

# The R package divDyn for quantifying diversity dynamics using fossil sampling data

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## 1 SUMMARY

- 2 1. Unbiased time series of diversity dynamics are vital for quantifying the grand  
3 history of life. Applications include identifying ancient mass extinctions and  
4 inferring both biotic and abiotic controls on diversification rates.
- 5 2. We introduce divDyn, a new R package that facilitates the calculation of  
6 taxonomic richness, extinction and origination rates from time-binned fossil  
7 sampling data. State-of-the-art sampling completeness metrics, counting  
8 protocols, and sampling standardisation functions permit the reconstruction  
9 of biologically meaningful time series. Additional functions permit the  
10 partitioning of turnover rates by trait and environmental affinity.
- 11 3. We display Phanerozoic-scale diversity dynamics of marine invertebrates  
12 using the divDyn package. Using the core function and standard  
13 subsampling options, we revisit earlier assessments of declining extinction  
14 and origination rates over time and of equilibrium diversity dynamics to  
15 assess their methodological dependency.
- 16 4. The modular and fast implementation of published methods ensures  
17 traceability, reproducibility, and comparability of future studies.

**Key-words:** diversity dynamics, fossil record, Paleobiology Database, extinction, origination, subsampling

## 1 INTRODUCTION

2 Reconstructions of global diversity (Sepkoski *et al.* 1981; Alroy *et al.* 2001; Alroy *et al.* 2008; Alroy  
3 2010a) as well as extinction and origination rates (Newell 1952; Carr & Kitchell 1980; Raup & Sepkoski  
4 1982; Sepkoski 1993; Benton 1995; Foote 2000; Bambach, Knoll & Wang 2004; Alroy 2008; Alroy 2014;  
5 Alroy 2015) have led to the recognition of ancient mass extinctions (Raup & Sepkoski 1982; Alroy 2008)  
6 and major insights about the interplay of evolutionary crisis and recovery. All of these results depend on  
7 the reconstruction of time series that characterise changes in the global biosphere. Calculating these time  
8 series from an incomplete fossil record is a fundamental task, as they serve as the basis for the statistical  
9 testing of grand questions in macroevolution.

10 Early studies largely relied on compendia of stratigraphic ranges, that is, they derived diversity metrics  
11 from overlapping durations of taxa (e.g. Sepkoski 1984). Since the advent of the Paleobiology Database  
12 (PaleoDB, <https://paleobiodb.org>) diversity dynamics have largely been inferred from large occurrence  
13 datasets that incorporate hundreds of thousands of items. Occurrence data allow for alternative counting  
14 methods and sampling standardisation, but implementing these methods in scripting languages is time-  
15 consuming and can be challenging for students and researchers with little programming experience.  
16 The algorithmic implementation of some procedures and the multiple steps of data filtering also permit  
17 considerable analytical freedom, which potentially compromises the comparability and traceability of  
18 results. Using a standardised toolkit will facilitate a fast and consistent workflow and allows researchers to  
19 focus on scientific questions rather than losing time with repeated implementation of established methods  
20 in computer scripts.

21 Here we present the R (2018) package *divDyn*, which facilitates the calculation of diversity dynamics  
22 from fossil occurrence datasets along with additional methods of palaeobiological inference. Our purpose  
23 is to establish a transparent, traceable and modular workflow from data acquisition to the calculation  
24 of biologically meaningful diversity metrics. The primary application of the package is expected to be  
25 for data from the Paleobiology Database (PaleoDB, <https://paleobiodb.org/>), the largest fossil occurrence  
26 dataset, which serves as a standard for palaeontological data analyses. However, any dataset for which  
27 diversity metrics are to be assessed in temporal or spatial intervals can also be processed in *divDyn*. The  
28 PaleoDB, Neptune (Lazarus 1994) and AMMON (Korn & Ilg 2007) databases are good examples of  
29 alternative datasets. To demonstrate the advantages of *divDyn*, we revisit results from an earlier study on  
30 Phanerozoic-scale diversity dynamics (Alroy 2008).

## 1 FEATURES

### 2 CALCULATION OF TIME SERIES

3 To prepare an occurrence dataset for analysis in `divDyn`, it must be formatted as a table with each row  
4 representing a single occurrence of a taxon. Occurrences should be assigned to discrete time intervals  
5 (bins). Alternatively, values in a continuous time-related dimension (e.g. years before present, or meters in  
6 a section) can be used that will be translated to discrete bins by the package.

7 The core function `divDyn()` calculates taxonomic richness, extinction and origination rate estimates  
8 using the presence-absence patterns of the bin-taxon matrix implied by the input dataset. It calculates a  
9 large suite of diversity metrics and rates in one go, ranging from classical sampled-in-bin richness to the  
10 recent second-for-third proportions (Alroy 2015, Table 1).

### 11 SAMPLING STANDARDISATION PROCEDURES

12 Sampling standardisation is a useful tool for smoothing out the effects of changing sampling intensity  
13 on the available data. Subsampling, the most common group of methods in this field of research, uses  
14 interpolation to answer the general question ‘What would the results look like if fewer data were  
15 available?’. The oldest and most widely used subsampling method is rarefaction (Sanders 1968; Miller &  
16 Foote 1996) but there are many others (Alroy *et al.* 2001; Bush, Markey & Marshall 2004; Alroy 2010a;  
17 Chao & Jost 2012). More implementations of these methods are available for estimating richness from  
18 an incomplete sample (Hammer, Harper & Ryan 2001; Hsieh, Ma & Chao 2016), but their application is  
19 more complicated in the context of time series reconstruction (Fig. 1), where information combined from  
20 multiple samples is to be extracted.

21 We formalized the subsampling process in the wrapper function `subsample()`. The arguments of  
22 the process are  $D$ ,  $g$ ,  $f$ ,  $K$ ,  $\alpha_f$  and  $\alpha_g$ , where  $D$  is the source dataset,  $g$  is the subsampling function,  $f$  is the  
23 user-supplied function,  $K$  is the number of iterations, and  $\alpha_f$  and  $\alpha_g$  are sets of additional function argu-  
24 ments for  $f$  and  $g$ , respectively. The desired result, based on all sampled data, is just a function of the data  
25 and its own arguments

$$26 \quad R = f(D, \alpha_f) \quad (1)$$

27 Given that the dataset is divisible into finite subsets, such as time bin-specific parts

$$28 \quad D := \{D^1, D^2, \dots, D^U\} \quad (2)$$

29 each bin-specific part has an abstract subset that features the same desired sampling characteristics (for  
30 instance, intensity), thus defining a set of data

$$31 \quad {}^{sub}D := \{g(D^1, \alpha_g), g(D^2, \alpha_g), \dots, g(D^u, \alpha_g)\} \quad (3)$$

32 With this  ${}^{sub}D$  abstract representation of the data, the desired results ( ${}^{sub}R$ ) would be just

1 
$${}^{sub}R = f({}^{sub}D, \alpha_p) \quad (4)$$

2 This can be approximated with Monte Carlo simulations, by generating multiple, randomly subsampled  
3 instances of  ${}^{sub}D_k$  (subsamped dataset in trial  $k$  out of  $K$ ) and allowing the naturally emerging variation  
4 to propagate to  ${}^{sub}R_k$  (subsamped result in trial  $k$ ). Thus, the simulation will lead to a vector of possible  
5 results.

6 From the point of implementation,  $f$  can be any function that is applicable to the original occurrence  
7 dataset  $D$  and the class of  ${}^{sub}R_k$  can be of any sort, such as vectors (time series) and complex structures, if  
8 they can be vectorized in the form of a list-class R object. In the case of primitive trial results (vectors and  
9 matrices), the averaging of time series can be automated. The current package version features Classical  
10 Rarefaction (Sanders 1968; Miller & Foote 1996), Occurrence-Weighted By-List Subsampling (O<sup>W</sup>,  
11 Alroy *et al.* 2001), and Shareholder Quorum Subsampling (SQS, Alroy 2010a).

## 12 **ADDITIONAL FUNCTIONALITY**

13 To facilitate the stratigraphic assignment of collections, we compiled tables using the dynamic timescale  
14 interpreter of Fossilworks (<http://fossilworks.org/>) that links entries to major geochronological intervals of  
15 two predefined timescales (the level of geological stages and the 10-million-year time scale). The package  
16 also includes additional tables to categorise the downloaded occurrences in terms of bathymetry (shallow,  
17 deep), substrate (siliciclastic vs. carbonate) and reef vs. non-reef environments.

18 Occurrence patterns of taxa allow the inference of preferred environments, which we can use to  
19 compare diversity dynamics between groups with different affinities such as tropical vs. extra-tropical  
20 or reef vs. non-reef (Alroy 2010a; Kiessling, Simpson & Foote 2010). As fossil sampling is biased and  
21 heterogeneous, we implemented methods to calculate likely environmental preferences with sampling  
22 patterns taken explicitly into account (Kiessling & Aberhan 2007), as well as test for selectivity of  
23 extinctions (Kiessling & Kocsis 2015).

24 The `divDyn()` function creates output in discretised time intervals. Results can be visualized effectively  
25 with the additional plotting functions that display the used time scale (`tsplot()`), stratigraphic ranges  
26 (`ranges()`), changes in composition (`parts()`) or distributions of values in time series (`shades()`).

27 The basic functionality of the package is elaborated in the accompanying vignette (Handout to the R  
28 package `divDyn` v0.6.0 for diversity dynamics from fossil occurrence data), with an example dataset of  
29 Scleractinian corals used by Kiessling and Kocsis (2015).

## 1 **EXAMPLE APPLICATION: PHANEROZOIC-SCALE DIVERSITY** 2 **DYNAMICS OF MARINE ANIMALS**

3 Tracing diversity through the entire Phanerozoic (the last 541 million years of Earth history) has been  
4 the focus of palaeobiological research ever since the first global diversity curves were published (Newell  
5 1952). Some patterns have been surprisingly robust to scientific scrutiny, whereas others are more volatile.  
6 For example, the temporal decline of turnover rates has largely gone unchallenged since its first observation  
7 (Raup & Sepkoski 1982), whereas the original ‘Big Five’ mass extinction events of Raup and Sepkoski  
8 (1982) have been repeatedly revisited, with different conclusions (Bambach, Knoll & Wang 2004; Alroy  
9 2008). Much discussion has focused on the dramatic rise of marine biodiversity over the last 100 myr,  
10 which is evident in older compilations (Valentine 1970; Sepkoski 1993) but much less so in sampling-  
11 standardised analyses (Alroy *et al.* 2008). Not yet formally contested are Alroy’s (2008, 2010b) analyses  
12 of the temporal relationship between diversity and rates. If these results are robust at different temporal  
13 resolutions, they strongly argue for equilibrium, diversity-dependent diversity dynamics (Sepkoski 1978;  
14 Sepkoski 1984; Alroy 1996) through biotic interactions. With the continuous expansion of both fossil  
15 occurrence data sets and the toolkit to analyse them, it is necessary to re-evaluate such scientific outcomes  
16 on a periodical basis. The objective of this case study is to assess the robustness of previous results in  
17 the face of the increase in the number of fossil occurrences and the number of choices we face when we  
18 express diversity dynamics over deep time.

## 19 **DATA PROCESSING AND APPLIED METHODS**

20 The analyses presented in this section can be reproduced with the second vignette accompanying  
21 the package (Phanerozoic-scale global marine biodiversity analysis with the R package *divDyn* v0.6;  
22 <http://github.com/adamkocsis/ddPhanero>). The occurrences used here were downloaded on 14 September  
23 2018, including all entries between the Ediacaran-Holocene interval. The data were filtered to marine taxa  
24 and binned to geological stages as well the often used 10 myr bins (Alroy *et al.* 2008). As the procedural  
25 treatment of stages in the Cambrian and Ordovician systems was influenced by considerable stratigraphic  
26 error, they were resolved using biozone and formation entries (Ordovician), and with data from previous  
27 analyses (Cambrian, Na & Kiessling 2015). In keeping with related literature (e.g. Sepkoski 1997), all  
28 analyses were carried out at the genus level. However, species-level analyses can be conducted with  
29 exactly the same procedures.

30 We computed diversity dynamics at both stratigraphic resolutions (stages and 10 myr), with three  
31 different treatments of the data (raw, CR and SQS). Four different rate metrics were applied: per capita  
32 rates (Foote 1999, used most frequently in studies), corrected three-timer rates (Alroy 2008), gap-filler  
33 equations (Alroy 2014), and second-for-third substitution rates of Alroy (2015). This resulted in 24  
34 different sets (2 timescales  $\times$  3 data treatments  $\times$  4 rate metrics) of richness, origination and extinction  
35 rate series, each affected in a different way by the distorting effects of incomplete, heterogeneous sampling

1 and estimation error. Simple correlation and normality tests were applied to each of those sets to check  
2 whether previous results are robust to varying protocols.

3 As indicated by Foote (2005), most taxonomic turnover was probably pulsed, likely at stage  
4 boundaries. This assertion is supported by the infrequent correlations between interval durations and rate  
5 values when the time dimension is excluded from the rate equations (Table 2 and Alroy 2008). For the  
6 analysis of distributions, outliers and cross correlations, we detrended the rates and the richness by applying  
7 LOESS with AICc-based smoothing parameters (Wang 2010) to describe long-term variation (Bambach,  
8 Knoll & Wang 2004). Mass extinctions are defined as statistical outliers (using boxplot statistics) after the  
9 LOESS trend has been removed.

## 10 RESULTS

11 The first order patterns of the time series acquired with the different methods match very well,  
12 but the estimates for the individual time slices (Fig. 2) and thus the derived conclusions (Table 2) vary  
13 considerably. Although the decline of extinction and origination rates can be confirmed if the Cambrian  
14 and Ordovician is included in the dataset, the rates are unlikely to have featured a solid decline after the  
15 Ordovician period. All detrended extinction-rate series feature the latest Permian value as a mass extinction,  
16 which is consistently identified as the highest value in the series. The number of mass extinctions vary  
17 considerably. Among the ‘Big Five’ mass extinctions (Raup & Sepkoski 1982), the end-Triassic and the  
18 end-Cretaceous values also show up as outliers, as was indicated by Alroy (2008). The cross-correlations  
19 that indicate equilibrational dynamics appear to be unstable and are likely affected by the estimation error of  
20 the values in the time series.

## 21 DISCUSSION

22 Most major results derived from the Phanerozoic-scale analyses of the marine fossil animal record  
23 are robust after the additional 10 years of data entry and methodological development since Alroy (2008).  
24 Sepkoski (1993) found a similar pattern in analysing an older, range-based Phanerozoic diversity data set.  
25 One notable exception is the decline of rates through time, which receives varying support if the first two  
26 Phanerozoic periods are excluded. Likewise, changing data treatments either question equilibrational diversity  
27 dynamics or point to the possibility that carrying capacities change through time (Sepkoski 1984; Alroy  
28 2010b; Marshall & Quental 2016).

29 Whichever the case, using a standard toolkit like divDyn enhances our ability to reproduce previous  
30 results and test the effect of added data or changing temporal resolution. We hope that our package will  
31 spur large-scale diversity analyses beyond the still small group of trained peers, such that results can be  
32 incorporated into broader evolutionary questions (Jablonski & Shubin 2015).

33 We intend to expand the set of output variables in the future, and the flexibility to write custom

1 subsampling functions will be incorporated into divDyn. Our package utilises methods developed mostly  
2 by palaeobiologists. Simulations are currently being developed to compare results with other approach-  
3 es such as PyRate (Silvestro, Salamin & Schnitzler 2014) or capture-mark-recapture methods (Liow &  
4 Nichols 2010).

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10 Paleobiology students of the FAU.

## 11 **AUTHOR CONTRIBUTIONS**

12 ATK conceived the project, wrote the first manuscript draft and the software using code from WK and  
13 JA as foundations. WK and CJR contributed to testing, interface and feature development, as well as the  
14 debugging of code. All authors contributed to writing the manuscript.

## 15 **DATA ACCESSIBILITY**

16 The package is accessible from its GitHub repository (<http://github.com/adamkocsis/divDyn>) and  
17 has been submitted to the CRAN servers. The occurrence data used here are freely available from the  
18 Paleobiology Database. All files needed to reproduce the specific example are available on GitHub  
19 (<http://github.com/adamkocsis/ddPhanero>).

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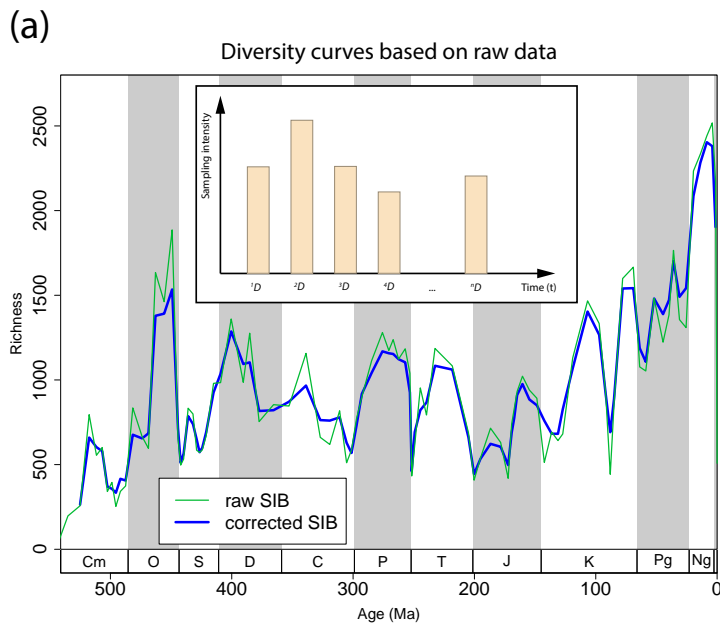
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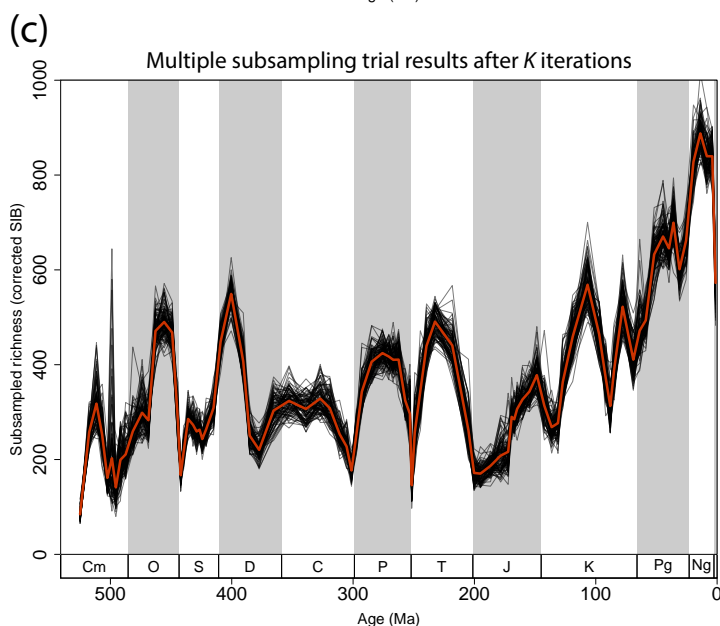
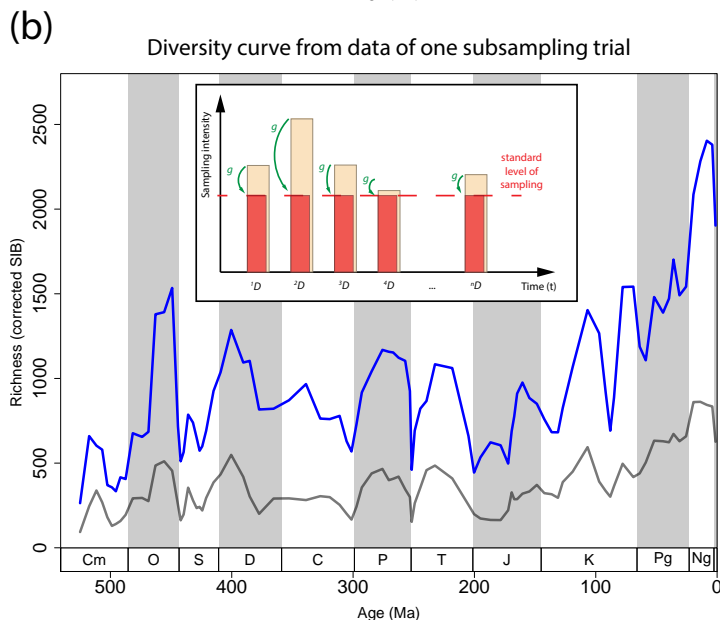
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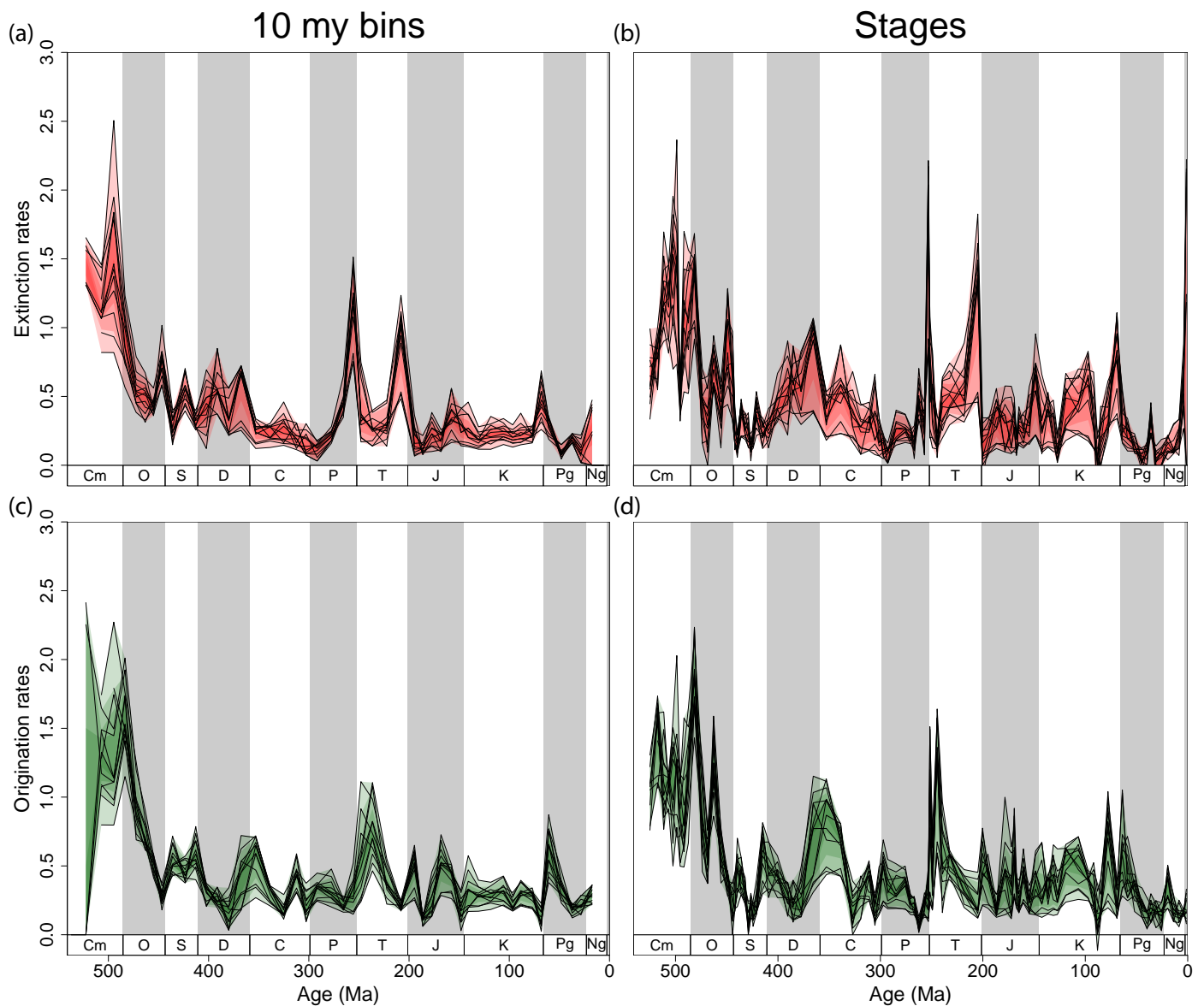
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## FIGURES



1 Figure 1. Demonstration of the procedures  
2 implemented in the subsampling wrapper  
3 function. (a) Calculation of raw results, (b)  
4 calculation of results from a single subsampling  
5 trial and (c) multiple trial results and averaging.  
6 The curves show genus richness from the  
7 Phanerozoic example dataset, standardized  
8 with SQS at the stratigraphic resolution of  
9 geologic stages. The number of iterations ( $K$ )  
10 was 100, the quorum for SQS is 0.7.





1 Figure 2. Genus-level Phanerozoic-scale extinction (a-b) and origination rates (c-d) calculated at the level of 10  
2 million year bins and stratigraphic stages. Each panel features twelve (three treatment x four rate metrics) curves,  
3 either raw, CR (quotas are 4,800 for the 10my bins and 1,100 for the stages) or SQS-standardized (quorum is 0.7  
4 for both) average per capita rates, corrected three-timer rates, gap-filler rates or second-for-third substitution rates.

## TABLES

1 Table 1. List of some of the variables output by the main function of the package.

Variable name	Metric name	Type	Reference
tSing, tOri, tExt, tThrough	range-based taxon patterns	counts	Foote, 1999
t2d, t2u, t3, tPart, tGFu, tGFd	occurrence-based taxon patterns	counts	Alroy, 2008; Alroy 2014
extProp, oriProp	proportional extinctions and originations	turnover	Newell, 1952
extPC, oriPC	per capita extinction and origination rates	turnover	Foote, 1999 (Alroy, 1996)
ext3t, ori3t	three-timer extinction and origination rates	turnover	Alroy, 2008
extC3t, oriC3t	corrected three-timer extinction and origination rates	turnover	Alroy, 2008
extGF, oriGF	gap-filler extinction and origination rates	turnover	Alroy, 2014
ext2f3, ori2f3	second-for-third substitution extinction and origination rates	turnover	Alroy, 2015
divSIB	sampled-in-bin diversity (SIB)	richness	Miller and Foote, 1996
divRT	range-through diversity (RT)	richness	Newell, 1952
divBC	boundary-crosser diversity (BC)	richness	Carr and Kitchell, 1980
divCSIB	corrected sampled-in-bin diversity	richness	Alroy et al., 2008
samp3t	three-timer sampling completeness	sampling completeness	Alroy, 2008
sampRange	range-based sampling completeness	sampling completeness	Foote and Miller, 2007

1 Table 2. Results of method-specific outcomes of the time series calculations for 10 myr bins (a) and stages (b).  
 2 Unless otherwise indicated, values are estimates of correlation coefficients. Significant results of Shapiro-Wilk tests  
 3 indicates deviation from log-normality. Formatting indicates significance (except for binary information): insignificant  
 4 values are not reported, regular entries indicate  $0.05 \geq p > 0.01$ , **bold** entries  $0.01 \geq p > 0.001$  and underscored  
 5 **bold** entries denote  $p \leq 0.001$ . Rate metrics are abbreviated: PC = the per capita rates (Foote 1999), C3t = corrected  
 6 three-timer rates (Alroy 2008), GF = gap-filler rates (Alroy, 2014) and 2f3 = second-for-third-substitution rates (Alroy,  
 7 2015).

(a)		10 MYR TIME SCALE											
		raw				CR				SQS			
		PC	C3t	GF	2f3	PC	C3t	GF	2f3	PC	C3t	GF	2f3
Pulsed/ continuous	ext. rates with durations												
	norm. ext. rates with durations	<b>-0.49</b>	<b>-0.44</b>	-0.34	-0.3	<b>-0.56</b>	<b>-0.58</b>	<b>-0.55</b>	<b>-0.55</b>	<b>-0.47</b>	<b>-0.46</b>	-0.32	-0.34
	orig. rates with durations			0.32									
	norm. orig. rates with durations	-0.37	<b>-0.42</b>			-0.36	<b>-0.4</b>				-0.35		
Declines	extinctions	<b>0.55</b>	<b>0.58</b>	<b>0.61</b>	<b>0.51</b>	<b>0.55</b>	<b>0.61</b>	<b>0.62</b>	<b>0.57</b>	<b>0.55</b>	<b>0.61</b>	<b>0.65</b>	<b>0.57</b>
	post-Ordovician extinctions		0.38	<b>0.42</b>			<b>0.45</b>	<b>0.44</b>	0.35		0.41	<b>0.44</b>	
	originations	<b>0.5</b>	<b>0.45</b>	<b>0.5</b>		<b>0.55</b>	<b>0.43</b>	<b>0.52</b>	<b>0.41</b>	<b>0.53</b>	<b>0.43</b>	<b>0.53</b>	
	post-Ordovician originations												
Mass extinctions	end-Permian ME	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
	end-Triassic ME	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
	end-Cretaceous ME	yes	yes	yes	yes	no	yes	yes	yes	no	yes	no	no
	end-Permian is highest	yes	no	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
	number of mass extinctions	5	3	4	3	2	4	3	3	2	3	2	3
Rate dist.	extinctions log-normal (p-values)						0.04						
	originations log-normal (p-values)				<b>&lt;0.001</b>							<b>0.01</b>	<b>0.01</b>
Equilibrial dyn.	origination and lagged diversity					0.35			0.32	<b>0.45</b>		0.31	0.35
	diversity and lagged extinction	<b>0.45</b>				0.35				<b>0.48</b>			
	diversity and lagged origination		<b>0.55</b>				<b>0.67</b>	<b>0.48</b>	<b>0.42</b>		<b>0.54</b>		

(b)		STAGE-LEVEL TIME SCALE											
		raw				CR				SQS			
		PC	C3t	GF	2f3	PC	C3t	GF	2f3	PC	C3t	GF	2f3
Pulsed/ continuous	ext. rates with durations	0.23		0.22	<b>0.28</b>				0.22				<b>0.27</b>
	norm. ext. rates with durations	<b>-0.45</b>	<b>-0.35</b>	<b>-0.34</b>		<b>-0.64</b>	<b>-0.53</b>	<b>-0.58</b>	<b>-0.42</b>	<b>-0.54</b>	<b>-0.51</b>	<b>-0.46</b>	<b>-0.28</b>
	orig. rates with durations	<b>0.35</b>		<b>0.32</b>	<b>0.33</b>					0.24		0.24	0.23
	norm. orig. rates with durations	<b>-0.52</b>	<b>-0.51</b>	<b>-0.4</b>	<b>-0.31</b>	<b>-0.66</b>	<b>-0.58</b>	<b>-0.55</b>	<b>-0.51</b>	<b>-0.59</b>	<b>-0.5</b>	<b>-0.41</b>	<b>-0.39</b>
Declines	extinctions	<b>0.52</b>	<b>0.39</b>	<b>0.39</b>	<b>0.36</b>	<b>0.59</b>	<b>0.43</b>	<b>0.46</b>	<b>0.46</b>	<b>0.59</b>	<b>0.4</b>	<b>0.39</b>	<b>0.37</b>
	post-Ordovician extinctions					0.27				0.29			
	originations	<b>0.44</b>	<b>0.36</b>	<b>0.39</b>	<b>0.35</b>	<b>0.58</b>	<b>0.39</b>	<b>0.43</b>	<b>0.43</b>	<b>0.52</b>	<b>0.36</b>	<b>0.39</b>	<b>0.38</b>
	post-Ordovician originations					0.24							
Mass extinctions	end-Permian ME	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
	end-Triassic ME	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
	end-Cretaceous ME	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
	end-Permian is highest	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
	number of mass extinctions	4	3	5	4	3	3	3	4	3	3	6	3
Rate dist.	extinctions log-normal (p-values)			0.01	<b>&lt;0.001</b>				<b>&lt;0.001</b>			<b>&lt;0.001</b>	<b>&lt;0.001</b>
	originations log-normal (p-values)		0.05	<b>&lt;0.001</b>					<b>&lt;0.001</b>	<b>&lt;0.001</b>		<b>&lt;0.001</b>	0.02
Equilibrial dyn.	origination and lagged diversity	<b>0.39</b>	0.3			<b>0.34</b>				<b>0.52</b>	<b>0.34</b>	<b>0.34</b>	0.28
	diversity and lagged extinction	<b>0.6</b>	<b>0.41</b>	<b>0.39</b>	<b>0.34</b>	<b>0.45</b>				<b>0.61</b>	0.23	<b>0.37</b>	<b>0.3</b>
	diversity and lagged origination						<b>0.46</b>	<b>0.46</b>	<b>0.38</b>				