

Genus-level versus species-level extinction rates

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ABSTRACT:

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The average extinction rates of index species per m. y. are computed by means of a count-of-biozones metric (Trammer 2014). These rates and the average extinction rates of genera belonging to biostratigraphically important groups, calculated according to three different methods, show congruent rises and falls from the Cambrian to the Neogene. The extinction rates of genera are, thus, a relatively good predictor of species extinction rates.

Key words: Extinction; Rates; Species; Genera; Fossil record.

INTRODUCTION

The extinction rates of fossil species are an important topic of evolutionary palaeobiology and Earth-life system research. Investigators who calculate these rates usually do not measure directly the extinction intensity of particular species. Instead, they study the rates for families and genera as a proxy for species extinction (e.g. Raup and Sepkoski 1984; Raup 1986; Raup and Boyajian 1988; Foote 1994, 2000, 2003; Peters and Foote 2002; Bambach *et al.* 2004; Kiessling and Baron-Szabo 2004; MacLeod 2004; Peters 2005, 2006, 2008; Stanley 2007; Mayhew *et al.* 2007, 2012; Alroy 2008, 2014; Kaminski *et al.* 2010).

The aim of the present contribution is to evaluate whether the rates calculated for genera are a good proxy for species extinction rates (see also e. g. Raup and Boyajian 1988, Alroy 2014).

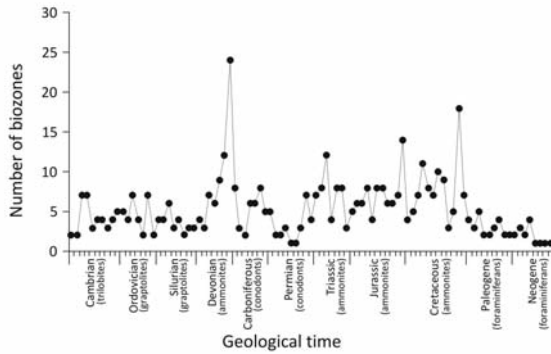
METHODS

Biozones mirror and record the origination and extinction of the index taxa on which they are based (for details see Trammer 2014). Thus, the “extinction rates” of

biozones are also a potential proxy for the extinction rates of index taxa (mostly species) that define those biozones.

I have counted the standard biozones ratified by the International Union of Geological Sciences (Ogg *et al.* 2008). For one geological period there is often more than one standard biostratigraphic zonation. For the calculation herein, I have always selected the zonal scheme with the largest number of biozones.

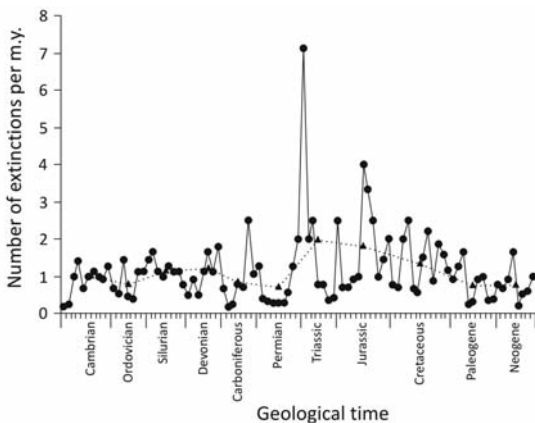
The selected biozonal schemes (compare Ogg *et al.* 2008) are thus as follows: for the Cambrian – the Australian trilobite zonation with the exception of the Terreneuvian series (archaeocyathan and small shelly fossil zonation); for the Ordovician – the Australasian graptolite biozones; for the Silurian – the graptolite zonation; for the Devonian – the ammonite scheme with the exception of the Lochkovian and the Pragian stages (graptolite zonation); for the Carboniferous and the Permian – the conodont zones; for the Triassic – Tethyan ammonite zones with the exception of the Upper Ladinian (Boreal ammonite zonation); for the Jurassic – the Tethyan and Boreal ammonite zones; for the Cretaceous – Tethyan ammonite zones for the Lower Cretaceous and the U. S. Western Interior ammonite zones for the Upper Cretaceous; and the planktonic foraminiferal biozones for the Paleogene and the Neogene.



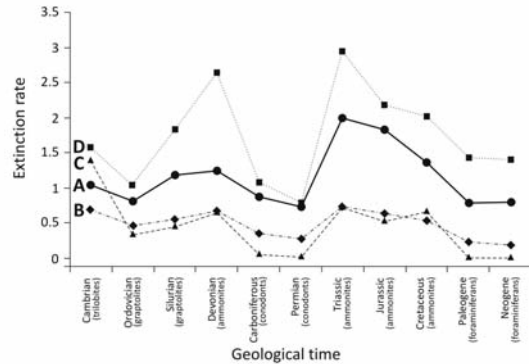
Text-fig. 1. The number of biozones in individual geological stages of the Phanerozoic. Intervals on the horizontal axis “Geological time” correspond to stages. Names of animal groups such as ammonites, conodonts etc. refer to the group on which the biozones of a given period are based

Knowing the number of biozones in the individual geological stages of the Phanerozoic (Text-fig. 1), and knowing the durations of the stages (International Chronostratigraphic Chart 2014; www.stratigraphy.org), I have divided the number of biozones of every stage by its duration achieving the average extinction rate per m. y. of the index species in each stage (Text-fig. 2). Such a procedure may be termed the “count-of-biozones” metric of extinction rates. As the index species are chiefly single-interval taxa (so called singletons), therefore the count-of-biozones metric is the calculation of the extinction rate of singletons.

To obtain the mean extinction rate of the index species for geological periods (Text-figs 2, 3 and 7) I have added the results for particular stages of a period and divided the sum by the number of stages included in that period.



Text-fig. 2. The number of extinctions of index taxa (mostly species) per m. y. in the individual geological stages of the Phanerozoic (= the number of biozones in a stage divided by its duration). The average number of extinction per m. y. in the geological periods (compare Text-fig. 7) is also shown (dotted line). Averaging does not include the Terreneuvian series of the Cambrian, where trilobites are absent; and the Lochkovian and Pragian stages of the Devonian, where index goniatites are missing. For animal groups to which index taxa belong see Text-fig. 1



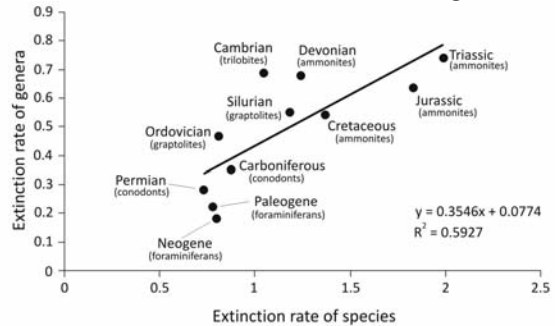
Text-fig. 3. Trajectories of average extinction rates in the Phanerozoic. A: Extinction rates per m. y. of the index species obtained by means of the count-of-biozones metric (Trammer 2014, and this paper). Durations of periods and average extinction rates are not significantly correlated ($r = 0.352$ at $p = 0.289$). B–D: Extinction rates of genera belonging to the biostratigraphically important groups. B: Proportional extinction. C: Extinction rates calculated according to the per-capita method of Foote (2000). D: Extinction rates computed according to the three-timer method of Alroy (2008). Names of animal groups such as ammonites, conodonts etc refer to the group on which the biozones of a given period are based. For numerical values of rates consult Text-fig. 7

Next I have measured the extinction rates of all genera belonging to the groups on which the biozones are based: Cambrian trilobites; Ordovician and Silurian graptolites; Devonian goniatites, Triassic, Jurassic and Cretaceous ammonites; Carboniferous and Permian conodonts; and Paleogene and Neogene foraminifers.

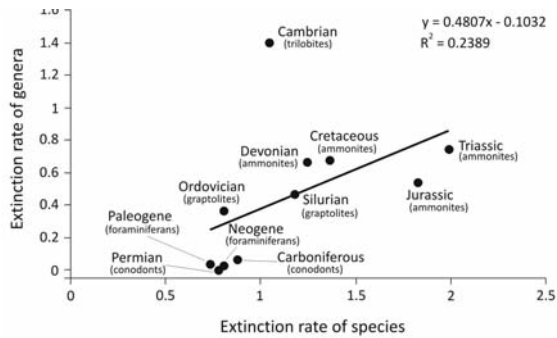
I have used three different measures of the extinction rates of genera: the proportional count (number of extinction / number of recorded taxa in an interval), the per-capita method of Foote (2000), and the three-timer method of Alroy (2008).

For the proportional and the per-capita (Foote 2000) metrics, data from the compendium of marine genera (Sepkoski 2002, and www.strata.geology.wisc.edu /jack/) were used. The Paleobiology Database (www.paleodatabase.org) was the source of data for the three-timer count (Alroy 2008).

To obtain the mean rate of extinction of genera in a



Text-fig. 4. Relationship between the average extinction rate per m. y. of the index species (curve A in Text-fig. 3) and the average proportional genus-level extinction rate (B in Text-fig. 3). Pearson’s $r = 0.77$ at $p = 0.006$, $r^2 = 0.593$; Spearman’s $r_s = 0.82$ at $p = 0.002$; first differences – Pearson’s $r = 0.93$ at $p = 0.0001$, Spearman’s $r_s = 0.89$ at $p = 0.0005$



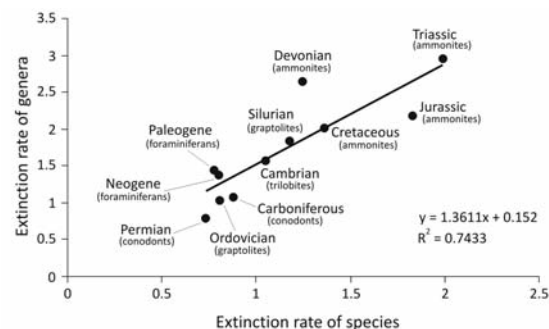
Text-fig. 5. Relationship between the average extinction rate per m.y. of the index species (curve A in Text-fig. 3) and the average genus-level extinction rate (C in Text-fig. 3) calculated by means of the per-capita method of Foote (2000). Pearson's $r = 0.49$ at $p = 0.13$, $r^2 = 0.24$; Spearman's $r_s = 0.8$ at $p = 0.003$; first differences – Pearson's $r = 0.72$ at $p = 0.019$, Spearman's $r_s = 0.67$ at $p = 0.033$. When data concerning the Cambrian are excluded from the regression then Pearson's $r = 0.82$ at $p = 0.004$, $r^2 = 0.67$; Spearman's $r_s = 0.915$ at $p = 0.0002$; first differences – Pearson's $r = 0.82$ at $p = 0.007$; Spearman's $r_s = 0.72$ at $p = 0.03$

given period (Text-figs 3, 7), I have averaged the results for particular stages in a period in the case of the per-capita and proportional metrics, and averaged the results for 11 m.y. bins in the case of the three-timer count.

Finally, I have examined the strength of the relationship between the species extinction rates and the extinction rates of genera by means of correlation and least-square regression analyses (Text-figs 4–6).

RESULTS

To a large extent, index species and all genera belonging to biostratigraphically important groups show congruent Phanerozoic trends in the average extinction intensity (Text-fig. 3). Moreover, there are strong correlative relationships between the extinction rates for the



Text-fig. 6. Relationship between the average extinction rate per m.y. of the index species (curve A in Text-fig. 3) and the average genus-level extinction rate (curve D in Text-fig. 3) computed by means of the three-timer method of Alroy (2008). Pearson's $r = 0.86$ at $p = 0.0006$, $r^2 = 0.74$; Spearman's $r_s = 0.89$ at $p = 0.0002$; first differences – Pearson's $r = 0.88$ at $p = 0.0008$; Spearman's $r_s = 0.78$ at $p = 0.008$

index species and for genera (both for raw data and first differences; Text-figs 4–6). The values of the genus-level rates, irrespective of the applied measuring method, all correlate significantly with the index species rates (Text-figs 4–6).

Close correspondence between the temporal changes in the species-level and the genus-level extinction rates has been presented also by Dera *et al.* (2010, fig. 4), as exemplified by the Early Jurassic ammonites, and by Aretz *et al.* (2014, fig. 5) for Devonian and Carboniferous foraminifers.

The extinction rates computed for genera are, thus, a relatively good predictor of the extinction rates for species and inversely, at least on a broad temporal scale and in the case of biostratigraphically important groups that supply geology with index fossils. A substantial relationship must have existed between the longevity of genera and the longevity of their constituent species.

DISCUSSION

The results presented above are also a little surprising, because the genus-level extinction patterns, obtained by means of three different methods are mutually consistent (compare Alroy 2014). Now, there is time normalization in the case of the three-timer method (11 m.y. bins), whereas the proportional and per-capita metrics are not normalized for time (varying durations of the stages). Furthermore, the proportional metric takes into account singletons among genera that are not taken into consideration by the per-capita and the three-timer metrics. In spite of this, all the methods used produced congruent period-level extinction patterns (Text-fig. 3)

It is also interesting that the extinction rates of index species, which are based on singletons, correlate well with the extinction rates of the genera measured (after Foote 2000 and Alroy 2008) while excluding singleton genera (compare Cascales-Miñana and Diez 2012).

CONCLUSIONS

The use of the “extinction rate” of biozones as a metric of extinction of the index species constituting biozones is proposed (see also Trammer 2014). This procedure may be termed the count-of-biozones metric of the index species extinction rates. Changes of these rates with time track closely the changes of the extinction rate of genera belonging to biostratigraphically important groups. Thus, the extinction rates computed for genera are a relative good predictor of the extinction rates of species at least over broad temporal scale.

Period (Animal group)	Index species per m.y.	Genera		
		Proportional measure	Per-capita measure	Three-timer measure
Cambrian (Trilobites)	1.045	0.687	1.4	1.568
Ordovician (Graptolites)	0.808	0.467	0.357	1.031
Silurian (Graptolites)	1.179	0.55	0.464	1.828
Devonian (Ammonites)	1.242	0.68	0.659	2.639
Carboniferous (Conodonts)	0.875	0.35	0.058	1.070
Permian (Conodonts)	0.731	0.28	0.031	0.780
Triassic (Ammonites)	1.992	0.74	0.734	2.95
Jurassic (Ammonites)	1.827	0.635	0.534	2.175
Cretaceous (Ammonites)	1.364	0.54	0.675	2.004
Paleogene (Foraminiferans)	0.78	0.223	0.00956	1.43
Neogene (Foraminiferans)	0.793	0.18	0.0166	1.395

Text-fig. 7. Average extinction rates of the index species and of all genera belonging to the biostratigraphically important groups. Numerical data used in Text-figs 3–6

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