APPLICATION

CRABS: Congruent rate analyses in birth–death scenarios

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Abstract

1. Diversification rates inferred from phylogenies are not identifiable if the rates are allowed to vary freely over time. There are infinitely many combinations of speciation and extinction rate functions that have the exact same likelihood score for a given phylogeny, building a congruence class. The specific shape and characteristics of such congruence classes have not yet been studied. Whether speciation and extinction rate functions within a congruence class share common features is also not known.

2. Prior hypotheses typically render diversification rates identifiable, but the results then depend on these a priori hypotheses and assumptions. To test the robustness of diversification results to these a priori hypotheses, we use two different approaches to explore congruence classes: (i) constructing congruent models under alternative hypotheses and (ii) sampling alternative rate function within the congruence class.

3. Our methods are implemented in the open-source R package CRABS (https://github.com/afmagee/CRABS). CRABS provides a flexible approach to explore the congruence class and provides summaries of rate functions within a congruence class. The summaries can highlight common trends, that is, increasing, flat or decreasing rates.

4. Although there are infinitely many equally likely diversification rate functions, these can share common features. CRABS can be used to assess if diversification rate patterns are robust despite the non-identifiability of the birth–death model. In our example, we clearly identify three phases of diversification rate changes that are common among all models which we sampled from the congruence class. Thus, congruence classes are not necessarily a problem for studying historical patterns of biodiversity from phylogenies.

KEYWORDS
birth–death models, congruence class, diversification rates, identifiability, macroevolution

1 | INTRODUCTION

In macroevolution, one prominent avenue of research is to estimate macroevolutionary rates of diversification from molecular phylogenies (Morlon, 2014; Ricklefs, 2007). Specifically, many studies are interested in inferring time-varying diversification rates. Time-varying diversification rates are used to study monotonic slowdowns/increases using continuous functions (e.g. Höhna, 2014; Morlon et al., 2011; Rabosky, 2006), abrupt shifts in diversification rates (e.g. Magee et al., 2020; May et al., 2016; Stadler, 2011), mass extinction (e.g. Culshaw et al., 2019; Höhna 2015; Magee & Höhna, 2021; May et al., 2016) and correlations to environmental factors (e.g. Condamine et al., 2013, 2019; Palazzesi et al., 2022). While these models are typically identifiable when estimated from time-calibrated phylogenies, they rely on specific a priori hypotheses in the form of the time variation of diversification rates (Morlon et al., 2022). Unfortunately, when relaxing these hypotheses by allowing for any continuous diversification rate function, time-varying diversification rates are no longer identifiable (Kubo & Iwasa, 1995; Louca & Pennell, 2020). That is, infinitely many combinations of speciation and extinction rate functions, summarized within a *congruence class*, result in the same likelihood given a phylogenetic tree (Kubo & Iwasa, 1995; Louca & Pennell, 2020).

However, the existence of infinitely many equivalently likely rate functions does not imply that one cannot draw any general conclusions (Morlon et al., 2022; O'Meara & Beaulieu, 2021). We do not know yet which diversification rate functions are within a congruence class, and if these diversification rate function share some specific features (e.g. rate changes at the same time). If we obtained estimates of diversification rate functions for our study group, then we could be interested in exploring all or a sample of diversification rate functions included in the congruence class to identify shared features. Furthermore, we could test if different specific diversification rate scenarios are included within a congruence class, for example, if a model with exponentially increasing/decreasing speciation rates is included in the congruence class. If the corresponding extinction rate is negative, which is biologically unrealistic and therefore not allowed, then the diversification scenario is not contained within the congruence class (see also Louca & Pennell, 2021). Similarly, we could assess if models with rate shifts at specific times, corresponding to alternative diversification scenarios, are included in the congruence class. These tests focus on the robustness of inferred diversification rate pattern.

Here we provide the R package CRABS (Congruent Rate Analyses in Birth–death Scenarios) that (1) converts between models within the same congruence class, (2) samples from the congruence class and (3) shows common trends among models within the same congruence class. Conversion between congruent models is useful if a researcher wants to explore alternative diversification scenarios, for example, 'what if the extinction rate was not constant but instead exponentially increased through time?' Sampling from the congruence class can highlight general features of a congruence class, for example, if a researcher has estimated a given pattern of diversification

rates and wants to know if most models within the congruence class show a certain trend (e.g. a rate shift at time *t*). Finally, all explored models can be analysed to show common patterns of diversification rate increases and decreases. With our R package CRABS, researchers can test which patterns are robust despite the non-identifiability of speciation and extinction rates.

2 | THEORY AND USAGE

In this section, we provide the theory behind CRABS, as well as a brief overview on how to use it. We start by explaining how CRABS processes any diversification rate function to construct the congruence class. Next, we explain how CRABS obtains alternative (congruent) matching pairs of speciation and extinction rates functions. Then, we show how to explore the congruence class by constructing specific diversification scenarios and using diversification rate functions generated from a process or a distribution. Finally, we demonstrate how alternative diversification rate models within the congruence class can be summarized to assess for shared trends.

2.1 | Reference speciation and extinction rates

Our exploration of the congruence class starts with obtaining a *reference* set of speciation and extinction rates. As an empirical example, we estimated speciation and extinction rates for the primates phylogeny from Springer et al. (2012) using a horseshoe Markov random field (HSMRF) prior distribution (Carvalho et al., 2010; Magee et al., 2020) as implemented in RevBayes (Höhna et al., 2016). The specific details about the dataset and Markov chain Monte Carlo settings are not important for this study, but can be found at https://revbayes.github.io/tutorials/divrate/ebd.html. We include the samples from the posterior distribution in our package for convenience. We will use this example to showcase how to explore the congruence class with CRABS.

CRABS accepts any type of function for the reference model. As an example, we will use here a first-order spline function, that is, a piecewise linear rate function for the reference model. In R, we can set up the piecewise linear rate functions as follows.

```
library(CRABS)
data(primates_ebd)
lambda <- approxfun(primates_ebd$time, primates_ebd$lambda)
mu <- approxfun(primates_ebd$time, primates_ebd$mu)
```

2.2 | Constructing the congruence class

The central idea in CRABS is to construct the congruence class given a speciation and extinction rate function. A congruence class is fully

specified by either the pulled net-diversification rate $r_p(t)$ and the speciation rate at the present (λ_0), or the pulled speciation rate $\lambda_p(t)$. That is, any combination of speciation and extinction rate function that result in the same pulled net-diversification rate $r_p(t)$ and speciation rate at the present (λ_0), or pulled speciation rate $\lambda_p(t)$, belong to the same congruence class (Louca & Pennell, 2020). We can therefore set up the congruence class by constructing the pulled net-diversification rate $r_p(t)$. The pulled net-diversification rate is defined as (Louca et al., 2018; Louca & Pennell, 2020)

$$r_p(t) = \lambda(t) - \mu(t) + \frac{1}{\lambda(t)} \frac{d\lambda(t)}{dt}. \tag{1}$$

The equation for the pulled speciation is (Louca et al., 2018; Louca & Pennell, 2020):

$$\lambda_p(t) = (1 - E(t))\lambda(t), \tag{2}$$

where $E(t)$ is the probability that the lineage observed at time t goes extinct before the present, and the equation for the pulled extinction rate is

$$\mu_p(t) = \lambda_0 - r_p(t). \tag{3}$$

Currently, we only use the pulled speciation rate and pulled extinction rate for visualization purposes (e.g. Figure 1). We use the pulled

net-diversification rate to construct the congruence class because it simplifies the equations.

Continuing with the primates data example, we can construct the congruence class in CRABS as follows.

```
times <- seq(0, max(primates_ebd$time), length.out = 1000)
my_model <- create.model(lambda, mu, times)
```

The pulled rates are computed for a set of pre-defined time points. Here, we use a fine grid of 1000 time points to achieve a high resolution in our plots. In our experience, 1000 time points are sufficient for plotting purposes because a higher resolution does not improve visibility.

Then, we can plot the diversification rates together with their pulled counterparts in CRABS using plot(my_model) (Figure 1). Studying the pulled speciation and pulled net-diversification rates itself can highlight aspects of the congruence class (Helmstetter et al., 2021; Louca et al., 2018).

2.3 | Transforming speciation and extinction rates

A researcher can either provide another speciation rate function (or extinction rate function) and CRABS computes the corresponding extinction rate function (or speciation rate function,
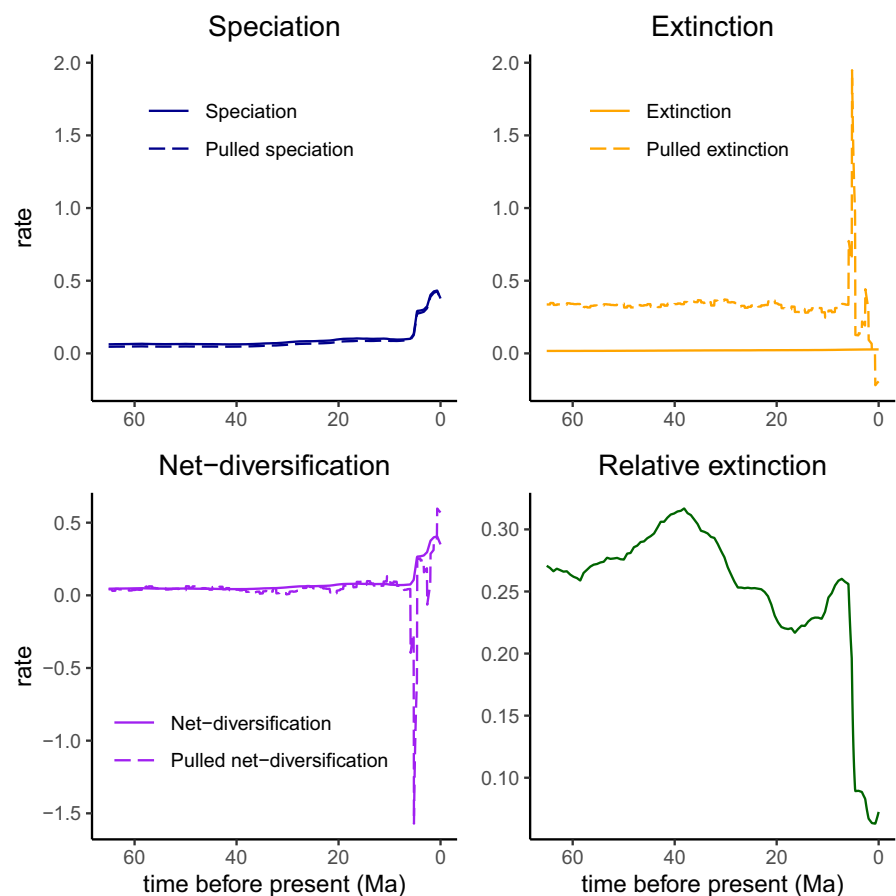

FIGURE 1 Estimated diversification rates for the primates phylogeny by Springer et al. (2012) using an episodic birth–death model with a horseshoe Markov random field prior (Magee et al., 2020) in RevBayes (Höhna et al., 2016). Here we show the speciation rate (λ), extinction rate (μ), net-diversification rate ($\lambda - \mu$) and relative extinction rate (μ / λ). The original rates define the *reference* model in CRABS (solid lines). CRABS automatically computes the pulled speciation rate, the pulled extinction rate, as well as the pulled net-diversification rate (dashed lines), which characterize the congruence class

respectively) so that the new pair also belongs to the same congruence class.

If a user provides a new extinction rate function, $\mu'(t)$, and wishes to know the corresponding speciation rate, $\lambda'(t)$, we can compute it from the following relationship, obtained by solving Equation (1) for λ:

$$\frac{d\lambda'}{dt} = -\left(\lambda'(t)\right)^2 + \lambda'(t)\left(\mu'(t) + r_p(t)\right). \tag{4}$$

We discuss in the Supplementary Material how this differential equation can be solved. We note that λ_0 is equal for all models in the congruence class. Conversely, if a user provides a new speciation rate function, then we can instead solve Equation (1) for μ and get

$$\mu'(t) = \lambda'(t) - r_p(t) + \frac{1}{\lambda'(t)}\frac{\lambda'(t)}{dt}. \tag{5}$$

These two transformations allow us to explore the congruence class. We only need to propose an alternative speciation rate function, or an alternative extinction rate function, and then compute their counterpart for the new model to be within the congruence class.

2.4 | Constructing congruent models under specific hypotheses

A first option to explore the congruence class is to test for specific alternative diversification scenarios. For example, one can explore if a linearly or exponentially decreasing speciation rate function is contained within the congruence class while restricting that extinction rates must be non-negative. In principle, there are no limitations to the choice of specific diversification scenarios and we provide several examples in our vignette (https://afmagee.github.io/CRABS). This option is useful when a researcher has a specific idea regarding when diversification rates could have changed and what shape the diversification rates function might have.

In our primates HSMRF analysis, we inferred that the speciation rate changed abruptly in the last few million years, but the extinction rate remained comparably constant (Figure 1). We note that the speciation rate appears to drive the changes in the 'observed' net-diversification rate, that is, in our originally inferred net-diversification rate. As an illustration, we explore here the alternative scenario if it instead was the extinction rate that drove the changes in the net-diversification rate. Because the net-diversification rate is defined as $\delta(t) = \lambda(t) - \mu(t)$, we construct our new diversification scenario for the extinction rate function as $\mu'(t) = \mu_0 - \lambda(t)$ where μ_0 is any arbitrary value with $\mu_0 \geq \sup(\lambda(t))$ to ensure that $\mu'(t) \geq 0$. In CRABS, we only need to specify the alternative extinction rate functions $\mu'(t)$ and then call congruent.models (which works similar to the function congruent_hbds_model in the R package castor [Louca & Doebeli, 2018]).

```
mu_scaling <- c(1.1, 1.2, 1.5, 2.0)
mu_0s <- max(lambda(my_model$times)) * mu_scaling

mu_prime <- list()
for (i in seq_along(mu_scaling)){
    mu_prime[[i]] <- local({
        mu_0 <- mu_0s[i]
        function(t) mu_0 - lambda(t)
    })
}

alt_models <- congruent.models(my_model, mus = mu_prime)
plot(alt_models)
```

Even though we constructed the extinction rate functions to be responsible for the changes in the net-diversification rates, we observe that the corresponding speciation rate functions of the same congruence class are never constant (Figure 2). This results in somewhat different net-diversification rate functions although both recent rate increases remain.

2.5 | Exploring congruent models, that is, sampling from the congruence class

A second option is to explore the congruence class. However, because there are infinitely many rate functions contained within the congruence class, we cannot explore every single model within the congruence class. Instead, we can sample randomly from a distribution of rate functions within the congruence class. We only need to specify how to create a random sample. For example, we could sample from different exponentially decreasing rate functions, or we could sample from a (discretized) Brownian motion process.

In CRABS, we provide ways to randomly sample from several flexible rate distributions. These distributions can be specified using the function sample.basic.models, and Table 1 provides an overview of the options for this function. A more detailed description is provided in our vignette (https://afmagee.github.io/CRABS).

As an example, we assume that an alternative extinction rate function corresponds to a (log-scale) Brownian motion. Note that we cannot sample from Brownian motion as a fully continuous function so we sample instead at specific time points and use a first-order spline function to interpolate between these time points. As a starting point for the Brownian motion at the present time $t_0 = 0$, we sample μ_0' from a lognormal distribution. The distribution is centred around the reference estimate μ_0. Each preceding μ_i is distributed as lognormal$\left(\mu_{i-1}, \sigma^2\right)$, where σ is drawn from a half-Cauchy distribution with parameters set following Magee et al. (2020). We select the variance for the initial lognormal such that the central 95% quantile of μ_0' spans 2.5 times two orders of magnitude on the rate scale. We repeat the entire procedure to draw each rate function.

FIGURE 2 Alternative models contained in the congruence class. The solid black line depicts the *reference* model (i.e. the model which we inferred and provided to CRABS). The four dashed lines in each plot show four different examples where we assumed that the extinction rate function was driving the net-diversification rates. The speciation rate functions, net-diversification rate functions and relative extinction rate functions are computed (i.e. deduced) given the extinction rate functions to enforce that the models remain in the congruence class
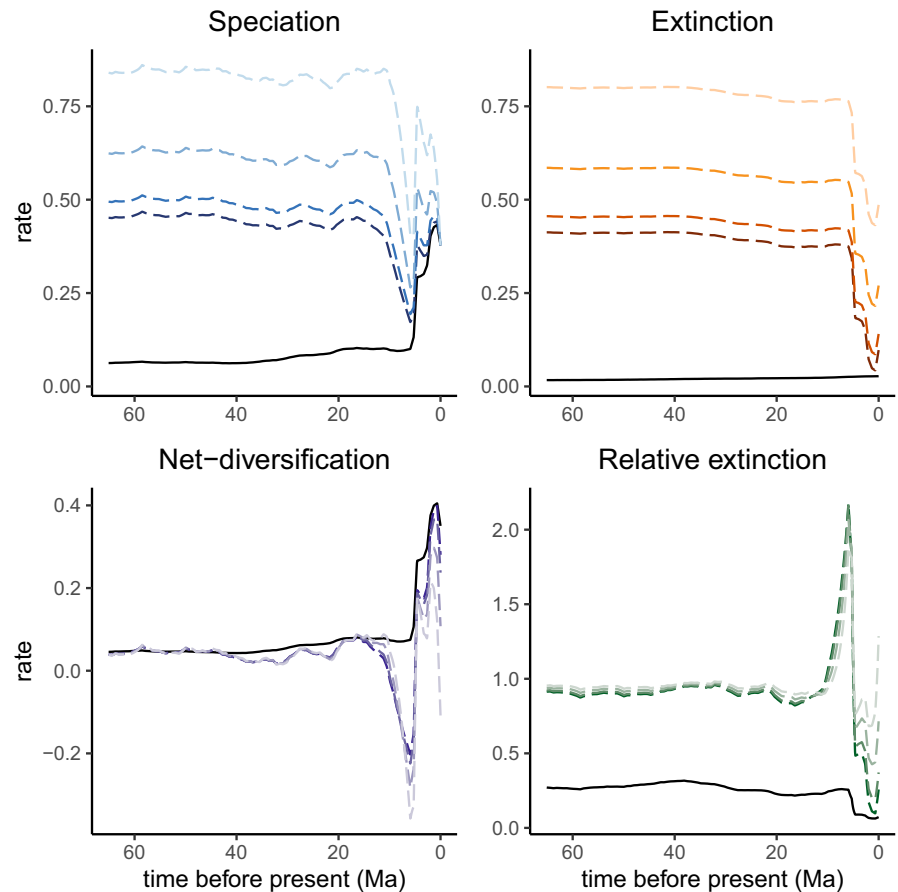

TABLE 1 Options for sampling basic models using sample.basic.models

Argument	Description
times	The vector of time points that we wish to sample at
rate0	The rate at the present. If not specified, will draw a random log-normally distributed rate at the present
rate0.median	Median rate at present
rate0.logsd	(log-scale) standard deviation of the rate at present
model	Either 'exponential', 'linear', 'episodic', 'MRF' for Markov random field
direction	Increase or decrease for the deterministic trend
noisy	Whether or not to add stochastic noise (the 'MRF' component)
MRF.type	One of 'HSMRF', for horseshoe-, or 'GMRF' for Gaussian Markov random field
monotonic	Whether to enforce that the rate always changes in the same direction
fc.mean	Mean fold-change
min.rate	Minimum rate value used for rejection sampling
max.rate	Maximum rate value used for rejection sampling

```
extinction_rate_samples <- function() {
    sample.basic.models(
        times = primates_ebd[["time"]],
        model = "MRF",
        MRF.type = "GMRF",
        max.rate = 0.5,
        mrf.sd.scale = 2.5,
        rate0.median = mu(0.0))
}
```

Then, we use this function extinction_rate_samples—which specifies how to generate new samples for the extinction rate function—to sample from the congruence class, which is done using the function sample.congruence.class. Here, we sample 20 new extinction rate functions and automatically compute the corresponding speciation rate functions.

```
samples <- sample.congruence.class(
    my_model,
```

```
num.samples=20,
rate.type="extinction",
sample.extinction.rates=extinction_rate_samples)
```

We can plot the BM samples in CRABS, using plot(samples) (Figure 3, left and middle columns). Note that we strongly recommend users to apply several different approaches for sampling more comprehensively from the congruence class (e.g. see our vignette: https://afmagee.github.io/CRABS) and to draw more samples than in this demonstrative example.

2.6 | Summarizing trends over congruent models

Once several models from the congruence class are obtained, we compute summaries of our sampled rate functions. Recall that we are primarily interested in changes in diversification rates over time for these models. Therefore, we compute the amount of rate change within a small interval Δt

$$\Delta \lambda_i = \frac{\lambda_{i-1} - \lambda_i}{\Delta t}, \tag{6}$$

where the index i refers to the ith grid point used for drawing. Next, we extract at which times the change in diversification rate ($\Delta \lambda$) is larger than a pre-defined threshold ϵ: if $\Delta \lambda$ is larger than ϵ then we paint this time as a rate increase, and if $\Delta \lambda$ is smaller than $-\epsilon$, then we paint this time as a rate decrease. Alternatively, we can compute the normalized rate change of the rate function:

$$\Delta \overline{\lambda}_i = \frac{\Delta \lambda_i}{\lambda_i}. \tag{7}$$

The absolute rate change represents the change in the speciation rate per time, while the normalized rate change represents the fold-change in the speciation rate per time. The absolute rate change has the advantage that we can easily specify a comparable threshold over the entire diversification history, while the normalized rate change has the advantage that we can easily specify a threshold that is comparable between analyses/datasets.
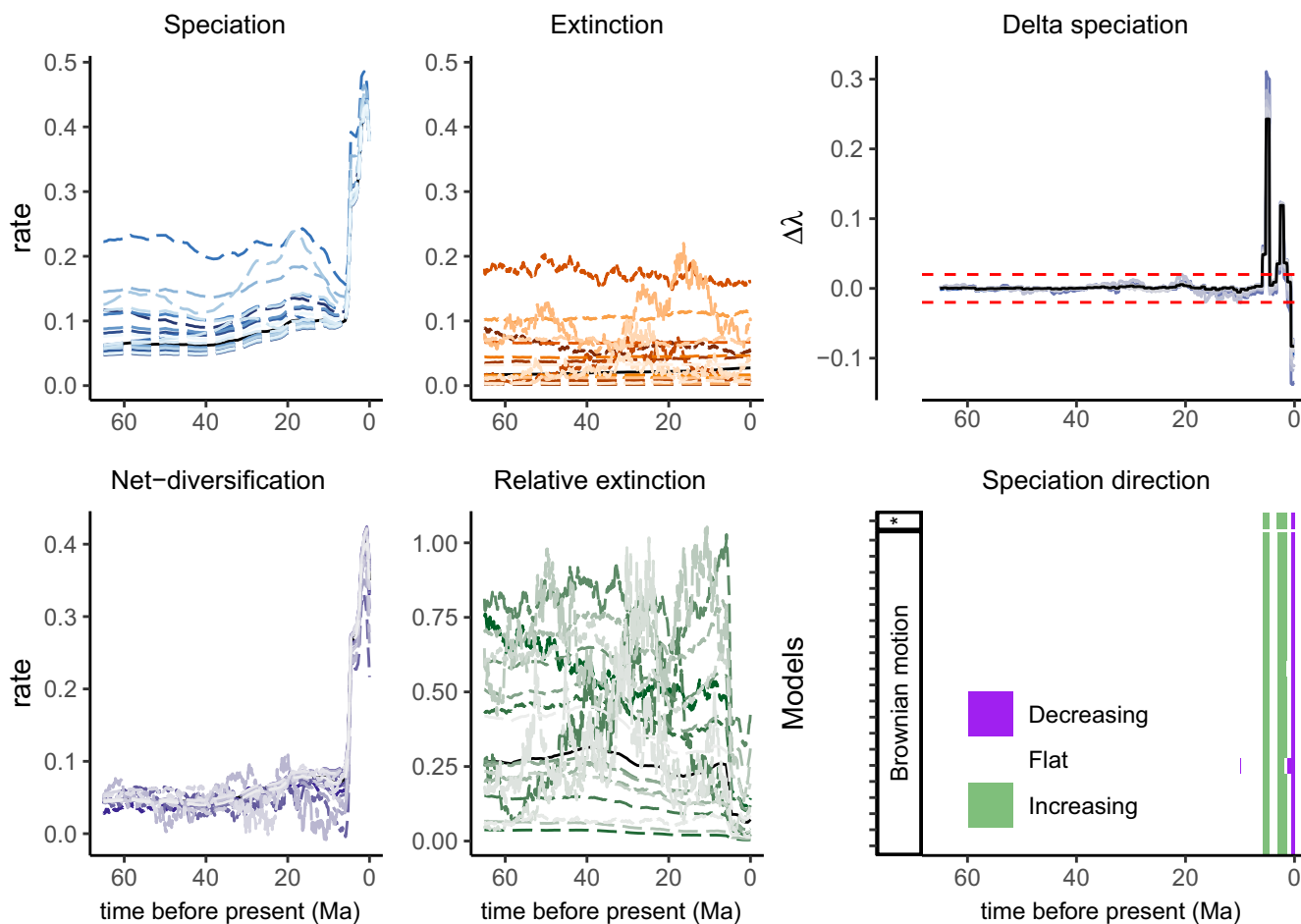

FIGURE 3 Congruent models where the extinction rates were sampled from a Brownian motion. The speciation rates were computed (i.e. deduced) to match the extinction rates so that the models remain within the same congruence class. The net-diversification rates and relative extinction rate functions result from the speciation and extinction rate functions. The right column depicts the change in the speciation rate ($\Delta \lambda = [\lambda_{i-1} - \lambda_i]/\Delta t$), and a summary indicating whether the speciation rate function is decreasing, flat or increasing assuming a threshold for $\Delta \lambda$ of $\pm \epsilon = 0.02$. The asterisk (*) in the trends plot (bottom row, right panel) and the solid black lines represent the reference model

Outliers can signal single rate changes detected by $\Delta\lambda$ but could also be noise. Therefore, we implemented an option to smooth trends (either increases or decreases) by removing singleton outliers. We define an outlier as a time interval where both neighbours share the same trend but the interval itself has a different trend. The outlier is then replaced with the same trend as both its neighbours. This smoothing can clarify the overall signal to detect the total number of directional changes. However, smoothing might delete sharp or instantaneous rate changes.

In CRABS, we summarize the directional changes in the congruence class by specifying a threshold ϵ, in units of rate change per time.

```
summarize.trends(samples, threshold = 0.02)
```

The summary provides us with an overview of the trends: how many of the sampled models have speciation rate functions that were increasing or decreasing at a given time. For the example primate dataset and our choice to generate model samples from the congruence class, we observe that sampled models had two speciation rate increases very recently, and one additional speciation rate decrease at the present (Figure 3). A more detailed description of how to summarize and interpret trends is provided in our vignette (https://afmagee.github.io/CRABS).

2.7 | Accommodating uncertainty in rates

In the above example, we explored the congruence class for the posterior median diversification rates. We can also explore congruence classes for samples from posterior distributions. That is, as an example, we compute the congruence class for 20 samples from the posterior distribution and draw 20 alternative rate functions for each posterior sample. First, we load our posterior samples.

```
data(primates_ebd_log)
posterior <- read.RevBayes(
                primates_ebd_log,
                n_times = 1000,
                max_t = 65,
                n_samples = 20)
```

We plot the speciation rate functions from the posterior sample in the left panel of Figure 4 (see Supplementary Scripts for information about plotting). Next, we generate congruent models for each of the samples from the posterior.

```
samples <- sample.congruence.class.posterior(
                posterior,
                num.samples = 20,
                rate.type = "extinction",
                model = "MRF",
                MRF.type = "GMRF",
```

```
                max.rate = 3.0,
                rate0.median = mu(0.0))
```

This selection yields 20 samples from the posterior, which are not congruent, but for each 20 samples we generated a subset of 20 additional congruent models. Next, we can summarize and plot the directions of change in the speciation rate function.

```
summarize.posterior(samples, threshold = 0.02)
```

Directional changes are summarized to show the number of models with an increase (or decrease, Figure 4, right panel), rather than to keep results from the same model consistent across rows. In contrast to results based solely on the posterior median model (Figure 3), the posterior samples show more disagreement between trends in direction of rate changes. Nevertheless, we observe general agreement among rate functions for the same three rate changes; two speciation rate increases in the last eight million years followed by one speciation rate decrease very close to the present.

2.8 | Summary of available functions

Finally, we present an overview of the most important functions available in CRABS (Table 2). We demonstrated the core functionality in the previous sections, and we also provide a vignette where we explore more detailed features of the package. We designed CRABS to have few, but generic functions, that allow for flexibility in exploration of the rate space in the congruence class.

We designed CRABS to use standard ggplot objects (Wickham, 2016) so that plots can easily be manipulated as any other ggplot objects. For example, it is possible to change the axis limits, axis labels or the time scale. This allows for flexibility in visualizing the congruence class for other datasets than we have exemplified here.

3 | DISCUSSION AND CONCLUSIONS

In this paper, we present the R package CRABS, Congruent Rate Analyses in Birth–death Scenarios. CRABS is available on CRAN and the source code is available from GitHub (https://github.com/afmagee/CRABS). CRABS enables easy testing of the impact of non-identifiable diversification rates. Specifically, with CRABS anyone can explore specific alternative diversification rate scenarios (e.g. explore if a model with constant speciation rates is included within the congruence class), or explore equally probable diversification rate models for shared characteristics. Thus, non-identifiability of diversification rates can be incorporated into conclusions about the process shaping historical biodiversity.

In this paper, we have numerically approximated the congruence class by computing the congruent models at given grid points. Between these grid points, we choose to linearly interpolate in
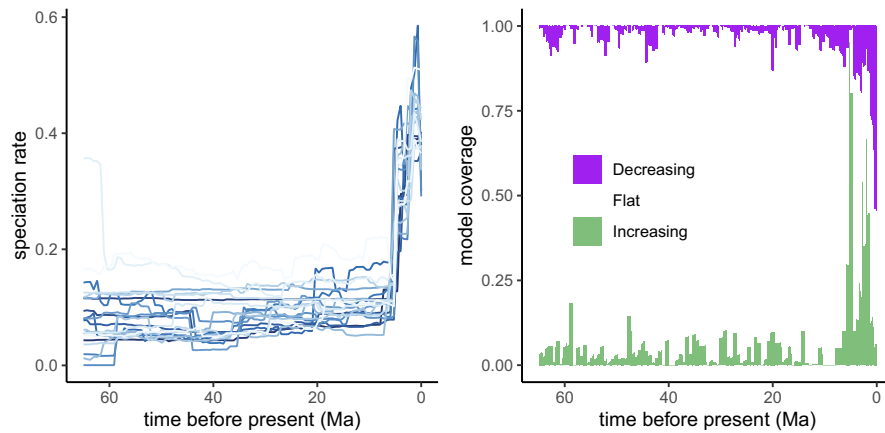
FIGURE 4 Left column: Twenty posterior samples from the primates analyses. Right column: Summary of trends over the posterior samples and congruence class samples for each posterior sample

TABLE 2 A summary of the core functions used in CRABS

Function	Description
congruent.models	Constructs models that are congruent with a reference model
create.model	Creates a CRABS model object
model2df	Converts a CRABS model object to a data frame, for example, for plotting
plot.CRABS	Plots a birth–death model
plot.CRABSset	Plots a set of congruent models
sample.basic.models	Samples rate functions from various distributions (see Table 1)
sample.congruence.class	Samples models from the congruence class
sample.congruence.class. posterior	Sample from the congruence classes of the posterior samples
sample.rates	Samples custom rate functions
summarize.posterior	Plots a summary of the directional trends in the posterior
summarize.trends	Plots a summary of the directional trends in the congruence class
read.RevBayes	Reads a RevBayes log file

our plotting functions. Importantly, our motivation for the exploration of the congruence class is primarily visual (see Figure 3). Alternative models produced by CRABS are not—in a strict mathematical sense—in the same congruence class as they do not yield the exact same likelihoods. However, the precision can be arbitrarily increased by selecting a finer time grid. The precision can be increased sufficiently so that the features are visually indistinguishable (see Figure S1).

In our main example of exploring a congruence class, we sampled alternative rate functions from a Brownian motion process. This choice reflects our belief that Brownian motion might be a good approximation of how diversification rates have changed over time, though other approaches should be considered. The biological motivation to apply Brownian motion is that diversification rates rarely change drastically from one time step to another and the change is instead gradual. We can also model rate changes with rapid shifts using a HSMRF model (Magee et al., 2020). Alternatively, we could assume that rates of speciation and extinction fluctuate around some central tendency, and model the behaviour of the rates using an Ornstein–Uhlenbeck process (see Condamine et al., 2018, Magee et al., 2020 and Palazzesi et al., 2022 for comparisons of

diversification rate models through time). To assist with this, CRABS provides functions to generate alternative rate functions with stochastic changes, as well as diversification rate functions with deterministic trends (e.g. exponential and linear). The existing functions to explore the congruence class can accept any type of rate functions. Although it remains unclear what the best approach to sample alternative rate functions is, we provide some guidelines here. First, we strongly recommend to use multiple different approaches to draw samples of rate function to suggest alternative rates. These multiple rate functions can be summarized together in the same trend plots. Second, we strongly recommend to explore both alternative speciation and extinction rate functions to not bias rate changes on only either the speciation or the extinction rate.

The primary output of CRABS is the congruence class and models belonging to this congruence class. Since changes in diversification rates are generally of interest, rather than the rates themselves, we focus on summaries of the congruence class showing directional trends in diversification rates (increasing, decreasing or flat). However, these summaries strongly depend on the chosen threshold for assessing whether the diversification rate was changing or not. We chose an arbitrary threshold of $\epsilon = 0.02$, which signifies

that any rate change of ±0.02 per million years is a significant trend. We recommend in practice testing summaries using a variety of thresholds. We strongly recommend researchers begin by exploring and visualizing specific models (as in Section 2.4), before examining broader sections of the congruence class (as in Section 2.5 and 2.6). Additionally, we strongly recommend users to apply different approaches with varying degrees of smoothness for sampling from the congruence class (e.g. see our vignette: https://afmagee.github.io/CRABS).

Finally, non-identifiability of diversification rates extends to diversification rates inferred from phylogenies with fossil taxa and phylodynamic models (Louca et al., 2021). In CRABS, we currently only focus on speciation and extinction rate functions and omit fossilization rates. However, it is possible to analyse a congruence class obtained from a phylogeny with fossil taxa using an approach analogous to what we described here. If a specific new extinction rate function was chosen, then both the speciation rate function and fossilization rate function can be computed given the congruence class. The results with CRABS are still valid for speciation and extinction rates, and could be considered as if the fossilization was simply not shown.

Non-identifiability of diversification rates has questioned the reliability and interpretation of diversification rate estimates from current approaches. Non-identifiability is a very real problem and should not be neglected. CRABS provides a new tool to assess if the conclusions drawn about patterns of diversification rates are robust despite the existence of infinitely many alternative diversification models.

AUTHOR CONTRIBUTIONS

Sebastian Höhna and Andrew F. Magee conceived the study; Sebastian Höhna, Bjørn T. Kopperud and Andrew F. Magee developed the R package CRABS; Sebastian Höhna and Bjørn T. Kopperud drafted the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors report no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.