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IMPACT OF THE LATE TRIASSIC MASS EXTINCTION ON FUNCTIONAL DIVERSITY AND COMPOSITION OF MARINE ECOSYSTEMS

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Abstract: Mass extinctions have profoundly influenced the history of life, not only through the death of species but also through changes in ecosystem function and structure. Importantly, these events allow us the opportunity to study ecological dynamics under levels of environmental stress for which there are no recent analogues. Here, we examine the impact and selectivity of the Late Triassic mass extinction event on the functional diversity and functional composition of the global marine ecosystem, and test whether post-extinction communities in the Early Jurassic represent a regime shift away from pre-extinction communities in the Late Triassic. Our analyses show that, despite severe taxonomic losses, there is no unequivocal loss of global functional diversity associated with the extinction. Even though no functional groups were lost, the extinction event was, however, highly selective against some modes of life, in particular sessile suspension feeders. Although taxa with heavily calcified skeletons suffered higher extinction than other taxa, lightly calcified taxa also appear to have been selected against. The extinction appears to have invigorated the already ongoing faunal turnover associated with the Mesozoic Marine Revolution. The ecological effects of the Late Triassic mass extinction were preferentially felt in the tropical latitudes, especially amongst reefs, and it took until the Middle Jurassic for reef ecosystems to fully recover to pre-extinction levels.

Key words: mass extinction, Triassic, Jurassic, functional diversity, niche, regime shift.

THE Late Triassic mass extinction event (LTE), which occurred ~201.6 million years ago (Blackburn *et al.* 2013), is the second biggest biodiversity loss (Alroy 2010) and the third biggest ecological crisis (McGhee *et al.* 2004) since the Cambrian. The proposed mechanism for the crisis was CO_2-induced environmental changes, including global warming (McElwain *et al.* 1999; Wignall 2001), sea-level changes (Hallam 1981), ocean anoxia (Hallam & Wignall 2000; Jaraula *et al.* 2013) and ocean acidification (Hautmann 2004; Hautmann *et al.* 2008*a*) as a result of the eruption of the Central Atlantic Magmatic Large Igneous Province (CAMP) (Whiteside *et al.* 2010; Blackburn *et al.* 2013). This makes the LTE an attractive candidate for drawing ecological comparisons with the current anthropogenically-driven biodiversity decline. Recognizing when ecosystems reach a threshold in response to environmental pressures, resulting in a change in ecosystem structure often characterized by a shift in dominance among organisms with different modes of life (i.e. a regime shift) is key to understanding mass extinction events (Barnosky *et al.* 2012; Aberhan & Kiessling 2015). The LTE has been understudied in comparison with other major Phanerozoic biotic crises (Twitchett 2006) and, despite the importance of functional diversity changes or ecological regime shifts on ecosystem function, a palaeoecological perspective on long-term trends through deep-time, including the effects of mass extinctions, is still lacking (Villéger *et al.* 2011). Consequently, little is known about the ecological impact of the LTE, aside from the preferential extinction of tropical taxa inhabiting shallow marine environments, particularly hypercalcifiers, and the subsequent reef crisis in the Early Jurassic (Kiessling & Aberhan 2007; Kiessling *et al.* 2007; Kiessling & Simpson 2011).

Understanding the nature and patterns of extinction selectivity during this event may help in better understanding the cause(s) of the event, and/or may help pinpoint sampling biases or deficiencies. Selective loss of reef ecosystems is a common outcome of past biotic crises

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driven by CO_2-induced environmental change (Flügel 2002; Veron 2008; Kiessling & Simpson 2011; Foster & Twitchett 2014) and may be interpreted as a consequence of their sensitivity to environmental change. Apart from selection against specific regions, ecosystems or habitats (Foster & Twitchett, 2014), other studies have suggested that traits such as skeletal composition, motility and feeding are also critical in explaining patterns of selectivity. Past extinction events associated with elevated CO_2 have been shown to be selective against epifaunal, sessile, suspension feeders (Bush & Bambach 2011; Foster & Twitchett 2014; Clapham 2017), and selective against heavily calcified organisms (Hautmann 2004; Knoll *et al.* 2007; Hautmann *et al.* 2008*a*; Clapham & Payne 2011; Kiessling & Simpson 2011; Bush & Pruss 2013; Payne *et al.* 2016*a*) but as epifaunal, sessile suspension feeders tend to be heavily calcified, it is unclear which of those traits is most important. Also, apparent selectivity may simply be an artefact of preservation or sampling biases that may exist between different modes of life, at least regionally (Mander & Twitchett 2008).

The main aim of this study is to understand the patterns of diversity change and extinction selectivity in marine ecosystems during the Triassic–Jurassic interval and, in particular, in relation to the LTE. In order to investigate the functional diversity of ecosystems and to study key traits such as feeding, tiering and motility, the ecospace model of Bambach *et al.* (2007) was used to provide a quantitative autecological analysis of all known Middle Triassic to Middle Jurassic marine animal genera. This approach has been previously successfully applied to analysis of the Cambrian radiation (Bambach *et al.* 2007), comparisons of Palaeozoic and modern ecosystems (Bush *et al.* 2007; Villéger *et al.* 2011; Knope *et al.* 2015) and studies of both the late Permian (Dineen *et al.* 2014; Foster & Twitchett 2014) and end-Cretaceous (Aberhan & Kiessling 2015) mass extinction events. The following individual hypotheses were tested: (1) in common with the Late Permian extinction (Foster & Twitchett 2014), despite significant taxonomic losses, the LTE did not result in a reduction in global functional diversity; (2) sessile suspension feeders were selected against, compared to other modes of life across the LTE; (3) heavily calcified organisms were selected against and suffered higher extinction rates than lightly calcified taxa; and (4) taxonomic and functional diversity loss was greater in the tropics than at higher latitudes.

MATERIAL AND METHOD

Marine animal database

A database of all Middle Triassic to Middle Jurassic marine animal genera was downloaded from the Paleobiology Database (PaleoDB) on 13 April 2016 (Clapham *et al.* 2016; Dunhill *et al.* 2017). This database consists of 55 608 occurrences of 2615 genera compiled at stage level. Filtering protocols were used to exclude ichnotaxa, form taxa and any uncertain generic assignments (e.g. aff., cf., ex gr., *sensu lato*, '[quotation marks]', and 'informal'). Although there is concern that some of the data within the PaleoDB is inaccurate in terms of taxonomic and stratigraphic assignment, a number of studies have shown that taxonomic errors in these datasets are randomly distributed and have only minimal effects on long-term diversification and extinction patterns (Miller 2000; Peters 2007; Wagner *et al.* 2007; Miller & Foote 2009). Erroneous taxonomic and/or stratigraphic assignments were identified and corrected as far as was possible. This process involved drawing on the expertise of the authors and consultation with experts in specific taxonomic groups where necessary (all cited in Acknowledgements below). As well as systematic information, from phylum to generic level, information relating to palaeolongitude and palaeolatitude, depositional environment, and both chrono- and lithostratigraphy were downloaded. Stratigraphic assignments were made to the stage level, and Triassic and Jurassic occurrences falling outside of a Ladinian to Aalenian range were omitted from the data set. Occurrences without stage-level designations were omitted. However, occurrence data do not capture Lazarus taxa (i.e. an organism that disappears from the fossil record, often for millions of years, before reappearing unchanged; Flessa & Jablonski 1983) which can lead to the overestimation of extinction rates, particularly across major extinction events (Twitchett 2001). A second database was therefore constructed by ranging-through 2844 genera between first and last occurrences at substage level derived from the PaleoDB and from Sepkoski *et al.* (2002). To avoid edge effects in the range database, pre-Middle Triassic and post-Middle Jurassic occurrences were used for determining the stratigraphic ranges of genera. This approach was used by Foster & Twitchett (2014) and compensates for the out-of-date nature of much of Sepkoski *et al.* (2002) such as truncation of generic ranges in the Norian which are now known to extend into the Rhaetian, whilst filling in the gaps of the incomplete PaleoDB. The occurrence-based PaleoDB also allows for the accounting of variation in sampling intensity which is not possible with a range-through data set. The PaleoDB bins data at the stage level whilst the ranged-through data (Sepkoski *et al.* 2002) is binned at the substage level. Therefore, taxonomic and functional richness data are calculated from ranged-through data at the substage level and occurrence data (raw and subsampled) at the stage level. As it is only possible to use the occurrence data in the regional subset analyses, all of these are at stage-level only.

Functional characterization of marine animal genera

Modes of life for all marine genera within the database were inferred using data from previous publications, functional morphology, online taxonomic databases and data from extant relatives. Each genus was assigned to a functional bin in the ecospace model of Bambach *et al.* (2007) based on its tiering, motility and feeding habits (Tables 1, 2). Scleractinian coral genera were all recorded as having suspension-feeding modes of life, despite evidence suggesting that many may have been photosymbiotic (Stanley & Swart 1995; Frankowiak *et al.* 2016; Stanley & Swart 2016). Modern scleractinian corals may employ a variety of feeding strategies, but most, including zooplankton microcarnivory, are consistent with suspension-feeding (Bambach *et al.* 2007; Bush *et al.* 2007). However, as the dominant organisms within this mode of life (which suffer the greatest reduction in generic richness and occurrences at the LTE) it would not alter the results of this analysis if corals were to be classified as photosymbiotic or predatory; this would only change the mode of life code from 261 to 265 or 266.

Some previous studies have also considered skeletal calcification to be an important trait that may confer selective advantage during extinction events (Pörtner *et al.* 2005; Knoll *et al.* 2007; Helmuth 2009; Payne *et al.* 2016*a*). In order to test this, the fossil genera were also assigned to one of three bins based on their calcification (i.e. light, moderate or heavy), following the classification scheme of Knoll *et al.* (2007). We do not go as far as to

TABLE 1. Mode of life categories for tiering, motility, and feeding following Bambach et al. (2007).

Ecologic category	Description
Tiering	
1	Pelagic: in the water column
2	Erect: benthic, extending into the water mass
3	Surficial: benthic, not extending significantly into the water column
4	Semi-infaunal: partly infaunal, partly exposed
5	Shallow infaunal: living in the top ~5 cm of the sediment
6	Deep infaunal: living more than ~5 cm deep in the sediment
Motility	
1	Freely, fast: regularly moving, unencumbered
2	Freely, slow: as above, but strong bond to substrate
3	Facultative, unattached: moving only when necessary, free-lying
4	Facultative, attached: moving only when necessary, attached
5	Non-motile, unattached: not capable of moving, free-lying
6	Non-motile, attached: not capable of moving, attached
Feeding	
1	Suspension: capturing food particles from the water
2	Surface deposit: capturing loose particles from a substrate
3	Mining: recovering buried food
4	Grazing: scraping or nibbling food from a substrate
5	Predatory: capturing prey capable of resistance
6	Other: e.g. photo- or chemosymbiosis, parasites

TABLE 2. Mode of life assignments (Bambach *et al.* 2007) present in Middle Triassic to Middle Jurassic marine environments.

Numeric	Mode of life defintion (tiering; motility; feeding mechanism)
115	Pelagic; freely, fast; predatory
141	Pelagic; facultative, attached; suspension
241	Erect; facultative, attached; suspension
261	Erect; non-motile, attached; suspension
312	Surficial; freely, fast; surface deposit
315	Surficial; freely, fast; predatory
321	Surficial; freely, slow; suspension
322	Surficial; freely, slow; surface deposit
324	Surficial; freely, slow; grazing
325	Surficial; freely, slow; predatory
331	Surficial; facultative, unattached; suspension
341	Surficial; facultative, attached; suspension
351	Surficial; non-motile, unattached; suspension
361	Surficial; non-motile, attached; suspension
415	Semi-infaunal; freely, fast; predatory
421	Semi-infaunal; freely, slow; suspension
422	Semi-infaunal; freely, slow; surface deposit
425	Semi-infaunal; freely, slow; predatory
441	Semi-infaunal; facultative, attached; suspension
442	Semi-infaunal; facultative, attached; surface deposit
451	Semi-infaunal; non-motile, unattached; suspension
456	Semi-infaunal; non-motile, unattached; other
461	Semi-infaunal; non-motile, attached; suspension
521	Shallow infaunal; freely, slow; suspension
522	Shallow infaunal; freely, slow; surface deposit
523	Shallow infaunal; freely, slow; mining
525	Shallow infaunal; freely, slow; predatory
526	Shallow infaunal; freely, slow; other
531	Shallow infaunal; facultative, unattached; suspension
532	Shallow infaunal; facultative, unattached; surface deposit
533	Shallow infaunal; facultative, unattached; mining
535	Shallow infaunal; facultative, unattached; predatory
541	Shallow infaunal; facultative, attached; suspension
546	Shallow infaunal; facultative, attached; other
621	Deep infaunal; freely, slow; suspension
631	Deep infaunal; facultative, unattached; suspension
641	Deep infaunal; facultative, attached; suspension
646	Deep infaunal; facultative, attached; other

consider skeletal mineralogy, however, previous results from Kiessling *et al.* (2007) found no overall selectivity associated with skeletal mineralogy.

Where sufficient geological information was available, fossil occurrences were assigned to one of three depositional settings: inshore, offshore or reef (Table 3). Occurrences with insufficient environmental data were not used in the depositional settings analyses. All occurrences were assigned to 30° palaeolatitudinal bands, irrespective of hemispheric orientation: polar (> 60°N or S), temperate (between 30 and 60°N or S) or tropical (< 30°N or S). All occurrences were, using palaeolatitude and palaeolongitude, plotted on to Triassic–Jurassic plate-tectonic basemaps (Scotese 2010) to identify which palaeo-oceanographic basin they were derived from (i.e. Tethys, Panthalassa, Boreal) (Dunhill *et al.* 2017, fig. S1).

TABLE 3. Categorization of depositional environments recorded in the PaleoDB following Kiessling *et al.* (2007).

PaleoDB classification	Category from this study
Coastal indet.	Inshore
Delta plain	Inshore
Deltaic indet.	Inshore
Estuary/bay	Inshore
Foreshore	Inshore
Lagoonal	Inshore
Lagoonal/restricted shallow subtidal	Inshore
Marginal marine indet.	Inshore
Open shallow subtidal	Inshore
Paralic indet.	Inshore
Peritidal	Inshore
Prodelta	Inshore
Sand shoal	Inshore
Shallow subtidal indet.	Inshore
Shoreface	Inshore
Transition zone/lower shoreface	Inshore
Basinal (carbonate)	Offshore
Basinal (siliciclastic)	Offshore
Deep subtidal (indet.)	Offshore
Deep subtidal ramp	Offshore
Deep subtidal shelf	Offshore
Deep-water indet.	Offshore
Offshore	Offshore
Offshore indet.	Offshore
Offshore ramp	Offshore
Offshore shelf	Offshore
Slope	Offshore
Submarine fan	Offshore
Basin reef	Reef
Intrashelf/intraplatform reef	Reef
Perireef or subreef	Reef
Platform/shelf-margin reef	Reef
Reef, buildup or bioherm	Reef
Slope/ramp reef	Reef

Statistical analyses

To account for biases brought about by uneven sampling across space and through time, we applied a subsampling regime to standardize both taxonomic and functional diversity on the basis of the number of fossil occurrences. Subsampling quotas were set at $n = 2000$ occurrences per bin for global analyses, and at $n = 350$ for the smaller-scale analyses pertaining to palaeolatitude, depositional setting and oceanic basin. Any time bins that did not reach the subsampling quota were omitted from the analyses. In each case, subsampling was carried out across 1000 iterations. We do not use shareholder quorum subsampling (SQS) (Alroy 2010), which has been proven to avoid the problems rarefaction has with dampening true differences in diversity, as our data show no trend in alpha diversity (i.e. number of taxa per collection) through time or across the Triassic–Jurassic boundary. Dissimilarity in ecological community structure between time bins was tested for using Bray–Curtis dissimilarity (Bray & Curtis 1957) tests on subsampled occurrence data to detect changes in relative abundances of functional groups and significance testing was achieved by randomly assigning fossil occurrences to pre- and post-extinction time bins across 1000 iterations and performing a Manly test (Manly 1997) to detect whether the observed dissimilarity is significantly different to the distribution of random occurrences. The simulations were achieved by randomly assigning Rhaetian and Hettangian occurrences to pre- and post-extinction assemblages and calculating Bray–Curtis dissimilarity across the boundary.

RESULTS

Global changes in functional diversity

Global genus-level extinction across the LTE is estimated at between 46% (using ranged-through data) and 72–73% (raw and subsampled occurrence) (Fig. 1A). There are considerable differences between the ranged-through and occurrence data throughout the results, with the former providing lower extinction estimates. This is unsurprising as the incomplete nature of the fossil record leads to inflated levels of extinction in occurrence data due to disappearances brought about by Lazarus taxa. The same difference between the datasets is evident in functional diversity loss too: seven modes of life apparently disappeared across the LTE according to the occurrence data, whereas five of those modes of life are recorded as being present by the range-through data (Fig. 1B). A maximum of two modes of life, therefore, disappeared across the Triassic–Jurassic (T–J) boundary: pelagic, facultatively mobile, suspension feeders and semi-infaunal, unattached non-motile, 'other' feeders, associated with the extinction of pelagic crinoids and megalodontid bivalves, respectively.

In the immediate aftermath of a mass extinction, it is hypothesized that there would be a radiation in functional diversity as taxa evolve to fill vacant ecospace left by the high levels of extinction (Bambach *et al.* 2007). Despite this, only one new mode of life originated in the aftermath of the LTE (Fig. 1B): semi-infaunal, slow-moving, deposit-feeding gastropods of the family Nerinellidae. However, a greater increase in ecospace occupation apparently preceded the LTE, in the Rhaetian, with the occupation or reoccupation of three modes of life: semi-infaunal, slow-moving, predators; shallow infaunal, slow-moving, 'other' feeders; shallow infaunal, facultatively mobile attached, 'other' feeders (Fig. 1B).

Similar losses of global functional diversity that are recorded in the aftermath of the LTE are also recorded between the Carnian–Norian (Tuvalian–Lacian) and across the Pliensbachian–Toarcian boundary (Fig. 1B). Neither of these reductions in functional diversity are reflected in the generic richness curve, but approximately correspond to known lesser extinction events: the Carnian Pluvial Event (CPE) in the mid-Carnian (Dal Corso *et al.* 2015) and the early Toarcian Ocean Anoxic Event (OAE) (Little & Benton 1995). The early Toarcian OAE is only detected in the occurrence (raw and subsampled) data and not in the ranged-through data, suggesting that extinctions may have been regional with functional groups rapidly recolonizing affected environments in the Middle Jurassic.

Regional changes in functional diversity

Based on subsampled data, the LTE records the biggest declines in both generic and functional richness in

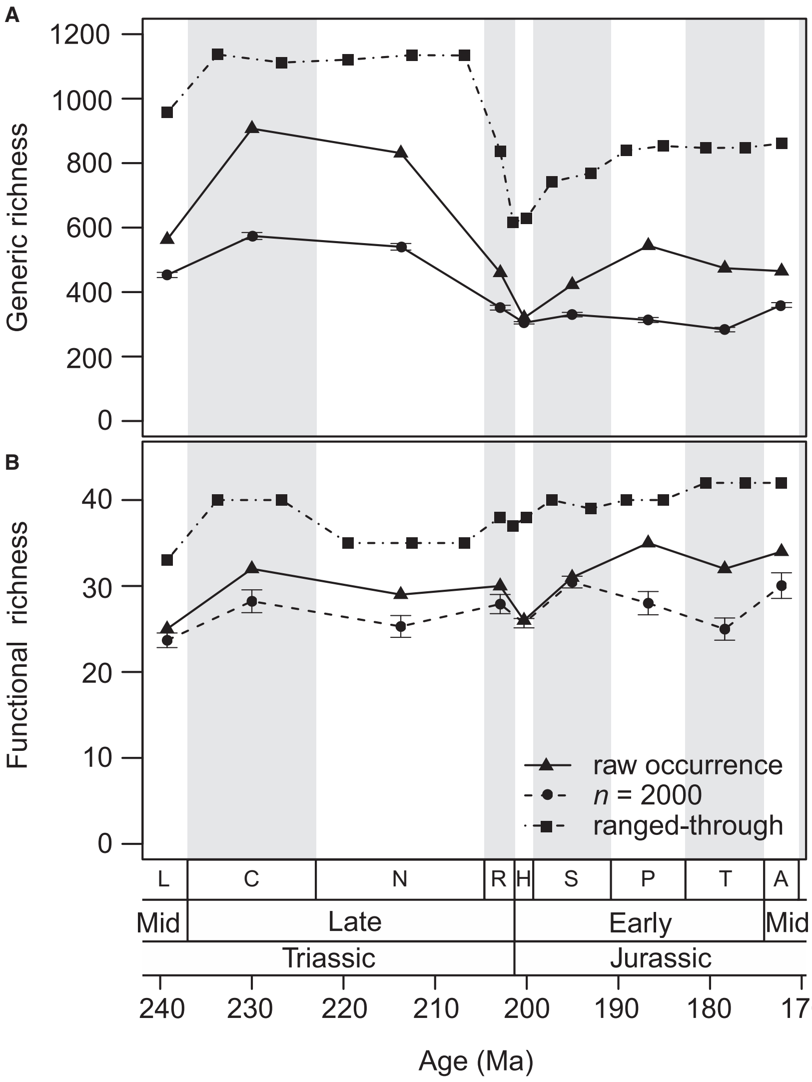

FIG. 1. Global diversity from the Middle Triassic to the Middle Jurassic. A, ranged, raw sampledand subsampled generic richness. B, ranged, raw sampled and subsampled functional diversity. Alternate white and grey bars represent chronostratigraphic stages (from left to right): L, Ladinian; C, Carnian; N, Norian; R, Rhaetian; H, Hettangian; S, Sinemurian; P, Pliensbachian; T, Toarcian; A, Aalenian.

tropical latitudes (Fig. 2A; Dunhill *et al.* 2017, fig. S2). Erect, facultatively mobile, suspension feeders disappeared from the tropics and did not return until the Middle Jurassic. A number of mostly suspension-feeding, surficial and infaunal modes of life also vacated the tropics, but returned in the Sinemurian–Pliensbachian. Tropical functional diversity returned to pre-extinction levels by the Sinemurian–Pliensbachian, but generic richness remained much lower than it was prior to the extinction, in the Carnian–Norian. Similar patterns are recorded in polar latitudes, but both generic and functional richness took longer to recover and remained low until the Aalenian (Fig. 2A; Dunhill *et al.* 2017, fig. S2).

In contrast, the mid-latitudes record a markedly different pattern, with only a slight decrease in generic and functional richness across the T–J boundary (Fig. 2A; Dunhill *et al.* 2017, fig. S2). Although pelagic suspension-feeders and a single guild of deep-infaunal suspension-feeders disappeared, most other guilds are present in the Hettangian. After subsampling, functional richness shows a much more pronounced drop from the Pliensbachian to the Toarcian, suggesting that although the LTE profoundly affected tropical and polar latitudes, the Toarcian OAE extinction was a more important event in the mid-latitudes. The drop in functional richness across the Pliensbachian–Toarcian boundary is associated with the temporary loss of ten infaunal modes of life, of which seven returned in the Aalenian.

The effects of the LTE are much more apparent in Panthalassa than in the Tethys or Boreal oceans (Fig. 2B). Pelagic suspension feeders apparently disappeared earlier in Panthalassa, at the end of the Carnian. Facultatively mobile, erect suspension feeders, all of which are crinoids, are absent from Panthalassa during the Hettangian. A number of epifaunal and infaunal suspension feeding guilds are also absent until the Sinemurian or Pliensbachian. Panthalassan generic and functional richness recovered to pre-extinction levels by the Sinemurian,

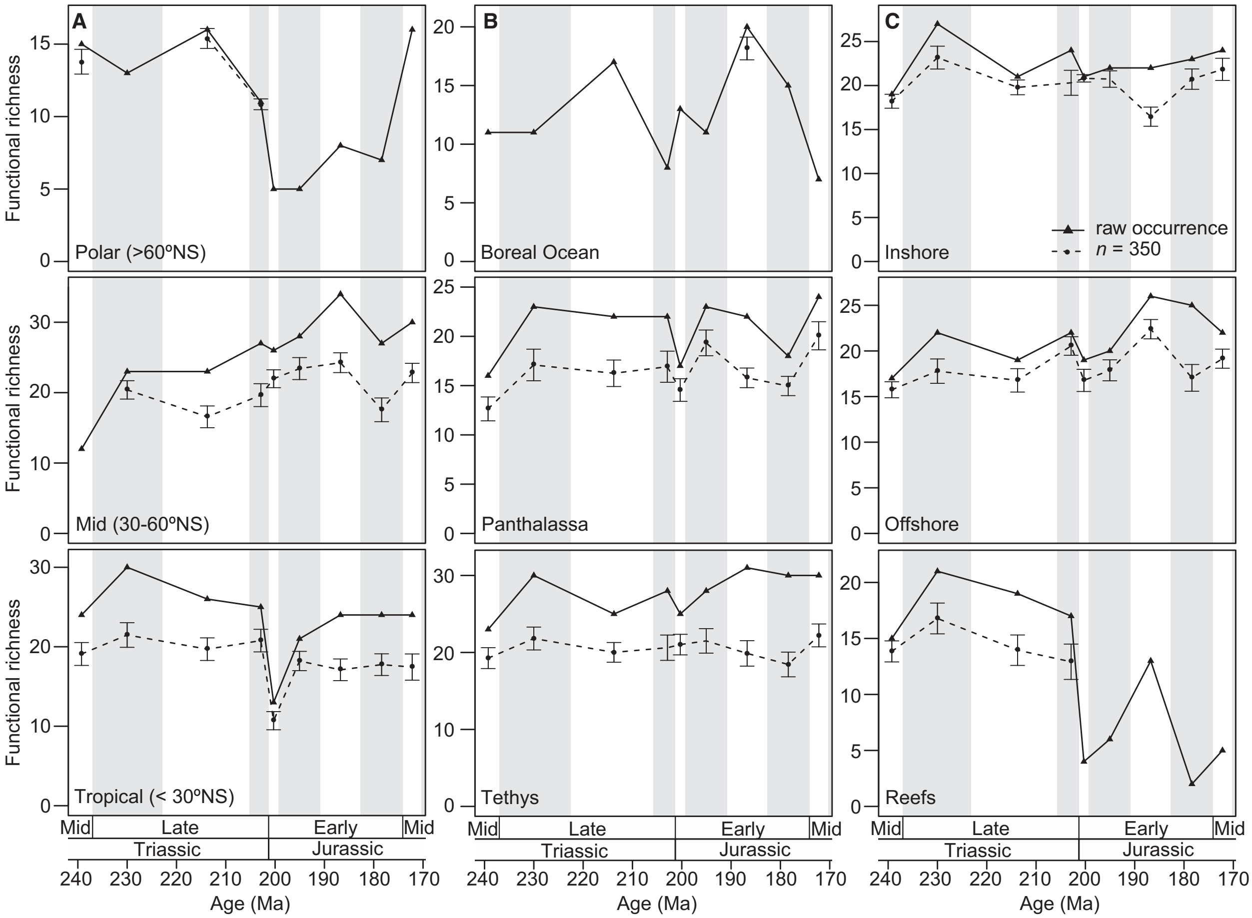

FIG. 2. Regional functional diversity from the Middle Triassic to the Middle Jurassic. A, subdivided by latitude (polar, mid-, tropical). B, subdivided by palaeo-oceanic basin (Boreal Ocean, Panthalassa, Tethys). C, subdivided by depositional environment (inshore, offshore, reef). Gaps in the subsampled time series represent time bins where the subsampling quotas were not met. Chronostratigraphic scale is the same as Figure 1.

although functional richness decreased once more through the Pliensbachian and Toarcian before recovering again in the Aalenian (Fig. 2B; Dunhill *et al.* 2017, fig. S2). The effects of the LTE appear less pronounced in the Tethys Ocean: the slight drop in raw generic and functional richness vanishes entirely after subsampling (Fig. 2B; Dunhill *et al.* 2017, fig. S2). Although generic richness was higher in the Late Triassic than the Early Jurassic, the decrease appears in the Norian–Rhaetian transition (Dunhill *et al.* 2017, fig. S2), rather than across the T–J boundary, and functional richness appears to be stable across the entire study interval. However, pelagic suspension feeders disappear at the LTE along with the temporary absence of some semi-infaunal and deep infaunal guilds until the Sinemurian and Pliensbachian. The Toarcian OAE is characterized by the temporary loss of some infaunal guilds, which all returned in the Aalenian. We see no evidence for a pronounced LTE or early Toarcian event in the Boreal Ocean (Fig. 2B), although the data are too sparse to carry out meaningful subsampling.

Reefs suffered greater losses than other depositional settings during the LTE (Fig. 2C). The generic and functional richness of reef environments plummeted across the T–J boundary, with the loss of over 90% of genera (Fig. 2C; Dunhill *et al.* 2017, fig. S2). With the exception of benthic suspension feeders, represented by one bivalve, one echinoid and seven coral genera, all functional guilds are absent from Hettangian reef ecosystems. All known Hettangian reefs are from mid-palaeolatitudes. The complete absence of tropical reefs is not due to sampling failure as there is a large sample size of Hettangian tropical occurrences in general. Reef ecosystems also record low functional diversity in the Toarcian (Fig. 2C). This decline in the Toarcian is similar to the LTE, with the temporary exclusion of most functional guilds apart from certain surficial suspension-feeding coral and bivalve genera. However, in contrast to the Hettangian, all Toarcian reefs are from the tropics, with none recorded from the mid-latitudes despite a large sample size of mid-latitude Toarcian occurrences in general.

Inshore environments record a drop in raw generic and functional richness across the T–J boundary, although this is not retained after subsampling (Fig. 2C; Dunhill *et al.* 2017, fig. S2). The LTE appears to driven the loss of some epifaunal and infaunal groups, which returned in the Sinemurian, but pelagic and facultatively mobile suspension feeding crinoids disappeared earlier. Neither of these functional guilds returned to inshore environments until the Middle Jurassic, suggesting that Early Jurassic shallow marine conditions remained inhospitable to some groups of motile, suspension feeding crinoids.

Offshore environments record modest drops in generic and functional richness across the T–J boundary, with the loss of a few infaunal guilds (Fig. 2C; Dunhill *et al.* 2017, fig. S2). Facultatively motile, erect suspension feeders (i.e. crinoids) are present in offshore environments during the Hettangian, suggesting that those settings remained hospitable to this mode of life whilst they were excluded from shallower ecosystems. There is a drop in functional richness, although not in generic richness, between the Pliensbachian and Toarcian in offshore environments (Fig. 2C; Dunhill *et al.* 2017, fig. S2), with the loss of many shallow and deep-infaunal guilds.

Changes in ecological structure

There is a significant reduction in within-mode-of-life richness from the Rhaetian to the lower Hettangian (Wilcoxon paired test: $V = 293$, $p < 0.001$) (Fig. 3A), with 19 modes of life, including the most taxonomically diverse groups, suffering a significant reduction in richness. Attached, erect, suspension feeders suffer a 50% reduction in their generic richness, whilst pelagic, fast-moving, predators and surficial, attached suspension feeders suffer a 30–40% reduction in generic richness. No change in generic richness was recorded for 11 modes of life, and increases in richness were recorded in 4 modes of life.

There is no significant reduction in the occurrence (i.e. number of occurrences within PaleoDB collections) of each mode of life across the T–J boundary (Wilcoxon paired test: $V = 256$, $p = 0.89$) (Fig. 3B). However, there is a reduction in the occurrence of attached, surficial suspension feeders of over 25% and attached, erect, suspension feeders suffer a decline of around 75%. There are reductions in the occurrence of many other suspension feeding groups whilst the number of occurrences of motile, surficial grazers, deposit feeders, and predators increase. There is also a dramatic increase in the number of occurrences of fast-moving, pelagic carnivores, which is unexpected given the reduction in generic richness recorded within this group.

Despite the significant losses to generic richness across all modes of life, the relative richness amongst modes of life does not deviate a great deal across the T–J boundary (Fig. 4A). Both erect and surficial, stationary, attached suspension feeders suffered a reduction in proportional richness across the LTE and remained at lower relative richness throughout the subsequent Early Jurassic. In contrast, infaunal groups and motile surficial modes of life show increases in proportional richness whilst pelagic predators suffer a reduction in proportional richness across the extinction but recover to pre-extinction levels by the late Hettangian (Fig. 4A). Long-term proportional occurrence patterns were, as expected, much more variable than the smoother trends of proportional richness, with the LTE appearing more pronounced (Fig. 4B). Surficial and erect, non-motile, suspension feeders suffered a

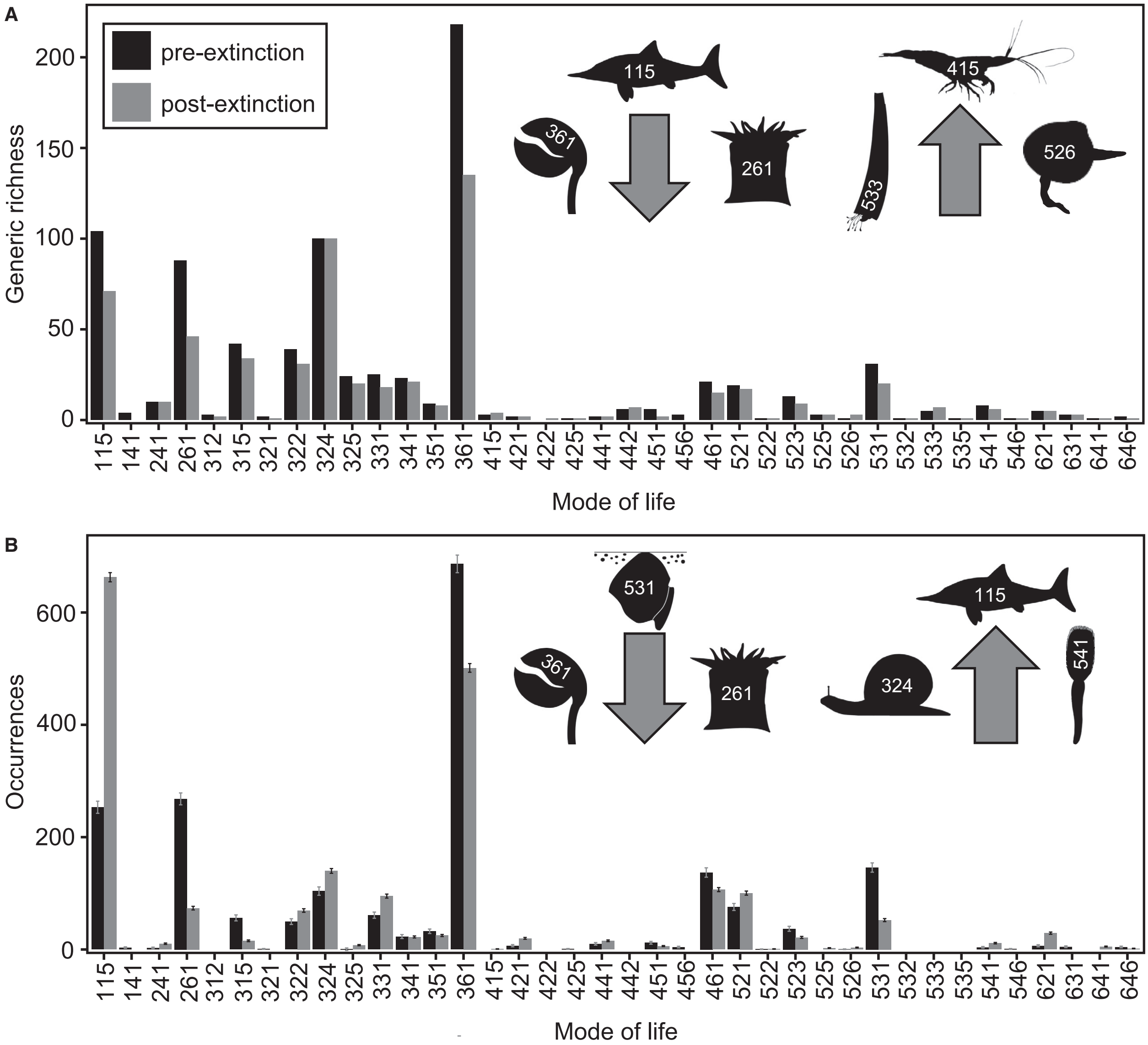

FIG. 3. A, pre-extinction (Rhaetian) and post-extinction (lower Hettangain) within-mode-of-life generic richness based on ranged-through richness data. B, pre-extinction (Rhaetian) and post-extinction (Hettangian) within-mode-of-life occurrence data based on subsampling to $n = 2000$. Silhouettes represent examples of modes of life that increased/decreased in richness/occurrence across the extinction event. See Tables 1 and 2 for mode of life definitions.

reduction in proportional richness whereas surficial, slow-moving grazers, deposit feeders and predators showed an increase. A large increase is also recorded in pelagic, fast-moving predators. Surficial, non-motile suspension feeders recovered quickly, reaching their pre-extinction level of proportional occurrence by the Sinemurian, but erect, non-motile suspension feeders (a guild dominated by scleractinian corals and crinoids) remained depressed in terms of number of occurrences with only a slight hint of recovery into the Aalenian. Another change in proportional occurrence occurs between the Pliensbachian and the Toarcian, which is coincident with the biotic crisis at that time.

Global ecological structure of the Rhaetian is more dissimilar to that of the Hettangian than would be expected by chance (Bray–Curtis dissimilarity value of 0.3, $p < 0.001$), and the change recorded across the LTE is greater than any other time period, bar the Toarcian–Aalenian (Fig. 5A and see Table 4 for Bray–Curtis scores). However, these dissimilarity values are only slightly higher than those recorded between other time bins (Fig. 5A). There is a clear dip in dissimilarity between the Hettangian and Sinemurian, before an increase in dissimilarity across the Pliensbachian–Toarcian boundary, and then a further increase in dissimilarity into the Middle Jurassic, possibly signifying the recovery of reef ecosystems (Fig. 5A). The

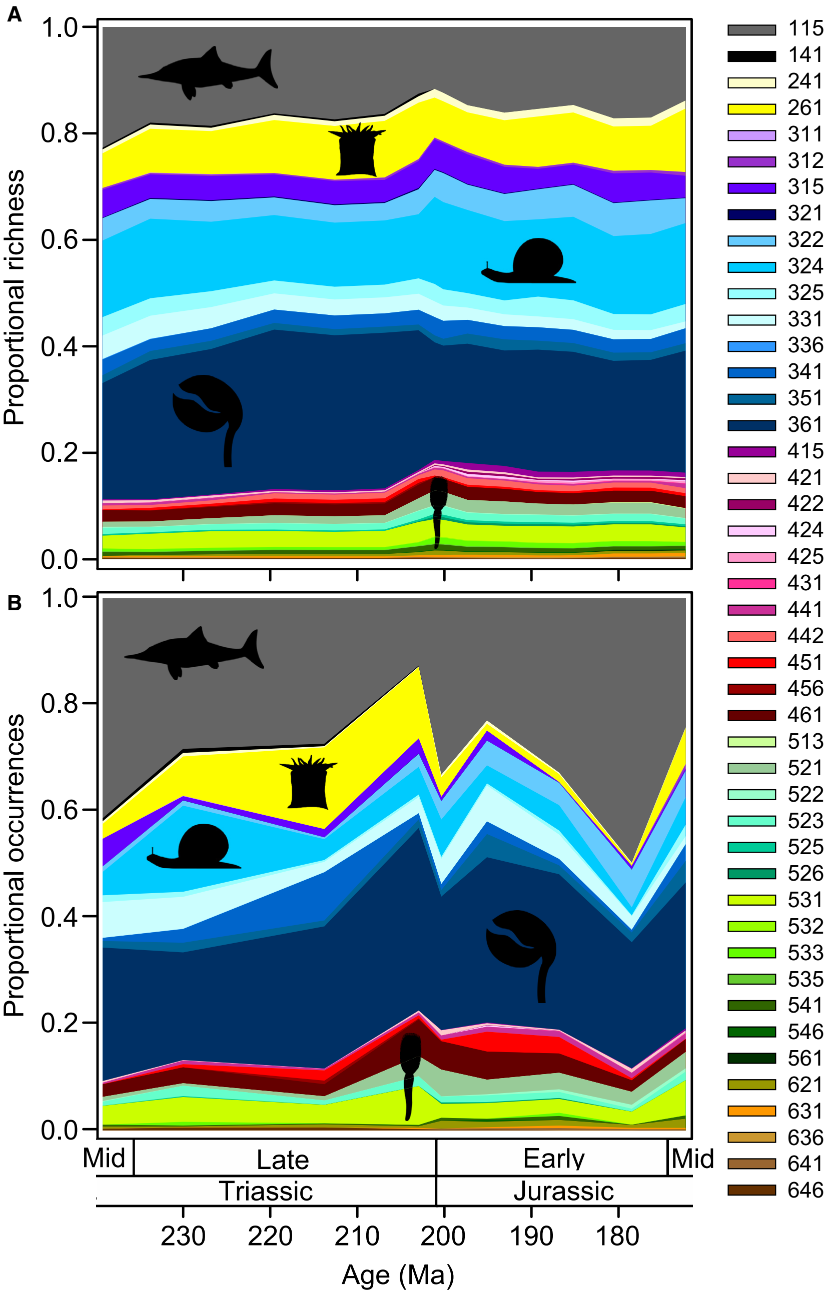

FIG. 4. Proportional richness and occurrence of modes of life from the Middle Triassic to the Middle Jurassic. A, proportional generic richness of modes of life, based on ranged-through data. B, proportional occurrence of modes of life based on occurrence data subsampled to *n* = 2000 occurrences. See Tables 1 and 2 for mode of life definitions.

Rhaetian is more ecologically similar to the Sinemurian than it is to the Hettangian, suggesting the onset of recovery through the Hettangian (Fig. 5A). However, the Pliensbachian and Toarcian are less similar to the Rhaetian than to the Hettangian or the Sinemurian. The functional composition of the Aalenian is more similar to the Rhaetian than any of the Early Jurassic stages (Fig. 5A).

Skeletal calcification appears to have had an influence on richness and proportional extinction across the T–J boundary (Fig. 6). Moderately calcified genera record a small net increase in relative richness, whereas the greatest loss of richness is recorded by the lightly and heavily calcified genera (Fig. 6A). This result is also reflected in extinction magnitude, where heavily calcified genera suffer the highest level of extinction, closely followed by light calcifiers, with much lower extinction among moderately calcified genera (Fig. 6C). Analyses were also carried out on just the benthic taxa, to test whether the erratic extinction rates of pelagic organisms, such as ammonoids, may have influenced these results, but no difference was recorded. Benthic taxa record very similar results, in terms of both generic richness (Fig. 6B) and extinction magnitude (Fig. 6D). However, in the benthic-only analyses, there is a slightly larger difference between the

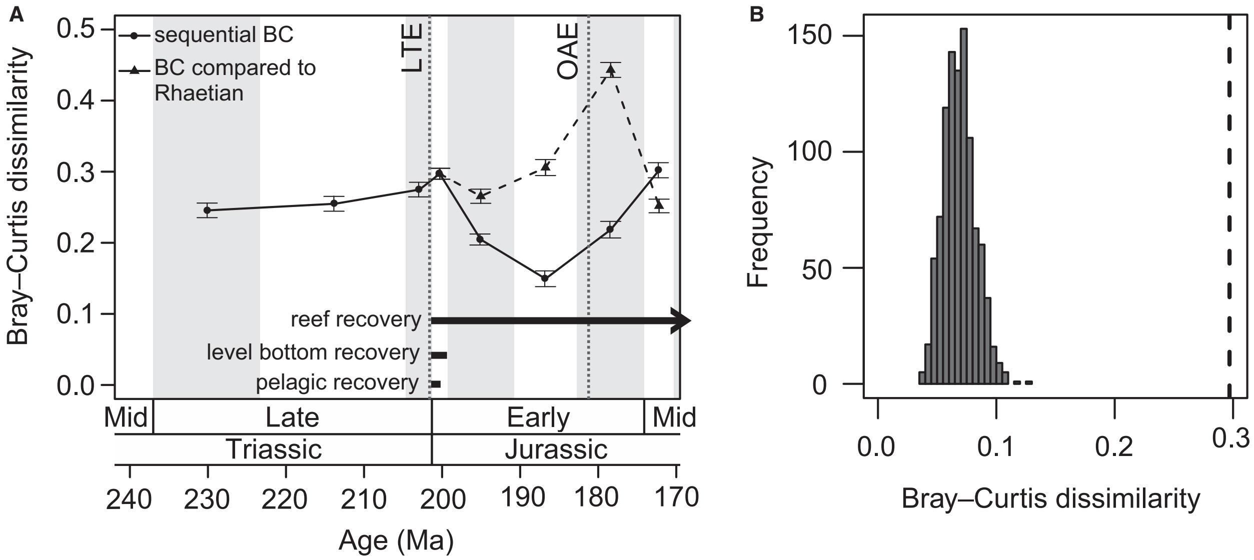

FIG. 5. Bray–Curtis dissimilarity analyses of global faunal composition from the Middle Triassic to the Middle Jurassic. A, Bray–Curtis dissimilarity values (BC) amongst sequential time bins (black); each point represents the dissimilarity between the time bin and the previous time bin and Bray–Curtis dissimilarity values between the Rhaetian and Jurassic time bins; all Bray–Curtis analyses were performed on occurrence data subsampled to $n = 2000$. B, Manly test for significance of Bray–Curtis dissimilarity between observed Rhaetian and Hettangian occurrences (dotted line) ($p \ll 0.001$) as compared to randomized occurrences across 1000 iterations (histogram).

TABLE 4. Bray–Curtis dissimilarity analyses.

Stage	Sequential		Dissimilarity to Rhaetian	
	Raw	$n = 2000$	Raw	$n = 2000$
Ladinian				
Carnian	0.37	0.25		
Norian	0.25	0.25		
Rhaetian	0.28	0.27		
Hettangian	0.38	0.3	0.38	0.3
Sinemurian	0.29	0.2	0.27	0.27
Pliensbachian	0.54	0.15	0.57	0.31
Toarcian	0.22	0.22	0.55	0.44
Aalenian	0.53	0.3	0.25	0.25

Sequential analyses represent mean value of dissimilarity across 1000 iterations from previous time bin to labelled time bin. Dissimilarity to Rhaetian analyses represent dissimilarity from Rhaetian to labelled time bin.

extinction magnitude of heavy and light calcifying genera, suggesting a slightly greater selection against heavy calcifiers (Fig. 6D). The only time interval that appears to be exclusively selective against heavily calcifying organisms is across the Pliensbachian–Toarcian boundary (Fig. 6D).

DISCUSSION

Although the LTE caused significant reductions in generic richness within almost all classes of animal life, we find very little evidence for significant reductions in global functional diversity. Global functional stability appears to be a common factor among mass extinction events, having been previously recorded for the Late Triassic (Kiessling *et al.* 2007), late Permian (Foster & Twitchett 2014) and the end-Cretaceous (Aberhan & Kiessling 2015). The LTE fits the 'skeleton crew hypothesis' of Foster & Twitchett (2014), in which each ecological guild survives, but is 'manned' by only a few individual taxa during the recovery period.

The two modes of life that are apparently lost across the extinction interval are both equivocal because of uncertain taxonomy and autecology. The pelagic, facultatively mobile, suspension feeders are all represented by one order of crinoids, the Roveacrinida, which originated in the Ladinian (Hess *et al.* 2016) and range-through to the Rhaetian when they apparently became extinct at the LTE. However, different taxa assigned to the Roveacrinida appear again in the Bajocian (Middle Jurassic) and range-through to the Miocene (Gorzelak *et al.* 2011). As this mode of life is re-occupied by the same order of organisms in the Middle Jurassic, we consider it unlikely that this mode of life was completely vacated at the LTE, and instead infer that the Roveacrinida persisted in abundances that were too low to be recorded in the fossil record, or in areas that have yet to be sampled for Early Jurassic fossils, as observed for Cenozoic occurrences of this group (Gorzelak *et al.* 2011). Alternatively, if the Roveacrinida is in fact paraphyletic, as has been suggested

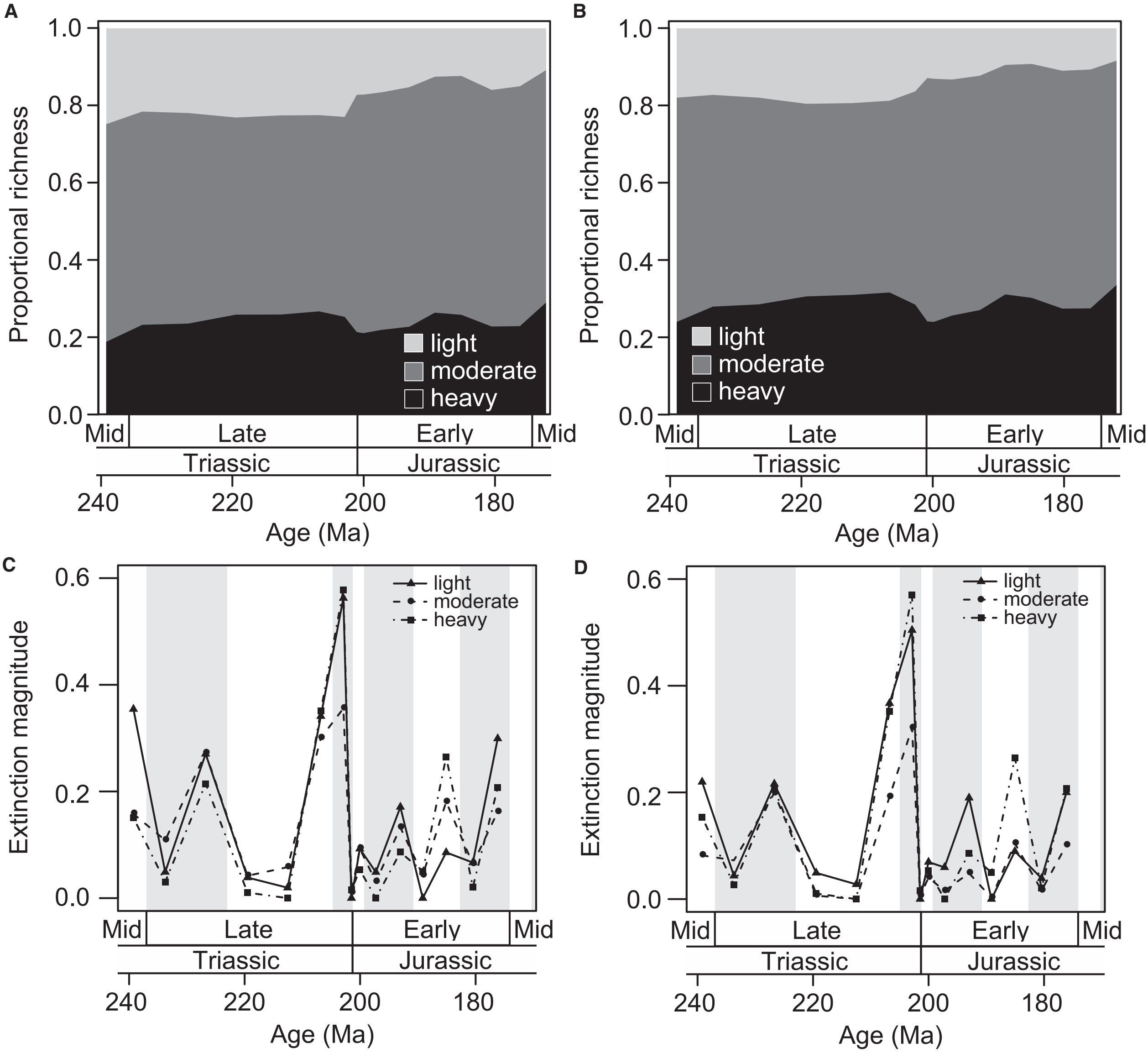

FIG. 6. Proportional generic richness and extinction magnitude of groups of calcifying organisms, from the Middle Triassic to the Middle Jurassic, distinguishing between light, moderate and heavy calcification. A–B, proportional generic richness; A, all groups; B, benthic groups. C–D, extinction magnitude; C, all groups; D, benthic groups.

(Simms 1990), then this may represent a real functional extinction and later re-occupation of the same niche by a different lineage of hemi-pelagic crinoids.

The surficial, unattached, 'other' feeders are represented by certain genera of megalondontid bivalves that have been interpreted as possessing photosynthetic symbionts (Yancey & Stanley 1999). A number of megalondontids that are not regarded as photosymbiotic are, however, known to have survived the extinction (Ros-Franch *et al.* 2014). Given that the identification and interpretation of photosymbiosis in alatoform bivalves is regarded as problematic (Yancey & Stanley 1999; Vermeij 2013) the apparent loss of this mode of life may be an artefact of palaeoecological interpretation, where either: (1) no megalodontids were photosymbiotic; or, (2) some photosymbiotic megalondontids also survived the extinction.

The single new mode of life that appears in the aftermath of the extinction and the three new modes of life that appear in the Rhaetian, immediately preceding the extinction, are all reoccurrences of niches that are found earlier in the Permian or Triassic, but not previously in the Late Triassic (i.e. Carnian and Norian). The reappearance of semi-infaunal, slow-moving, deposit feeders and predators, represented by nuculoid bivalves, gastropods, asteroids and ophuiroids, which were apparently absent through the Carnian and Norian, is probably an artefact.

These taxa are rare throughout the entire sequence and their absence from the Carnian and Norian is probably due to sampling failure. A further two modes of life in the Rhaetian are reoccupied following gaps in the Middle–Late Triassic and are represented by shallow infaunal, slow moving or facultatively mobile, chemosymbiotic bivalves of the family Lucinidae known also from the Early Triassic (Hautmann & Nützel 2005). Therefore, as has been recorded for the late Permian mass extinction (Erwin *et al.* 1987; Foster & Twitchett 2014), even though taxonomic richness was low in the aftermath of the Late Triassic extinction, global ecosystem functioning of keystone species was maintained with each functional group occupied by only a few individual genera.

As happened in the late Permian mass extinction, the LTE was felt most intensely in the tropics and disproportionally affected reef-dwelling organisms with suspension and/or photosymbiotic feeding habits, whilst deposit-feeding modes of life appear to benefit (Kiessling & Aberhan 2007; Kiessling *et al.* 2007; Martindale *et al.* 2012). The strong extinction signal in the tropical latitudes and the preferential extinction of reef taxa supports the hypothesis of a CAMP-driven, climate-warming kill mechanism driving high sea surface temperatures and anoxia for the LTE (Hallam & Wignall 2000; Kiessling *et al.* 2007; McRoberts *et al.* 2012; Jaraula *et al.* 2013; Bond & Wignall 2014; van de Schootbrugge & Wignall 2016).

Previous studies have suggested that global warming driven by rapid CO_2 release should also preferentially impact heavily calcified marine organisms, due to the effects of acidification (Hautmann 2004; Knoll *et al.* 2007). Although heavily calcified organisms do record the highest extinction rates across the T–J boundary, it is not clear that acidification was driving extinction because lightly calcified organisms also record high rates of extinction. This result contrasts with those of some previous studies where there appear to be clear differences in extinction rates between physiologically buffered and unbuffered organisms (Hautmann *et al.* 2008*a*; Kiessling & Simpson 2011). In other warming-related extinctions in the study interval, such as the early Toarcian, selection against heavily calcified organisms is much clearer (Fig. 6). The extinction pattern across the LTE is consistent with that of previous studies, which show that although heavy calcifiers experienced higher extinction rates, there are not huge differences between light, moderate and heavy calcifiers (Bush & Pruss 2013) and that selectivity against heavy calcifiers only becomes apparent after the removal of other confounding factors (Payne *et al.* 2016*b*). Therefore, it appears that even if acidification contributed to the LTE and reef collapse, other kill mechanisms (i.e. temperature change) were also important.

The reductions in suspension-feeder richness contrast with the slow moving, surficial, deposit feeders, grazers and predators, which increase in relative richness in the early Hettangian and maintain this throughout the Early Jurassic and into the Middle Jurassic. This is a common pattern that is also recorded in the aftermath of the late Permian (Twitchett 2006; Foster & Twitchett 2014; Foster *et al.* 2016, 2017) and end-Cretaceous (Aberhan & Kiessling 2015) extinction events, when suspension feeders suffered a crash primarily attributed to epicontinental shelf turbidity (Foster & Twitchett 2014) or a productivity crisis (Aberhan & Kiessling 2015) respectively. Given the similarities between the causal mechanisms of the late Permian and LTE events, it seems more likely that high sediment fluxes and eutrophication-driven dysoxia caused by increased runoff from the terrestrial realm may have spelled the downfall of benthic suspension feeding groups at the LTE (Algeo & Twitchett 2010; Jaraula *et al.* 2013; Foster *et al.* 2015; Schobben *et al.* 2015, 2016). Such a scenario may also explain the earlier exclusion of suspension feeding guilds after the Carnian as a result of the CPE (Dal Corso *et al.* 2015; Ruffell *et al.* 2016). Increased runoff and subsequent eutrophication of shallow shelf sea settings would have simultaneously choked suspension feeders, pushing them offshore, whilst benefiting deposit-feeding organisms (Algeo & Twitchett 2010). It is also possible that reductions in suspension feeder richness may be, in part, because many are heavily calcified (i.e. crinoids, brachiopods etc.), and heavily calcified organisms, particularly in reef settings, were selected against.

Although the LTE appears to have been concentrated in the tropical latitudes, the Toarcian OAE appears to have been felt most severely in the mid-latitudes, with the temporary exclusion of infaunal taxa being consistent with widespread dysoxia and/or anoxia being the main driving force of the early Toarcian extinction (Little & Benton 1995). This is further supported by the complete absence of reef environments in the tropics during the Hettangian and the mid-latitudes during the Toarcian. High extinction levels in Panthalassa, as compared to Tethys, particularly amongst erect suspension feeders and infaunal taxa may be a real signal, or may be a consequence of the high levels of extinction recorded in tropical latitudes and reef ecosystems. Further investigation of the determinants of extinction is required to answer this.

Although we see a general trend of reduced generic richness within modes of life across the LTE, a number of modes of life actually show an increase in richness. These functional groups, although not particularly diverse, all display feeding strategies that are expected to fare well in a stressed, post-extinction world (i.e. deposit-feeding, mining and chemosymbiosis) (Foster & Twitchett 2014; Clapham 2017). Some functional groups, such as pelagic, fast-moving carnivores, suffered a significant reduction in relative richness at the LTE, but then quickly recovered to pre-extinction levels by the late Hettangian, reinforcing the idea that both vertebrates (Thorne *et al.* 2011) (excluding conodonts which become extinct) and cephalopods (Longridge & Smith 2015) passed through an evolutionary bottleneck at the T–J boundary where rapid turnover rates aided rapid recovery. Despite this reduction in relative richness across the LTE, we see an increase in relative occurrences of pelagic, fast-moving carnivores. An explanation for this discrepancy is that the ranged-through richness data is compiled at the substage-level, and thus distinguishes the lower and upper Hettangian, whereas the occurrence data from the PaleoDB is compiled at the stage-level, and thus bins together the entire Hettangian. Several studies have demonstrated that recovery was rapid and complete by the upper Hettangian (Barras & Twitchett 2007; Hautmann *et al.* 2008*b*; Mander *et al.* 2008) and it is likely that some of the extinction effects are being masked due to the resolution of this study. Nevertheless, some of the pre–post-extinction changes are still evident in the occurrence data, most notably the reduction in non-motile suspension feeders and the increase in motile grazers, deposit feeders and predators.

Whilst dissimilarity analyses show that the global ecological shift from Rhaetian to Hettangian communities was greater than would be expected by chance, it is not notably larger than the ecological shifts witnessed at many other stage-level transitions and is similar to the ecological shift witnessed between the Toarcian and Aalenian (the Early to Middle Jurassic transition). Comparing the dissimilarity between the Rhaetian and each Jurassic time bin in turn shows that dissimilarity is higher between the Rhaetian and Hettangian than it is between the Rhaetian and Sinemurian, indicating that the global ecosystem was returning to its pre-extinction state by the Sinemurian. This is followed by a slight increase in dissimilarity between the Rhaetian and Pliensbachian, followed by a large increase in dissimilarity between the Rhaetian and Toarcian, as a result of the early Toarcian OAE. However, the Aalenian has a more similar ecological composition to the Rhaetian than the latter does to any of the Early Jurassic time intervals, thus signifying a recovery to something more similar to pre-extinction levels at the onset of the Middle Jurassic, probably driven by the beginning of the recovery of reef ecosystems (Hautmann 2012, 2016).

Benthic marine deposit-feeders, predators and grazers, dominated by gastropods, echinoderms and malacostracans, flourished during the earliest Jurassic in the aftermath of the crisis. Non-motile epifauna declined across the LTE, but infauna, motile epifauna and pelagic predators all increased in taxonomic richness and number of occurrences. This trend is associated with the Mesozoic Marine Revolution and was ongoing throughout the Late Triassic (Tackett & Bottjer 2016), before being invigorated by the preferential extinction of non-motile, suspension-feeding benthic guilds at the LTE. Our findings are somewhat at odds with previous studies of a single clade (i.e. bivalves) which showed selectivity against infaunal taxa (McRoberts & Newton 1995; McRoberts *et al.* 1995). Apparent high rates of extinction seen in infaunal bivalves are most likely to be the result of preservational biases (Mander & Twitchett 2008). Also, similar increases in deposit-feeders, grazers and predators, as well as in predation-resistant modes of life, have also been recorded in the aftermath of the late Permian (Foster & Twitchett 2014) and end-Cretaceous mass extinctions (Aberhan & Kiessling 2015). Although initial recovery from the LTE was rapid in level-bottom and pelagic communities, full benthic recovery, i.e. the reestablishment of reef ecosystems, appears to have been delayed by the subsequent crisis in the Early Toarcian. Overall, the similarities in functional, environmental and biogeographical extinction selectivity and recovery between the late Permian and the Late Triassic events are striking, although not surprising given the similarities in the causal mechanisms of the two events (van de Schootbrugge & Wignall 2016).

CONCLUSIONS

Although the LTE does not appear to have resulted in the extinction of any ecological guilds or a permanent global ecological regime shift, it had very profound regional and environmental effects, with the temporary complete collapse of tropical reef ecosystems (McGhee *et al.* 2004; Kiessling & Simpson 2011; Martindale *et al.* 2012) that did not fully recover until the Middle Jurassic. The effects of the LTE were largely confined to the tropical latitudes and there was significant selection against some modes of life, particularly stationary suspension feeders. We did not find any conclusive evidence that heavily calcifying organisms were selected against during the LTE, as compared to light calcifiers, but this may well have been the case during the early Toarcian OAE. The lack of evidence of permanent global regime shifts across major mass extinction events (Foster & Twitchett 2014), coupled with reduced estimates of taxonomic extinction (Stanley 2016), suggest that mass extinctions may not have been as ecologically catastrophic as once suspected. However, profound regional ecological effects and global taxonomic losses of 30–80% of species (Stanley 2016) still represent global biotic catastrophes of unimaginable magnitudes when thought of in terms of modern biodiversity. It therefore remains that the mass extinctions of the distant past, particularly those linked to rapid greenhouse warming, ocean anoxia, and ocean acidification (e.g. late Permian and Late Triassic), offer a stark reminder of the possible future consequences of anthropogenic influences on the biosphere (Harnik *et al.* 2012; Hull 2015).

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.bg30k

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