

1 The error in Bayesian phylogenetic reconstruction
2 when speciation co-occurs

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7 December 4, 2018

8 **Abstract**

9 There exist millions of species on Earth, all originating from a common
10 ancestor billions of years ago. The field of phylogenetics uses heritable
11 material to determine which species are closest related and what are the
12 mathematics that shape speciation.

13 In Bayesian phylogenetics, a DNA/RNA/protein alignment is used to
14 infer a distribution of phylogenies and parameter estimates. To do so,
15 we use assumptions that may be biologically unrealistic, but may give
16 tolerable errors.

17 Contemporary inference assumes that speciation never co-occurs.

18 Here we show the error we make in our inference, when nature has
19 varying degrees of co-occurring speciation.

20 **Keywords:** computational biology, evolution, phylogenetics, Bayesian anal-
21 ysis, tree prior

1 Introduction

- There are many contemporary tools that provide the possibility to infer a phylogeny from genetic data (DNA, RNA, proteins). A popular Bayesian phylogenetic tool is called BEAST (Drummond & Rambaut 2007) and its cousin BEAST2 (Bouckaert *et al.* 2014).
- BEAST is very flexible, providing the user with the option to set up all possible phylogenetic priors (e.g. site/clock/speciation model).
- However, currently available priors can be not suitable to analyze some specific datasets. With this work we aim to test whether or not the implementation of a new prior model is beneficial to study a specific kind of diversification process.
- BEAST2 gives us the possibility to introduce new tree priors to infer phylogenies based on different assumptions on how the speciation process takes place.
- One of such speciation processes is the multiple birth hypothesis, a new model (described below) and thus currently absent in BEAST.
- The Multiple birth hypothesis can be useful to explain a phenomenon that has always puzzled evolutionary biologists: what are the drivers of the diversification processes for those phylogenies that show an impressive amount of speciation events in relatively short times? The (constant-rate) birth-death (BD) model embodies the common assumption that only a single speciation event can occur at any given time. The multiple-birth-death (MBD) model relaxes this assumption, allowing events in which large-scale environmental changes lead to a great number of species in relatively short time intervals. Such a hypothesis may be a better fit to

describe the burst in systems like cichlid fish diversification in the African Great Lakes: Malawi, Tanganyika and Victoria (Janzen *et al.* 2016, Janzen *et al.* 2017).

- However, it may be that current BD tree priors are good enough at detecting such events, with a (preferred) lower level of complexity. If this is the case one should always be more keen to adopt the simplest model.
- Here we present our study with the aim of exploring when using a more complex MBD tree prior is warranted. To do so, we simulate phylogenies using the MBD process, with varying degrees of that process. To be explicit, we define that degree, s , as the number of extinct and extant species created during a co-occurring speciation event, $n_{\mathbb{M}}$, from the total number of extinct and extant species:

$$s = \frac{n_{\mathbb{M}}}{n_{\mathbb{M}} + n_{\mathbb{B}}} \quad (1)$$

Here, $n_{\mathbb{B}}$ is the number of extinct and extant species created during a default single-birth speciation event.

From such phylogenies with different degrees of s , we measure the inference error we make today, would nature follow such a phylogeny. The inference error we make today is caused by the assumption of a BD process and by inherent noise in this inference.

We have the hypothesis \mathcal{H}_1 that, for a higher s , the inference error e will increase:

$$e = f(s) \quad (2)$$

Where f is a monotonously increasing function of unknown shape.

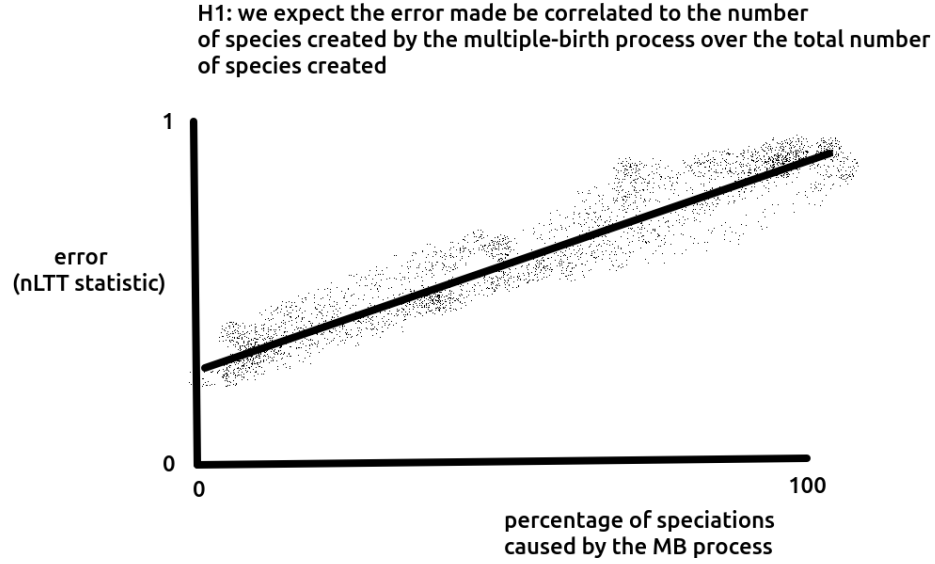


Figure 1: Hypothesis 1: we expect the error made be correlated to the number of species created by the multiple-birth process over the total number of species created

68 The MBD process has multiple components, that may cause different val-
69 ues of e for identical values of s .

70 One MBD component that may cause different values of e for identical
71 values of s is the MBD regime: which can be many modest multiple-
72 speciation events, or few intense ones. As we have no prior expectations,
73 we have the (null) hypothesis, \mathcal{H}_7 , that the MBD regime has no effect on
74 e .

75 Another MBD component that may cause different values of e for identical
76 values of s is the effect of extinction. As extinctions will hit lineages
77 created by both speciation processes equally, and we have no additionaly
78 prior expectations, we have the (null) hypothesis, \mathcal{H}_2 , that extinction has
79 no effect on e .

80 Another MBD component that may cause different values of e for identical

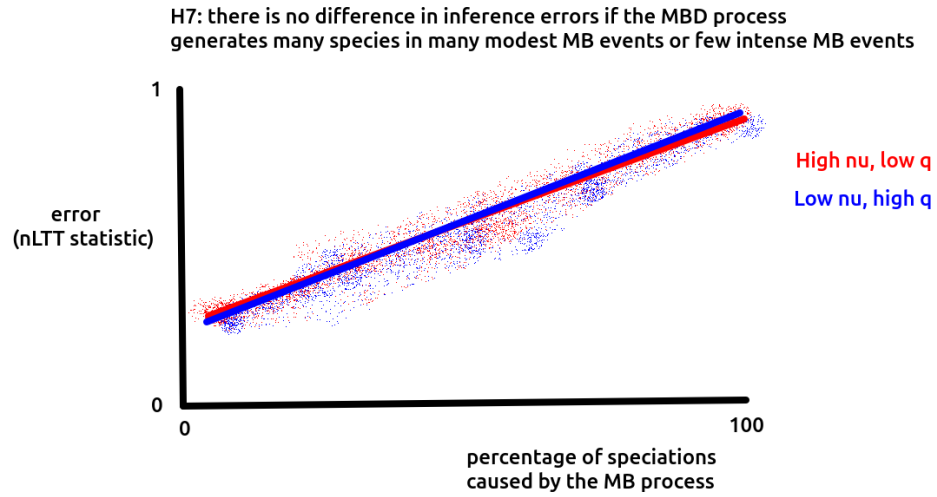


Figure 2: Hypothesis 7: there is no difference in inference errors if the MBD process generates many species in many modest MB events or few intense MB events

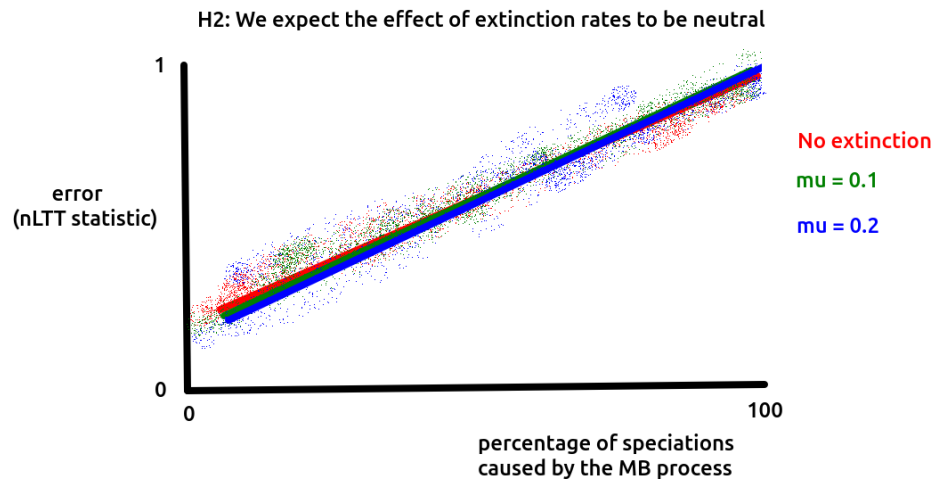


Figure 3: Hypothesis 2: the effect of extinction rates is neutral

81 values of s , is the timing of a multiple-birth event: be it close to the crown
 82 age or close to the present. Compared to a late multiple birth event, an
 83 early multiple birth event may have a longer-lasting effect (as the next
 84 speciation event will be later), but it will create less new species, as there
 85 are still fewer taxa. As we have no prior expectations, we have the (null)
 86 hypothesis, \mathcal{H}_3 , that the timing of multiple-birth events has no effect on
 87 e .

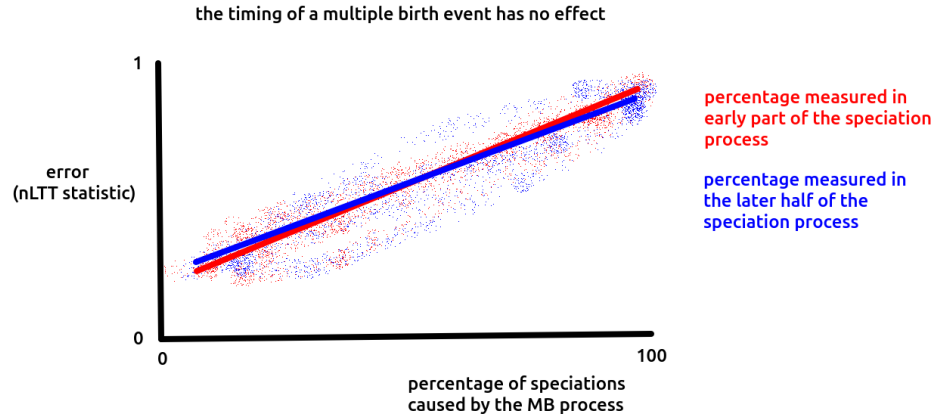


Figure 4: Hypothesis 3: the timing of a multiple birth event has no effect.

88 Another MBD component that may cause different values of e for identical
 89 values of s , is the number of taxa in a phylogeny. As there is no diversity
 90 dependency in any of the processes and we have no further prior expecta-
 91 tions, we have the (null) hypothesis \mathcal{H}_5 , that the number of taxa has no
 92 effect on e . As a higher number of taxa increases the information content
 93 in a phylogeny, we have hypothesis \mathcal{H}_6 that the variance in e decreases.

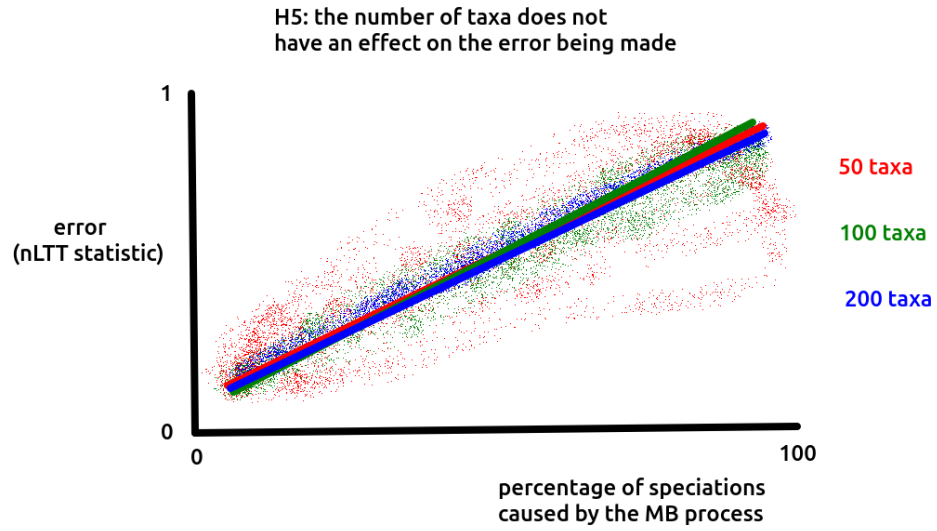


Figure 5: Hypothesis 5: the number of taxa does not have an effect on the error being made

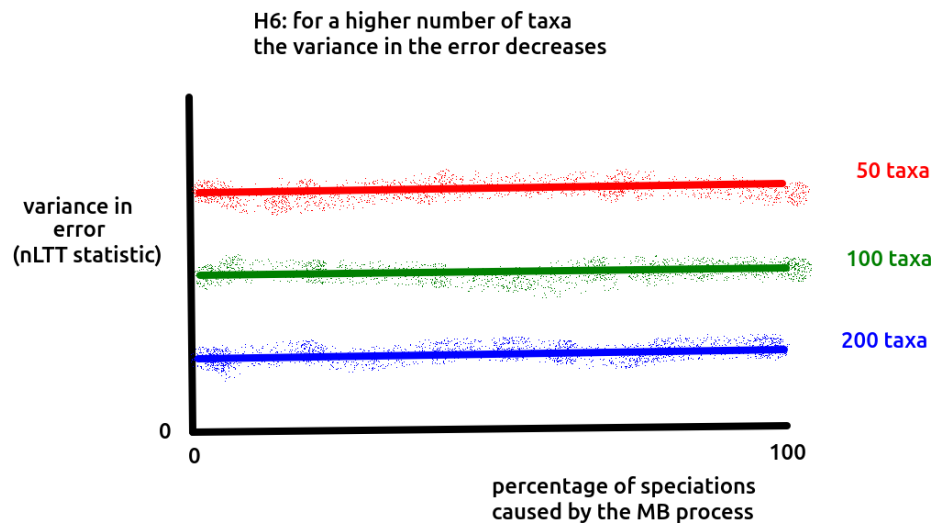


Figure 6: Hypothesis 6: for a higher number of taxa the variance in the error decreases

94 2 Methods

95 2.1 Model

96 • Current phylogenetic tools assume that only a single speciation event can
97 occur at any given time. While this assumption is useful to construct
98 a wide variety of successful models (e.g Maddison *et al.* 2007, Valente
99 *et al.* 2015, Etienne *et al.* 2012, Etienne *et al.* 2014), they disallow for
100 environmental changes that trigger speciations in multiple clades at a same
101 point in time.

102 [RJCB: duplicate paragraph!]

103 • The (constant-rate) birth-death (BD) model embodies the common as-
104 sumption that only a single speciation event can occur at any given time.
105 The multiple-birth-death (MBD) model relaxes this assumption, allowing
106 events in which large-scale environmental changes lead to a great num-
107 ber of species in relatively short time intervals. Such hypothesis can be
108 useful to describe, for example, systems like cichlid fish diversification in
109 the African Great Lakes: Malawi, Tanganyika and Victoria (Janzen *et al.*
110 2016, Janzen *et al.* 2017).

111 • In the MBD model, parameters λ and μ correspond, respectively, to the
112 common per-species speciation and extinction rates present also in the
113 standard BD model. Additionally, MBD relies on two additional param-
114 eters. Parameter ν is the rate at which an environmental change is trig-
115 gered. When such event is triggered, all species present in the phylogeny
116 at that moment have a probability q to speciate at that time, which is
117 independent on λ . Polytomies are not allowed in such process as each
118 species can speciate only once at the time.

- It is also possible to write down a likelihood function for such processes as in Laudanno 2018.

2.2 Simulations

- To prove our hypothesis we simulate two twin datasets. All the simulations are produced in continuous time, using the Doob-Gillespie algorithm.
- We start simulating $N_S = 1000$ MBD trees, with either 50, 100 and 200 taxa.
- From each MBD tree, a DNA sequence alignment is simulated. For each sequence alignment we then perform a Bayesian analysis to recover a posterior distribution of trees, each composed of N_P phylogenies. Such analysis is performed using the 'pirouette' package (Bilderbeek 2018) to call the BEAST2 tool suite from R. We let the Bayesian analysis assume a BD prior in both cases, to investigate the extent of the error we make under this assumption.
- For each tree generated under the MBD model we aim to generate a "twin" tree under the BD model. With the word "twin" we denote a tree generated starting from the respective MBD tree, in order to perform a fair comparison with it. This operation has to be done, because we want to compare two trees that are generated by different processes. To do so we infer the parameters λ_{BD} and μ_{BD} from the MBD maximizing the likelihood under a BD model. To perform this operation we use the function "bd_ML" from the package "DDD" (Etienne *et al.* 2012).
- We then exploit such parameters to generate a BD tree using the function "tess.sim.taxa.age" from the package "TESS" (Hhna 2013). We simulate the tree in such a way the new tree has the same number of tips

144 and the same crown age as the MBD tree. We furthermore require that
 145 the BD tree conserve the topology of the MBD tree. We have hypothesis
 146 H4 that, compared to the MBD trees, the error will be less in the BD
 147 twin tree. The difference between the errors made in MBD and twin BD
 148 trees indicates the impact the MBD process has on the error we make in
 149 inference using a contemporary BD prior.

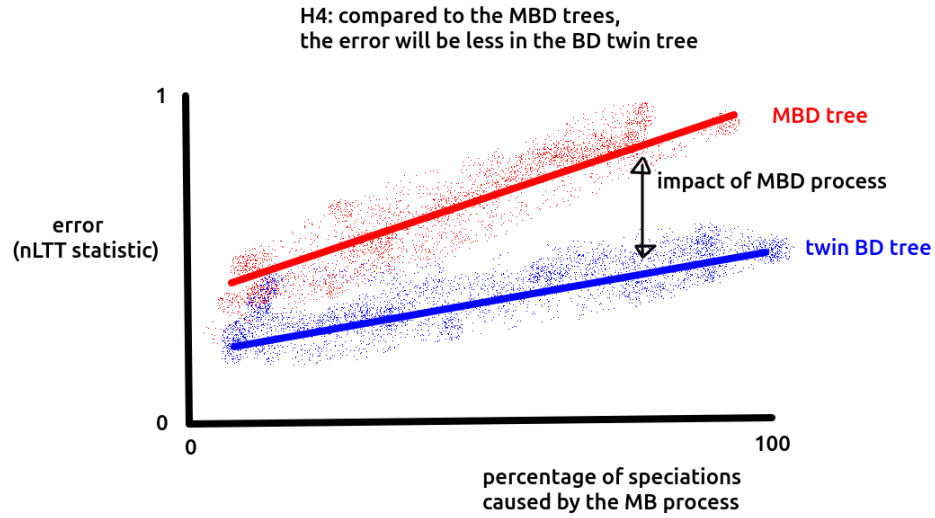


Figure 7: Hypothesis 4: compared to the MBD trees, the error will be less in the BD twin tree

150 We want the MBD and twin BD trees to contain the same amount of in-
 151 formation, i.e. the same number of DNA mutations and the same number
 152 of taxa at the present:

$$m_{MBD} = m_{BD} \quad (3)$$

153 The expected number of mutations m of a phylogeny with crown age $-T$
 154 (with $T > 0$) in fact is given by [RJC: So one of use likes '-T', the
 155 other likes 'T'. How to resolve this?]

$$m = L \cdot \rho \cdot \int_0^T n(t) dt \quad (4)$$

156 where L is the number of DNA nucleotides, ρ is the per-site per-species
157 mutation rate and $n(t)$ the number of species at each time.

158 The parameter we'll tune is ρ ... **[RJCB: elaborate here :-)]**

159 Since we cannot know $n_{BD}(t)$ before running simulations we need to re-
160 place it with a proxy. For this reason we will use the average number of
161 species in time according to the BD model. It's well known that this is
162 equal to **[GL: insert proper citation]**

$$< n_{BD} > (t) = n_0 \cdot e^{(\mu_{BD} - \lambda_{BD})t} \quad (5)$$

163 where $n_0 = n_{BD}(-T) = n_{MBD}(-T)$ is the initial number of species at
164 the crown age. From 3, 4 and 5 follows:

$$m_{MBD} = L \cdot \rho \cdot \int_0^T < n_{BD} > (t) dt = L \cdot \rho \cdot n_0 \cdot \left[\frac{e^{(\mu_{BD} - \lambda_{BD})T} - 1}{\mu_{BD} - \lambda_{BD}} \right] \quad (6)$$

165 If we set $\mu_{BD} = \mu_{MBD}$ and reverse this relation we can extrapolate the
166 value of λ_{BD} to use to generate BD trees.

- 167 • We explained how we set the parameters for each twin BD tree. Using
168 this rules we generate a BD dataset. We repeat the analysis, producing
169 alignments for each tree and subsequently using BEAST to produce a
170 posterior for each of them.

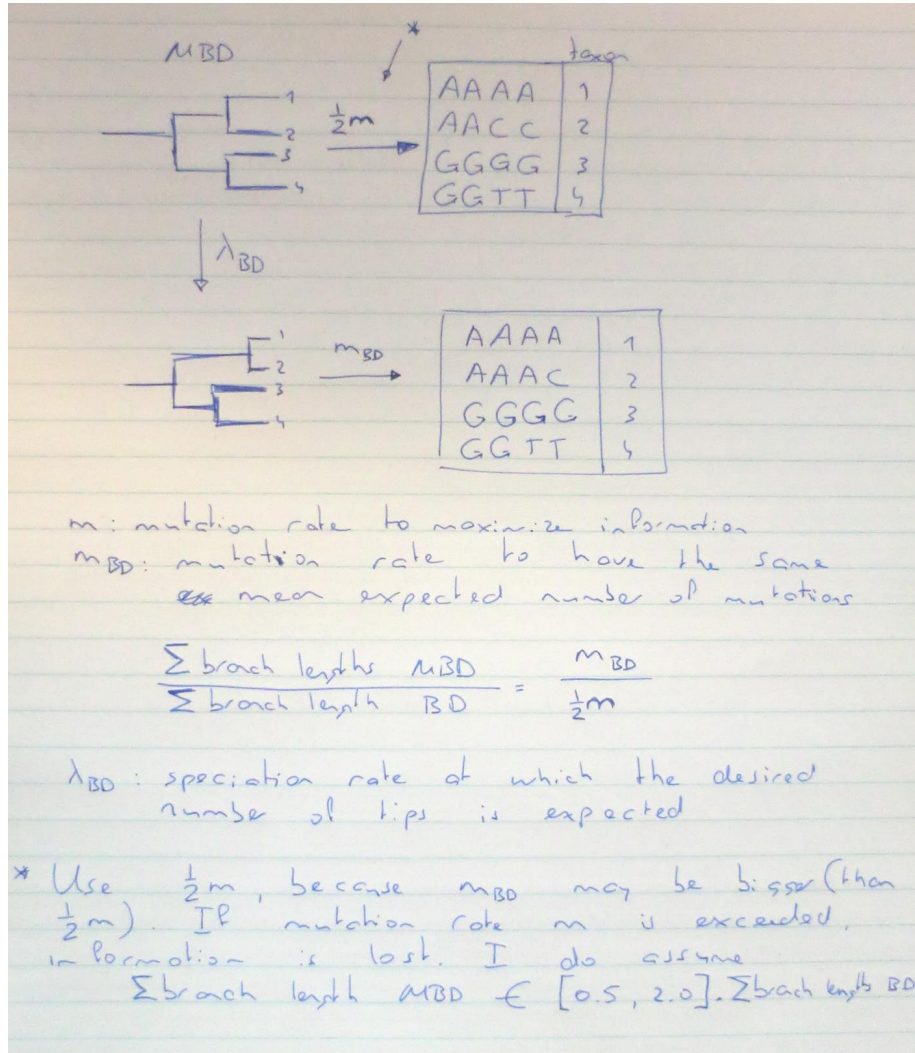


Figure 8: How to create twin trees and alignments. From a focal MBD tree, a twin tree is produced as such: (1) estimate the λ_{BD} to get the same expected number of tips, (2) simulate a BD tree with that amount of tips (discard trees with different number of tips), (3) estimate a mutation rate to get an alignment with the same expected number of mutations, (4) simulate alignments with that amount of mutations (discard those that don't, the picture shows an alignment that should be discarded)

2.3 Measuring the inference error

- So far we have simulated two datasets of trees under the two models: $\{T_i^{BD}\}_{i=1}^{N_S}$ and $\{T_i^{MBD}\}_{i=1}^{N_S}$. We used them to generate a dataset of alignments for each model: $\{X_i^{BD}\}_{i=1}^{N_S}$ and $\{X_i^{MBD}\}_{i=1}^{N_S}$. From each dataset we produced a posterior distribution from a BD prior: $P_i(\theta|X_i^{BD}, BD)$ and $P_i(\theta|X_i^{MBD}, BD)$. [GL: 1) We might want to rename the models, e.g. BD = (0) and MBD = (1). These names with capital letters are too big and ugly;] [RJCB: I would strongly prefer MBD and BD, as I feel replacing the big ugly capital letters by short pretty numbers hurts readability even more]
- To compare the results for the two models we measure the inference error using the nLTT statistic between known/true tree and posterior/inferred trees (Janzen 2015). To obtain such statistics the procedure is the following:
 - From each tree $T_{i,j}^M$ (with $j = 1, \dots, N_S$) belonging to the posterior $P_i(\theta|X_i^M, BD)$ and relative to the model M , we extrapolate the lineage-through-time (LTT), in other words we measure the number of species as a function of time $n_{i,j}(t)$. To allow a comparison we normalize dividing by the maximum number of species of each tree, i.e. the number of tips at the present $N_{i,j}(t) = \frac{n_{i,j}(t)}{n_{i,j}^{max}}$. We then define the nLTT measure as
$$nLTT_{i,j} = \int_0^T |N_{i,j}(t) - N_{T_i}| dt$$

[GL: I am running out of letters :(] [RJCB: Haha! I suggest to use the same equation and symbols as equation 1 in the nLTT article of Janzen, Hoehna and Etienne, 2015:]

$$\Delta nLTT = \int_0^1 |nLTT_1(t) - nLTT_2(t)| dt$$

2.4 Model selection

We simulate alignments using the simplest nucleotide substitution model (JC69), the simplest clock model (strict). It is thus imminent to assume these models in our Bayesian inference. Nevertheless, the phylogeny the alignment was based on, could have followed either an MBD or BD tree model, where we in both cases assume a BD tree model. This will have an unknown effect on our inference: it may theoretically be that an MBD model generates (a tree that generates) an alignment in which a different site and/or clock model is favored.

We investigate this by measuring if the generative model (with the simplest nucleotide substitution and simplest clock model) is indeed selected to be the best fitting model. To be precise, we look at the model with the highest marginal likelihood (also called evidence MacKay & Mac Kay 2003), $f(D|M)$, which is the probability of the data D given model M. In the context of this research, D consists of the DNA alignment, and M is the combination of site, clock and tree models.

To estimate the marginal likelihood, we use an algorithm named nested sampling Skilling *et al.* 2006. Nested sampling is attractive to use in a phylogenetic context, as it gives a good estimation, requires little tuning Russel *et al.* 2018. Nested sampling is available as a BEAST2 package and can be used by babette Bilderbeek & Etienne 2018.

The nested sampling algorithm stops its run when the marginal likelihood estimation error reaches below a certain tolerance. Similar to Russel *et al.* 2018, we use a (relative) error tolerance ϵ of 10^{-13} , 1 particle to explore the parameter space and 100 active points. To achieve the latter, we use the MCMC chain length L_c of 1M (as also used in the parameter estimates), and a sub-chain length L_{sc} of 10K.

222 The models we use in our model comparison are the four combinations
 223 of two site models and two clock models. We use the JC69 site model,
 224 which is the (generative and) simplest model and GTR, the site model
 225 with most degrees of freedom. For the clock models, we use the strict
 226 clock model, which is the (generative and) simplest clock model, and the
 227 RLN clock model. [RJC: Could also just be all site models and
 228 clock models = 8 models]

229 From these four marginal likelihood estimates, we calculate the weight of
 230 the generative model and plot this in figure 2. We do this for both the
 231 alignments derived from the MBD tree and the BD twin tree. We expect
 232 that the generative model has the heighest weight in both the MBD and
 233 BD alignments. We expect this weight to be higher in the BD alignments.

234 3 Results

- 235 •
- 236 •

237 References

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	Description
e	Inference error
$n_{\mathbb{M}}$	Number of extinct and extant taxa created by a multiple-birth event
$n_{\mathbb{B}}$	Number of extinct and extant taxa created by a single-birth event
s	Extent/strength of the multiple birth process
L_c	MCMC chain length
L_{sc}	MCMC sub-chain length
ϵ	relative error tolerance in marginal likelihood estimation

Table 1: Overview of the symbols.

Symbol	Expectation	Figure
\mathcal{H}_1	For a higher s , e will increase monotonously	1
\mathcal{H}_2	Extinction rates have no effect on e	2
\mathcal{H}_3	The timing of multiple-birth events has no effect on e	3
\mathcal{H}_4	An MBD tree will have a higher e than its twin BD counterpart	4
\mathcal{H}_5	The number of taxa has no effect on e	5
\mathcal{H}_6	A higher number of taxa decreases the variance in e	6
\mathcal{H}_7	The MBD regime has no effect on e	7

Table 2: Overview of the symbols.

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	Value(s)
L_c	10^6
L_{sc}	10^4
ϵ	10^{-13}

Table 3: Overview of the simulation parameters.

idx	n_{taxa}	f_{taxa}^{MB}	μ	MB regime	n_ν evts	q	λ
1	50	0	0	many modest	8	1 / 8	derive
2	50	0	0	intermediate	4	1 / 4	derive
3	50	0	0	few intense	2	1 / 2	derive
4	50	0	0.1	many modest	8	1 / 8	derive
5	50	0	0.1	intermediate	4	1 / 4	derive
6	50	0	0.1	few intense	2	1 / 2	derive
7	50	0	0.2	many modest	8	1 / 8	derive
8	50	0	0.2	intermediate	4	1 / 4	derive
9	50	0	0.2	few intense	2	1 / 2	derive
10	50	0	0.2	many modest	8	1 / 8	derive
11	50	0.25	0	intermediate	4	1 / 4	derive
12	50	0.25	0	few intense	2	1 / 2	derive
13	50	0.25	0	many modest	8	1 / 8	derive
14	50	0.25	0.1	intermediate	4	1 / 4	derive
15	50	0.25	0.1	few intense	2	1 / 2	derive
16	50	0.25	0.1	many modest	8	1 / 8	derive
17	50	0.25	0.2	intermediate	4	1 / 4	derive
18	50	0.25	0.2	few intense	2	1 / 2	derive
19	50	0.25	0.2	many modest	8	1 / 8	derive
20	50	0.25	0.2	intermediate	4	1 / 4	derive
21	50	0.5	0	few intense	2	1 / 2	derive
22	50	0.5	0	many modest	8	1 / 8	derive
23	50	0.5	0	intermediate	4	1 / 4	derive
24	50	0.5	0.1	few intense	2	1 / 2	derive
25	50	0.5	0.1	many modest	8	1 / 8	derive
26	50	0.5	0.1	intermediate	4	1 / 4	derive
27	50	0.5	0.2	few intense	2	1 / 2	derive
28	50	0.5	0.2	many modest	8	1 / 8	derive
29	50	0.5	0.2	intermediate	4	1 / 4	derive
30	50	0.5	0.2	few intense	2	1 / 2	derive
31	50	0.75	0	many modest	8	1 / 8	derive
32	50	0.75	0	intermediate	4	1 / 4	derive
33	50	0.75	0	few intense	2	1 / 2	derive
34	50	0.75	0.1	many modest	8	1 / 8	derive
35	50	0.75	0.1	intermediate	4	1 / 4	derive
36	50	0.75	0.1	few intense	2	1 / 2	derive
37	50	0.75	0.2	many modest	8	1 / 8	derive
38	50	0.75	0.2	intermediate	4	1 / 4	derive
39	50	0.75	0.2	few intense	2	1 / 2	derive
40	50	0.75	0.2	many modest	8	1 / 8	derive
41	50	1	0	intermediate	4	1 / 4	0
42	50	1	0	few intense	2	1 / 2	0
43	50	1	0	many modest	8	1 / 8	0
44	50	1	0.1	intermediate	4	1 / 4	0
45	50	1	0.1	few intense	2	1 / 2	0
46	50	1	0.1	many modest	8	1 / 8	0
47	50	1	0.2	intermediate	4	1 / 4	0
48	50	1	0.2	few intense	2	1 / 2	0
49	50	1	0.2	many modest	8	1 / 8	0
50	50	1	0.2	intermediate	4	1 / 4	0

Table 4: Overview of the MBD parameters 1/3.

idx	n_{taxa}	f_{taxa}^{MB}	μ	MB regime	n_ν evts	q	λ
51	100	0	0	few intense	2	1 / 2	derive
52	100	0	0	many modest	8	1 / 8	derive
53	100	0	0	intermediate	4	1 / 4	derive
54	100	0	0.1	few intense	2	1 / 2	derive
55	100	0	0.1	many modest	8	1 / 8	derive
56	100	0	0.1	intermediate	4	1 / 4	derive
57	100	0	0.2	few intense	2	1 / 2	derive
58	100	0	0.2	many modest	8	1 / 8	derive
59	100	0	0.2	intermediate	4	1 / 4	derive
60	100	0	0.2	few intense	2	1 / 2	derive
61	100	0.25	0	many modest	8	1 / 8	derive
62	100	0.25	0	intermediate	4	1 / 4	derive
63	100	0.25	0	few intense	2	1 / 2	derive
64	100	0.25	0.1	many modest	8	1 / 8	derive
65	100	0.25	0.1	intermediate	4	1 / 4	derive
66	100	0.25	0.1	few intense	2	1 / 2	derive
67	100	0.25	0.2	many modest	8	1 / 8	derive
68	100	0.25	0.2	intermediate	4	1 / 4	derive
69	100	0.25	0.2	few intense	2	1 / 2	derive
70	100	0.25	0.2	many modest	8	1 / 8	derive
71	100	0.5	0	intermediate	4	1 / 4	derive
72	100	0.5	0	few intense	2	1 / 2	derive
73	100	0.5	0	many modest	8	1 / 8	derive
74	100	0.5	0.1	intermediate	4	1 / 4	derive
75	100	0.5	0.1	few intense	2	1 / 2	derive
76	100	0.5	0.1	many modest	8	1 / 8	derive
77	100	0.5	0.2	intermediate	4	1 / 4	derive
78	100	0.5	0.2	few intense	2	1 / 2	derive
79	100	0.5	0.2	many modest	8	1 / 8	derive
80	100	0.5	0.2	intermediate	4	1 / 4	derive
81	100	0.75	0	few intense	2	1 / 2	derive
82	100	0.75	0	many modest	8	1 / 8	derive
83	100	0.75	0	intermediate	4	1 / 4	derive
84	100	0.75	0.1	few intense	2	1 / 2	derive
85	100	0.75	0.1	many modest	8	1 / 8	derive
86	100	0.75	0.1	intermediate	4	1 / 4	derive
87	100	0.75	0.2	few intense	2	1 / 2	derive
88	100	0.75	0.2	many modest	8	1 / 8	derive
89	100	0.75	0.2	intermediate	4	1 / 4	derive
90	100	0.75	0.2	few intense	2	1 / 2	derive
91	100	1	0	many modest	8	1 / 8	0
92	100	1	0	intermediate	4	1 / 4	0
93	100	1	0	few intense	2	1 / 2	0
94	100	1	0.1	many modest	8	1 / 8	0
95	100	1	0.1	intermediate	4	1 / 4	0
96	100	1	0.1	few intense	2	1 / 2	0
97	100	1	0.2	many modest	8	1 / 8	0
98	100	1	0.2	intermediate	4	1 / 4	0
99	100	1	0.2	few intense	2	1 / 2	0
100	200	1	0.2	many modest	8	1 / 8	0

Table 5: Overview of the MBD parameters 2/3.

idx	n_{taxa}	f_{taxa}^{MB}	μ	MB regime	n_ν evts	q	λ
101	200	0	0	intermediate	4	1 / 4	derive
102	200	0	0	few intense	2	1 / 2	derive
103	200	0	0	many modest	8	1 / 8	derive
104	200	0	0.1	intermediate	4	1 / 4	derive
105	200	0	0.1	few intense	2	1 / 2	derive
106	200	0	0.1	many modest	8	1 / 8	derive
107	200	0	0.2	intermediate	4	1 / 4	derive
108	200	0	0.2	few intense	2	1 / 2	derive
109	200	0	0.2	many modest	8	1 / 8	derive
110	200	0	0.2	intermediate	4	1 / 4	derive
111	200	0.25	0	few intense	2	1 / 2	derive
112	200	0.25	0	many modest	8	1 / 8	derive
113	200	0.25	0	intermediate	4	1 / 4	derive
114	200	0.25	0.1	few intense	2	1 / 2	derive
115	200	0.25	0.1	many modest	8	1 / 8	derive
116	200	0.25	0.1	intermediate	4	1 / 4	derive
117	200	0.25	0.2	few intense	2	1 / 2	derive
118	200	0.25	0.2	many modest	8	1 / 8	derive
119	200	0.25	0.2	intermediate	4	1 / 4	derive
120	200	0.25	0.2	few intense	2	1 / 2	derive
121	200	0.5	0	many modest	8	1 / 8	derive
122	200	0.5	0	intermediate	4	1 / 4	derive
123	200	0.5	0	few intense	2	1 / 2	derive
124	200	0.5	0.1	many modest	8	1 / 8	derive
125	200	0.5	0.1	intermediate	4	1 / 4	derive
126	200	0.5	0.1	few intense	2	1 / 2	derive
127	200	0.5	0.2	many modest	8	1 / 8	derive
128	200	0.5	0.2	intermediate	4	1 / 4	derive
129	200	0.5	0.2	few intense	2	1 / 2	derive
130	200	0.5	0.2	many modest	8	1 / 8	derive
131	200	0.75	0	intermediate	4	1 / 4	derive
132	200	0.75	0	few intense	2	1 / 2	derive
133	200	0.75	0	many modest	8	1 / 8	derive
134	200	0.75	0.1	intermediate	4	1 / 4	derive
135	200	0.75	0.1	few intense	2	1 / 2	derive
136	200	0.75	0.1	many modest	8	1 / 8	derive
137	200	0.75	0.2	intermediate	4	1 / 4	derive
138	200	0.75	0.2	few intense	2	1 / 2	derive
139	200	0.75	0.2	many modest	8	1 / 8	derive
140	200	0.75	0.2	intermediate	4	1 / 4	derive
141	200	1	0	few intense	2	1 / 2	0
142	200	1	0	many modest	8	1 / 8	0
143	200	1	0	intermediate	4	1 / 4	0
144	200	1	0.1	few intense	2	1 / 2	0
145	200	1	0.1	many modest	8	1 / 8	0
146	200	1	0.1	intermediate	4	1 / 4	0
147	200	1	0.2	few intense	2	1 / 2	0
148	200	1	0.2	many modest	8	1 / 8	0
149	200	1	0.2	intermediate	4	1 / 4	0
150	200	1	0.2	few intense	2	1 / 2	0

Table 6: Overview of the MBD parameters 3/3.