Identifying the most surprising victims of mass extinction events: an example using Late Ordovician brachiopods

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Mass extinction events are recognized by increases in extinction rate and magnitude and, often, by changes in the selectivity of extinction. When considering the selective fingerprint of a particular event, not all taxon extinctions are equally informative: some would be expected even under a ‘background’ selectivity regime, whereas others would not and thus require special explanation. When evaluating possible drivers for the extinction event, the latter group is of particular interest. Here, we introduce a simple method for identifying these most surprising victims of extinction events by training models on background extinction intervals and using these models to make per-taxon assessments of ‘expected’ risk during the extinction interval. As an example, we examine brachiopod genus extinctions during the Late Ordovician Mass Extinction and show that extinction of genera in the deep-water ‘Foliomena fauna’ was particularly unexpected given preceding Late Ordovician extinction patterns.

1. Introduction

Mass extinction events in the fossil record offer the opportunity to study extinction processes during a wide range of biological and environmental perturbations. One of the most striking and informative features of such events is their selectivity. Extinction patterns are rarely consistent with a random ‘field of bullets’ model, but are often strongly selective with respect to ecological, environmental and biogeographic factors [1–4].

Selectivity patterns can be powerful sources of information about the drivers of extinction events, but it is important to consider selectivity patterns during mass extinctions in the context of the intervals of ‘background extinction’ that precede them [5,6]. Extinctions during background intervals are also often highly non-random with respect to a variety of factors [2,5–7]. Consequently, when evaluating a mass extinction event, the critical question is how and to what degree selectivity patterns during the event differ from those observed during previous intervals. Some taxon extinctions are more unexpected—that is, they represent a more surprising departure from background extinction patterns—than others.

Here, we outline a simple method for determining which specific extinctions represent the greatest departures from background patterns. Our approach is to create models of extinction selectivity based on observed extinction/survival patterns during the background extinction intervals leading up to the mass extinction event. We then use these models to predict the expected
extinction risk of each taxon during the mass extinction interval based on the risks observed for taxa with similar traits during background intervals.

As an example, we use this approach to examine extinctions of rhynchonelliform (articulate) brachiopods during the Late Ordovician Mass Extinction (LOME), one of the ‘Big 5’ largest extinctions of the past 500 Myr [8,9]. This extinction event occurred in two distinct pulses: a latest Katian (approx. 444.7 Ma) pulse broadly associated with cooling, glaciation and sea-level fall and a mid-Late Hirnantian pulse (at the base of the persculptus graptolite biozone) associated with warming, melting of ice sheets and continental flooding [10,11]. The LOME has long been notable for exhibiting relatively little taxonomic selectivity compared with other mass extinction events, but recent analyses of benthic macroinvertebrates have detected significant selectivity related to habitat preference, depth range, abundance and inferred thermal tolerance range [12–17].

2. Material and methods

(a) Database

We base our analyses on a large and taxonomically standardized database of the local stratigraphic ranges of rhynchonelliform brachiopods compiled from the literature and from ongoing research programmes in Durham and Copenhagen [15–17]. Ranges are expressed in terms of the British chronostratigraphic system, which we adapt accordingly: Early Caradoc (Sandbian 1), Mid Caradoc (Sandbian 2), Late Caradoc (Katian 1), Pusgillian (Katian 2), Cauleyan (Katian 3), Rawtheyan (Katian 4) and Hirnantian. These stage subdivisions overlap with, but are not identical to, those of Bergstrom et al. [18]. Palaeogeographic coordinates for each local region are based on reconstructions by Cocks & Torsvik [19,20].

(b) Extinction and risk predictors

Data manipulations and analyses were carried out in the R programming environment [21]. Although it would be desirable to analyse species extinction risk, there is still considerable uncertainty about Ordovician brachiopod taxonomy at the species level. Consequently, we follow many previous analyses of the marine invertebrate fossil record in conducting analyses at the genus level [4,6,22] with the recognition that genera are to some degree artificial constructs. Within each of the seven Late Ordovician intervals analysed, we tabulated several aspects of geographical, bathymetric, environmental and macrostratigraphic distribution for each genus. See ‘Description of predictors’, in the electronic supplementary material, for descriptions of how predictors were calculated and standardized.

(c) Modelling relationships between predictors and background extinction risk

We examined relationships between the predictors described above and ‘background’ extinction patterns in five pre-extinction intervals (Sandbian 1 and 2, Katian 1–3) and the two pulses of the LOME (Katian 4, Hirnantian). We used stepwise regression (direction = ‘both’) to choose from among the predictors described above and build additive logistic regression models for each interval, in each case selecting the model with the lowest Akaike information criterion. We chose logistic regression as an analytical framework, because it is an established method with well-understood properties that has previously been applied.

Figure 1. Summary of multiple logistic regression models for different Late Ordovician intervals. Each column represents an interval and each row a predictor. Colours indicate sign of log-odds associated with the predictor in a given interval and text gives the log-odds. Positive log-odds (magenta) indicate that as the predictor value increases marginal extinction risk increases; negative log-odds (green) indicate that as the predictor value increases marginal extinction risk decreases. Only predictors that are significant at the 95% confidence level are plotted. S1: Sandbian 1, S2: Sandbian 2, K1: Katian 1, K2: Katian 2, K3: Katian 3, K4: Katian 4, H: Hirnantian. (Online version in colour.)
to many analyses of extinction/survival in the fossil record [4,6,7,22].

3. Results and discussion
Logistic regression coefficients (log-odds ratios) of risk predictors show considerable variability across intervals, demonstrating that the determinants of apparent extinction risk vary both between the mass extinction intervals and the background intervals and among background intervals (figure 1). Consistent with earlier analyses using a different statistical methodology [13], number of localities, proportional stratigraphic truncation, absolute latitudinal range and minimum depth are significantly associated with apparent extinction risk in the latest Katian interval (Katian 4), but of these only number of localities and, to a lesser degree, proportional stratigraphic truncation are consistent predictors of apparent extinction risk during background intervals. We focus the remainder of our discussion on the latest Katian extinction pulse both because it is larger and because it has a more distinct selective signature than the second, Hirnantian pulse [12,13] (figure 1).
Ranking genera present during the Katian 4 and Hirnan-
tian intervals from lowest to highest based on the median risk
prediction from the full suite of background models provides
an overall measure of expected risk conditioned on prior
extinction selectivity patterns (electronic supplementary
material, table S1; figure 2). As would be expected consider-
ing the consistent importance of predictors such as number of
localities and proportional truncation, there is some corre-
spondence between expected risk and observed extinctions:
during both intervals most of the genera that go extinct come
from the high end of the predicted risk spectrum and most
of the genera that survive have low predicted risk. Given
that 112 of 219 genera appear to go extinct during
Katian 4, the degree of correspondence can be evaluated by
comparing observed extinction versus survival with pro-
jected extinction versus survival if the 112 genera with the
highest expected risk (lower half of figure 2a) had gone
extinct and the 107 genera with the lowest expected risk
(upper half of figure 2a) had survived. In total, 79 of 112
observed extinctions fall within this set (true positive
percentage = 71%) and 74 of 107 observed survivors are
among the projected survivors (true negative percentage =
69%). Of more interest when considering changes in selective
regime between the LOME and preceding intervals are the 33
genera with relatively high expected risk that did not go
extinct and, especially, the 33 genera that went extinct despite
having relatively low expected risk.

No obvious commonalities unite the members of the
former group, but conspicuous within the latter group are
the members of the 'Foliomena fauna', a distinctive assem-
blage of small, thin-shelled genera that were widely
distributed in tropical and subtropical seas and inhabited
deeper-water (BA 4–6) environments during the Late Ordo-
vician [23,24] (highlighted genera in figure 2a). Of seven
genera identified as core members of this fauna by Cocks &
Rong [25], all but Cyclopspra disappear in the latest Katian.
Simultaneous extinction of graptolite clades associated with
oxygen minimum zones [26,27] and proxy evidence for
enhanced ventilation of the shelves at this time [28,29]
suggest that extinction of the Foliomena fauna may represent
loss of a distinctive deep-water biotope adapted to low-
oxygen conditions widespread during the Katian greenhouse
climate state [13] (but see Hammarlund et al. [28] for an
alternative interpretation). We assessed the probability of
observed Foliomena fauna extinctions happening by chance
given background selectivity patterns and latest Katian
extinction rates by randomly drawing 112 genera 10,000
times for each of the five background interval models, in
each case using per-genus expected risk estimates from that
model as sampling probabilities. The expected probability
of extinction of six or more of the core Foliomena fauna mem-
ers is low for all background models, ranging from 0.0133
(Sandbian 1) to <0.0001 (Katian 1 and Katian 3) (electronic
supplementary material, figure S1), with an overall probability across all models of 0.0039.

The consistency of number of localities and, to a lesser
degree, proportional stratigraphic truncation as predictors
of apparent extinction risk (figure 1) may be a genuine
signal, as narrowly distributed taxa are at greater risk of
extinction under most extinction scenarios, including
regression and draining of regional seaways [12,30]. How-
ever, this association could also be an artefact of sampling
bias. Genera that are only sampled in a single locality are
likely to have prematurely truncated stratigraphic ranges,
especially if that locality exhibits a hiatus [31,32]. The local
range-based nature of our dataset precludes use of occur-
cence-based approaches to assessing time of extinction
[33,34], but to reduce the potential influence of sampling
biases we re-ran our analysis after excluding both genera
sampled in only a single region and genera sampled in only
a single interval. Owing to edge effects Sandbian 1
cannot be included in this analysis, but observed selectivity
patterns in the remaining intervals are broadly comparable
to those in the full dataset (electronic supplementary
material, figure S2). There is a moderately strong positive cor-
relation between median expected risk estimates based on
the full dataset and those based on the culled dataset (electronic
supplementary material, figure S3), and extinctions of core
members of the Foliomena fauna remain among the least
expected given background extinction patterns (electronic
supplementary material, figures S4, and S5). Consequently,
we tentatively conclude that, although sampling biases
doubtless have an influence on apparent extinction risk pat-
terns, these biases are unlikely to account for the very low
expected risk of the Foliomena fauna. The extinction of these
genera appears to be a genuinely unexpected and potentially
informative selective pattern that merits further investigation.

The approach outlined here provides a simple framework
for determining which taxa are most likely to have been vic-
tims of unusual stresses and which are most likely to have
been the expected casualties of ‘normal’ extinction processes.
In this example, we have used logistic regression because of
its familiarity and simplicity, but a wide variety of statistical
methods could be employed. Ecological, physiological and
phylogenetic factors could also be considered in assessing
expected risk and, when available, taxon occurrence data
and data on the spatio-temporal distribution of the strati-
graphic record could be incorporated to estimate and
reduce the influence of sampling biases. Our approach can
be applied to examine other mass extinction events in the
fossil record, but could also be used to scan for particularly
surprising extinctions that may shed light on extinction
processes during background intervals.

Data accessibility. Input data (electronic supplementary material, Appen-
dix S1) and R code to replicate our analyses (electronic
supplementary material, Appendix S2) are reposed at Data Dryad:
http://dx.doi.org/10.5061/dryad.03v3n [35].

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