-fitting points from million-year increments between  
363 215-20 Ma (the best fit relative fit supports a single shift model at 171 Ma) plotted using  
364 `timeSliceSummary` (c). The Akaike weights for various *timeSlice* and *modeSlice* models  
365 (d), showing the overwhelming support for the model of OU to 66 Ma followed by a BM  
366 with a rate increase with a subsequent shift to a lower rate in another OU model. Full details  
367 of each model are shown in Table 2.