

# Phylogenetic Inference using RevBayes

## *Episodic Diversification Rate Estimation*

Sebastian Höhna

## 1 Overview: Diversification Rate Estimation

Models of speciation and extinction are fundamental to any phylogenetic analysis of macroevolutionary processes (*e.g.*, divergence time estimation, diversification rate estimation, continuous and discrete trait evolution, and historical biogeography). First, a prior model describing the distribution of speciation events over time is critical to estimating phylogenies with branch lengths proportional to time. Second, stochastic branching models allow for inference of speciation and extinction rates. These inferences allow us to investigate key questions in evolutionary biology.

Diversification-rate parameters may be included as nuisance parameters of other phylogenetic models—*i.e.*, where these diversification-rate parameters are not of direct interest. For example, many methods for estimating species divergence times—such as BEAST (Drummond et al. 2012), MrBayes (Ronquist et al. 2012), and RevBayes (Höhna et al. 2016)—implement ‘relaxed-clock models’ that include a constant-rate birth-death branching process as a prior model on the distribution of tree topologies and node ages. Although the parameters of these ‘tree priors’ are not typically of direct interest, they are nevertheless estimated as part of the joint posterior probability distribution of the relaxed-clock model, and so can be estimated simply by querying the corresponding marginal posterior probability densities. In fact, this may provide more robust estimates of the diversification-rate parameters, as they accommodate uncertainty in the other phylogenetic-model parameters (including the tree topology, divergence-time estimates, and the other relaxed-clock model parameters). More recent work, *e.g.*, Heath et al. (2014), uses macroevolutionary models (the fossilized birth-death process) to calibrate phylogenies and thus to infer dated trees.

In these tutorials we focus on the different types of macroevolutionary models to study diversification processes and thus the diversification-rate parameters themselves. Nevertheless, these macroevolutionary models should be used for other evolutionary questions, when an appropriate prior distribution on the tree and divergence times is needed.

### 1.1 Types of Hypotheses for Estimating Diversification Rates

Many evolutionary phenomena entail differential rates of diversification (speciation – extinction); *e.g.*, adaptive radiation, diversity-dependent diversification, key innovations, and mass extinction. The specific study questions regarding lineage diversification may be classified within three fundamental categories of inference problems. Admittedly, this classification scheme is somewhat arbitrary, but it is nevertheless useful, as it allows users to navigate the ever-increasing number of available phylogenetic methods. Below, we describe each of the fundamental questions regarding diversification rates.

**(1) Diversification-rate through time estimation** *What is the (constant) rate of diversification in my study group?* The most basic models estimate parameters of the stochastic-branching process (*i.e.*, rates of speciation and extinction, or composite parameters such as net-diversification and relative-extinction

rates) under the assumption that rates have remained constant across lineages and through time; *i.e.*, under a constant-rate birth-death stochastic-branching process model (Nee et al. 1994). Extensions to the (basic) constant-rate models include diversification-rate variation through time (Stadler 2011; Höhna 2015). First, we might ask whether there is evidence of an episodic, tree-wide increase in diversification rates (associated with a sudden increase in speciation rate and/or decrease in extinction rate), as might occur during an episode of adaptive radiation. A second question asks whether there is evidence of a continuous/gradual decrease in diversification rates through time (associated with decreasing speciation rates and/or increasing extinction rates), as might occur because of diversity-dependent diversification (*i.e.*, where competitive ecological interactions among the species of a growing tree decrease the opportunities for speciation and/or increase the probability of extinction, *e.g.*, Höhna (2014)). Third, we can ask whether changes in diversification rates are correlated with environmental factors, such as environmental CO<sub>2</sub> or temperature (Condamine et al. 2013). A final question in this category asks whether our study tree was impacted by a mass-extinction event (where a large fraction of the standing species diversity is suddenly lost, *e.g.*, May et al. (2016)). The common theme of these studies is that the diversification process is tree-wide, that is, all lineages of the study group have the exact same rates at a given time.

**(2) Diversification-rate variation across branches estimation** *Is there evidence that diversification rates have varied significantly across the branches of my study group?* Models have been developed to detect departures from rate constancy across lineages; these tests are analogous to methods that test for departures from a molecular clock—*i.e.*, to assess whether substitution rates vary significantly across lineages (Alfaro et al. 2009; Rabosky 2014). These models are important for assessing whether a given tree violates the assumptions of rate homogeneity among lineages. Furthermore, these models are important to answer questions such as: *What are the branch-specific diversification rates?*; and *Have there been significant diversification-rate shifts along branches in my study group, and if so, how many shifts, what magnitude of rate-shifts and along which branches?*

**(3) Character-dependent diversification-rate estimation** *Are diversification rates correlated with some variable in my study group?* Character-dependent diversification-rate models aim to identify overall correlations between diversification rates and organismal features (binary and multi-state discrete morphological traits, continuous morphological traits, geographic range, etc.). For example, one can hypothesize that a binary character, say if an organism is herbivorous/carnivorous or self-compatible/self-incompatible, impact the diversification rates. Then, if the organism is in state 0 (*e.g.*, is herbivorous) it has a lower (or higher) diversification rate than if the organism is in state 1 (*e.g.*, carnivorous) (Maddison et al. 2007).

## 2 Models

We begin this section with a general introduction to the stochastic birth-death branching process that underlies inference of diversification rates in RevBayes. This primer will provide some details on the relevant theory of stochastic-branching process models. We appreciate that some readers may want to skip this somewhat technical primer; however, we believe that a better understanding of the relevant theory provides a foundation for performing better inferences. We then discuss a variety of specific birth-death models, but emphasize that these examples represent only a tiny fraction of the possible diversification-rate models that can be specified in RevBayes.

### 2.1 The birth-death branching process

Our approach is based on the *reconstructed evolutionary process* described by Nee et al. (1994); a birth-death process in which only sampled, extant lineages are observed. Let  $N(t)$  denote the number of species at time

$t$ . Assume the process starts at time  $t_1$  (the ‘crown’ age of the most recent common ancestor of the study group,  $t_{\text{MRCA}}$ ) when there are two species. Thus, the process is initiated with two species,  $N(t_1) = 2$ . We condition the process on sampling at least one descendant from each of these initial two lineages; otherwise  $t_1$  would not correspond to the  $t_{\text{MRCA}}$  of our study group. Each lineage evolves independently of all other lineages, giving rise to exactly one new lineage with rate  $b(t)$  and losing one existing lineage with rate  $d(t)$  (Figure 1 and Figure 2). Note that although each lineage evolves independently, all lineages share both a common (tree-wide) speciation rate  $b(t)$  and a common extinction rate  $d(t)$  (Nee et al. 1994; Höhna 2015). Additionally, at certain times,  $t_{\text{M}}$ , a mass-extinction event occurs and each species existing at that time has the same probability,  $\rho$ , of survival. Finally, all extinct lineages are pruned and only the reconstructed tree remains (Figure 1).

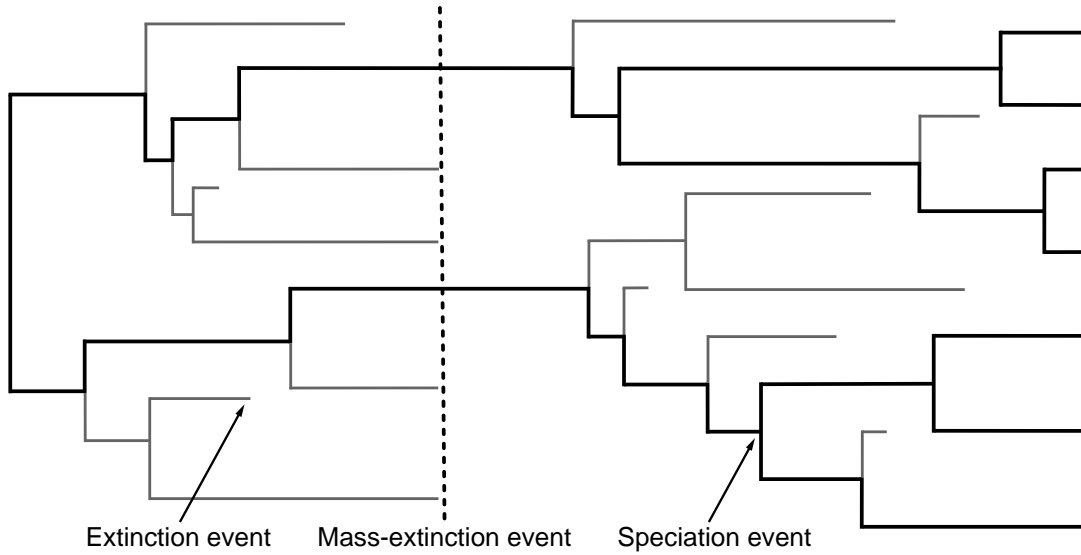


Figure 1: A realization of the birth-death process with mass extinction. Lineages that have no extant or sampled descendant are shown in gray and surviving lineages are shown in a thicker black line.

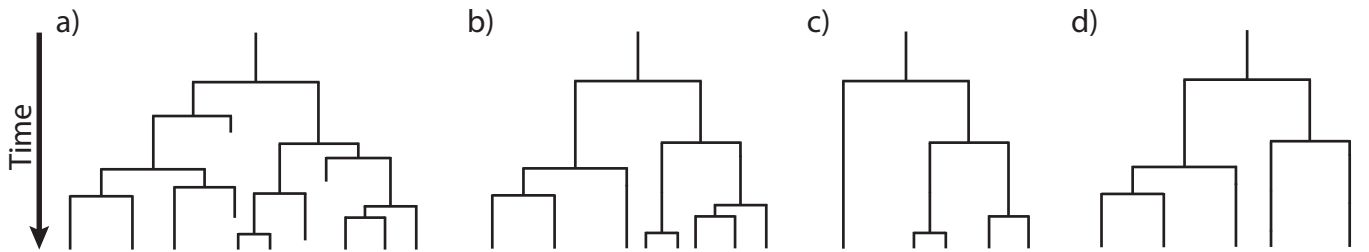


Figure 2: **Examples of trees produced under a birth-death process.** The process is initiated at the first speciation event (the ‘crown-age’ of the MRCA) when there are two initial lineages. At each speciation event the ancestral lineage is replaced by two descendant lineages. At an extinction event one lineage simply terminates. (A) A complete tree including extinct lineages. (B) The reconstructed tree of tree from A with extinct lineages pruned away. (C) A *uniform* subsample of the tree from B, where each species was sampled with equal probability,  $\rho$ . (D) A *diversified* subsample of the tree from B, where the species were selected so as to maximize diversity.

To condition the probability of observing the branching times on the survival of both lineages that descend from the root, we divide by  $P(N(T) > 0 | N(0) = 1)^2$ . Then, the probability density of the branching times,

$\mathbb{T}$ , becomes

$$P(\mathbb{T}) = \frac{\overbrace{P(N(T) = 1 \mid N(0) = 1)^2}^{\text{both initial lineages have one descendant}}}{\underbrace{P(N(T) > 0 \mid N(0) = 1)^2}_{\text{both initial lineages survive}}} \times \prod_{i=2}^{n-1} \overbrace{i \times b(t_i)}^{\text{speciation rate}} \times \overbrace{P(N(T) = 1 \mid N(t_i) = 1)}^{\text{lineage has one descendant}},$$

and the probability density of the reconstructed tree (topology and branching times) is then

$$P(\Psi) = \frac{2^{n-1}}{n!(n-1)!} \times \left( \frac{P(N(T) = 1 \mid N(0) = 1)}{P(N(T) > 0 \mid N(0) = 1)} \right)^2 \times \prod_{i=2}^{n-1} i \times b(t_i) \times P(N(T) = 1 \mid N(t_i) = 1) \quad (1)$$

We can expand Equation (1) by substituting  $P(N(T) > 0 \mid N(t) = 1)^2 \exp(r(t, T))$  for  $P(N(T) = 1 \mid N(t) = 1)$ , where  $r(u, v) = \int_u^v d(t) - b(t)dt$ ; the above equation becomes

$$\begin{aligned} P(\Psi) &= \frac{2^{n-1}}{n!(n-1)!} \times \left( \frac{P(N(T) > 0 \mid N(0) = 1)^2 \exp(r(0, T))}{P(N(T) > 0 \mid N(0) = 1)} \right)^2 \\ &\quad \times \prod_{i=2}^{n-1} i \times b(t_i) \times P(N(T) > 0 \mid N(t_i) = 1)^2 \exp(r(t_i, T)) \\ &= \frac{2^{n-1}}{n!} \times \left( P(N(T) > 0 \mid N(0) = 1) \exp(r(0, T)) \right)^2 \\ &\quad \times \prod_{i=2}^{n-1} b(t_i) \times P(N(T) > 0 \mid N(t_i) = 1)^2 \exp(r(t_i, T)). \end{aligned} \quad (2)$$

For a detailed description of this substitution, see [Höhna \(2015\)](#). Additional information regarding the underlying birth-death process can be found in ([Thompson 1975](#); Equation 3.4.6) and [Nee et al. \(1994\)](#) for constant rates and [Höhna \(2013; 2014; 2015\)](#) for arbitrary rate functions.

To compute the equation above we need to know the rate function,  $r(t, s) = \int_t^s d(x) - b(x)dx$ , and the probability of survival,  $P(N(T) > 0 \mid N(t) = 1)$ . [Yule \(1925\)](#) and later [Kendall \(1948\)](#) derived the probability that a process survives ( $N(T) > 0$ ) and the probability of obtaining exactly  $n$  species at time  $T$  ( $N(T) = n$ ) when the process started at time  $t$  with one species. Kendall's results were summarized in Equation (3) and Equation (24) in [Nee et al. \(1994\)](#)

$$P(N(T) > 0 \mid N(t) = 1) = \left( 1 + \int_t^T \left( \mu(s) \exp(r(t, s)) \right) ds \right)^{-1} \quad (3)$$

$$\begin{aligned} P(N(T) = n \mid N(t) = 1) &= (1 - P(N(T) > 0 \mid N(t) = 1) \exp(r(t, T)))^{n-1} \\ &\quad \times P(N(T) > 0 \mid N(t) = 1)^2 \exp(r(t, T)) \end{aligned} \quad (4)$$

An overview for different diversification models is given in [Höhna \(2015\)](#).

*Sidebar: Phylogenetic trees as observations*

The branching processes used here describe probability distributions on phylogenetic trees. This probability distribution can be used to infer diversification rates given an “observed” phylogenetic tree. In reality we never observe a phylogenetic tree itself. Instead, phylogenetic trees themselves are estimated from actual observations, such as DNA sequences. These phylogenetic tree estimates, especially the divergence times, can have considerable uncertainty associated with them. Thus, the correct approach for estimating diversification rates is to include the uncertainty in the phylogeny by, for example, jointly estimating the phylogeny and diversification rates. For the simplicity of the following tutorials, we take a shortcut and assume that we know the phylogeny without error. For publication quality analysis you should always estimate the diversification rates jointly with the phylogeny and divergence times.

### 3 Estimating Speciation & Extinction Rates Through Time

#### 3.1 Outline

This tutorial describes how to specify an episodic branching-process models in `RevBayes`; a birth-death process where diversification rates vary episodically through time model by piecewise constant rates ([Stadler 2011](#); [Höhna 2015](#)). The probabilistic graphical model is given once at the beginning of this tutorial. Your goal is to estimate speciation and extinction rates through-time using Markov chain Monte Carlo (MCMC).

#### 3.2 Requirements

We assume that you have read and hopefully completed the following tutorials:

- [Getting started](#)
- [Rev basics](#)
- [Basic Diversification Rate Estimation](#)

Note that the [Rev basics tutorial](#) introduces the basic syntax of `Rev` but does not cover any phylogenetic models. You may skip the [Rev basics tutorial](#) if you have some familiarity with `R`. We tried to keep this tutorial very basic and introduce all the language concepts and theory on the way. You may only need the [Rev basics tutorial](#) for a more in-depth discussion of concepts in `Rev`.

### 4 Data and files

We provide the data file(s) which we will use in this tutorial. You may want to use your own data instead. In the `data` folder, you will find the following files

- `primates_tree.nex`: Dated primates phylogeny including 233 out of 367 species from [Magnuson-Ford and Otto \(2012\)](#).

→ Open the tree `data/primates_tree.nex` in FigTree.

## 5 Episodic Birth-Death Model

The basic idea behind the model is that speciation and extinction rates are piecewise constant but can be different for different time intervals. Thus, we will divide time into equal time interval with the only exception that the first 20% of the time do not have any rate changes. Our only reason to do so is because there are too few lineages in the reconstructed tree at that time to obtain reliable parameter estimates. An overview of the underlying theory of the specific model and implementation is given in [Höhna \(2015\)](#). Figure 3 shows an example of a constant rate birth-death process and an episodic birth-death process.

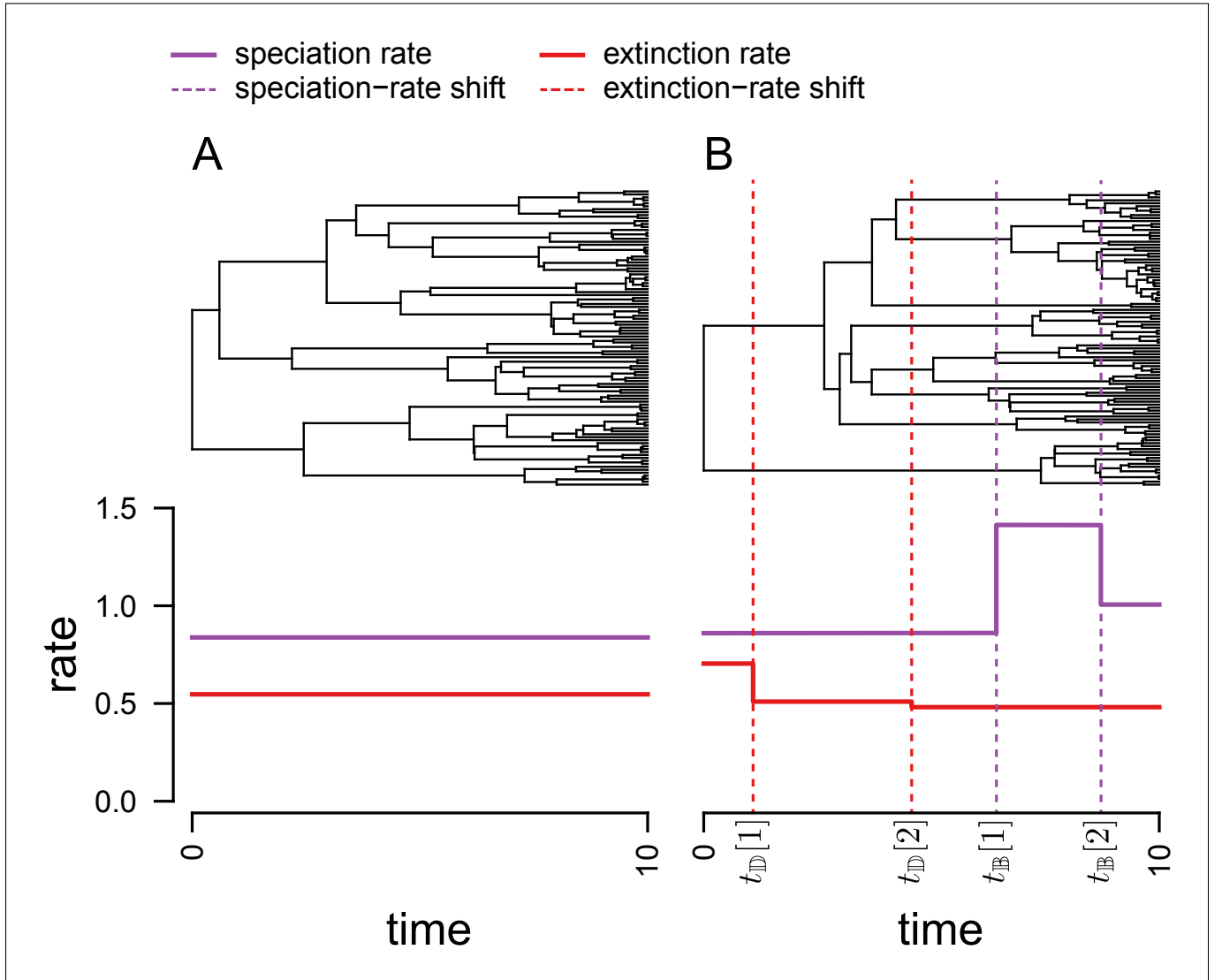


Figure 3: Two scenarios of birth-death models. On the left we show constant diversification. On the right we show an example of an episodic birth-death process where rates are constant in each time interval (epoch). The top panel of this figure shows example realization under the given rates.

We assume that the log-transformed rates are drawn from a normal distribution. Furthermore, we will assume that rates are autocorrelated, that is, rates in the next time interval will be centered around the rates in the current time interval. Thus, we model (log-transformed) diversification rates by a Brownian

motion. The assumption of autocorrelated rates does not only makes sense biologically but also improves our ability to estimate parameters. We show a graphical model of the episodic birth-death process with

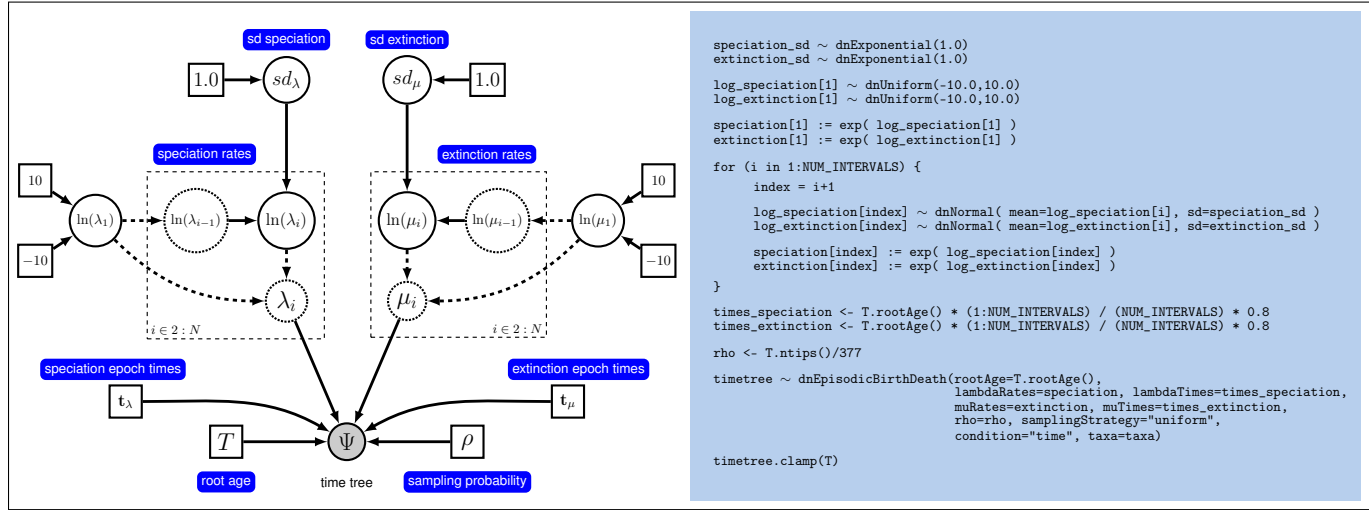


Figure 4: A graphical model with the outline of the Rev code. On the left we see the graphical model describing the correlated (Brownian motion) model for rate-variation through time. On the right we show the correspond Rev commands to instantiate this model in computer memory. This figure gives a complete overview of the model that we use here in this analysis.

autocorrelated rates in Figure 4. This graphical model shows you which variables are included in the model, and the dependency between the variables. Thus, it makes the structure and assumption of the model clear and visible instead of a black-box (Höhna et al. 2014). For example, you see how the speciation and extinction rates in each time interval depend on the rates of the previous rates, and that we use a hyperprior for the standard deviation of rates between time intervals.

## 5.1 Read the tree

Begin by reading in the “observed” tree.

```
T <- readTrees("data/primates_tree.nex")[1]
```

From this tree, we get some helpful variables, such as the taxon information which we need to instantiate the birth-death process.

```
taxa <- T.taxa()
```

Additionally, we initialize an iterator variable for our vector of moves and monitors.

```
mvi = 0
mni = 0
```

Finally, we create a helper variable that specifies the number of intervals.

```
NUM_INTERVALS = 10
```

Using this variable we can easily change our script to break-up time into many (*e.g.*, `NUM_INTERVALS = 100`) or few (*e.g.*, `NUM_INTERVALS = 4`) intervals.

## 5.2 Specifying the model

### 5.2.1 Priors on amount of rate variation

We start by specifying prior distributions on the rates. Each interval-specific speciation and extinction rate will be drawn from a normal distribution. Thus, we need a parameter for the standard deviation of those normal distributions. We use an exponential hyperprior with rate 1.0 to estimate the standard deviation, but assume that all speciation rates and all extinction rates share the same standard deviation. The motivation for an exponential hyperprior is that it has the highest probability density at 0 which would make the variance of rates between consecutive time intervals 0 and thus represent a constant rate process. The data will tell us if there should be much variation in rates through time. (You may want to experiment with this hyperprior if you are interested.)

```
speciation_sd ~ dnExponential(1.0)
extinction_sd ~ dnExponential(1.0)
```

We apply a simple scaling move on each prior parameter.

```
moves[++mvi] = mvScale(speciation_sd,weight=5.0)
moves[++mvi] = mvScale(extinction_sd,weight=5.0)
```

### 5.2.2 Specifying episodic rates

As we mentioned before, we will apply normal distributions as priors for each log-transformed rate. We begin with the rate at the present which is our initial rate parameter. The rates at the present will be specified slightly differently because they are not correlated to any previous rates. This is because we are actually modeling rate-changes backwards in time and there is no previous rate for the rate at the present. Modeling rates backwards in time makes it easier for us if we had some prior information about some event affected diversification sometime before the present, *e.g.*, 25 million years ago.

We use a uniform distribution between -10 and 10 because of our lack of prior knowledge on the diversification rate. This actually means that we allow speciation and extinction rates between  $e^{-10}$  and  $e^{10}$  we should clearly cover the true values. (Note that for diversification rate estimates  $e^{-10}$  is virtually 0 since the rate is so slow).



```
log_speciation[1] ~ dnUniform(-10.0,10.0)
log_extinction[1] ~ dnUniform(-10.0,10.0)
```

Notice that we store the diversification rate variables in vectors. Storing the rate parameters in vectors will be useful and important later when we pass the rates into the birth-death process.

We apply simple sliding window moves for the rates. Normally we would use scaling moves but in this case we work on the log-transformed parameters and thus sliding moves perform better. (If you are keen you can test the differences.)

```
moves[++mvi] = mvSlide(log_speciation[1], weight=2)
moves[++mvi] = mvSlide(log_extinction[1], weight=2)
```

Now we transform the diversification rate parameters into actual rates using an exponential parameter transformation.

```
speciation[1] := exp( log_speciation[1] )
extinction[1] := exp( log_extinction[1] )
```

Next, we specify the speciation and extinction rates for each time interval (*i.e.*, epoch). This can be done efficiently using a **for**-loop. We will use a specific index variable so that we can easier refer to the rate at the previous interval. Remember that we want to model the rates as a Brownian motion, which we achieve by specify a normal distribution as the prior distribution on the rates centered around the previous rate (*i.e.*, the mean is equal to the previous rate).

```
for (i in 1:NUM_INTERVALS) {
  index = i+1

  log_speciation[index] ~ dnNormal( mean=log_speciation[i], sd=speciation_sd )
  log_extinction[index] ~ dnNormal( mean=log_extinction[i], sd=extinction_sd )

  moves[++mvi] = mvSlide(log_speciation[index], weight=2)
  moves[++mvi] = mvSlide(log_extinction[index], weight=2)

  speciation[index] := exp( log_speciation[index] )
  extinction[index] := exp( log_extinction[index] )
}
```

Finally, we apply moves that slide all values in the rate vectors, *i.e.*, all speciation or extinction rates. We will use an **mvVectorSlide** move.

```
moves[++mvi] = mvVectorSlide(log_speciation, weight=10)
moves[++mvi] = mvVectorSlide(log_extinction, weight=10)
```

Additionally, we apply a **mvShrinkExpand** move which changes the spread of several variables around their mean.

```
moves[++mvi] = mvShrinkExpand( log_speciation, sd=speciation_sd, weight=10 )
moves[++mvi] = mvShrinkExpand( log_extinction, sd=extinction_sd, weight=10 )
```

Both moves considerably improve the efficiency of our MCMC analysis.

### 5.2.3 Setting up the time intervals

In **RevBayes** you actually have the possibility to specify unequal time intervals or even different intervals for the speciation and extinction rate. This is achieved by providing a vector of times when each interval ends. Here we simply break-up the most recent 80% of time since the root in equal-length intervals.

```
interval_times <- T.rootAge() * (1:NUM_INTERVALS) / (NUM_INTERVALS) * 0.8
```

This vector of times will be used for both the speciation and extinction rates. Also, remember that the times of the intervals represent ages going backwards in time.

### 5.2.4 Incomplete Taxon Sampling

We know that we have sampled 233 out of 367 living primate species. To account for this we can set the sampling parameter as a constant node with a value of 233/367. For simplicity, and since almost all species have been sampled, we assume *uniform* taxon sampling ([Höhna et al. 2011](#); [Höhna 2014](#)),

```
rho <- T.ntips()/377
```

### 5.2.5 Root age

The birth-death process requires a parameter for the root age. In this exercise we use a fix tree and thus we know the age of the tree. Hence, we can get the value for the root from the [Magnuson-Ford and Otto \(2012\)](#) tree.

```
root_time <- T.rootAge()
```

### 5.2.6 The time tree

Now we have all of the parameters we need to specify the full episodic birth-death model. We initialize the stochastic node representing the time tree.

```
timetree ~ dnEpisodicBirthDeath(rootAge=T.rootAge(), lambdaRates=speciation,  
    lambdaTimes=interval_times, muRates=extinction, muTimes=interval_times, rho=rho,  
    samplingStrategy="uniform", condition="survival", taxa=taxa)
```

You may notice that we explicitly specify that we want to condition on survival. It is possible to change this condition to the *time of the process* or the *number of sampled taxa* too.

Then we attach data to the **timetree** variable.

```
timetree.clamp(T)
```

Finally, we create a workspace object of our whole model using the **model()** function.

```
mymodel = model(speciation)
```

The **model()** function traversed all of the connections and found all of the nodes we specified.

## 5.3 Running an MCMC analysis

### 5.3.1 Specifying Monitors

For our MCMC analysis, we need to set up a vector of *monitors* to record the states of our Markov chain. First, we will initialize the model monitor using the **mnModel** function. This creates a new monitor variable that will output the states for all model parameters when passed into a MCMC function.

```
monitors[++mni] = mnModel(filename="output/primates_EBD.log", printgen=10, separator =  
    TAB)
```

Additionally, we create four separate file monitors, one for each vector of speciation and extinction rates and for each speciation and extinction rate epoch (*i.e.*, the times when the interval ends). We want to have the speciation and extinction rates stored separately so that we can plot them nicely afterwards.

```
monitors[++mni] = mnFile(filename="output/primates_EBD_speciation_rates.log", printgen  
    =10, separator = TAB, speciation)  
monitors[++mni] = mnFile(filename="output/primates_EBD_speciation_times.log", printgen  
    =10, separator = TAB, interval_times)
```

```
monitors[++mni] = mnFile(filename="output/primates_EBD_extinction_rates.log",printgen
  =10, separator = TAB, extinction)
monitors[++mni] = mnFile(filename="output/primates_EBD_extinction_times.log",printgen
  =10, separator = TAB, interval_times)
```

Finally, create a screen monitor that will report the states of specified variables to the screen with **mnScreen**:

```
monitors[++mni] = mnScreen(printgen=1000, extinction_sd, speciation_sd)
```

### 5.3.2 Initializing and Running the MCMC Simulation

With a fully specified model, a set of monitors, and a set of moves, we can now set up the MCMC algorithm that will sample parameter values in proportion to their posterior probability. The **mcmc()** function will create our MCMC object:

```
mymcmc = mcmc(mymodel, monitors, moves)
```

First, we will run a pre-burnin to tune the moves and to obtain starting values from the posterior distribution.

```
mymcmc.burnin(generations=10000,tuningInterval=200)
```

Now, run the MCMC:

```
mymcmc.run(generations=50000)
```

When the analysis is complete, you will have the monitored files in your output directory. You can then visualize the rates through time using R using our package **RevGadgets**. If you don't have the R-package **RevGadgets** installed, or if you have trouble with the package, then please read the separate tutorial about the package.

Just start R in the main directory for this analysis and then type the following commands:

```
library(RevGadgets)

tree <- read.nexus("data/primates_tree.nex")
```

```

rev_out <- rev.process.div.rates(speciation_times_file = "output/
  primates_EBD_speciation_times.log", speciation_rates_file = "output/
  primates_EBD_speciation_rates.log", extinction_times_file = "output/
  primates_EBD_extinction_times.log", extinction_rates_file = "output/
  primates_EBD_extinction_rates.log", tree, burnin=0.25,numIntervals=100)

pdf("EBD.pdf")
par(mfrow=c(2,2))
rev.plot.output(rev_out,use.geoscale=FALSE)
dev.off()

```

(Note, you may want to add a nice geological timescale to the plot by setting `use.geoscale=TRUE` but then you can only plot one figure per page.)

→ The Rev file for performing this analysis: [mcmc\\_EBD.Rev](#).

## 5.4 Exercise 1

- Run an MCMC simulation to estimate the posterior distribution of the speciation rate and extinction rate.
- Visualize the rate through time using R.
- Do you see evidence for rate decreases or increases? What is the general trend?
- Is there evidence for rate variation? Look at the estimates of `speciation_sd` and `extinction_sd`: Is there information in the data to change the estimates from the prior?
- Run the analysis using a different number of intervals, *e.g.*, 5 or 50. How do the rates change?

## 5.5 Exercise 2

- In our results we see that the extinction rate is fairly constant. Modify the model by using a constant-rate for the extinction rate parameter but still let the speciation rate vary through time.
  - Remove all previous occurrences of the extinction rates (*i.e.*, priors, parameters and moves).
  - Specify a lognormal prior distribution on the constant extinction rate (`extinction ~ dnLognormal(-5,sd=2*0.587405)`)
  - Add a move for the new extinction rate parameter `moves[++mvi] = mvScale(extinction,weight=5.0)`.
  - Remove the argument `muTimes=interval_times` from the birth-death process.
- How does this influence your estimated rates?

## References

Alfaro, M., F. Santini, C. Brock, H. Alamillo, A. Dornburg, D. Rabosky, G. Carnevale, and L. Harmon. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences* 106:13410–13414.

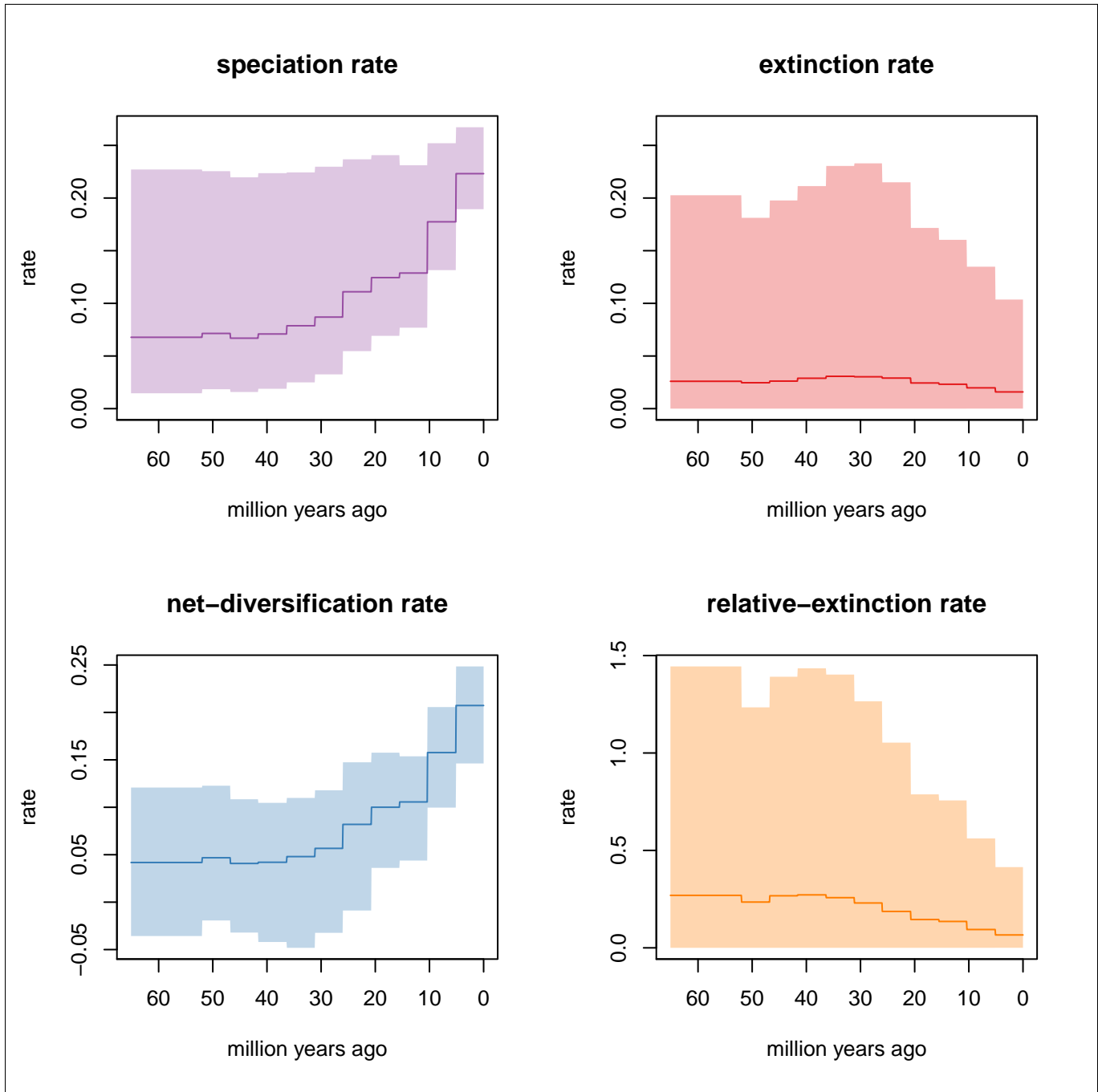


Figure 5: Resulting diversification rate estimations when using 10 intervals. You should obtain similar results when you use 10 intervals. The estimated rates might change when you use a different resolution, *i.e.*, a different number of intervals.

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