***Title***

# Estimating clade-specific diversification rates and palaeodiversity dynamics from reconstructed phylogenies

***Authors***

Nathan Mazet[1]*, Hélène Morlon[2], Pierre-Henri Fabre[1,3,4] and Fabien L. Condamine[1]

***Affiliations***

[1]*Institut des Sciences de l'Evolution de Montpellier, CNRS, IRD, EPHE, Université de Montpellier, 34095 Montpellier, France*

[2]*Institut de Biologie de l'École Normale Supérieure (IBENS), École Normale Supérieure, CNRS, INSERM, Université PSL, 75005 Paris, France*

[3] Mammal Section, Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

[4]Institut Universitaire de France (IUF), Paris, France

***Corresponding author (*)***

Nathan Mazet

Email: nathan.mazet@umontpellier.fr

***Abstract***

One of the central goals of macroevolution is to understand palaeodiversity dynamics through time and space, and its potential drivers. Estimating palaeodiversity dynamics has been historically addressed with the fossil record because it directly reflects the past variations of biodiversity. Unfortunately, some groups or regions lack a good fossil record, and dated phylogenies can be useful to estimate deep-time diversification dynamics. Recent methodological developments have unlocked the possibility to investigate palaeodiversity dynamics with dated phylogenies by using birth-death models with non-homogeneous rates through time and across clades. One of them, which models rate heterogeneity as a local clock, seems particularly promising to detect clades whose diversity has declined through time. However, empirical applications of the method have been hampered by its lack of automation as leading the analysis by hand was costly and error-prone.

Here we propose an automation with additional features accounting for recent developments and we implement it in the R package RPANDA. We also test the approach with simulations focusing on its ability to detect shifts of diversification and to infer palaeodiversity dynamics. Finally, we illustrate the automation by investigating the palaeodiversity dynamics of Cetacea, Vangidae, Parnassiinae, and Cycadales.

Simulations showed that we accurately detected shifts of diversification although false shift detections were higher for complex diversification models. The median global error of palaeodiversity dynamics estimated with the automated model is low showing that the method can capture diversity declines. We detected shifts of diversification for three of the four empirical examples considered (Cetacea, Parnassiinae and Cycadales). These heterogeneities of diversification rates unveil a waxing-and-waning pattern due to a phase of negative net diversification rate embedded in the trees after isolating recent radiations.

Our work allows to easily apply non-homogeneous models of diversification in which rates can vary through time and across clades to reconstruct palaeodiversity dynamics. By doing so, we detected palaeodiversity declines among three of the four groups tested, highlighting that such periods of negative net diversification might be common. We discuss the extent to which this approach might provide reliable estimates of extinction rates and we provide guidelines for users.

*Keywords*

Birth-death model, macroevolution, palaeodiversity, rate heterogeneity, RPANDA.

## 1 | Introduction

Estimating palaeodiversity dynamics over geological timescales is a thrilling goal of macroevolution (Alroy et al. 2008; Quental and Marshall 2010; Morlon et al. 2011). This question is generally addressed with paleontological data because fossil records are direct witnesses of past diversity dynamics (Marx and Uhen 2010; Ezard et al. 2011). Unfortunately, the fossil record is not homogeneous over time, space, and groups (Close et al. 2020). Consequently, investigating evolutionary history of poorly fossilised groups relies on diversification analyses based on dated phylogenies (time-trees) mainly composed of extant species. Methodological developments in the field have focused on estimating the speciation rate (λ) and extinction rate (μ), which represent the pace at which lineages appear and go extinct, respectively, as well as the net diversification rate (denoted r) defined as the difference between them (Ricklefs 2007; Stadler 2013; Morlon 2014). A large variety of phylogenetic models allows testing evolutionary hypotheses on whether diversification rates are constant, vary over time (Rabosky and Lovette 2008; Morlon et al. 2010), across clades (Morlon et al. 2011; Rabosky et al. 2013; Maliet et al. 2019) or in association with species' traits (Maddison et al. 2007; FitzJohn 2012; Beaulieu and O'Meara 2016) or with environmental changes (Condamine et al. 2013, Condamine, Rolland & Morlon 2019). However, early studies have shown that reconstructed dated phylogenies can display heterogeneity of diversification rates across clades (Rabosky et al. 2007, Esquerré et al. 2019).

Among the methods developed to detect this heterogeneity (Alfaro et al. 2009; Stadler and Bokma 2013; Rabosky et al. 2013; Maliet et al. 2019; Barido-Sottani et al. 2020; Maliet & Morlon 2022), the model developed by Morlon et al. (2011) considers heterogeneity in diversification rate by testing for shifts in rates of diversification at specific branching points in the phylogeny. The diversification of subclades identified *a priori* based on taxonomy or

ecological traits, and the diversification of the ancestral group leading to these clades, hereafter called the backbone, can be analysed separately. The main advantage of this method is that each part of a phylogeny (subclades and backbone) can follow a different birth-death model, offering the opportunity to test biological hypotheses that create heterogeneity of diversification rate and thus reconstruct palaeodiversity dynamics for each part of the tree (Nee et al. 1992; Morlon et al. 2011; Morlon 2014). Doing so for Cetacea, Morlon et al. (2011) showed a good consistency in the trend of the palaeodiversity dynamics between the molecular phylogeny and the fossil record. Recent advances have improved palaeodiversity estimation with a probabilistic approach providing confidence intervals of palaeodiversity values (Billaud et al. 2020). Subclades might experience recent adaptive radiations due to the acquisition of key innovations (Jønsson et al. 2012; Drummond et al. 2012) while the backbone tree might display a different dynamic such as a waxing-waning pattern of diversification. The resulting heterogeneity of diversification rates cannot be detected in clade-homogeneous birth-death models because recently radiating clades can overshadow the estimation of extinction in other parts of the tree, and likely hamper the inference of a negative net diversification rate ($r < 0$, $\mu > \lambda$) that may explain such a period of diversity decline (Morlon et al. 2011). The waxing-waning pattern detected by Morlon et al. (2011) was promising, yet the approach developed in that paper, part of which was made accessible in the R package RPANDA (Morlon et al. 2016), has been applied to only a few empirical cases since it was proposed (Bacon et al. 2013; Legendre and Condamine 2018; Billaud et al. 2020; Chazot et al. 2021) because of the lack of automation.

The method developed by Morlon et al. (2011) requires manually isolating subclades and backbones, accounting for all pruned speciation events, applying diversification models, and testing all backbone(s)/subclade(s) combinations by hand. This is time-consuming, error-prone, and makes the method underutilized. In addition to making this method more

automatic and user-friendly, several aspects of its performance remain to be tested. It was shown that the method recovers unbiased rates of diversification and can detect periods of diversity decline (Morlon et al. 2011), but its ability to detect clade-specific shifts of diversification remains untested and can make the palaeodiversity dynamic challenging to recover (Burin et al. 2019). More generally, several studies have questioned our ability to estimate extinction rate from molecular phylogenies (Rabosky 2010, 2016; Louca and Pennell 2020; but see Nee et al. 1994; Morlon 2014; Beaulieu and O'Meara 2015). Historically, Nee et al. (1994) have demonstrated how to estimate constant extinction rate from molecular-dated phylogenies with extant species only. Some studies relaxed the assumption of constant rates (Rabosky and Lovette 2008, Stadler 2011a), but these models are homogeneous across clades. By being non-homogeneous across clades, the model of Morlon et al. (2011) brings better extinction rate estimates by revealing ancient periods of palaeodiversity decline (Stadler 2011b) in line with the fossil record (Marx and Uhen 2010). This model opens the possibility to investigate palaeodiversity dynamics for groups without good fossil records.

In this study, we automatize the approach developed by Morlon el al. (2011) and implement it in the R package RPANDA (Morlon et al. 2016). In addition, we provide several advances compared to the original method. In particular, we implement the possibility to test for a shift at the crown age of subclades, whereas the original version of the method tested shifts at the stem age of subclades (Morlon et al. 2011; Billaud et al. 2020). This rationale is motivated by the idea that clade radiations – may it be adaptive or simply rapid compared to the rest of the tree – are characterized by long stem branches at the crown of subclades, with fast speciation starting at the crown. We provide functions to calculate rates and diversity dynamics through time, including recent developments from Billaud et al. (2020) with new functions using automation outputs. Using simulations, we assess the performance of the approach to detect shifts and to infer palaeodiversity dynamics under various diversification

scenarios. We further illustrate the approach empirically by investigating the evolutionary history of four groups with well-sampled molecular-dated phylogenies (Cetacea, Vangidae, Parnassiinae and Cycadales), which have been previously analysed with other methods. We finally discuss both simulations and empirical cases to provide guidelines and recommendations when using this approach.

## 2 | Methods

### 2.1 | The clade-dependent time-dependent diversification model of Morlon et al. (2011)

Morlon et al. (2011) developed an exact analytical expression of a birth-death model of cladogenesis that estimates rate variation through time while accounting for undersampling thanks to a sampling fraction (denoted by $f$, $f$=1 if all described species are included in the phylogeny). The expression is defined backwards in time such that values for λ and μ for time-dependent models correspond to rate values at present ($t$=0) and α and β are their dependency parameters, respectively. Then, the assumed changes of diversification rates occur at specific branching points (nodes) of the reconstructed phylogeny, meaning that potential rate shifts on unobserved (extinct or unsampled) lineages are ignored (Moore et al. 2016; Barido-Sottani et al. 2020). Under such assumptions, their analytical expression holds and in particular their expressions of the probability that a lineage alive at time $t$ has no descendant in the sample at $t$=0 ($\Phi(t)$), and the probability that a lineage alive at time $t$ leaves exactly one descendant lineage at time $s < t$ ($\Psi(s, t)$, *i.e.* the probability of survival from $t$ to $s$, see Appendix S8 and S9 from Morlon et al. 2011). These two expressions allow expressing the likelihood of the backbone phylogeny by including the speciation event corresponding to the subclade. The probability $1 - \Phi(t_1^{cl})$ that the subclade survives from this branch point $t_1^{cl}$ is then included in the likelihood of the subclade expressed with the same formula. Finally, the

product of the likelihood of the subtree and the backbone phylogeny gives the global likelihood of the phylogeny while accounting for heterogeneity of diversification rates across clades. This global likelihood can be compared to the likelihood of a diversification model with a homogeneous model of diversification to see if the shift of diversification rate is supported. This can be extended to a phylogeny with multiple subclades following their own diversification rates and even shifts of diversification rates inside the backbone creating multiple backbones.

## 2.2 | Automation

### 2.2.1 | Implementation in RPANDA

Few empirical studies have applied the approach using a manual and sequential approach (Morlon et al. 2011; Bacon et al. 2013; Billaud et al. 2020; Chazot et al. 2021). Each shift was selected one by one among subclades defined *a priori* until either the inclusion of a new shift was no longer statistically supported or shifts at all nodes were supported. Our automated approach still relies on the *a priori* definition of a limited number of subclades in which shifts may have occurred, but contrary to the sequential approach it compares all combinations of these potential shifts at the same time. The simplest way to make an *a priori* selection of subclades is to follow the approach of Morlon et al. (2011) by choosing taxonomic subclades such as families. Moreover, taxonomic databases then often provide the information required to compute sampling fractions (i.e. clade-level taxonomic diversity) that are required by phylogenetic diversification models. The tested subclades can also correspond to clades of species sharing key-innovations or colonisation events to test the role of these biological events on the clade's diversification. Once subclades have been chosen *a priori*, the whole analysis is divided in four steps: (1) calculating sampling fractions for the subclades from the taxonomic database, (2) calculating all potential combinations of subclade(s) and

corresponding backbone(s) from the set of preselected subclades, (3) applying a set of diversification models (see section 2.2.2) to each part (subclades and backbone) of each combination to calculate global likelihoods and the corrected Akaike Information Criterion (AICc) for each combination and comparing their statistical support, and (4) computing the palaeodiversity dynamics with deterministic or probabilistic approaches. The four steps of the whole analysis are illustrated in **Figure 1**. By default, two constraints are applied: (1) $\lambda$ and $\mu$ must be strictly positive, and (2) $r$ ($\lambda$ - $\mu$) must be positive ($r > 0$) at the beginning of the diversification history(otherwise the clade goes extinct immediately).

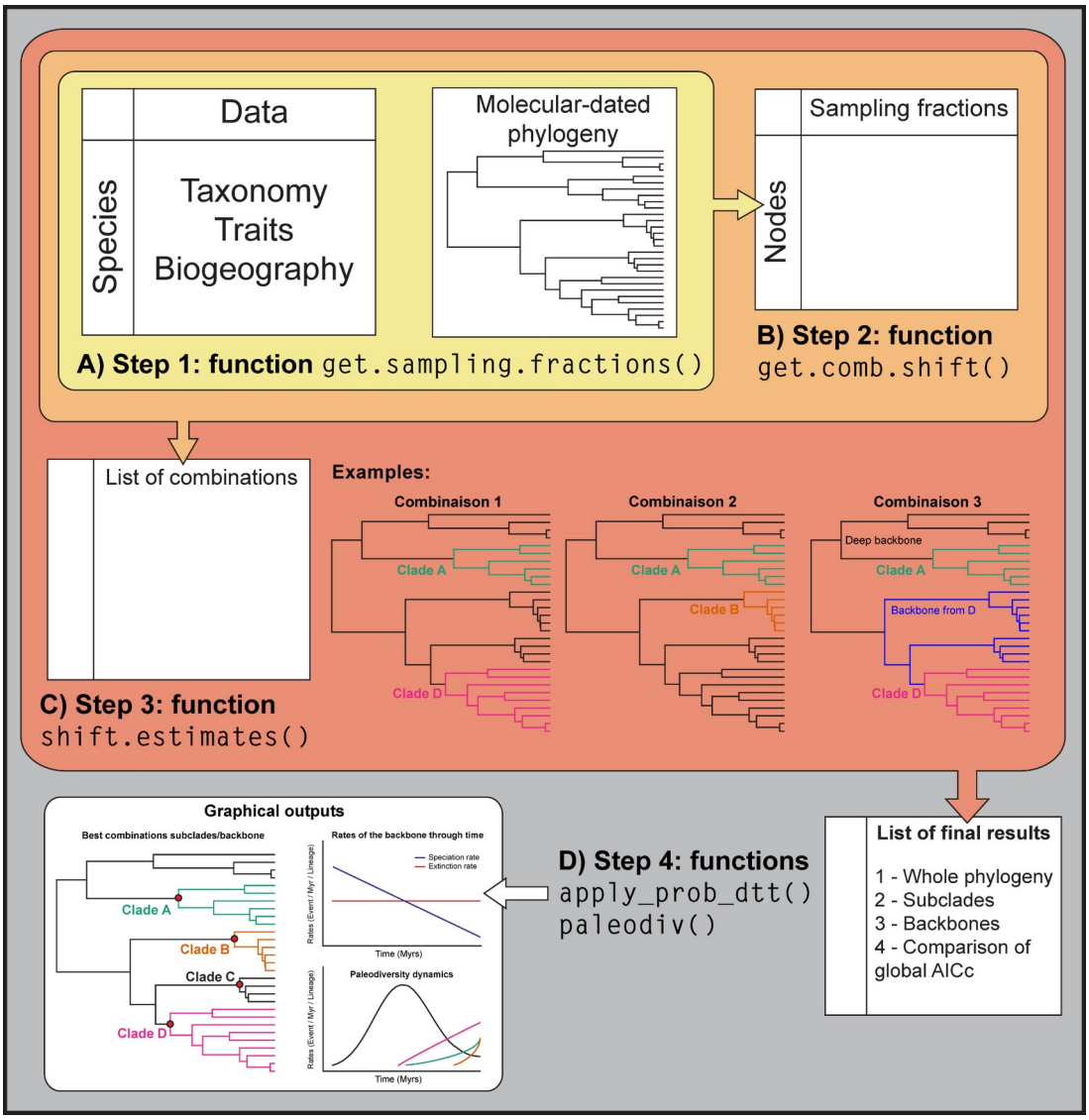


**Figure 1. Conceptualization of the analytical pipeline for the automation of the method presented in Morlon et al. (2011).** A) Step 1 calculates sampling fractions (*f*) from a database that contains all described species of the clade of interest and monophyletic subgroups (based on taxonomy or ecology); B) Step 2 calculates all the possible combinations of shifts (*e.g.* combination 1 has two shifts Clade A and D, the rest of the tree is included into the backbone tree); C) Step 3 applies a model comparison to select the best model for each part (subclades and backbone) of each combination. Then, it computes the likelihood and AICc of each combination, when using the best models. Finally, it selects the best supported combination. The final result is a list containing four elements: the model comparison for (1) the phylogeny analysed as a whole, (2) all subclades apart, (3) all backbones apart, and (4) the

comparison of all combinations of heterogeneous diversification models based on their global AICc (see Appendix S4 for example). D) Step 4 computes palaeodiversity dynamics either with the deterministic (function *paleodiv*) or probabilistic approach (function *apply_prob_dtt*).

### 2.2.2 | Set of diversification models

Several features have been implemented to perform different analyses. The minimum clade size for applying diversification can be defined at each step and should be the same during the application of the whole pipeline (argument clade.size, default is 5 tips). The set of diversification models applied by default in the model comparison corresponds to the six following birth-death models: (1) constant pure-birth model (BCST), (2) constant birth-death model (BCST_DCST), (3) pure-birth model with exponential time-dependency such as $\lambda(t) = \lambda_0 \times \exp(\alpha \times t)$ (BVAR), (4) birth-death model with exponential time-dependency for speciation rate and constant extinction rate (BVAR_DCST), (5) birth-death model with constant speciation rate and exponential time-dependency for extinction rate such as $\mu(t) = \mu_0 \times \exp(\beta \times t)$ (BCST_DVAR), and (6) birth-death model with exponential time-dependency for both speciation rate and extinction rate (BVAR_DVAR). A subset of these models can be used for all parts (subclades and backbones) with the argument models or only for subclades if, for example, extinction is not expected among subclades but only in the backbone(s) (see help files in RPANDA).

### 2.2.3 | Testing shifts at crown or stem age

Originally, the probability of the speciation event at the stem age was included in the likelihood of the backbone, while the probability that the stem of the subclade survives to the crown age was included in the likelihood of the subclade. Hence, the shift of diversification is

located at the stem age. However, when phylogenies are usually analysed with diversification models, the stem branch is rarely included. Moreover, adaptive or rapid radiations are expected to start at the crown age of the clade. We implemented the possibility to test for shifts at crown ages of subclades by including the probability that the stem of the subclade survives to the crown age in the likelihood of the backbone. In other words, it means that the change in diversification rates synchronously occurs with the cladogenesis event as it could be expected under an adaptive radiation. Users can choose to test for a shift at the stem age (backbone.option="stem.shift") as in Morlon et al. (2011), or at the crown age of the subclade (backbone.option="crown.shift", see Appendix S1 for more details).

#### 2.2.4 | Multiple backbones

Shifts of diversification can also be nested creating combinations of shifts with more than one backbone (multiple backbones) in the phylogeny (Figure 1B, combination 3). We recommend to start investigating the heterogeneity of diversification with a simple backbone (no shift in the backbone) to first capture the main tendency of the backbone (option multi.backbone=F in function shift.estimates). This might be interesting if there are a lot of combinations with multiple backbones. Combinations with multiple backbones can then be analysed using the option multi.backbone=T or all combinations can be analysed at once with the option multi.backbone="all".

#### 2.2.5 | Palaeodiversity dynamic estimation and constraints

Morlon et al. (2011) used a deterministic calculation of the palaeodiversity dynamics corresponding to the solution of the differential equation relating the time variation in the number of lineages to the rate values of the birth-death model (see Box 4 in Morlon 2014 for more details). Our automation also includes recent developments on palaeodiversity dynamic

estimates (Billaud et al. 2020), a probabilistic approach to infer a confidence interval around the palaeodiversity curve. Functions that are already included in the R package RPANDA 2.0 (Morlon et al. 2016) have been slightly modified to be used with outputs of the shift.estimates() through a new function called apply_prob_dtt(). Palaeodiversity dynamics are computed independently for subclades and backbones. Two optional constraints are embedded in the optimisation process: maximum rate value and maximum number of species estimates can be constrained with a maximum value (argument rate.max and n.max) for each part of the combinations. The constraint applied on palaeodiversity uses the deterministic approach to calculate maximum values of palaeodiversity dynamics and penalised the likelihood during the optimisation process if the maximum values exceed the constraint.

**2.3 | Simulations**

We used simulations to test whether the approach successfully detects diversification shifts and correctly estimates palaeodiversity dynamics (**Figure 2**). We simulated four diversification scenarios following Billaud et al. (2020). All trees were simulated forward in time over 100 million years (Myrs, $T_{max}$=100) with the R package TESS 2.1.0 (Höhna et al. 2016). For both waxing-waning models, α and β values were defined such that the diversity decline starts between the last third and the last quarter of the phylogenetic tree (*i.e.* between 33 and 25 Myrs ago in our case). Rate values were selected such as they respect the following conditions:

1. Expanding diversity: constant pure-birth model (BCST) with $\lambda \in [0.05; 0.25]$ and $\mu$=0 (**Figure 2A**).
2. Saturing diversity: pure-birth model with exponential time-dependency (BVAR) with $\lambda_{(t)}=\lambda_0\exp(-\alpha t)$ with $\lambda_0 \in [0.05; 0.25]$ and $\alpha$ such that $T_{eq}$ satisfies $\exp(-\alpha T_{eq})=0.5$ is in $[T_{max}2/3; T_{max}3/4]$ and μ=0 (**Figure 2B**).

3 Waxing-waning (with decreasing speciation): birth-death model with exponential time-dependency for speciation rate and constant extinction rate (BVAR_DCST) with $\lambda_{(t)}=\lambda_0\exp(-\alpha t)$ with $\lambda_0 \in [0.2; 0.4]$ and $\mu=\lambda_0/2$ and $\alpha$ such that $T_{eq}$ satisfies $\exp(\alpha T_{eq})=\mu/\lambda$ in $[T_{max}2/3; T_{max}3/4]$ (**Figure 2C**).

4 Waxing-waning (with increasing extinction): birth-death model with constant extinction rate and exponential time-dependency for speciation rate (BCST_DVAR) $\lambda \in [0.2; 0.4]$ and $\mu(t)=\mu_0\exp(\beta t)$ with $\mu_0=\lambda/2$ and $\beta$ such that $T_{eq}$ satisfies $\exp(\beta T_{eq})=\lambda/\mu$ in $[T_{max}\ 2/3; T_{max}3/4]$ (**Figure 2D**).

We retained the simulated trees containing at least 40 species. We simulated the diversification shift by grafting a new simulated tree at a specific node defined as the more recent node among nodes between 33 and 25 Myrs ago (**Figure 2F**). This node must have a minimum of five extant descendant species to avoid applying diversification models on a species-poor clade when testing for the detection of a shift on raw phylogenies (*i.e.* when there is no shift). For trees with a shift of diversification, the grafted tree follows a pure-birth model (BCST) with $\lambda$=0.1 (**Figure 2E**). This tree was grafted at its crown age and must contain at least 15 species. Because the shift was simulated at the crown age, the search for shift was also conducted at crown ages.

We quantified whether the model detected a shift of diversification while no shift was simulated (*i.e.* false detection of shifts). Following Billaud et al. (2020), we also calculated the global error *D* between the estimated and the expected diversity curves, calculated with the deterministic approach for each simulation (see Appendix S2 for details). Simulations were set up with Snakemake 5.2.4 and R 3.6.3 using the R packages ape 5.5 (Paradis et al. 2019), phytools 0.7-80 (Revell 2012), TESS 2.1.0 (Höhna et al. 2016), phangorn 2.7.0 (Schliep 2011), and RPANDA 2.0 (Morlon et al. 2016, see Appendix S2 for more details).

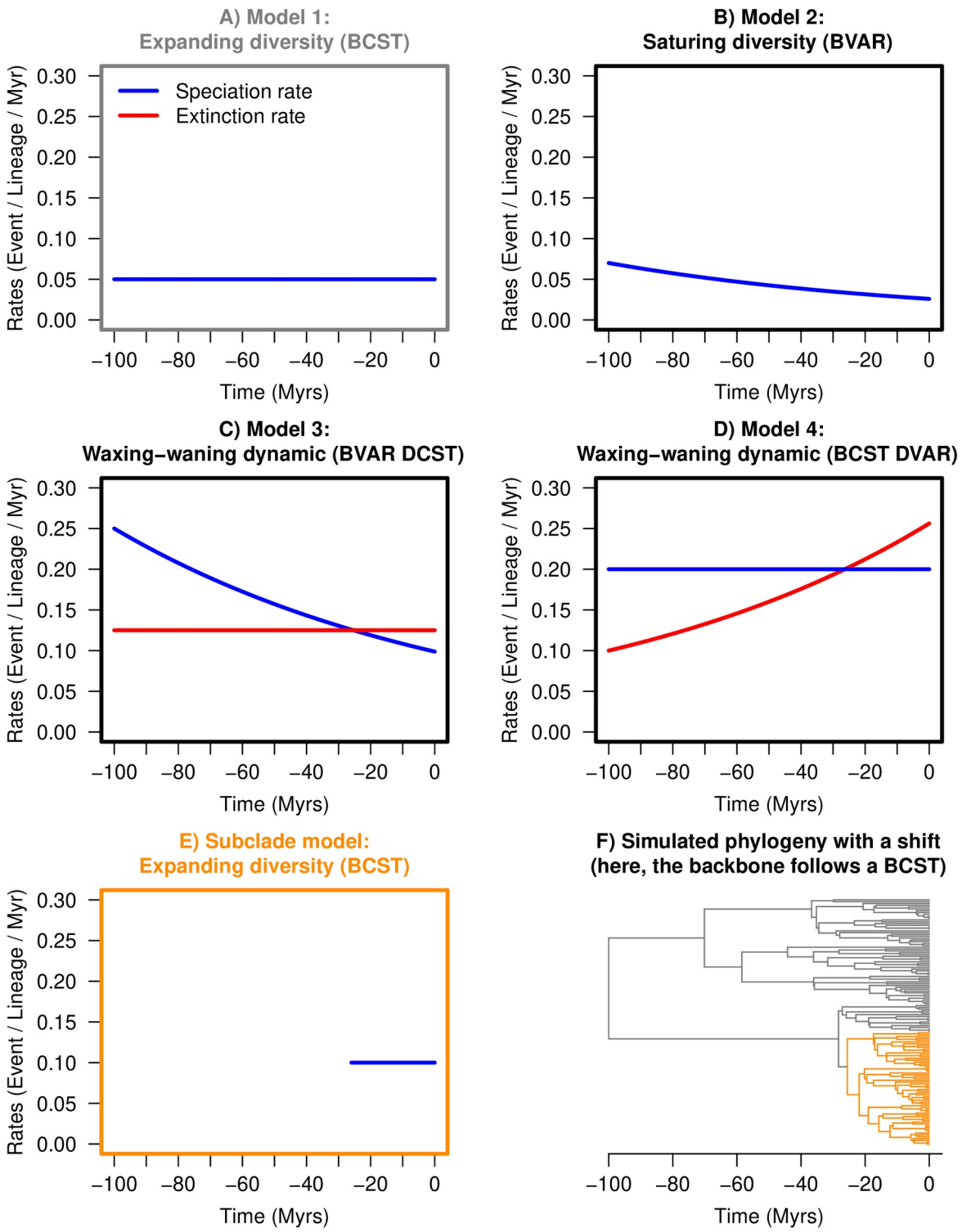


**Figure 2. Simulation pipeline.** A) to D) Diversification rates through time for the models used to simulate the backbone (grey). E) Diversification model used for the subclade (orange). F) Example of a simulated phylogeny with a rate shift shown in orange (the backbone is simulated with the Model 1).

## 2.4 | Applications to empirical phylogenies

We tested the automated pipeline on four clades representing a large diversity of taxa to illustrate the potential of the approach. First, we applied the approach to the original example of Morlon et al. (2011), the cetacean phylogeny published by Steeman et al. (2009). To compare with previous results, we used the same taxonomy as in Morlon et al. (2011) with a global sampling fraction of 98% (87/89 species). We looked for diversification shifts for the four main families (Balaenopteridae, Delphinidae, Phocoenidae and Ziphiidae) and for the two parvorders (Odontoceti and Mysticeti). We tested shifts at the crown age (backbone.option="crown.shift") of subclades but also at the stem age (backbone.option="stem.shift" see Appendix S2) as in Morlon et al. (2011) to compare both approaches.

Second, we tested a group without expected diversity decline, and studied the phylogeny of Vangidae (Jønsson et al. 2012), which is a small but fully sampled group (32/32 species). In their study, the authors detected two diversification shifts and concluded that this group has experienced adaptive radiation involving changes in beak size and body mass. We thus tested these hypotheses.

Third, we applied the approach to Parnassiinae, a subfamily of swallowtail butterflies (Condamine et al. 2018) with a good sampling fraction (96.6%, 85/88 species). Shifts of diversification can also come from ecological changes such as colonisation of new environments (Yoder et al. 2010) or host-plant shifts (Ehrlich and Raven 1964). We tested hypotheses related to host-plant shifts, Himalayan Mountain colonisations, and taxonomic groups.

Finally, we investigated the diversification history of Cycadales (Nagalingum et al. 2011). The sampling fraction of this group is equal to 72.5% (231/327 species, IUCN 2021). This group originated 275 Myr ago and almost all extant species emerge from recent radiations during the Miocene (Condamine et al. 2015). We tested shifts for all genera with

more than five species described except *Dioon*, which is the least sampled (8/13 species). To account for uncertainty in divergence time estimates, we applied the approach to posterior trees and calculated the corresponding range of the palaeodiversity dynamics with the deterministic approach. This allows measuring variation of palaeodiversity estimates on a large panel of posterior trees and therefore accounting for uncertainties on divergence time estimates. We also calculated the palaeodiversity dynamics with the probabilistic approach to account for uncertainty of diversity estimates (Billaud et al. 2020).

For all empirical cases, we did not use the BVAR_DVAR model because it often produced unrealistic estimates and has already been discussed as problematic (Burin et al. 2019). We also detailed an example with the BVAR_DVAR model in Appendix S4 to illustrate our choice.

### 2.5 | Posterior predictive analyses

To support the results on empirical phylogenies, we implemented posterior predictive analyses to test whether data simulated from empirical results are similar to empiricial data. For each empirical case where shifts of diversification are identified, we simulated 500 phylogenies with the same combination of shifts that the best result by using the crown age and the diversification rates of subclade(s) and backbone(s). We developed the simul_posteriors() function to simulate those phylogenies, which are then analysed by looking at the proportion of points of the empirical LTT contained in the 95% confidence interval of the LTT from the simulated trees (explained in detail in Appendix S4 for each case).

## 3 | Results

### 3.1 | Simulations

The simulation plan was set up to test both shift detections and palaeodiversity dynamic estimates. The analyses of the simulations initially revealed high proportions of false detections of shift (>11%, **Figure 3**, light orange). These false detections of shift led us to look at what they would be without the model selection procedure, *i.e.* if we fitted only the true (simulated) models rather than selecting the best model from the set of models applied to subclades, backbones and the whole phylogeny. By doing this, proportions of false detections of shift dropped below 10% (**Figure 3**, light blue). This finding sheds light on two problems: (1) the model selection, and (2) even with the simulated models, proportions of false detections of shift are higher than 5%. This latter problem shows that when a homogeneous model is simulated, splitting the optimisation of this model into a subclade and a backbone provides a gain of likelihood at the subclade level that is not penalised enough to avoid selecting a shift. We solved this by arbitrarily adding an extra penalisation with an additional parameter for the shift in the AICc calculation. This additional parameter can be thought as corresponding to the shift location as in previous methods such as MEDUSA (Alfaro et al. 2009); although the locations of the shifts are less free to vary in our approach that in MEDUSA, where all nodes are tested, they still need to be selected among a set. With this additional parameter and when fitting the models that were simulated, proportions of false detections of shift decreased below 5% (**Figure 3**, dark blue). If we use this additional parameter but used models that were selected rather than those that were simulated, proportions of false detections of shift are equal to 3.3% for BCST, 2.4% for BVAR, 13.8% for BVAR_DCST, and 22.7% for BCST_BVAR (**Figure 3**, dark orange). These results are satisfactory for simple models (BCST and BVAR) but false detections of shift are still important for more complex models.

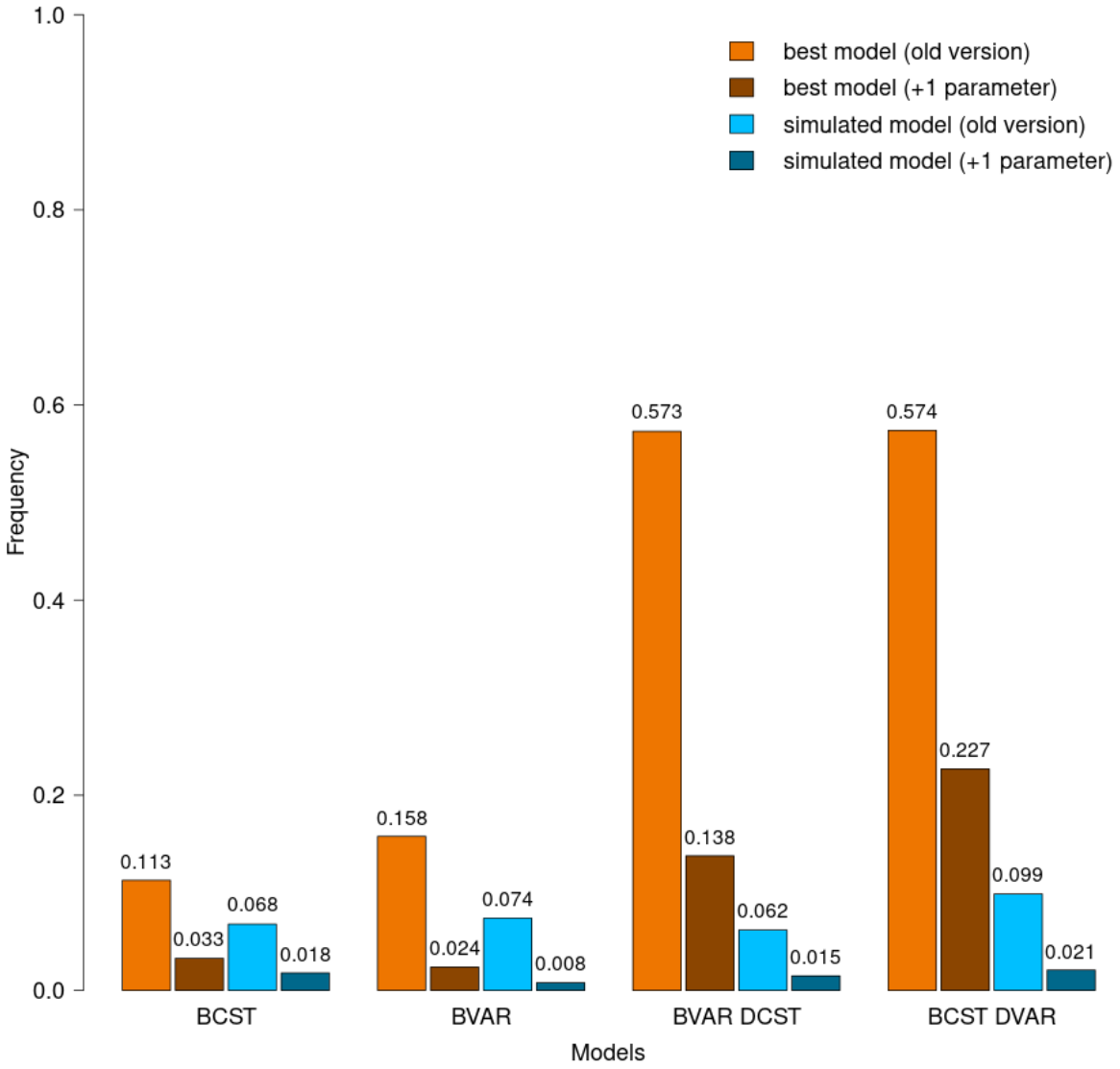


**Figure 3. Proportions of false detection of shifts by models used to simulate the backbone depending on the method.** Values for best-fitting models (in shades of orange) include the step of model selection for each part (subclade and backbone) while values for simulated models (in shades of blue) are calculated using the simulated models (no model selection). "Old version" corresponds to the AICc calculation from Morlon et al. (2011) and "+1 parameter" corresponds to the addition of one parameter for the location of the shift.

Concerning palaeodiversity dynamics, the main tendency (decline or not) is well recovered (BCST=97.35%, BVAR=84.6%, BVAR_DCST=89.5%, BCST_DVAR=92.65%).

More precisely, we compared palaeodiversity curves from simulated rate values with palaeodiversity curves from estimated rate values. Figure 4 represents these comparisons for simulations that get a global median error *D* equal to the three quartiles of *D* for each model. We found rather low global median errors *D* for simpler models (BCST and BVAR models) (**Figure 4**). More complex models have slightly higher median values of *D* (BVAR_DCST and BCST_DVAR models), **Figure 4**). First and third quartiles follow the same tendency as the median across models, with higher values of *D* for more complex models. The mean of median values of *D* across the different models is equal to 0.233. There is no specific bias neither towards overestimation nor underestimation of palaeodiversity (Appendix S3).

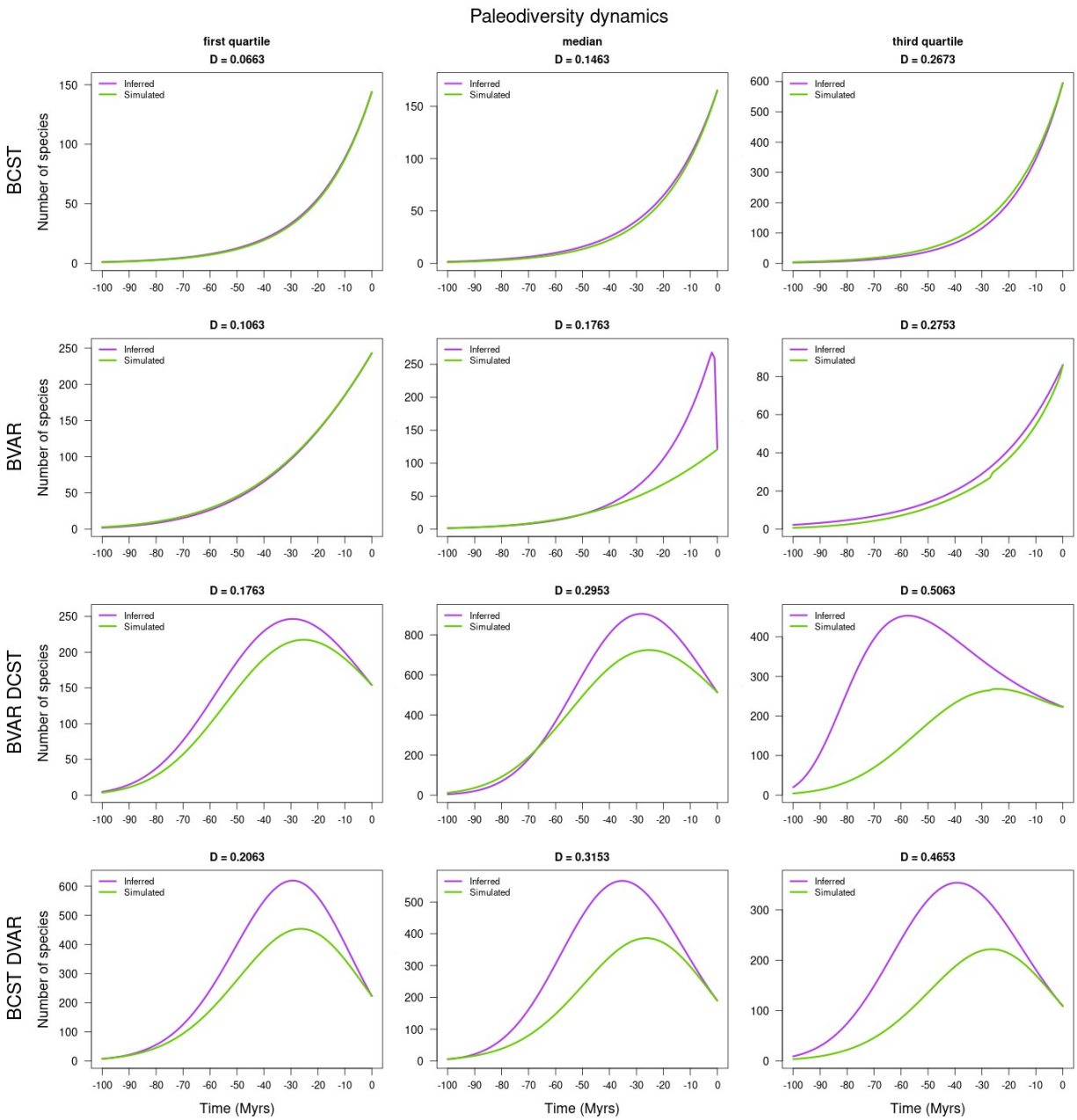


**Figure 4. Comparison of inferred versus simulated palaeodiversity dynamics by model, with increasing global error *D*.** For each model (in row) inferred palaeodiversity (purple) and simulated palaeodiversity (in green) are compared for the three quartiles of the global error *D* distributions by model (in column); see Appendix S3 for details. Note that the inferred palaeodiversity with the BVAR model (median) corresponds to a false detection of shift with the selection of a BVAR DCST model for the backbone creating this decline.

## 3.2 | Empirical evidence of extinction from phylogenies

### 3.2.1 | Cetacea

As in Morlon et al. (2011), we tested the presence of shifts in diversification at the base of the four main and recently diverged families (Balaenopteridae, Delphinidae, Phocoenidae and Ziphiidae) and the two parvorders (Mysteceti and Odotonceti) of Cetacea. This selection of subclades creates 25 combinations of shifts with a single backbone and 47 combinations of shifts if we add combinations with multiple backbones. When testing the shifts at the crown of subclades, we detected a single best combination with shifts for the four families tested (Table S1, ΔAICc=8.50). All the subclades follow a model with a decreasing speciation rate through time (see Appendix S4 for details). The simple backbone of this combination follows a model of diversification with a constant speciation rate and an increasing extinction rate leading to a phase of decline starting at 10 Ma before present, with a peak of palaeodiversity at 596 species (**Figure 5**). The same analysis with shifts tested at stem ages provides a best combination with a lower global AICc (Appendix S1, Table S5).

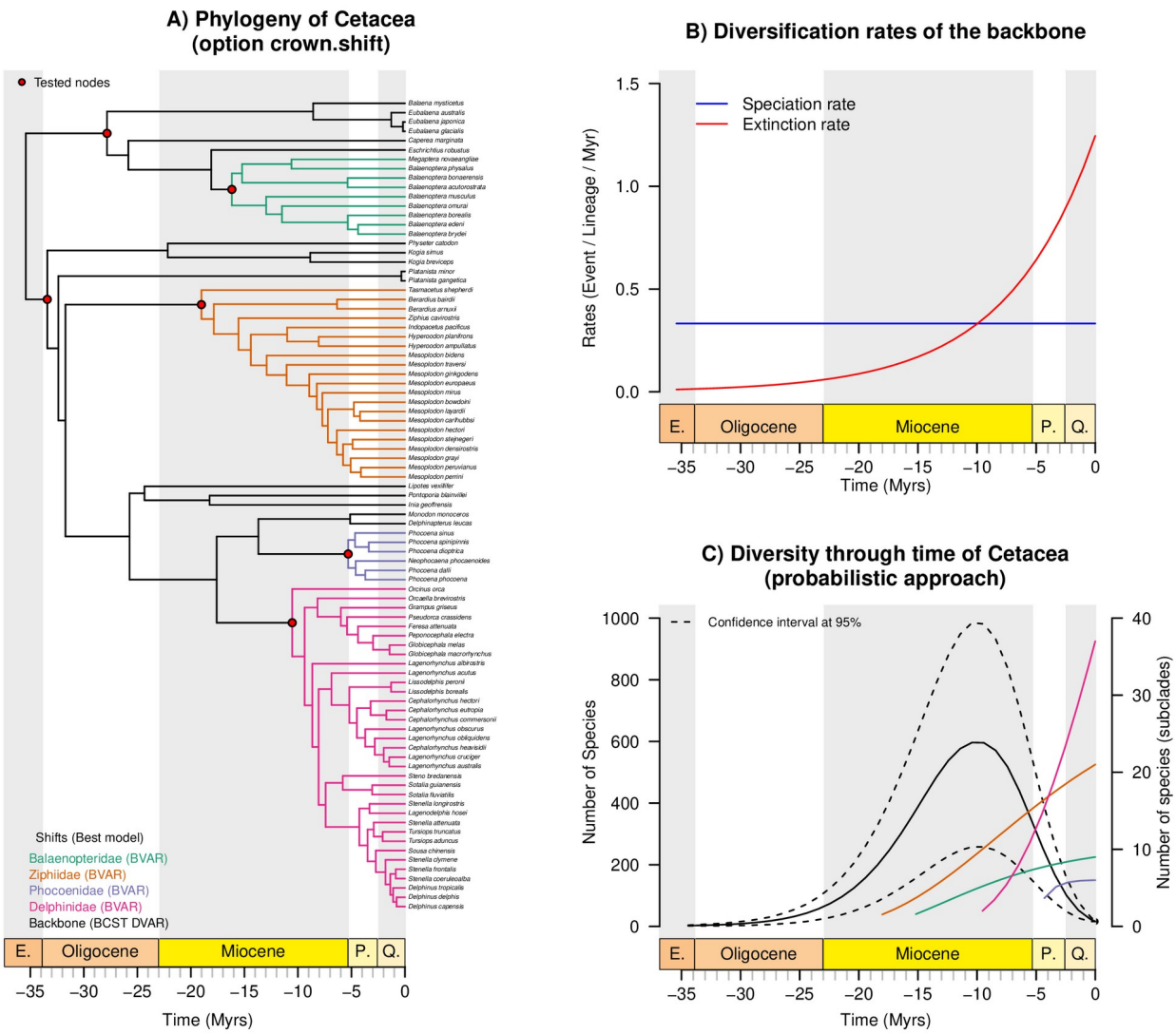


**Figure 5. Diversification shifts and palaeodiversity dynamics estimated for Cetacea with shifts tested at crown ages.** A) The phylogeny of Cetacea with shifts highlighted in colours and best models in parenthesis. Red dots correspond to all tested nodes. B) The evolution of diversification rates through time. C) The palaeodiversity dynamic estimated with the probabilistic approach. Dotted line represents the confidence interval of diversity estimates for the backbone at 95% calculated with the probabilistic approach. For the sake of clarity, confidence intervals of diversity estimates for subclades are not represented.

### 3.2.2 | Vangidae

We tested shifts at three nodes in the Vangidae phylogeny corresponding to the Malagasy Vangidae clade and two nodes where shifts of morphological evolution have been detected in a previous study (Jønsson et al. 2012). Because these nodes are nested and there are only 32 species, only five combinations result from this initial selection of subclades. We did not detect any shift of diversification, and a model for the phylogeny without shift remains better (Table S2, ΔAICc=3.38) than other combinations. The whole phylogeny follows a model with a decreasing speciation rate resulting in a palaeodiversity increase through time, which slows down to present and reaches the current diversity of 32 species (**Figure 6**).

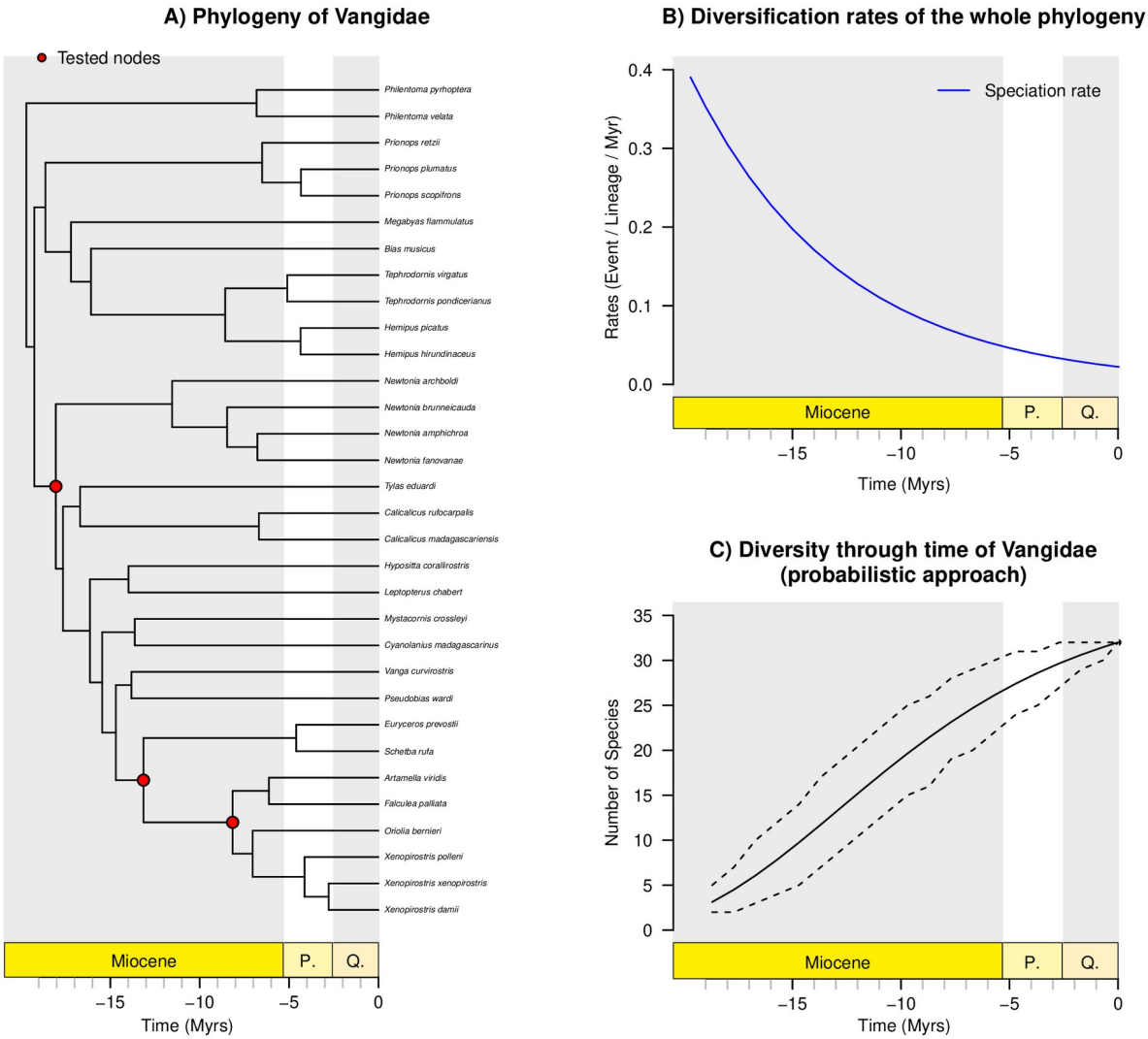

**Figure 6. Diversification shifts and palaeodiversity dynamics estimated for Vangidae with stems included in backbone analysis.** A) The phylogeny of Vangidae without shift detected (crown shifts). B) Diversification rates through time. C) The palaeodiversity dynamic estimated with the probabilistic approach. Dotted line represents the confidence interval of diversity estimates for the backbone at 95% calculated with the probabilistic approach.

### 3.2.3 | Parnassiinae

We tested 11 shifts corresponding to tribes (Luehdorfiini, Parnassiini, Zerynthiini), genera (*Allancastria*, *Parnassius*), subgenera (*Driopa*, *Tadumia*, *Kailasius*, *Koralius*, *Parnassius*), of which some match with host-plant shifts (genus *Parnassius*) or colonisation of Himalayan mountains (*Kailasius*, *Koramius*). This selection creates 392 combinations to compare with a single backbone and 1079 by adding combinations with multiple backbones. First results showed unrealistically high rates of diversification leading to unlikely palaeodiversity curves highlighting limits of some models (see Appendix S4 for details). We then repeated the analysis by constraining the rates to a maximum value of 2 and found three best combinations among the 1079 combinations (Table S3, ΔAICc=2.13). Among these three best combinations, the first and the third combination of shifts showed highly unrealistic palaeodiversity dynamics despite the applied constraint on rate values. Given that the three combinations are statistically equivalent (ΔAICc < 2), we only kept the second combination that was more biologically realistic (ΔAICc=1.11 with the first combination, see Appendix S4 for details). Among the tested shifts, seven shifts compose the best combination with tribes (Luehdorfiini, Zerynthiini) and subgenera (*Driopa*, *Tadumia*, *Koramius*, *Kailasius* and *Parnassius*, **Figure 7**). The tribes Luehdorfiini, Zerynthiini and both subgenera *Parnassius* and *Tadumia* follow a model with a constant speciation rate while subgenera *Driopa*, *Kaliasius* and *Koramius* follow a model with a decreasing speciation rate through time. The

backbone follows a model with a constant speciation rate and an increasing extinction rate through time (**Figure 7b**), leading to a period of negative net diversification rate from the beginning of the Miocene (19 Myrs ago) from the peak of the palaeodiversity of 324 species to the diversity of 88 extant species. This creates a palaeodiversity decline at the beginning of the Miocene.

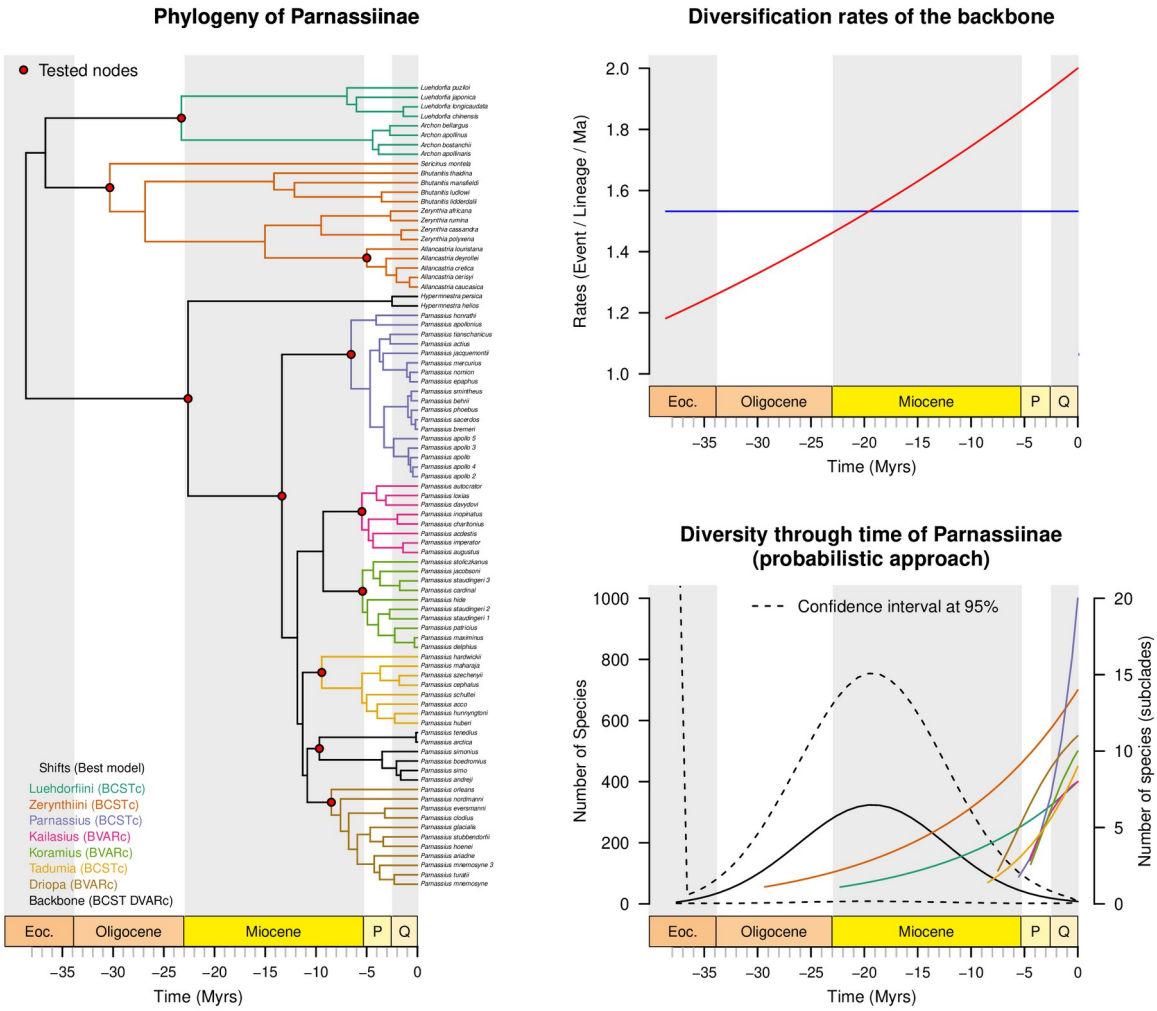


**Figure 7. Diversification shifts and palaeodiversity dynamics estimated for Parnassiinae with stems included in backbone analysis.** A) The phylogeny of Parnassiinae with shifts highlighted (crown shifts) in colours and best models in parenthesis. Red dots correspond to all tested nodes. B) Diversification rates through time. C) The palaeodiversity dynamic estimated with the probabilistic approach. Dotted line represents the confidence interval of

diversity estimates for the backbone at 95% calculated with the probabilistic approach. For the sake of clarity, confidence intervals of diversity estimates for subclades are not represented.

### 3.2.4 | Cycadales

We tested five shifts with the genera *Cycas*, *Ceratozamia*, *Zamia*, *Macrozamia*, and *Encephalartos*. This selection creates 32 combinations with a simple backbone and none with multiple backbones. The best combination is composed of all the tested subclades (Table S4, ΔAICc=11.96). The genera *Cycas*, *Ceratozamia* and *Macrozamia* follow pure-birth models with a constant speciation rate, while *Zamia* and *Encephalartos* follow models with a decreasing speciation rate (**Figure 8a,** Appendix S4). The diversification model of the backbone has a constant speciation rate and an increasing extinction rate, creating a negative net diversification rate starting 130 Myrs ago during the Early Cretaceous (**Figure 8b**). The global palaeodiversity increased again and reached the extant diversity thanks to the radiations of extant genera during the Miocene. The peak of palaeodiversity calculated with the deterministic approach reaches 200 species and ranges on posterior trees from 500 to 100 species (**Figure 8c**). The probabilistic approach estimates 150 species at the palaeodiversity with a confidence interval ranging from 400 to 0 species (**Figure 8d**).

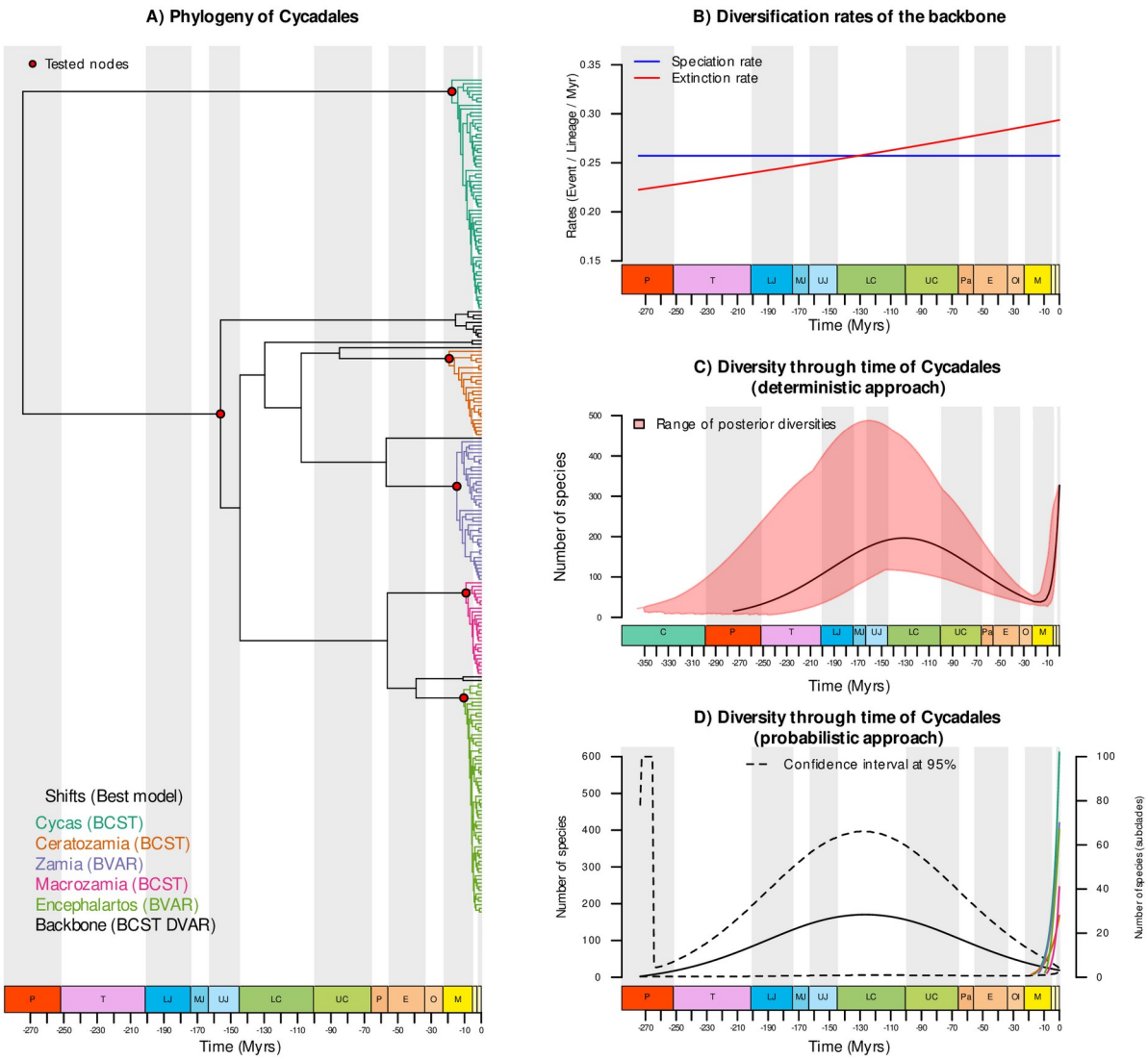


**Figure 8. Diversification shifts and palaeodiversity dynamics estimated for Cycadales with stems included in backbone analysis.** A) The phylogeny of cycads with shifts highlighted (crown shifts) in colours and best models in parenthesis. Red dots correspond to all tested nodes. B) The evolution of diversification rates through time. C) The palaeodiversity estimated with the deterministic approach. The red area represents the range of palaeodiversity estimates calculated on posterior trees. D) The palaeodiversity dynamic estimated with the probabilistic approach. Dotted line represents the confidence interval of diversity estimates for the backbone at 95% calculated with the probabilistic approach. For the sake of clarity, confidence intervals of diversity estimates for subclades and species names are not represented.

## 3.3 | Posterior predictive analyses

The posterior predictive analyses allowed us to check how empirical data were close to a set of trees simulated from the parameters of the best combinations of shifts for each empirical case. Overall, 98.7% of the empirical LTT values of the Cetacea falls into the 95% confidence interval defined on the LTT from the posterior predictive trees (Figure S5A). This statistic is a bit lower for Parnassiinae with 82.5% and slightly higher for Cycadales with 99.6% (Figure S5B and C; see Appendix S4 for details).

## 4 | Discussion

In this study, we automated and implemented in RPANDA, tested with simulations, and illustrated with empirical cases the approach developed by Morlon et al. (2011) that allows detecting shifts of diversification and estimating palaeodiversity dynamics through time from dated phylogenies. Several options and functions have been added to make this approach largely accessible to address an array of questions about heterogeneity of diversification rates and palaeodiversity dynamics by consolidating the challenging field of macroevolution in adopting hypothesis-driven approaches (Morlon et al. 2022). This emphasises the importance of additional information from biological knowledge on the focal groups to compare scenarios motivated by biological hypotheses (*e.g.* Legendre and Condamine 2018). In this sense, integrative taxonomic work is fundamental as it summarises broad morphological, ecological, and geographical divergences without neglecting historical divergence of clades thanks to phylogenetic analyses. Beyond taxonomy, ecological data, or other analyses such as ancestral state estimations can ground hypotheses for selecting subclades if the sampling fraction is known.

From a biological point of view, diversification histories are more complex than birth-death models. Accordingly, one should keep in mind that underlying assumptions of models influence the results. Among time- and clade-heterogeneous approaches, the most popular model, BAMM, investigates shifts along branches and does not allow periods of decline of

diversity (Rabosky et al. 2013). The Multi-Type Birth-Death model developed by Barido-Sottani et al. (2020) provides a Bayesian framework that investigates shifts thanks to type-specific birth and death rate without defining location of the type changes. ClaDS models rate heterogeneity with small but frequent shifts (Maliet et al. 2019). MiSSE is an extension of HiSSE models that focuses on trait-free shifts and investigates heterogeneity of diversification rates at the tips of phylogenies (Vasconcelos et al. 2022). These alternative approaches can be used in a complementary way to study heterogeneity of diversification but will not necessarily provide similar results because of their underlying assumptions on diversification rates. Globally, each model is better at finding what it is made for: BAMM performs better to find large discrete shifts and will underestimate finer heterogeneity while ClaDS and, to a lesser degree MiSSE, will perform relatively worst in looking for large shifts but will be more accurate for small and more frequent changes of diversification rates (see Vasconcelos et al. 2022 for a comparison between BAMM, ClaDS and MiSSE). In our model, rates of birth-death models are either constant or exponentially variable over time and shifts occur at specific branch points. Despite the uncertainty being higher deep in the past, the main advantage of our approach is to provide inference of palaeodiversity dynamics by better estimating palaeodiversity values during deep periods, with the probabilistic approach to calculate palaeodiversity dynamics (see Billaud et al. 2020).

Previous studies on Vangidae (Jønsson et al. 2012), on Cetacea (Rabosky 2014), on Parnassiinae (Condamine et al. 2018), and on Cycadales (Condamine et al. 2015) have investigated heterogeneity of diversification with other methods. The cladogenesis test used for the Vangidae found one significant and one marginal shift among the nodes we tested. Contrary to the cladogenesis test that looks at the number of descendants from a node relatively to what is expected under a null birth-death model, our method applies and compares various birth-death models. Finding no shift can then come from the small size of

the phylogeny but might also highlight that our approach is more conservative in detecting shifts in small phylogenies. Interestingly, BAMM analyses on the three other empirical cases estimated less diversification shifts (one in Cetacea vs. four here, one in Parnassiinae vs. seven here, and four in Cycadales vs. five here). This confirms that BAMM might be conservative in rate shift detection, although it has been shown to concern shifts with small clade sizes (Mitchell et al. 2019). Moreover, BAMM did not detect palaeodiversity decline contrary to our inferences. For instance in Parnassiinae, we found a decline starting at 19 Ma from a peak at 324 species to the current diversity of the backbone (8 species). This is consistent with Condamine et al. (2018) who applied models assuming instantaneous drops of diversity through time at specific time points (Stadler 2011a; May et al. 2016). This study found a sudden extinction around 15 Ma, 4 Myrs later, with a loss of 89% of the diversity (from 90 species to 10). Both methods recover a decline of diversity, although different assumptions behind each model (mass extinction vs. exponential dependency to time) influence the inferred timing and the scale of the decline.

The approach we automated has already been recognized for its ability to better estimate extinction rates (Stadler 2011b). Our simulations confirm the capacity of the model to recover non-zero extinction rate in the backbone that can exceed speciation rate, resulting in a diversity decline. Despite the high values of false detection of shifts for complex models, the difference between observed and simulated palaeodiversity was reasonable with a mean of median global error $D$=0.233 on average over models and close to the value found in Billaud et al. (2020) with a $D$=0.22. This result shows that even with an error on the detection of shift, the model estimates a trustworthy palaeodiversity dynamic (**Figure 4**). Moreover, our empirical analyses, confirmed by posterior predictive analyses, suggest diversity declines are more widespread than previously considered. Cetacea, Parnassiinae, and Cycadales show a common pattern with a single period of decline, but we can address the question to what

extent patterns with many diversity declines might be detected. Indeed, the main limit of our approach is that important levels of extinction are likely to erode both diversity and statistical power. Splitting a phylogeny into backbones and subclades requires enough species to be shared in different parts that will be analysed separately. Dated phylogenies with only a few extant species cannot be investigated by our approach although we sometimes know from the fossil record that they experienced extinction. The clade of Ginkgophyta is a caricatural example of this problem as it only contains one lineage (*Ginkgo biloba*) despite 275 Ma of evolution, and probably experienced a lot of extinction events (Royer et al. 2003). An interesting perspective will be to simulate more complex patterns of extinction with multiple backbones and multiple periods of decline to see whether we can properly recover these patterns.

Concerning subclades, we recovered only models without extinction, although some subclades are quite ancient (*e.g.* in Parnassiinae). We ran some simulations that tend to confirm the difficulty to select models with extinction in subclades (see Appendix S3 for details). This is not surprising given the small size of subclades (*e.g.* six species of Phocoenidae in Cetacea), which do not provide sufficient sample size to select parameter-rich models (i.e. with extinction). Low extinction rates in subclades can also be a real pattern in some cases. For the Cetacea, the phylogenetic placement of fossils indicates that extinct taxa are concentrated in the backbone (in particular along stems of the four main families (Lloyd and Slater 2021), which is consistent with our results indicating that the backbone bears most of the extinction signal in the tree.

Given the difficulty to estimate extinction rates (Morlon 2014; Beaulieu and O'Meara 2015; Rabosky 2016), studies have repeatedly raised debates about models in macroevolution (Kubo and Iwasa 1995; Rabosky and Lovette 2008; Crisp and Cook 2009; Burin et al. 2019; Pannetier et al. 2021). Recently, Louca and Pennell (2020) argued that diversification rates

should not be estimated from birth-death models with clade-homogeneous rates because any reconstructed phylogeny can be equally well explained with an infinite number of alternative models. Here we adopt a hypothesis-testing approach, in which we consider a limited set of alternative models chosen *a priori*, some of which will explain the phylogeny better than others (Helmstetter et al. 2022, Morlon et al. 2022). Even when allowing for potential rate shifts in only few clades, our approach sometimes compared thousands of combinations of shifts; still, cases with many statistically equivalent combinations were rare. Methodological developments and collecting more data (*e.g.* to update taxonomy, to increase sampling fractions) are required to investigate questions in such a challenging field while keeping in mind that rates inferred from extant time-trees are tentative estimates of a long history and should be interpreted cautiously (Helmstetter et al. 2022).

In conclusion, the automated implementation of the approach originally developed by Morlon et al. (2011) provides a user-friendly tool to investigate heterogeneity of diversification. We improved this approach by (1) adding the possibility to test shifts at crown age that seems to drastically improve the global likelihood of the approach (see Cetacea for example), (2) select a set of constant or time-dependent diversification models, (3) easily set up multiple backbone investigation, (4) make it possible to constrain rate estimates, (5) infer palaeodiversity dynamics while considering uncertainty both within rate estimation (probabilistic approach) and across many trees that can differ in terms of topology or divergence times, and (6) confirm empirical results with posterior predictive analyses. Nonetheless, we encourage users to adopt a hypothesis-driven approach and to be parsimonious concerning the number of nodes to test. We also recommend being critical on results of inferred palaeodiversity of the backbone in terms of raw number of species that results from rate values. We also caution that the most complex model where both speciation and extinction rates vary exponentially (BVAR_DVAR) is prone to provide highly unrealistic

patterns of palaeodiversity dynamics as shown in an example with Cetacea (Appendix S4). Echoing the results from Burin et al. (2019), the BVAR_DVAR model should be avoided or constrained. Keeping in mind these limitations, our study highlights that extinction signature and palaeodiversity declines can be investigated in groups without species-level fossil records.

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**Conflict of interest**

None declared.

**Authors’ contributions**

N.M. and F.L.C. designed the research with advice from P.-H.F.; N.M. performed the research and analysed the data with advice from H.M. and F.L.C.; and N.M. wrote the manuscript, and all authors edited the text.

**Data availability statement**

This open-source software is written entirely in the R language and is freely available through the Comprehensive R Archive Network (CRAN) at: https://cran.r-project.org/web/packages/RPANDA/index.html. The scripts used, simulation results, model fits and case study data are available at: https://figshare.com/s/6e8924774165b5ed81ec

**ORCID**

Nathan Mazet: https://orcid.org/0000-0002-6611-0312

Hélène Morlon: https://orcid.org/0000-0002-3195-7521

Pierre-Henri Fabre: https://orcid.org/0000-0002-3414-5625

Fabien L. Condamine: https://orcid.org/0000-0003-1673-9910

**References**

Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L., Carnevale, G., Harmon, L.J., (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* 106, 13410–13414. https://doi.org/10.1073/pnas.0811087106

Alroy, J., (2008). Dynamics of origination and extinction in the marine fossil record. *Proceedings of the National Academy of Sciences of the United States of America* 105, 11536–11542. https://doi.org/10.1073/pnas.0802597105

Bacon, C.D., Michonneau, F., Henderson, A.J., McKenna, M.J., Milroy, A.M., Simmons, M.P., (2013). Geographic and Taxonomic Disparities in Species Diversity: Dispersal and Diversification Rates Across Wallace's Line. *Evolution* 67, 2058–2071. https://doi.org/10.1111/evo.12084

Barido-Sottani, J., Vaughan, T.G., Stadler, T., (2020). A Multitype Birth–Death Model for Bayesian Inference of Lineage-Specific Birth and Death Rates. *Systematic Biology* 69, 973–986. https://doi.org/10.1093/sysbio/syaa016

Beaulieu, J.M., O'Meara, B.C., (2016). Detecting Hidden Diversification Shifts in Models of Trait-Dependent Speciation and Extinction. *Systematic Biology* 65, 583–601. https://doi.org/10.1093/sysbio/syw022

Beaulieu, J.M., O'Meara, B.C., (2015). Extinction can be estimated from moderately sized molecular phylogenies. *Evolution* 69, 1036–1043. https://doi.org/10.1111/evo.12614

Billaud, O., Moen, D.S., Parsons, T.L., Morlon, H., (2020). Estimating Diversity Through Time Using Molecular Phylogenies: Old and Species-Poor Frog Families are the Remnants of a Diverse Past. *Systematic Biology* 69, 363–383. https://doi.org/10.1093/sysbio/syz057

Burin, G., Alencar, L.R.V., Chang, J., Alfaro, M.E., Quental, T.B., (2019). How Well Can We Estimate Diversity Dynamics for Clades in Diversity Decline? *Systematic Biology* 68, 47–62. https://doi.org/10.1093/sysbio/syy037

Chazot, N., Blandin, P., Debat, V., Elias, M., Condamine, F.L., (2021). Punctuational ecological changes rather than global factors drive species diversification and the

evolution of wing phenotypes in Morpho butterflies. *Journal of Evolutionary Biology* 34, 1592–1607. https://doi.org/10.1111/jeb.13921

Close, R.A., Benson, R.B.J., Saupe, E.E., Clapham, M.E., Butler, R.J., (2020). The spatial structure of Phanerozoic marine animal diversity. *Science*. https://doi.org/10.1126/science.aay8309

Condamine, F.L., Rolland, J., Morlon, H., (2013). Macroevolutionary perspectives to environmental change. *Ecology Letters* 16, 72–85. https://doi.org/10.1111/ele.12062

Condamine, F.L., Nagalingum, N.S., Marshall, C.R., Morlon, H., (2015). Origin and diversification of living cycads: a cautionary tale on the impact of the branching process prior in Bayesian molecular dating. *BMC Evolutionary Biology* 15, 65. https://doi.org/10.1186/s12862-015-0347-8

Condamine, F.L., Rolland, J., Höhna, S., Sperling, F.A.H., Sanmartín, I., (2018). Testing the Role of the Red Queen and Court Jester as Drivers of the Macroevolution of Apollo Butterflies. *Systematic Biology* 67, 940–964. https://doi.org/10.1093/sysbio/syy009

Condamine, F.L., Rolland, J., Morlon, H., (2019). Assessing the causes of diversification slowdowns: temperature-dependent and diversity-dependent models receive equivalent support. *Ecology Letters* 22, 1900–1912. https://doi.org/10.1111/ele.13382

Condamine, F.L., Romieu, J., Guinot, G., (2019). Climate cooling and clade competition likely drove the decline of lamniform sharks. *Proceedings of the National Academy of Sciences of the United States of America* 116, 20584–20590. https://doi.org/10.1073/pnas.1902693116

Condamine, F.L., Silvestro, D., Koppelhus, E.B., Antonelli, A., (2020). The rise of angiosperms pushed conifers to decline during global cooling. *Proceedings of the National Academy of Sciences of the United States of America* 117, 28867–28875. https://doi.org/10.1073/pnas.2005571117

Crisp, M.D., Cook, L.G., (2009). Explosive Radiation or Cryptic Mass Extinction? Interpreting Signatures in Molecular Phylogenies. *Evolution* 63, 2257–2265. https://doi.org/10.1111/j.1558-5646.2009.00728.x

Drummond, C.S., Eastwood, R.J., Miotto, S.T.S., Hughes, C.E., (2012). Multiple Continental Radiations and Correlates of Diversification in Lupinus (Leguminosae): Testing for Key Innovation with Incomplete Taxon Sampling. *Systematic Biology* 61, 443–460. https://doi.org/10.1093/sysbio/syr126

Ehrlich, P.R., Raven, P.H., (1964). Butterflies and Plants: A Study in Coevolution. *Evolution* 18, 586–608. https://doi.org/10.2307/2406212

Esquerré, D., Brennan, I.G., Catullo, R.A., Torres-Pérez, F., Keogh, J.S., (2019). How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae). *Evolution* 73, 214–230. https://doi.org/10.1111/evo.13657

Etienne, R.S., Rosindell, J., (2012). Prolonging the Past Counteracts the Pull of the Present: Protracted Speciation Can Explain Observed Slowdowns in Diversification. *Systematic Biology* 61, 204. https://doi.org/10.1093/sysbio/syr091

Ezard, T.H.G., Aze, T., Pearson, P.N., Purvis, A., (2011). Interplay Between Changing Climate and Species' Ecology Drives Macroevolutionary Dynamics. *Science* 332, 349–351. https://doi.org/10.1126/science.1203060

FitzJohn, R.G., (2012). Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution* 3, 1084–1092. https://doi.org/10.1111/j.2041-210X.2012.00234.x

Helmstetter, A.J., Glemin, S., Käfer, J., Zenil-Ferguson, R., Sauquet, H., de Boer, H., Dagallier, L.-P.M.J., Mazet, N., Reboud, E.L., Couvreur, T.L.P., Condamine, F.L., 2021. Pulled Diversification Rates, Lineages-Through-Time Plots and Modern

Macroevolutionary Modelling. *Systematic Biology* syab083. https://doi.org/10.1093/sysbio/syab083

Höhna, S., May, M.R., Moore, B.R., (2016). TESS: an R package for efficiently simulating phylogenetic trees and performing Bayesian inference of lineage diversification rates. Bioinformatics 32, 789–791. https://doi.org/10.1093/bioinformatics/btv651

IUCN. 2021. *The IUCN Red List of Threatened Species. Version 2021-3*. https://www.iucnredlist.org. Accessed on [11 05 2021]

Jonsson, K.A., Fabre, P.-H., Fritz, S.A., Etienne, R.S., Ricklefs, R.E., Jorgensen, T.B., Fjeldsa, J., Rahbek, C., Ericson, P.G.P., Woog, F., Pasquet, E., Irestedt, M., (2012). Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Sciences of the United States of America* 109, 6620–6625. https://doi.org/10.1073/pnas.1115835109

Legendre, F., Condamine, F.L., (2018). When Darwin's Special Difficulty Promotes Diversification in Insects. *Systematic Biology* 67, 873–887. https://doi.org/10.1093/sysbio/syy014

Lloyd, G.T., Slater, G.J., 2021. A Total-Group Phylogenetic Metatree for Cetacea and the Importance of Fossil Data in Diversification Analyses. *Systematic Biology 70*, 922–939. https://doi.org/10.1093/sysbio/syab002

Louca, S., Pennell, M.W., (2020). Extant timetrees are consistent with a myriad of diversification histories. *Nature*. https://doi.org/10.1038/s41586-020-2176-1

Maddison, W.P., Midford, P.E., Otto, S.P., (2007). Estimating a Binary Character's Effect on Speciation and Extinction. *Systematic Biology* 56, 701–710. https://doi.org/10.1080/10635150701607033

Maliet, O., Hartig, F., Morlon, H., (2019). A model with many small shifts for estimating species-specific diversification rates. *Nature Ecology & Evolution* 3, 1086–1092. https://doi.org/10.1038/s41559-019-0908-0

Maliet, O., Morlon, H., (2022). Fast and Accurate Estimation of Species-Specific Diversification Rates Using Data Augmentation. *Systematic Biology* 71, 353–366. https://doi.org/10.1093/sysbio/syab055

Marx, F.G., Uhen, M.D., (2010). Climate, Critters, and Cetaceans: Cenozoic Drivers of the Evolution of Modern Whales. *Science* 327, 993–996. https://doi.org/10.1126/science.1185581

Mitchell, J.S., Etienne, R.S., Rabosky, D.L., 2019. Inferring Diversification Rate Variation From Phylogenies With Fossils. *Systematic Biology* 68, 1–18. https://doi.org/10.1093/sysbio/syy035

Moen, D., Morlon, H., (2014). Why does diversification slow down? *Trends in Ecology & Evolution* 29, 190–197. https://doi.org/10.1016/j.tree.2014.01.010

Moore, B.R., Höhna, S., May, M.R., Rannala, B., Huelsenbeck, J.P., 2016. Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures. *Proceedings of the National Academy of Sciences of the United States of America* 113, 9569–9574. https://doi.org/10.1073/pnas.1518659113

Morlon, H., Potts, M.D., Plotkin, J.B., (2010). Inferring the Dynamics of Diversification: A Coalescent Approach. *PLoS Biology* 8, e1000493. https://doi.org/10.1371/journal.pbio.1000493

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. https://doi.org/10.1073/pnas.1102543108

Morlon, H., (2014). Phylogenetic approaches for studying diversification. *Ecology Letters* 17, 508–525. https://doi.org/10.1111/ele.12251

Morlon, H., Lewitus, E., Condamine, F.L., Manceau, M., Clavel, J., Drury, J., (2016). RPANDA: an R package for macroevolutionary analyses on phylogenetic trees. *Methods in Ecology and Evolution* 7, 589–597. https://doi.org/10.1111/2041-210X.12526

Morlon, H., Robin, S., Hartig, F., (2022). Studying speciation and extinction dynamics from phylogenies: addressing identifiability issues. *Trends in Ecology & Evolution.* https://doi.org/10.1016/j.tree.2022.02.004

Nagalingum, N.S., Marshall, C.R., Quental, T.B., Rai, H.S., Little, D.P., Mathews, S., (2011). Recent Synchronous Radiation of a Living Fossil. *Science*. https://doi.org/10.1126/science.1209926

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 of the United States of America* 89, 8322–8326. https://doi.org/10.1073/pnas.89.17.8322

Nee, S., Holmes, E.C., May, Robert Mccredie, Harvey, P.H., Lawton, J.H., May, Robert McCredie, (1994). Extinction rates can be estimated from molecular phylogenies. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 344, 77–82. https://doi.org/10.1098/rstb.1994.0054

Pannetier, T., Martinez, C., Bunnefeld, L., Etienne, R.S., (2021). Branching patterns in phylogenies cannot distinguish diversity-dependent diversification from time-dependent diversification. *Evolution* 75, 25–38. https://doi.org/10.1111/evo.14124

Paradis, E., Schliep, K., (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Quental, T.B., Marshall, C.R., (2010). Diversity dynamics: molecular phylogenies need the fossil record. *Trends in Ecology & Evolution* 25, 434–441. https://doi.org/10.1016/j.tree.2010.05.002

Rabosky, D.L., Donnellan, S.C., Talaba, A.L., Lovette, I.J., (2007). Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proceedings of the Royal Society B: Biological Sciences* 274, 2915–2923. https://doi.org/10.1098/rspb.2007.0924

Rabosky, D.L., Lovette, I.J., (2008). Explosive Evolutionary Radiation: Decreasing speciation or increasing extinction through time? *Evolution* 62, 1866–1875. https://doi.org/10.1111/j.1558-5646.2008.00409.x

Rabosky, D.L., (2010). Extinction Rates Should Not Be Estimated from Molecular Phylogenies. *Evolution* 64, 1816–1824. https://doi.org/10.1111/j.1558-5646.2009.00926.x

Rabosky, D.L., Santini, F., Eastman, J., Smith, S.A., Sidlauskas, B., Chang, J., Alfaro, M.E., (2013). Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communication* 4, 1958. https://doi.org/10.1038/ncomms2958

Rabosky, D.L., 2014. Automatic Detection of Key Innovations, Rate Shifts, and Diversity-Dependence on Phylogenetic Trees. *PLOS One* 9, e89543. https://doi.org/10.1371/journal.pone.0089543

Rabosky, D.L., (2016). Challenges in the estimation of extinction from molecular phylogenies: A response to Beaulieu and O'Meara. *Evolution* 70, 218–228. https://doi.org/10.1111/evo.12820

Revell, L.J., (2012). phytools: an R package for phylogenetic comparative biology (and other things): *phytools: R package*. *Methods in Ecology and Evolution* 3, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Ricklefs, R.E., (2007). Estimating diversification rates from phylogenetic information. Trends in Ecology & Evolution 22, 601–610. https://doi.org/10.1016/j.tree.2007.06.013

Royer, D.L., Hickey, L.J., Wing, S.L., 2003. Ecological conservatism in the "living fossil" Ginkgo. *Paleobiology* 29, 84–104. https://doi.org/10.1666/0094-8373(2003)029<0084:ECITLF>2.0.CO;2

Schliep, K.P., (2011). phangorn: phylogenetic analysis in R. *Bioinformatics* 27, 592–593. https://doi.org/10.1093/bioinformatics/btq706

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. https://doi.org/10.1073/pnas.1016876108

Stadler, T., (2011b). Inferring speciation and extinction processes from extant species data. *Proceedings of the National Academy of Sciences of the United States of America* 108, 16145–16146. https://doi.org/10.1073/pnas.1113242108

Stadler, T., (2013). How Can We Improve Accuracy of Macroevolutionary Rate Estimates? *Systematic Biology* 62, 321–329. https://doi.org/10.1093/sysbio/sys073

Stadler, T., Bokma, F., (2013). Estimating Speciation and Extinction Rates for Phylogenies of Higher Taxa. *Systematic Biology* 62, 220–230. https://doi.org/10.1093/sysbio/sys087

Steeman, M.E., Hebsgaard, M.B., Fordyce, R.E., Ho, S.Y.W., Rabosky, D.L., Nielsen, R., Rahbek, C., Glenner, H., Sørensen, M.V., Willerslev, E., (2009). Radiation of Extant

Cetaceans Driven by Restructuring of the Oceans. *Systematic Biology* 58, 573–585. https://doi.org/10.1093/sysbio/syp060

Yoder, J.B., Clancey, E., Roches, S.D., Eastman, J.M., Gentry, L., Godsoe, W., Hagey, T.J., Jochimsen, D., Oswald, B.P., Robertson, J., Sarver, B. a. J., Schenk, J.J., Spear, S.F., Harmon, L.J., (2010). Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology* 23, 1581–1596. https://doi.org/10.1111/j.1420-9101.2010.02029.x