

APPLICATION

RPANDA: an R package for macroevolutionary analyses on phylogenetic trees

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Summary

1. A number of approaches for studying macroevolution using phylogenetic trees have been developed in the last few years. Here, we present RPANDA, an R package that implements model-free and model-based phylogenetic comparative methods for macroevolutionary analyses.
2. The model-free approaches implemented in RPANDA are recently developed approaches stemming from graph theory that allow summarizing the information contained in phylogenetic trees, computing distances between trees, and clustering them accordingly. They also allow identifying distinct branching patterns within single trees.
3. RPANDA also implements likelihood-based models for fitting various diversification models to phylogenetic trees. It includes birth–death models with i) constant, ii) time-dependent and iii) environmental-dependent speciation and extinction rates. It also includes models with equilibrium diversity derived from the coalescent process, as well as a likelihood-based inference framework to fit the individual-based model of Speciation by Genetic Differentiation, which is an extension of Hubbell's neutral theory of biodiversity.
4. RPANDA can be used to (i) characterize trees by plotting their spectral density profiles (ii) compare trees and cluster them according to their similarities, (iii) identify and plot distinct branching patterns within trees, (iv) compare the fit of alternative diversification models to phylogenetic trees, (v) estimate rates of speciation and extinction, (vi) estimate and plot how these rates have varied with time and environmental variables and (vii) deduce and plot estimates of species richness through geological time.
5. RPANDA provides investigators with a set of tools for exploring patterns in phylogenetic trees and fitting various models to these trees, thereby contributing to the ongoing development of phylogenetics in the life sciences.

Key-words: diversification rates, extinction, graph Laplacian, likelihood, macroevolution, speciation, Speciation by Genetic Differentiation, spectral density profiles

Introduction

Phylogenetic approaches have become a central component of various areas of the life sciences. A number of packages are available to handle and utilize phylogenetic trees (e.g. 'ape' Paradis, Claude & Strimmer 2004), in order to understand, for example, community assembly (e.g. 'picante' Kembel *et al.* 2010; 'DAMOCLES' Pigot & Etienne 2015), trait evolution (e.g. 'Coevol' Lartillot & Poujol 2011; 'geiger' Pennell *et al.* 2014) and diversification (e.g. 'BayesRate' Silvestro, Schnitzler & Zizka 2011; 'TreePar' Stadler 2011a; 'diversitree' FitzJohn 2012; 'DDD' Etienne *et al.* 2012; 'geiger' Pennell *et al.* 2014; 'BAMM' Rabosky 2014).

Here, we present and describe the R package RPANDA, which implements both model-free and model-based phyloge-

netic approaches that are not implemented in previous packages. The model-free approaches are inspired from graph theory and described in detail in Lewitus & Morlon (2015). They are designed to compare and classify phylogenetic trees without any *a priori* formulation of a model of cladogenesis underlying tree shape. The model-based approaches aim to fit various models of cladogenesis to phylogenetic trees by maximum likelihood. They are described in detail in Morlon, Potts & Plotkin (2010), Morlon, Parsons & Plotkin (2011), Condamine, Rolland & Morlon (2013) and Manceau, Lambert & Morlon (2015).

Within the category of model-based approaches, the package includes three main classes of models: birth–death models, coalescent models and individual-based models (see Morlon 2014 for a review of these three different types of models). Birth–death models are those that were originally considered by Nee, Mooers & Harvey (1992) and are at the basis of most

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diversification models used today. The present package allows fitting of birth–death models: (i) with speciation and extinction rates varying as a function of time, with any type of functional form and with potential periods of diversity decline (Morlon, Parsons & Plotkin 2011), and (ii) with speciation and extinction rates varying as a function of any variable that has been measured through geological time (e.g. temperature, Condamine, Rolland & Morlon 2013). Models based on the coalescent process were designed to consider scenarios of equilibrium diversity (Morlon, Potts & Plotkin 2010). Finally, individual-based models have been extensively studied in ecology, but likelihood-based inferences from phylogenies are typically not available. The present package allows likelihood inference for the model of Speciation by Genetic Differentiation (Manceau, Lambert & Morlon 2015), which is an extension of the neutral theory of biodiversity (Hubbell 2001).

Description

RPANDA is an R package (R Development Core Team 2014) that can be installed from the CRAN repository (<http://cran.r-project.org>). RPANDA relies on the R packages ‘ape’ (Paradis, Claude & Strimmer 2004), ‘picante’ (Kembel *et al.* 2010), ‘phytools’ (Revell 2012), ‘deSolve’ (Soetaert, Petzoldt & Setzer 2010) and ‘igraph’ (Csardi & Nepusz 2006).

The main functions of the package are listed in Table 1, classified into functions related to the model-free and model-based approaches. Nearly every function is associated with a plot function that helps visualize the results of the analyses.

To illustrate the use of RPANDA, we analyse the phylogeny of the bat family Phyllostomidae. This phylogeny is the maximum clade credibility tree used in Rolland *et al.* (2014),

which originally comes from the mammalian supertree (Bininda-Emonds *et al.* 2007; Fritz, Bininda-Emonds & Purvis 2009); it contains 150 of the 165 known bat species (i.e. it is 91% complete). To begin, we open an R console, and we install and load the RPANDA package as well as the example data sets.

```
> install.packages('RPANDA', dependencies=TRUE)
> library(RPANDA)
> data(Phyllostomidae)
> data(Phyllostomidae_genera)
```

‘Phyllostomidae’ is the family-level phylogeny and ‘Phyllostomidae_genera’ is a list of 25 phylogenies corresponding to Phyllostomidae genera with more than one species.

Characterizing and comparing phylogenies using spectral densities

We recently developed a new approach, described in detail in Lewitus & Morlon (2015), to efficiently summarize the shape of a phylogenetic tree. This approach can be used to measure similarities between trees and to cluster them accordingly, for example in order to identify phylogenies shaped by similar versus dissimilar diversification patterns. It can also help in identifying regions of a tree that have distinct branching patterns, which can for example reflect shifts in modes or rates of diversification. We summarize the shape of a phylogeny by its spectral density, which is a smoothed version of the frequencies of eigenvalues associated with a matrix (the graph Laplacian) built from the pairwise phylogenetic distances between nodes (see Lewitus & Morlon 2015 for a more detailed description). The function `spectR` computes the eigenvalues associated with a given phylogeny, and characteristics associated

Table 1. Major functions available in RPANDA

Function	Description
Characterizing and comparing phylogenies using spectral densities	
<code>BICcompare</code>	computes BIC values assessing the support of modalities in a phylogeny
<code>JSDtree</code>	computes the Jensen–Shannon distance between phylogenies
<code>JSDtree_cluster</code>	clusters phylogenies using hierarchical and k-medoids clustering
<code>spectR</code>	computes the eigenvalues of a phylogeny, and returns the principal eigenvalue, the skewness, and kurtosis of the spectral density profile, and the eigengap
<code>plot_BICcompare</code>	plots modalities on a phylogenetic tree
<code>plot_spectR</code>	plots the spectral density and eigenvalues of a phylogeny ranked in descending order
Fitting models of diversification to phylogenies	
<code>fit_bd</code>	fits a birth–death model to a phylogeny
<code>fit_coal_cst</code>	fits an equilibrium model with constant diversity through time to a phylogeny, using the coalescent model
<code>fit_coal_var</code>	fits a model with expanding diversity through time to a phylogeny, using the coalescent model
<code>fit_env</code>	fits a birth–death model with environmental dependency to a phylogeny
<code>fit_sgd</code>	fits the model of Speciation by Genetic Differentiation to a phylogeny
<code>likelihood_bd</code>	computes the likelihood corresponding to the birth–death model
<code>likelihood_coal_cst</code>	computes the likelihood corresponding to the coalescent model with constant diversity through time
<code>likelihood_coal_var</code>	computes the likelihood corresponding to the coalescent model with expanding diversity through time
<code>likelihood_sgd</code>	computes the likelihood corresponding to the model of Speciation by Genetic Differentiation
<code>plot_fit_bd</code>	plots diversification rates through time curves
<code>plot_fit_env</code>	plots diversification rates as a function of one or several environmental variables and time
<code>plot_dtt</code>	computes and plots diversity through time curves
<code>sim_sgd</code>	simulates a phylogeny arising from the model of Speciation by Genetic Differentiation

with the spectrum of eigenvalues, namely the principal eigenvalue, asymmetry (skewness), two measures of peakedness (kurtosis and peak height) and eigengap. The eigengap is given by the position of the largest difference between successive eigenvalues listed in descending order. This number is related to the number of peaks in the spectral density plot and is indicative of the number of modalities (i.e. distinct branching patterns) in a phylogeny.

```
> res<-spectR(Phyllostomidae)
```

returns the above information for the Phyllostomidae phylogeny. In particular, `res$eigengap` returns the number of modalities, suggesting three distinct branching patterns in this bat family.

```
> plot_spectR(res)
```

displays the spectral density profile and a plot of the eigenvalues ranked in descending order (Fig. 1).

Once the putative number of modalities is identified, the `BICcompare` function can be used to assess the significance of these modalities and to identify their location on the phylogeny. The statistical significance of the modalities is assessed by comparing the Bayesian Information Criterion (BIC) for detecting i clusters in the distance matrix of the empirical phylogeny and in randomly bifurcating trees parameterized on that tree (Lewitus & Morlon 2015). The function also identifies the location of the distinct branching patterns on the phylogeny by k-means clustering and returns the ratio of between-cluster sum of squares (BSS) to total sum of squares (TSS) for the clustering identified by the algorithm. The highest the BSS/TSS ratio, the more distinct the modalities are from each other. Different iterations of the k-means clustering algorithm can lead to different modality configurations, and BSS/TSS values allow the comparison between these configurations (configurations with high BSS/TSS should be preferred).

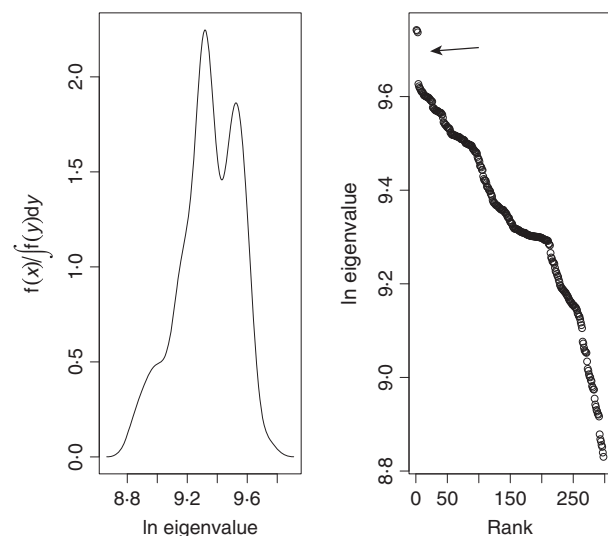


Fig. 1. Spectral density plot of the Phyllostomidae (left panel) and corresponding eigenvalues ranked in descending order (right panel). There is a clear gap between the third and fourth eigenvalue (indicated by an arrow), suggesting three modes of division in the phylogeny.

```
> res<-BICcompare(Phyllostomidae,3)
```

returns the above information for the Phyllostomidae phylogeny. The BIC score for the Phyllostomidae phylogeny is nearly a magnitude smaller than it is for the randomly bifurcating trees parameterized on that phylogeny, suggesting that the three modalities are significant. Typically, a BIC ratio ≤ 0.25 is deemed significant.

```
> plot_BICcompare(Phyllostomidae,res)
```

displays the Phyllostomidae phylogeny with branches coloured according to the modality they belong to, as assessed by the k-means clustering algorithm (Fig. 2).

Spectral densities are particularly useful for comparing phylogenies. The `JSDtree` function computes the pairwise distances between a list of phylogenies, measured as the Jensen–Shannon distance between their spectral densities. The `JSDtree_cluster` function uses these pairwise distances (or potentially other distance metrics) to cluster phylogenies into groups. The clustering is implemented using the hierarchical clustering and k-medoid clustering algorithms. To illustrate this approach, we compare the 25 phylogenies corresponding to Phyllostomidae genera with more than one species.

```
> res<-JSDtree(Phyllostomidae_genera)
```

returns the matrix containing the pairwise Jensen–Shannon distances between the 25 phylogenies.

```
> JSDtree_cluster(res)
```

plots the heatmap and hierarchical cluster (Fig. 3) as well as the hierarchical cluster with bootstrap support (not shown here). It also returns the optimal number of clusters given by the k-medoids algorithm, here suggesting that Phyllostomidae genera cluster into two meaningful groups. The function returns the assignment of each phylogeny to each of the two groups, as well as a measure of statistical support for this assignment.

Fitting models of diversification to phylogenies

One of the most popular approaches for analysing the diversification of clades consists in fitting various models of diversification to molecular phylogenies using maximum likelihood inference, comparing the likelihood support of the different models, and estimating the parameters of the model (see Morlon 2014 for a review). The different types of functions available in RPANDA reflect this general approach (Table 1): the `likelihood` functions compute the likelihood associated with different diversification models, the `fit` functions fit the corresponding models by maximum likelihood, and the `plot` functions plot estimates of how various variables (e.g. speciation and extinction rates, species richness) have varied as a function of time or various environmental factors (e.g. temperature). Simulating phylogenies under the different models is often useful, for example, to test the power of the approach to recover true parameter values or to measure type I and II error rates. We do not generally provide functions to simulate phylo-

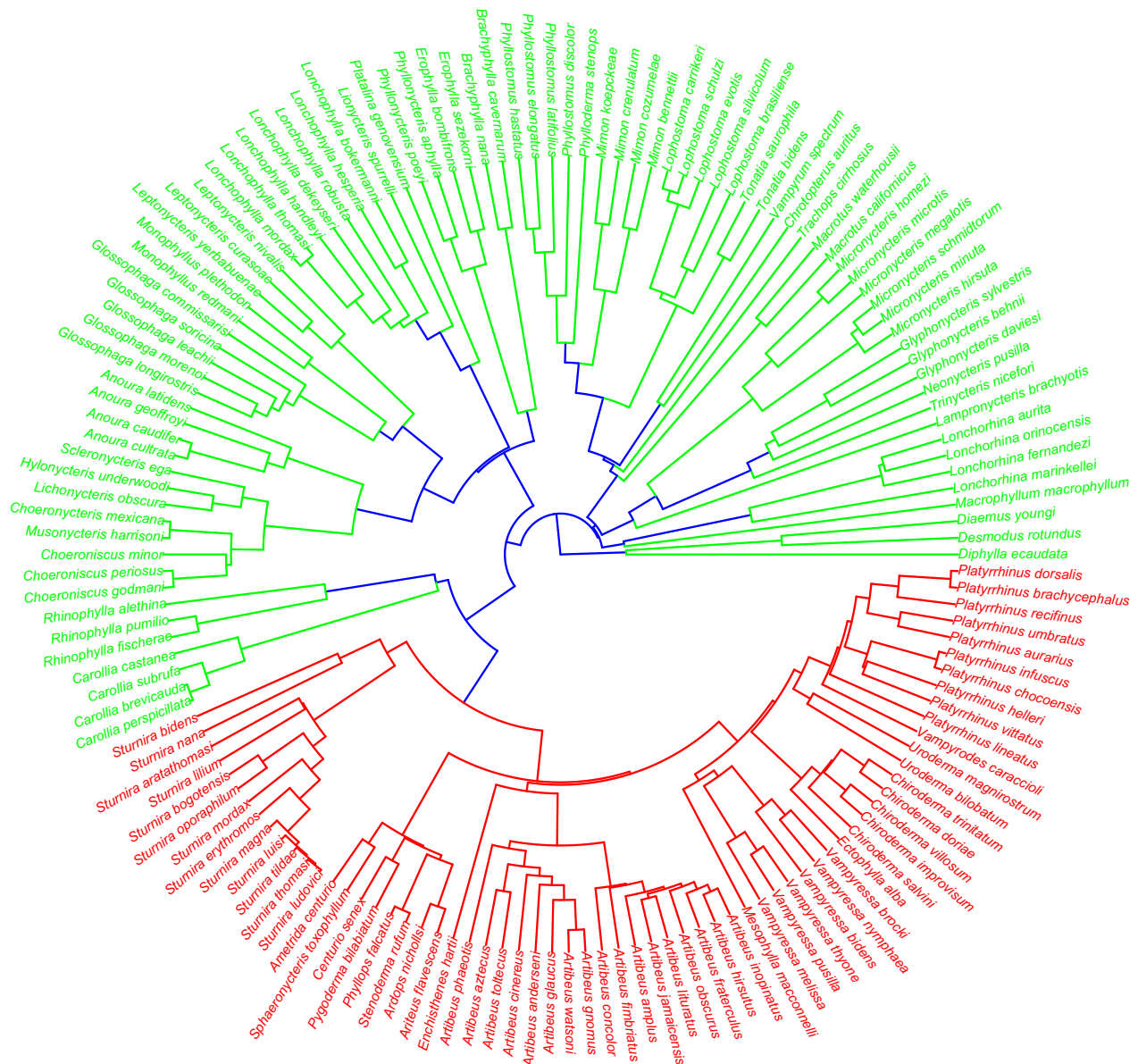


Fig. 2. Phyllostomidae phylogeny with branches coloured according to the 3 branching patterns (or modalities) identified by the eigengap, as given by k-medoid clustering.

genies, as they are available in other packages such as TreeSim (Stadler 2011b) and TESS (Höhna 2013). The one exception is the `sim_sgd` function that simulates phylogenies under the model of Speciation by Genetic Differentiation (Manceau, Lambert & Morlon 2015).

Fitting a diversification model to a phylogeny consists in finding the parameters that maximize the likelihood associated with the model. The `fit` functions, therefore, take as argument, at minimum, a phylogeny (`phylo`), initial parameter values (`par`) and the maximization algorithm to be used (`meth`). The various likelihood expressions all depend on the fraction of extant species that are sampled in the phylogeny; this fraction (`f`), therefore, also needs to be specified. Finally, `tot_time` specifies the age of the phylogeny. We often have access only to the crown age, in which case `tot_time` is

given by `max(node.age(phylo)$ages)`. If the stem age is known, specifying this older age in `tot_time` can provide a different and complementary inference.

TIME-DEPENDENT DIVERSIFICATION MODELS

RPANDA can be used to test whether (and how) diversification rates varied through time (Morlon, Parsons & Plotkin 2011). To illustrate the approach, we fit a birth–death model with time-varying rates to the Phyllostomidae phylogeny. We first need to specify the assumed functional form of the time dependency. For example, if we want to fit a model with an exponential variation of the speciation rate with time (`f.lamb`), and a constant extinction rate (`f.mu`), we define these functions as follows:

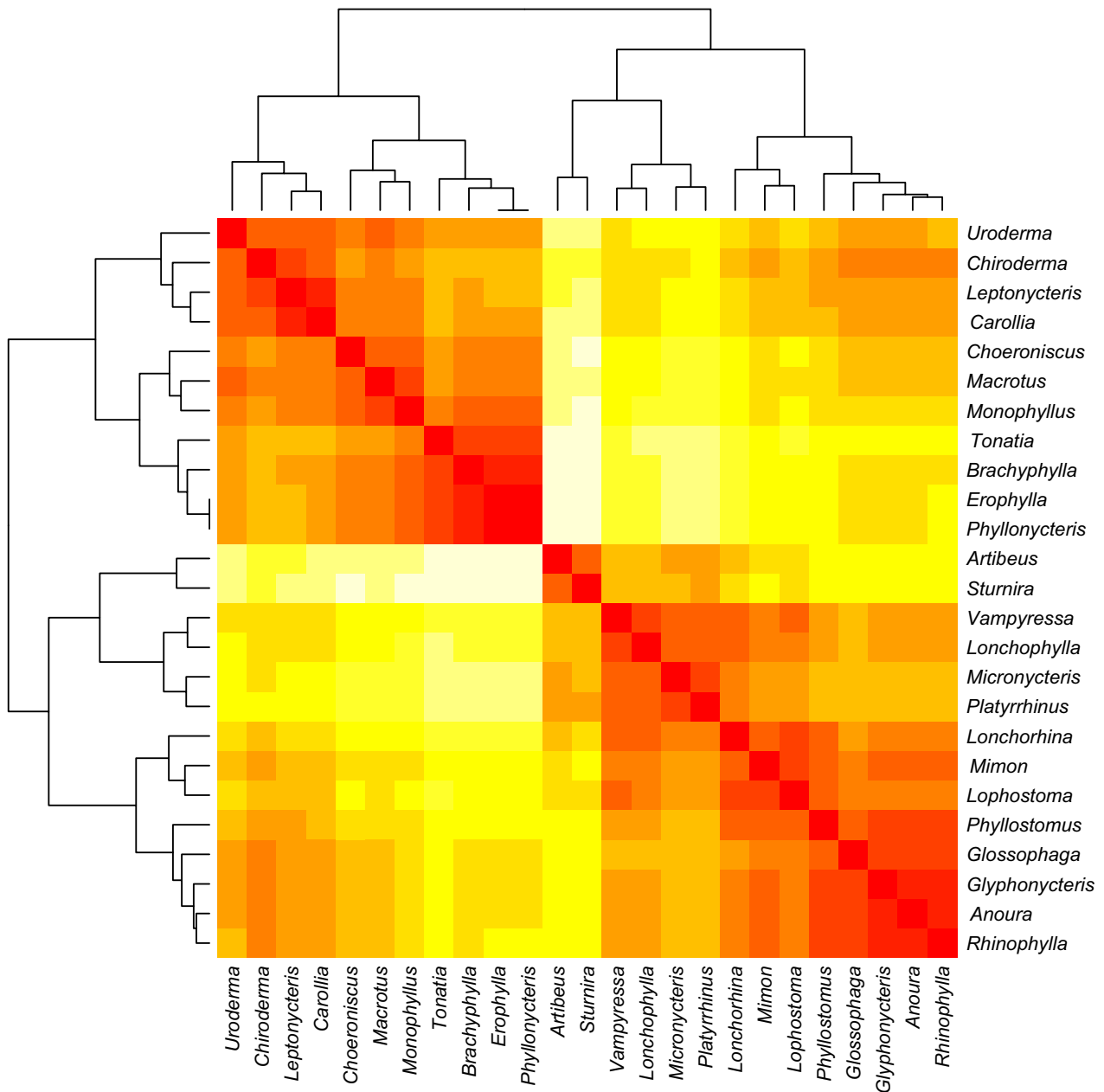


Fig. 3. Heatmap and hierarchical cluster showing the pairwise similarities between the 25 Phyllostomidae genera with more than one species.

```
> f.lamb<-function(t,y){y[1]*exp(y[2]*t)}
> f.mu<-function(t,y){y[1]}
```

For a linear dependency of the speciation rate, the function would be as follows:

```
> f.lamb.lin<-function(t,y){y[1]+y[2]*t}
```

The variable t represents time, running from the present to the past, while the variable y is a vector containing the different parameters involved in the definition of the temporal dependency. The parameters in y are therefore the parameters that will be estimated by maximum likelihood. We need to specify initial values for these parameters, for example

```
> lamb_par_init<-c(0.05,0.01)
```

sets the initial parameter values defining the `f.lamb` speciation function, and

```
> mu_par_init<-c(0.005)
```

sets the initial parameter values defining the `f.mu` extinction function. The result of the fitting procedure should not depend on the choice of the initial parameter values, which can be checked by running the model with several sets of (realistic) initial values. For example, the speciation rate at present (`lamb_par_init[1]`) typically takes value ranging between 0.01 and 1 (event per lineage, per million years). The rate of variation of the speciation rate (`lamb_par_init`

[2]) can then be chosen such that the resulting speciation rate (output of `f.lamb(t, lamb_par_init)`) remains within this realistic range throughout the clade history (i.e. for `t` ranging from 0 to crown or stem age). And finally, the initial extinction parameters set in `mu_par_init` can be chosen such that the resulting extinction rate (output of `f.mu(t, mu_par_init)`) is smaller than the speciation rate at the beginning of clade's history (i.e. for `t` set to the crown or stem age) and remains positive throughout the clade history (i.e. for `t` ranging from 0 to crown or stem age).

We can now fit the model. If we knew the stem age of Phyllostomidae, we could specify this age in `tot_time`. As we do not have this information, we define the following:

```
> tot_time<-max(node.age(Phyllostomidae)$ages)
```

Finally, we fit the model by maximum likelihood using the following command:

```
> res<-fit_bd(Phyllostomidae,tot_time,f.lamb,
f.mu,lamb_par_init,
mu_par_init,f=150/165,expo.lamb=TRUE,cst.mu=TRUE)
```

The two options `expo.lamb=TRUE` and `cst.mu=TRUE` are set to `TRUE` to speed up the computation by using analytical solutions; such solutions have been implemented for exponential, linear and constant functions. If the options are set to `TRUE` when the time dependency is not of the proper form (exponential, linear or constant), the code will not return the proper answer. When in doubt, it is better to prefer the default `FALSE` option. There is an additional `dt` option (not used in the examples here) that can also speed up the computation by using piecewise constant approximations in the computation of the integrals. There is also an option that specifies whether we are working with crown or stem ages, which has consequences for the conditioning that should be used in the computation of the likelihood: the process should be conditioned on survival when working with stem ages, and conditioned on a speciation event at the crown and survival of the two descending lines when working with crown ages (Morlon, Parsons & Plotkin 2011). The default (used here) is the `cond=crown` option, but it should be set to `cond=stem` if `tot_time` is the stem age. The output `res` of the fit contains

the maximum log-likelihood value (-469.36), the corrected Akaike Information Criterion (AICc) (944.89) and the maximum likelihood parameter estimates. For example,

```
> res$lamb_par[1]
```

returns the maximum parameter estimate of `y[1]`, which is the speciation rate at time `t=0`, that is the present (here 0.099).

```
> res$lamb_par[2]
```

returns the maximum parameter estimate of `y[2]`, which is the rate of change in speciation rate, with time running from the present to the past (here 0.022). A positive rate of change with time running from the present to the past – as estimated here – suggests a negative rate of change (decline in speciation rate) during the clade's history.

```
> plot_fit_bd(res,tot_time)
```

returns three plots, which represent speciation, extinction and net diversification (i.e. speciation minus extinction) rates through time (Fig. 4). If a model without extinction is fitted,

```
> f.mu<-function(t,y){0}
> mu_par_init<-c()
> res_noext<-fit_bd(Phyllostomidae,tot_time,
f.lamb,f.mu,
lamb_par_init,mu_par_init,f=150/165,
expo.lamb=TRUE,fix.mu=TRUE)
> plot_fit_bd(res_noext,tot_time)
```

returns two plots, which represent speciation and net diversification rates through time (in this case, these two rates are equal).

Once estimates of the temporal variation in speciation and extinction rates have been obtained (as described above), estimates of how species richness varied through time can be computed by resolving the appropriate differential equation (Morlon, Parsons & Plotkin 2011; Morlon 2014).

```
> plot_dtt(res,tot_time,N0=165)
```

plots the result of this estimation procedure, as illustrated in Fig. 5.

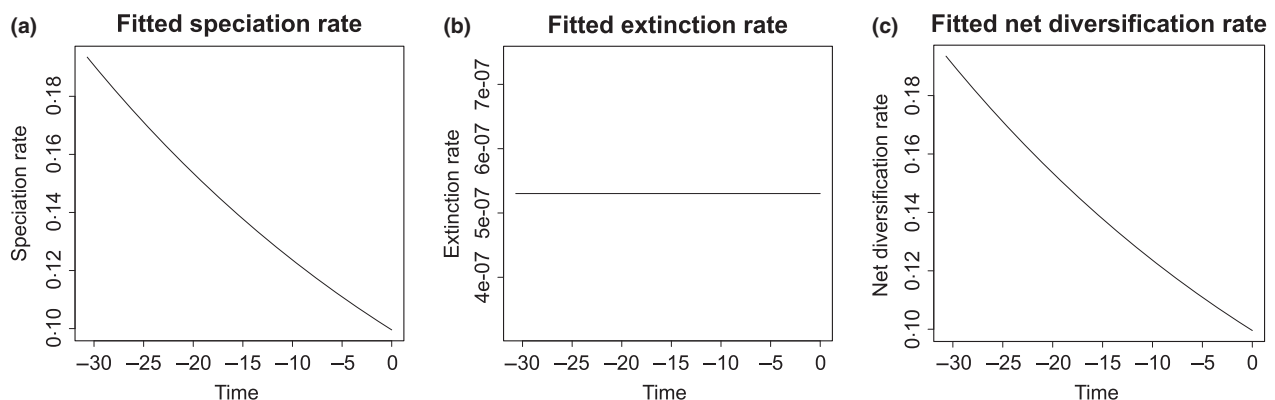


Fig. 4. Plots showing the estimated a) speciation, b) extinction and c) net diversification rates through time for the Phyllostomidae phylogeny, output of the `plot_fit_bd` function.

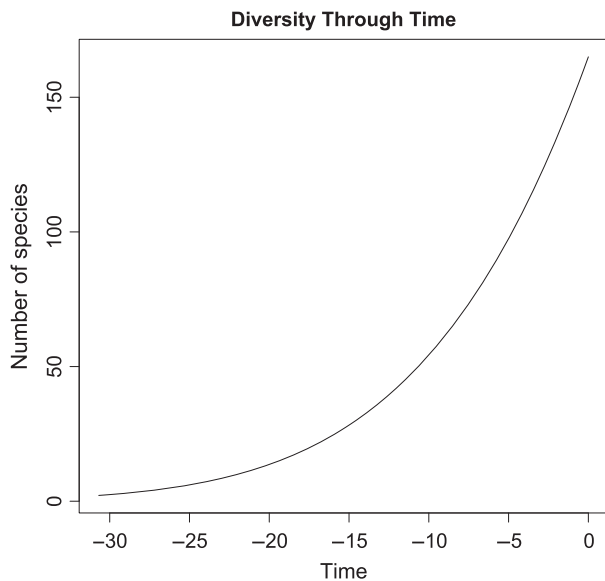


Fig. 5. Plot showing the estimated accumulation of species richness through time for the Phyllostomidae phylogeny, output of the `plot_dtt` function.

ENVIRONMENTAL-DEPENDENT DIVERSIFICATION MODELS

RPANDA can also be used to test the potential effect that past environmental conditions had on diversification (Condamine, Rolland & Morlon 2013). Fitting the environmental-dependent birth–death model is very similar to fitting the time-dependent birth–death model. In addition to a phylogeny, this model requires knowledge (typically an estimate) of how a given environmental variable varied through time. The example provided in RPANDA is temperature variation through the Cenozoic, estimated using oxygen isotope ratios (Zachos, Dickens & Zeebe 2008). We begin by loading the temperature data:

```
> data(InfTemp)
```

`InfTemp` is a two-column dataframe in which the first column reports time (measured from the present to the past) and the second column reports the corresponding estimated temperature at each time (Condamine, Rolland & Morlon 2013). Any other (abiotic or biotic) environmental variable in this format can be used in place of `InfTemp` in order to test the potential effect that this variable had on diversification (e.g. sea-level fluctuations, Condamine *et al.* 2015). Here, diversification rates can depend on time as well as on the environmental variable; the `f.lamb` and `f.mu` functions therefore take two arguments (time `t` and the environmental variable `x`) in addition to the parameters `y` to be estimated. We fit a simple model with an exponential dependence of the speciation rate on the environmental variable, no time dependence, and no extinction. We thus define the following:

```
> f.lamb<-function(t,x,y){y[1]*exp(y[2]*x)}
```

and

```
> f.mu<-function(t,x,y){0}
```

as well as initial parameter estimates:

```
> lamb_par_init<-c(0.10,0.01)
```

```
> mu_par_init<-c()
```

Finally, we fit the model:

```
> res<-fit_env(Phyllostomidae,InfTemp,tot_time,
f.lamb,f.mu,
lamb_par_init,mu_par_init,f=150/165,fix.mu=TRUE,
dt=1e-3)
```

Note that we do not use the option `expo.lamb=TRUE`, as `f.lamb` is an exponential function of the environmental variable, not an exponential function of time. Setting `expo.lamb` to `TRUE` would yield spurious results. However, we can speed up the computation by specifying `dt=1e-3`, which uses a piece-wise constant approximation in the evaluation of integrals. The output `res` of the fit contains the maximum log-likelihood value (−468.44), the AICc (940.97) and the maximum likelihood parameter estimates. For example,

```
> res$lamb_par[1]
```

returns the maximum parameter estimate of `y[1]`, which is the speciation rate that would correspond to a temperature of 0°C (here 0.077).

```
> res$lamb_par[2]
```

returns the maximum parameter estimate of `y[2]`, which is the rate of change in speciation rate with temperature (here 0.083). A positive value thus suggests a positive effect of the environmental variable (here temperature) on speciation rates. Note that the environmental model fitted here receives a better support than the model with an exponential dependency of speciation rate with time ($\Delta\text{AICc} = 944.89 - 940.97 = 3.92$).

```
> plot_fit_env(res,InfTemp,tot_time)
```

plots diversification rates as a function of the environmental variable and time (Fig. 6).

THE MODEL OF SPECIATION BY GENETIC DIFFERENTIATION

RPANDA also contains functions to fit a modified version of Hubbell's neutral model of biodiversity (Hubbell 2001): the model of Speciation by Genetic Differentiation, which is described in detail in Manceau, Lambert & Morlon 2015. We can fit the model following a similar procedure. The model is individual based and involves parameters describing the birth and death of individuals, as well as a per-individual mutation rate. We define initial parameter values for the birth, growth (birth minus death) and mutation rates (given in events per Myr if the branch lengths of the phylogeny are measured in Myrs), for example:

```
> par_init<-c(1e7,1e7-0.5,0.8)
```

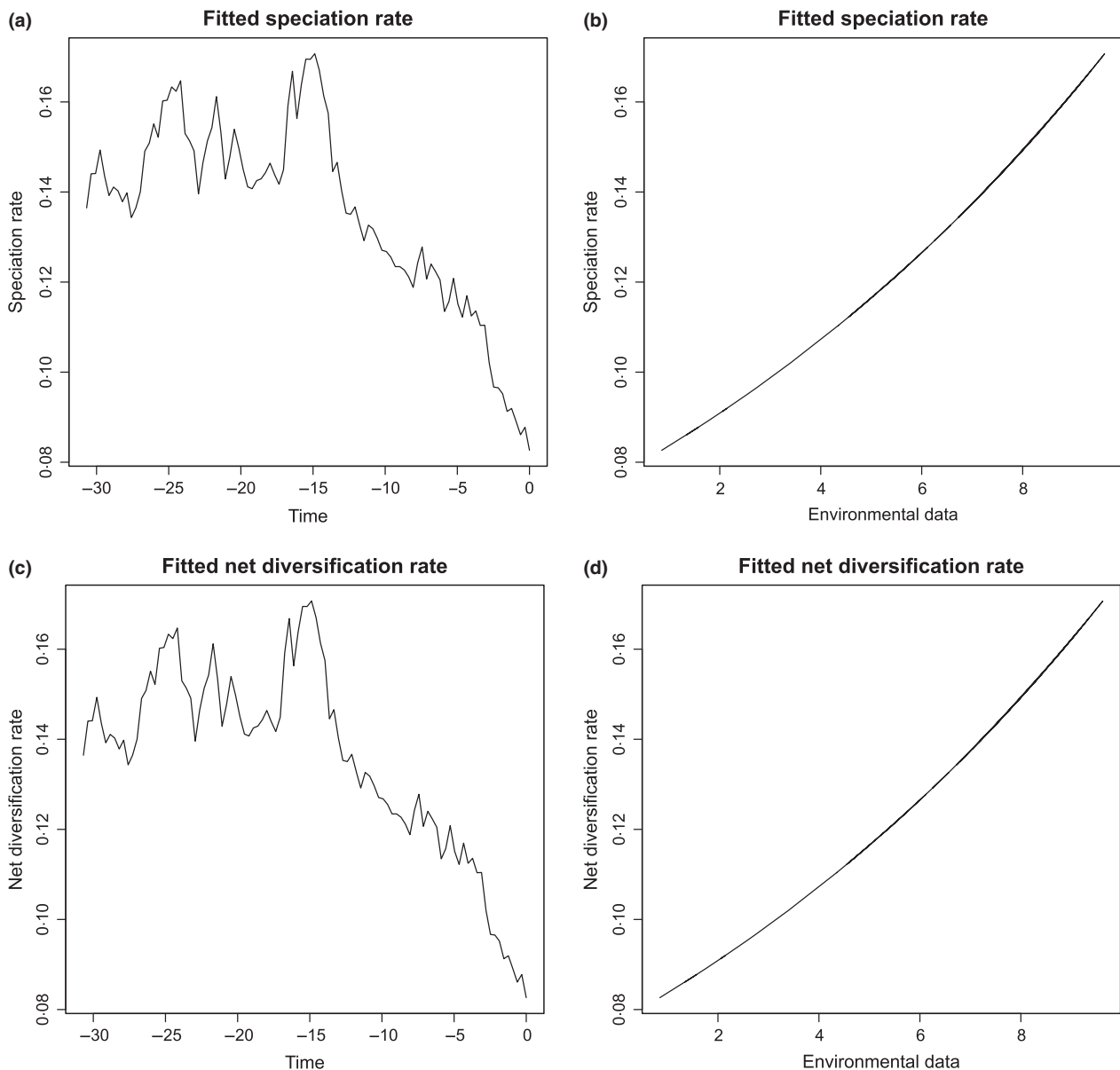


Fig. 6. Plots showing the estimated speciation (a,b) and net diversification (c,d) rates as a function of time (a,c) and temperature (b,d) for the Phyllostomidae phylogeny, output of the `plot_fit_env` function.

We can then fit the model (this takes more time than the previous examples, as computing likelihoods requires integrating a set of coupled differential equations along the tree, Manceau, Lambert & Morlon 2015):

```
> fit_sgd(Phyllostomidae, tot_time, par_init,
f=150/165)
```

returns the maximum log-likelihood (−466), the AICc (938), and the estimated birth ($1e7$), growth (0.157) and mutation (0.198) rates. As explained in Manceau, Lambert & Morlon (2015), the likelihood surface is quite flat with respect to the birth rate, such that this parameter cannot be estimated with confidence. Birth rate estimates are thus sensitive to the choice of the initial parameter values and should not be trusted.

Resources

RPANDA is an open-source package available for download on the CRAN repository at <https://cran.r-project.org/web/packages/RPANDA/index.html>. It includes illustrative data and a detailed manual. The package is constantly evolving. Bayesian implementations and functions that allow fitting new models of phenotypic evolution, such as the matching competition model (Drury *et al.* 2015), are already under development. Contributions are welcome; automatic tests have been implemented to facilitate a collaborative development and to insure the replicability of results. The most recent version is available on github at <https://github.com/hmorlon/PANDA>.

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Data accessibility

All data used in this manuscript are available through the R package RPANDA, available on CRAN <https://cran.r-project.org/web/packages/RPANDA/index.html>.

References

- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R. *et al.* (2007) The delayed rise of present-day mammals. *Nature*, **446**, 507–512.
- Condamine, F.L., Rolland, J. & Morlon, H. (2013) Macroevolutionary perspectives to environmental change. *Ecology Letters*, **16**, 72–85.
- Condamine, F.L., Toussaint, E.F.A., Clamens, A.-L., Genson, G., Sperling, F.A.H. & Kergoat, G.J. (2015) Deciphering the evolution of birdwing butterflies 150 years after Alfred Russel Wallace. *Scientific Reports*, **5**, 11860. http://www.nature.com/articles/srep11860?WT.ec_id=SREP-704-20150707&spMailingID=49041677&spUserID=ODkwMTM2NjQzMwS2&spJobID=720800808&spReportId=NzIwODAwODA4S0.
- Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research. *InterJournal, Complex Systems*, **1695**, 1–9.
- Drury, J., Clavel, J., Manceau, M., & Morlon, H. (2015) Estimating the effect of competition on trait evolution using maximum likelihood. *bioRxiv*, 023473. <http://dx.doi.org/10.1101/023473> See <http://biorxiv.org/content/early/2015/11/10/023473.abstract>.
- Etienne, R.S., Haegeman, B., Stadler, T., Aze, T., Pearson, P.N., Purvis, A. & Phillimore, A.B. (2012) Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1300–1309.
- FitzJohn, R.G. (2012) Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution*, **3**, 1084–1092.
- Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538–549.
- Höhna, S. (2013) Fast simulation of reconstructed phylogenies under global time-dependent birth–death processes. *Bioinformatics*, **29**, 1367–1374.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Lartillot, N. & Poujol, R. (2011) A phylogenetic model for investigating correlated evolution of substitution rates and continuous phenotypic characters. *Molecular Biology and Evolution*, **28**, 729–744.
- Lewitus, E. & Morlon, H. (2015) Characterizing and comparing phylogenies from their Laplacian spectrum. *bioRxiv*, doi: 10.1093/sysbio/syv116. <http://sysbio.oxfordjournals.org/content/early/2015/12/11/sysbio.syv116.abstract>.
- Manceau, M., Lambert, A. & Morlon, H. (2015) Phylogenies support out-of-equilibrium models of biodiversity. *Ecology Letters*, **18**, 347–356.
- Morlon, H. (2014) Phylogenetic approaches for studying diversification. *Ecology Letters*, **17**, 508–525.
- Morlon, H., Parsons, T.L. & Plotkin, J.B. (2011) Reconciling molecular phylogenies with the fossil record. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 16327–16332.
- Morlon, H., Potts, M.D. & Plotkin, J.B. (2010) Inferring the dynamics of diversification: a coalescent approach. *PLoS Biology*, **8**, e1000493.
- Nee, S., Mooers, A.O. & Harvey, P.H. (1992) Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences*, **89**, 8322–8326.
- Paradis, E., Claude, J. & Strimmer, K. (2004) APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics*, **20**, 289–290.
- Pennell, M.W., Eastman, J.M., Slater, G.J., Brown, J.W., Uyeda, J.C., FitzJohn, R.G., Alfaro, M.E. & Harmon, L.J. (2014) geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics*, **15**, 2216–2218.
- Pigot, A.L. & Etienne, R.S. (2015) A new dynamic null model for phylogenetic community structure. *Ecology Letters*, **18**, 153–163.
- R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rabosky, D.L. (2014) Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE*, **9**, e89543.
- Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.
- Rolland, J., Condamine, F.L., Jiguet, F. & Morlon, H. (2014) Faster Speciation and Reduced Extinction in the Tropics Contribute to the Mammalian Latitudinal Diversity Gradient. *PLoS Biology*, **12**, e1001775.
- Silvestro, D., Schnitzler, J. & Zizka, G. (2011) A Bayesian framework to estimate diversification rates and their variation through time and space. *BMC Evolutionary Biology*, **11**, 311.
- Soetaert, K.E.R., Petzoldt, T. & Setzer, R.W. (2010) Solving differential equations in R: package deSolve. *Journal of Statistical Software*, **33**, https://pure.knaw.nl/portal/files/462308/Soetaert_ea_4748.pdf.
- Stadler, T. (2011a) Mammalian phylogeny reveals recent diversification rate shifts. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 6187–6192.
- Stadler, T. (2011b) Simulating Trees with a Fixed Number of Extant Species. *Systematic Biology*, **60**, 676–684.
- Zachos, J.C., Dickens, G.R. & Zeebe, R.E. (2008) An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, **451**, 279–283.

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