

## APPLICATION

# BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees

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## Summary

1. Understanding the dynamics of speciation, extinction and phenotypic evolution is a central challenge in evolutionary biology. Here, we present BAMMtools, an R package for the analysis and visualization of macroevolutionary dynamics on phylogenetic trees. BAMMtools is a companion package to BAMM, an open-source program for reversible-jump MCMC analyses of diversification and trait evolution.
2. Functions in BAMMtools operate directly on output from the BAMM program. The package is oriented towards reconstructing and visualizing changes in evolutionary rates through time and across clades in a Bayesian statistical framework.
3. BAMMtools enables users to extract credible sets of diversification shifts and to identify diversification histories with the maximum *a posteriori* probability. Users can compare the fit of alternative diversification models using Bayes factors and by directly comparing model posterior probabilities.
4. By providing a robust framework for quantifying uncertainty in macroevolutionary dynamics, BAMMtools will facilitate inference on the complex mixture of processes that have shaped the distribution of species and phenotypes across the tree of life.

**Key-words:** computational biology, macroevolution, Bayesian, statistics, speciation, extinction, traits

## Introduction

In recent years, a number of methods have been developed for inferring rates of speciation, extinction and phenotypic evolution using time-calibrated phylogenies of extant species. These methods have enabled researchers to address a range of questions about the causes of macroevolutionary rate variation through time and among lineages. For example, how do rates of speciation and extinction contribute to geographic variation in species richness (Rabosky & Glor 2010; Goldberg, Lancaster & Ree 2011; Rolland *et al.* 2014)? How do ecological and other traits influence rates of species diversification (Seddon, Merrill & Tobias 2008; Hardy & Cook 2012)? What is the tempo and mode of phenotypic evolution during adaptive radiation (Harmon *et al.* 2003; Burbrink *et al.* 2012)? What is the correlation between speciation and morphological evolution (Adams *et al.* 2009; Mahler *et al.* 2010; Rabosky *et al.* 2013)? These are merely some of the questions that have been asked in recent years via the application of phylogenetic comparative methods to phylogenetic trees. A number of R-based software packages are now available to facilitate the modelling of evolutionary rates on phylogenetic trees (e.g. Paradis, Claude & Strimmer 2004; Harmon *et al.* 2008; FitzJohn 2012;

Revell 2012; Thomas & Freckleton 2012; Ingram & Mahler 2013).

In this note, we describe the R package 'BAMMtools'. BAMMtools is a companion package to the BAMM program (Bayesian analysis of macroevolutionary mixtures; Rabosky *et al.* 2013; Rabosky 2014) and is oriented entirely around the analysis and visualization of complex evolutionary dynamics on phylogenetic trees. BAMM ([www.bamm-project.org](http://www.bamm-project.org)) is a program written in C++ that uses reversible-jump Markov chain Monte Carlo (rjMCMC) to quantify heterogeneous mixtures of dynamic processes on phylogenetic trees. BAMM can be used to study diversification (speciation and extinction) as well as phenotypic evolution. BAMM simulates a posterior density of diversification models on a phylogenetic tree; each sample from the posterior includes a potentially unique configuration of macroevolutionary rate regimes. A regime, in this sense, is a potentially time-varying process of speciation, extinction or phenotypic evolution. The raw output from BAMM includes, for each sample from the posterior, a mapping of one or more distinct sets of evolutionary rate parameters to specific locations in a phylogenetic tree. Because the number of rate regimes is itself a random variable, the potential number of such sets is countably infinite.

We created the BAMMtools package to facilitate the interpretation of macroevolutionary dynamics with BAMM. We

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believe that the accessibility, technical support and graphical capabilities of R make it an ideal computing environment for developing and distributing BAMMtools. BAMMtools enables the user to create a data structure that includes all information from the posterior density simulated with BAMM; once this data structure is created, the user does not need to interact directly with raw BAMM output. This data structure, referred to as a ‘bammdata’ object, can be used and recycled for a number of subsequent analyses. In addition, functions are provided to perform a number of specific analyses and visualizations.

## Conceptual background

Describing results and analyses in the BAMM framework requires a number of new terms (Table 1). To facilitate understanding of these concepts, we have provided extensive documentation and example code at [www.bamm-project.org](http://www.bamm-project.org). Two of the most important concepts are the notion of a ‘distinct shift configuration’ and a ‘marginal shift probability’. A distinct shift configuration is a mapping of evolutionary rate regimes (e.g. ‘rate shifts’) to a particular topology of possible shift locations. Consider a simple rooted phylogenetic tree of two taxa; there are two non-root branches, which we designate A and B. This tree defines four possible distinct shift configurations: a shift on branch A only, on B only, on both A and B and on neither A nor B. Every sample in the posterior distribution simulated with BAMM would correspond to one of these four distinct shift configurations. To be clear, BAMM allows multiple rate shifts to occur on any branch of the phylogeny, but for the purposes of enumerating the set of distinct shift configurations, we simply note whether or not at least one shift occurred on a given branch.

The second major concept is the notion of the ‘marginal shift probability’. This is the marginal probability that a rate shift event occurred on a particular branch. This is simply the percentage of samples in the posterior that included a rate shift on a particular branch. Consider our two-taxon (A, B) tree exam-

ple above: suppose that 70% of all samples in the posterior had shifts on branch A, 25% had shifts on branch B alone, 3% had shifts on both A and B and 2% included no rate shifts. The marginal shift probabilities would be 0.73 (on branch A) and 0.28 (on branch B). However, the probability of at least one rate shift occurring in the data is 0.98, because 98% of samples in the posterior include a rate shift.

## Description

BAMMtools is an R package (R Development Core Team 2014) that is distributed via the CRAN repository (<http://cran.r-project.org>) as well as the BAMM project website ([www.bamm-project.org](http://www.bamm-project.org)). BAMMtools uses the package ‘ape’ (Paradis, Claude & Strimmer 2004; Popescu, Huber & Paradis 2012) for loading phylogenetic trees. Several BAMMtools functions make use of compiled C code to speed execution time. A list of major BAMMtools functions is given in Table 2.

### WORKING WITH BAMM OUTPUT

The first step in a BAMMtools analysis is to create a data object that contains the set of diversification parameters sampled with BAMM during simulation of the posterior. This object, of class ‘bammdata’, is created using the function `getEventData`. The `bammdata` object is a fundamental component of most analyses that can be performed with BAMMtools. Functions are available to extract specific samples from the posterior (`subsetEventData`) or to create a subtree from a `bammdata` object for arbitrary sets of taxa (`subtreeBAMM`).

### VISUALIZING DYNAMIC RATES AND RATE SHIFTS

BAMMtools enables users to create ‘phylorate’ plots to visualize dynamic shifts in macroevolutionary rates along the branches of a phylogenetic tree. A phylorate plot makes use of colour to show instantaneous rates of diversification or

**Table 1.** Glossary of terminology used in BAMM and BAMMtools

Term	Definition
Core shift	A rate shift with a marginal probability greater than expected under the prior distribution of rate shifts; a ‘significant’ rate shift
Credible set (95%) of shift configurations	The smallest set of distinct shift configurations sampled with BAMM that can account for 95% of the posterior distribution
Cumulative shift probability	The probability that evolutionary rates are decoupled from the root process
Distinct shift configuration	A shift configuration that is topologically distinct from all other shift configurations, based on the presence or absence of at least one rate shift
Marginal shift probability	The marginal probability of a rate shift on a particular branch of a phylogenetic tree
Maximum a posteriori probability (MAP) shift configuration	The distinct shift configuration with the highest posterior probability
Phylorate plot	A visualization of macroevolutionary dynamics where colours are used to represent instantaneous macroevolutionary rates along branches
Regime	A macroevolutionary rate dynamic that applies to some part of a phylogenetic tree. All lineages that share a common regime have exactly the same macroevolutionary rate at a given point in time
Root process / root regime	The set of macroevolutionary rate parameters at the root of the tree; the ‘background’ diversification process
Topological shift location	A branch or ‘edge’ of a phylogenetic tree where a rate shift can occur

Table 2. Major BAMMtools functions

Function	Description
<code>addBAMMshifts</code>	Add locations of macroevolutionary regime shifts to a phylorate plot
<code>as.phylo.bammdata</code>	Convert between class <code>bammdata</code> and class <code>phylo</code> objects
<code>computeBayesFactors</code>	Compute pairwise matrix of Bayes factors between macroevolutionary models from BAMM output
<code>credibleShiftSet</code>	Extract the 95% (or any other percentage) set of distinct rate shift configurations from BAMM output
<code>distinctShiftConfigurations</code>	Identify all distinct rate shift configurations in the posterior density simulated with BAMM
<code>getBestShiftConfiguration</code>	Identify the rate shift configuration with the highest posterior probability and return it as a <code>bammdata</code> object
<code>getBranchShiftPriors</code>	Find upper bound on the number of rate shifts that should occur on each branch under the prior
<code>getCladeRates</code>	Get mean macroevolutionary rates for specific clades
<code>getCohortMatrix</code>	Compute pairwise probabilities that any two taxa share a common macroevolutionary rate regime
<code>getEventData</code>	Turn raw BAMM output into a <code>bammdata</code> object
<code>getMeanBranchLengthTree</code>	Get a copy of a phylogenetic tree where branch lengths are equal to the mean of the corresponding marginal rate distribution (phenotypic evolution or diversification)
<code>getTipRates</code>	Compute marginal rates of speciation, extinction or phenotypic evolution for each tip in a phylogenetic tree
<code>getRateThroughTimeMatrix</code>	Compute rate-through-time curves for each sample in the posterior
<code>marginalShiftProbsTree</code>	Compute marginal rate shift probabilities for each branch
<code>maximumShiftCredibility</code>	Estimate the maximum shift credibility configuration
<code>plot.bammdata</code>	Generate a phylorate plot from a <code>bammdata</code> object
<code>plot.credibleshiftset</code>	Plot the credible set of rate shift configurations sampled with BAMM
<code>plot.bammshifts</code>	Plot random rate shift configurations sampled with BAMM
<code>plotRateThroughTime</code>	Plot macroevolutionary rates through time
<code>samplingProbs</code>	Construct an input file for BAMM analysis of diversification dynamics with incomplete taxon sampling
<code>setBAMMpriors</code>	Choose appropriate prior parameters for BAMM analysis
<code>subtreeBAMM</code>	Extract subtree from a <code>bammdata</code> object

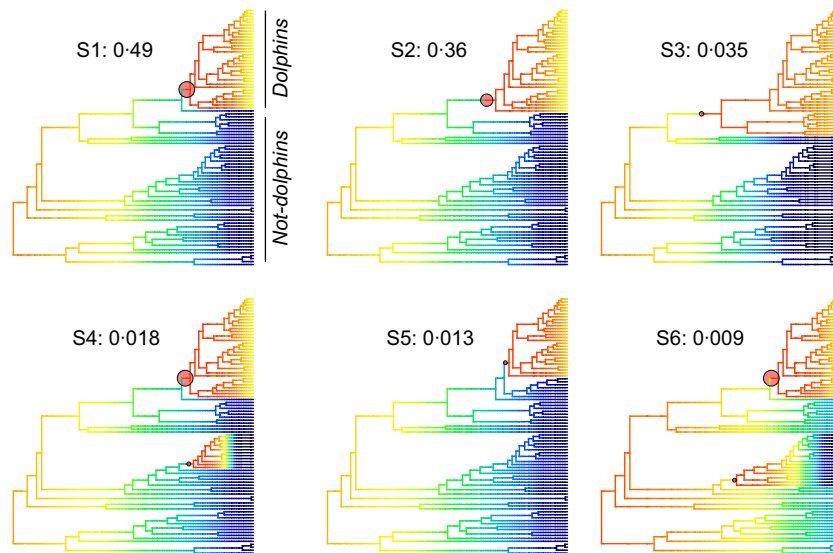
trait evolution for arbitrarily small intervals of time. This is useful, because the models of diversification and trait evolution implemented in BAMM allow rates to change continuously through time. This enables the user to plot continuous changes in rates along single branches and is similar to the visualization developed by Revell (2013) for character states. To calculate rates, each branch of the phylogeny is discretized into a number of small segments, and the mean of the marginal posterior density of the rate of speciation/extinction or trait evolution is calculated for each such segment. Rates are mapped to colours such that cool colours represent slow rates and warm colours represent fast rates. The function `plot.bammdata` will generate a phylorate plot for any set of samples from the posterior. The user is able to create both 'polar' and 'phylogram' versions of phylogenetic trees with coloured branches to denote changes in evolutionary rates through time.

The function `credibleShiftSet` will extract the 95% credible set of distinct shift configurations sampled using BAMM (Fig. 1), and the user can extract this frequency distribution (`summary.credibleshiftset`). In addition, the user can plot a specified number of shift configurations (as phylorate plots) in the credible set, along with text labels indicating the frequency, using `plot.credibleshiftset`. The function also displays the positions of rate shifts for each distinct shift configuration, scaled by the corresponding marginal shift probability.

The function `addBAMMshifts` will show rate shifts for any sample on a plotted `bammdata` object, and `plot.bammshifts` will generate phylorate plots for random samples from the posterior to give users a sense of the heterogeneity in macroevolutionary rates within the posterior sampled with BAMM. Users can also extract the marginal probability of a rate shift for any branch in the phylogeny with `marginalShiftProbsTree`. Finally, several functions are available for identifying the overall most-probable set of rate shifts under several optimality criteria (`getBestShiftConfiguration`; `maximumShiftCredibility`).

#### EVOLUTIONARY RATES THROUGH TIME

The function `plotRateThroughTime` is a flexible and general plotting function that will plot evolutionary rate reconstructions from a `bammdata` object (Fig. 2). A variety of options are available for displaying confidence in rate estimates, and the function enables users to extract and plot rate-through-time curves for specific subclades. `plotRateThroughTime` calls the function `getRateThroughTimeMatrix`, which computes rate-through-time trajectories for every sample in the posterior. The user can work directly with these matrices to summarize marginal distributions of evolutionary rates at any point in time.



**Fig. 1.** Speciation dynamics during the radiation of modern whales. Plots illustrate the six most-probable distinct shift configurations sampled with BAMM. Visualization was performed using `plot.credibleshiftset` in BAMMtools. Warmer colours denote faster rates of speciation. Rates change continuously along branches under BAMM model and have generally decelerated through time during the whale radiation; some discretization of rates is necessary for plotting. Red circles denote locations of rate shifts for each distinct shift configuration; circle size is proportional to the overall marginal probability of a shift on the branch. S1 (upper left) is the maximum *a posteriori* probability shift configuration and accounts for nearly 50% of the samples in the posterior. The dolphin clade (labelled in shift configuration S1) has accelerated rates of speciation relative to background lineages. These six shift configurations account for 92.5% of the posterior distribution of rate shift configurations sampled with BAMM.

#### CLADE- AND TIP-SPECIFIC RATES

The `bammdata` object includes components for the mean model-averaged rate of speciation, extinction or trait evolution at each tip in a phylogenetic tree. Marginal densities of rates for any tip can be extracted from the `bammdata` object with the function `getTipRates`. These tip-specific rates can be used for a variety of downstream analyses, including direct modelling of the relationship between diversification rates and character states. The function `getCladeRates` will compute marginal distributions of mean clade-specific evolutionary rates, potentially excluding or including specific clades.

#### MODEL SELECTION VIA BAYES FACTORS

Model selection can be performed by comparing posterior probabilities of evolutionary models sampled with BAMM; the function `summary.bammdata` will extract this information from a `bammdata` object. To minimize the effects of the prior density on the number of rate shifts, the user can also compute Bayes factors from BAMM output (`computeBayesFactors`).

#### Example: Speciation–extinction dynamics during the radiation of modern whales

We demonstrate several features of BAMMtools by applying it to a BAMM analysis of diversification rates during the radiation of modern whales. Note that all BAMMtools functions

described below can be applied to rates of phenotypic evolution as well, and BAMM enables explicit modelling of time-varying rates of phenotypic evolution. We analysed a time-calibrated phylogenetic tree of 89 extant species of cetaceans; this phylogeny was originally published in Steeman *et al.* (2009). Results from these BAMM analyses are distributed as example data sets in BAMMtools. Here, we will first analyse dynamic changes in speciation rates along the cetacean phylogeny, and we will extract the 95% credible set of rate shift configurations. We will then analyse the tempo of speciation through time. Finally, we will analyse the distribution of evolutionary rates for two sets of lineages separately: the dolphins and non-dolphins.

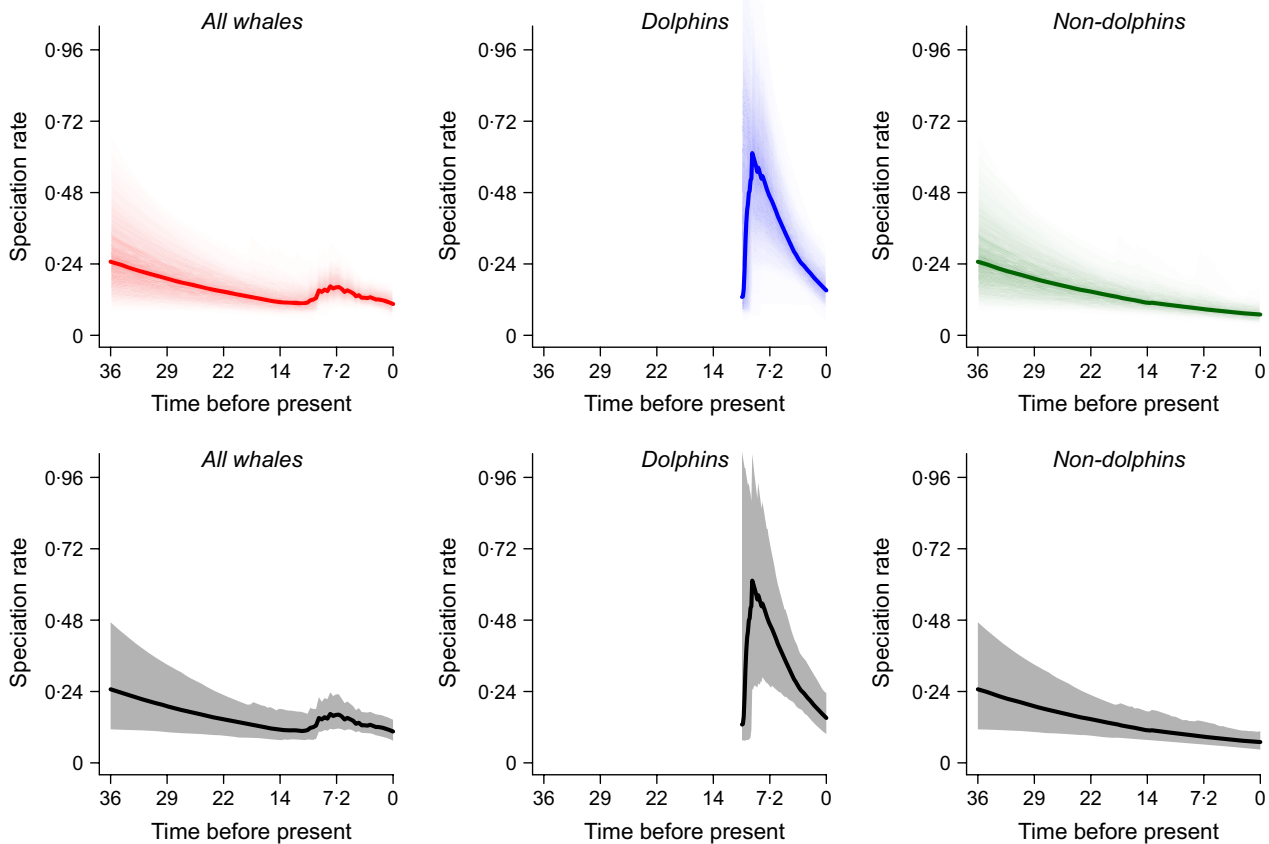
To begin, we load the BAMMtools package and the example data sets:

```
library(BAMMtools)
data(whales)
data(events.whales)
data(prior.whales)
```

`whales` is our time-calibrated phylogeny, `events.whales` is the raw ‘event data’ from a BAMM analysis, and `prior.whales` is an MCMC simulation of the prior density on the number of shift events. Now, we create a `bammdata` object for further analysis:

```
x <- getEventData(whales, events.whales, burnin = 0.1)
```

Executing `summary.bammdata(x)` will give us the posterior distribution of the number of shift events. Indeed,



**Fig. 2.** Speciation-through-time trajectories for the whale data set included as an example in BAMMtools. Columns show speciation rates for the entire whale radiation (left), the dolphins (middle) and all lineages except the dolphins (right). Upper panel uses colour density shading to illustrate the relative probability of a rate at any point in time; lower panel uses grayscale to illustrate the 95% credible interval on the distribution of rates through time. All visualization was performed using the BAMMtools function `plotRateThroughTime`. Note the massive spike in speciation rates associated with the origin of the dolphin clade (compare to Fig. 1).

classes of objects created with BAMMtools are S3 classes with `plot`, `print` and `summary` methods. We can generate a mean phylorate plot (Fig. 1) as follows:

```
plot.bammdata(x)
```

`plot.bammdata` also provides us with the ability to add an interpretive frequency histogram if `legend = TRUE` (Fig. 1). Note that we can simply call `plot(x)` because `x` is an S3 class with a default plotting method. Now, we will estimate the 95% credible set of rate shift configurations. To do so, we first must estimate the prior density on the number of shift events for each branch:

```
pset <- getBranchShiftPriors(whales, prior.whales)
```

Now getting the credible set:

```
css <- credibleShiftSet(x, threshold=pset)
```

We can summarize the frequency distribution of the credible set with

```
summary.credibleShiftSet(css)
```

We can visualize the six most-probable distinct shift configurations with:

```
plot.credibleShiftSet(css, plotmax=6,
pal="temperature")
```

We can see that just two shift configurations account for approximately 85% of the posterior (Fig. 1), and we can also see that the same general rate pattern (fast speciation in dolphins) holds for all six plotted shift configurations.

#### RATE-THROUGH-TIME ANALYSIS

It is straightforward to analyse and visualize rates of speciation, extinction and phenotypic evolution through time using a `bammdata` object:

```
plotRateThroughTime(x)
```

This plots a speciation rate-through-time (RTT) curve for the whale data set using a colour density gradient to show confidence in rates at any point in time (Fig. 2). We can also generate RTT curves while including or excluding specific subtrees. For example, node number '140' is the internal node number assigned to the common ancestor of the dolphin subclade; we can visualize this information using the `ape` function `nodeLabels`. Now, we plot only the RTT curve for dolphins:



```
plotRateThroughTime(x, node=140)
```

And here, we generate an RTT plot after excluding the dolphins, such that we only consider the ‘background’ rate of speciation:

```
plotRateThroughTime(x, node=140, nodetype=
"exclude")
```

These RTT curves are shown in Fig. 2, along with several colour schemes for displaying confidence in rates. While these results pertain to speciation, the user can also plot extinction and net diversification rates by specifying the `ratetype` parameter in the call to `plotRateThroughTime`.

#### CLADE-SPECIFIC RATES

We can extract posterior distributions of clade-specific rates from a `bammdata` object. For example, we can analyse speciation and extinction rates for the dolphin clade as follows:

```
rts<-getCladeRates(x, node=140)
```

`rts` is a list with components `lambda` and `mu`, where each component is a vector of mean speciation rates for the dolphin clade for each sample in the posterior. We can work directly with these rate distributions. Because BAMB allows rates to vary through time, the rates returned by `getCladeRates` are time-averaged rates. For any time-dependent rate function  $r(t)$ , these are computed as

$$\hat{r} = \frac{1}{T} \sum_{i=1}^N \int_{t_{i,0}}^{t_{i,1}} r(t) dt$$

where  $T$  is the total sum of branch lengths for the clade,  $N$  is the number of branches in the clade,  $t_{i,0}$  is the start time of the  $i$ th branch and  $t_{i,1}$  is the end time of the  $i$ th branch. These rates may be less useful for clades that have undergone strong temporal changes in rates through time. Here, we will compute the mean and 90% credible interval on speciation:

```
mean(rts$lambda)
```

```
[1] 0.263
quantile(rts$lambda, c(0.05, 0.95))
[1] 0.185 0.373
```

We can compare these to the corresponding distributions of speciation rates for all other whales (e.g. excluding the dolphin clade):

```
nd<-getCladeRates(x, node=140, nodetype="exclude")
mean(nd$lambda)
[1] 0.106
quantile(nd$lambda, c(0.05, 0.95))
[1] 0.072 0.153
```

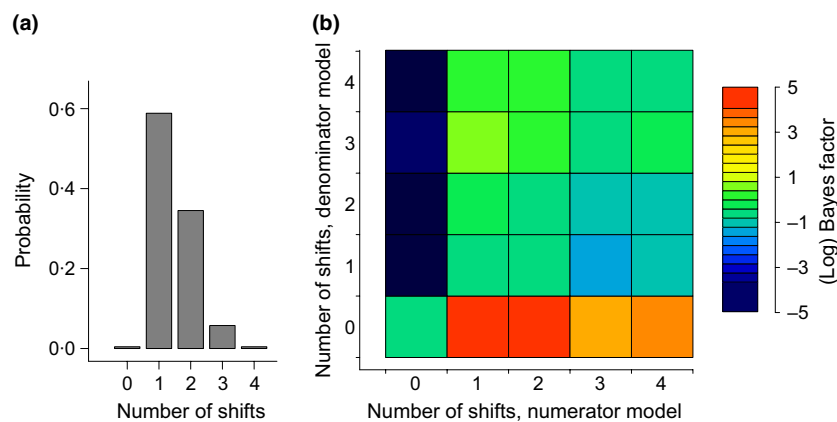
We can see that rates in the dolphin clade are much higher than the background rate of speciation; this is clearly visible in Figs 1 and 2.

#### MODEL SELECTION

In the BAMB framework, a model  $M_k$  is a diversification model with  $k$  rate shifts. Hence, model  $M_0$  is a model with zero rate shifts and model  $M_1$  has a single rate shift. We can compute the posterior probability of each model sampled with BAMB with summary methods for the `bammdata` object:

```
pprobs<-summary.bammdata(x)
```

This returns a `data.frame` with the posterior probability of each model; posterior probabilities of each sampled model are shown in Fig. 3a. The total probability of all models where  $k > 0$  is equivalent to the posterior probability that our data set contains among-lineage variation in diversification rates. For the whale example, this probability exceeds 0.99. Finally, the posterior probabilities in `pprobs` are a function of both the likelihood and the prior probability on the number of rate shifts. To minimize the effect of the prior, we can compute Bayes factor evidence in favour of any model over another model. This essentially standardizes the posterior odds ratio for any two models by their prior odds ratio. The Bayes



**Fig. 3.** Model selection using BAMBtools. (a) Posterior distribution of the number of rate shifts in the whale data. (b) Bayes factor matrix illustrating pairwise model comparisons. Each element of the matrix is a pairwise comparison between models, with colours indicating the logarithm of the Bayes factor; log Bayes factor scores of 0 imply that the models are equivalent. Here, models with one or more rate shifts outperform a model with a single evolutionary dynamic ( $M_0$ ). Model  $M_1$  is the overall best model.

factor for two models  $M_0$  and  $M_1$  is computed as

$$B_{01} = \frac{P(M_0|D) \pi(M_1)}{P(M_1|D) \pi(M_0)}$$

where  $P(M|D)$  and  $\pi(M)$  are the posterior and prior probabilities of each model, respectively. The odds ratios  $P(M_0|D)/P(M_1|D)$  and  $\pi(M_1)/\pi(M_0)$  are immediately available from BAMM output. The posterior odds are simply the ratio of model posterior probabilities described above (Fig. 3a). To obtain the prior odds, BAMM – by default – simulates the distribution of models under the prior alone. This enables calculation of the Bayes factor without the use of coarse approximations (e.g. harmonic mean estimator; Newton & Raftery 1994) or computationally-intensive methods to estimate marginal likelihoods (Lartillot & Philippe 2006). Bayes factors  $>1$  imply increased support for the numerator model ( $M_0$  in this example), and Bayes factors  $<1$  imply greater support for the denominator model ( $M_1$  here). To compute a pairwise matrix of Bayes factors for the whales data set, we first load our raw BAMM MCMC output as well as the simulated prior density on the number of shifts. Bayes factors are then computed with `computeBayesFactors`:

```
data(mcmc.whales, prior.whales)
bmat <- computeBayesFactors(mcmc.whales,
  prior.whales, burnin=0.1)
```

In general, pairwise Bayes factors in excess of 20 provide strong support for one model over another (Kass & Raftery 1995). In the case of whales, the Bayes factor evidence in favour of a model with a single rate shift over a model with zero rate shifts is very high (81.5). A visualization of pairwise Bayes factors is shown in Fig. 3b. R code to generate colour matrix plots of Bayes factors using output from `computeBayesFactors` is available at [www.bamm-project.org](http://www.bamm-project.org) and as supplementary information to this article.

## Online resources

A number of extensions to BAMMtools and BAMM are currently in the development stage. New features will be documented on the project website, [www.bamm-project.org](http://www.bamm-project.org). In addition, we have created a dedicated Google Group (see our 'Contact Us' web page) for questions, comments and bug reports for BAMMtools and BAMM. The most recent version of BAMMtools is available on Github at <http://github.com/macroevolution/bammtools>.

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## Data accessibility

Everything used in this manuscript is available through the R package BAMMtools, available on CRAN: <http://cran.r-project.org/web/packages/BAMMtools/index.html>. A demo script is uploaded as supplementary information.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Data S1.** R code for BAMMtools analysis of the whale dataset.