Marine extinction risk shaped by trait–environment interactions over 500 million years

EMILY A. ORZECHOWSKI[1], ROWAN LOCKWOOD[2], JARRETT E. K. BYRNES[3],
SEAN C. ANDERSON[4], SETH FINNEGAN[1], ZOE V. FINKEL[5], PAUL G. HARNIK[6],
DAVID R. LINDBERG[1], LEE HSIANG LIOW[7], HEIKE K. LOTZE[8], CRAIG R. MCCLAIN[9],
JENNY L. MCGUIRE[10], AARON O'DEA[11], JOHN M. PANDOLFI[12], CARL SIMPSON[13] and
DEREK P. TITTENSOR[14,15]
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referred to here as ‘extinction selectivity’, is defined as the identification of traits that distinguish taxa that go extinct from taxa that survive across a particular extinction event or time interval (Lockwood, 2008).

Much of what we know about extinction selectivity in the marine realm is derived from the rich fossil record of benthic marine invertebrates. Paleontological studies provide empirical support for the influence of a number of biological factors on extinction selectivity over the >500-million-year history of skeletonized marine animals (e.g., Jablonski, 2005; Kiessling & Aberhan, 2007; Knoll et al., 2007; Liow, 2007; Payne & Finnegan, 2007; O’Dea & Jackson, 2009; Simpson & Harnik, 2009; Crampton et al., 2010; Finnegan et al., 2012; Harnik et al., 2012b). The extent to which biological characteristics have influenced extinction selectivity, and changes in environmental state have amplified or weakened these effects, is valuable information for predicting extinction selectivity given future environmental conditions (Harnik et al., 2012a; Blois et al., 2013). Quantitainfaunal life habit may be advantageous under normal geochemical conditions, when predation pressure on epifaunal organisms can be intense (Stanley, 1977, 1982,

Calculating extinction selectivity

To calculate the log-odds ratio (Mantel & Haenszel, 1959; Cooper et al., 2009), we began with a 2 × 2 matrix describing the number of preserved and sampled species going extinct or surviving in either trait category. For example, a taxon is either epifaunal or infaunal and can either go extinct or survive. The odds ratio of extinction selectivity is the ratio of the probability of survival (p_1) and extinction ($1 - p_1$) in one trait category divided by the ratio of survival (p_2) and extinction ($1 - p_2$) in the other trait category. The extinction log-odds ratio (OR) is defined as:

$$\ln(OR) = \ln \frac{p_1/(1 - p_1)}{p_2/(1 - p_2)}$$

ratTm [(no)-274741offo.33941 1 Ttheiother,er several important extinction events (e.g., Ordovician –Silurian, Late Permian events) are associated with d^{34}S excursions.

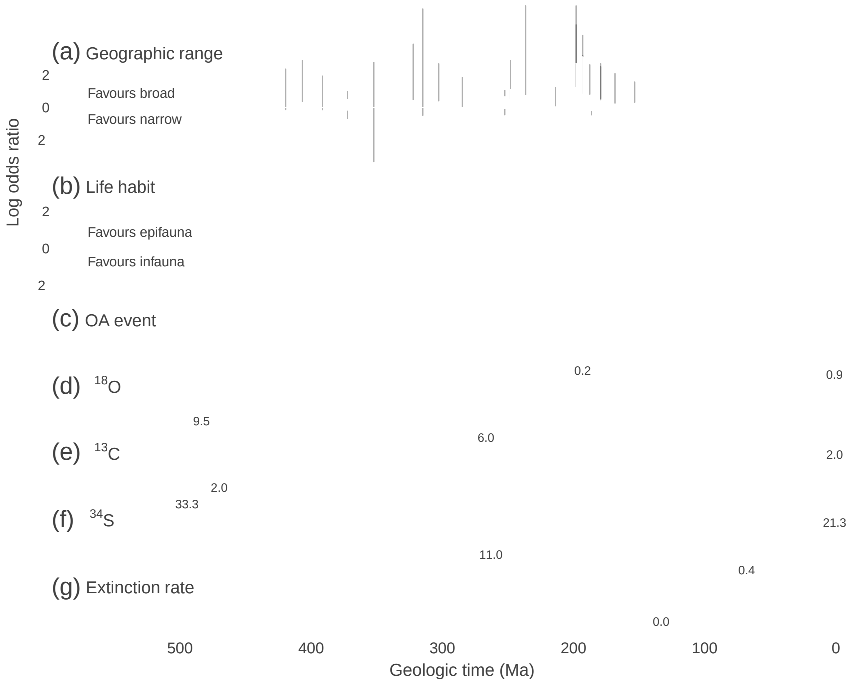
confidence interval (CI) = 0.84–1.25, (odds ratio: 2.8, 95% CI = 2.3–3.5)). When pooled across intervals characterized by different environmental conditions, there is no significant difference in extinction selectivity according to life habit (Figs 1b, 3; estimate of log-odds ratio = 0.06, 95% CI= 0.32–0.20).

The variation in log-odds ratios throughout the Phanerozoic (Fig. 1a) suggests that the importance of geographic range in promoting survivorship may vary across different extinction events or geological stages, but not with any discernible trend through time (Fig. 1a). We did not find strong evidence for an effect of observed extinction rate on geographic range or life-habit extinction selectivity (Figs 1, 4; Table S4). Our meta-regression shows no statistically significant relationships between geographic range selectivity and environmental proxies (Fig. 4a; Table S4a). Although the relationship with d^{34}S is borderline statistically significant (estimate of log-odds ratio: 0.07, 95% confidence interval (CI) = 0.13–0.001), it does not alter the direction of selectivity (i.e., although extinction selectivity appears to weaken slightly, broad-ranging taxa are still significantly more buffered from extinction than narrow taxa within the observed range of d^{34}S, see Fig. S3).

In contrast, we found some evidence suggesting a weak relationship between environmental conditions and the selectivity of extinction with respect to life habit (Fig. 4b, Table S4b). Our data sho positive association between d^{18}O and epifaunal survivorship (Fig. 4b). Accounting for all other predictors, decreases in d^{18}O (tied to climate warming) corresponded to preferential infaunal survivorship; increases in d^{18}O (tied to climate cooling) were associated with less selectivity (Fig. 5a; log-odds ratio: 0.42, 95% CI = 0.03–0.81). We used the detrended residuals of d^{18}O to account for the long-term Phanerozoic trend toward heavier values, which is controversial and poorly understood (Jaffrés et al., 2007). These residuals yielded even stronger results (Fig. 5b; Table S5b), such that increases in detrended d^{18}O (tied to climate cooling) corresponded to preferential epifaunal survivorship. Once again, decreases in detrended d^{18}O (tied to climate warming) corresponded to preferential infaunal survivorship (Fig. 5b; log-odds ratio: 0.52, 95% CI = 0.14–0.90). We did not find strong evidence that life-habit selectivity was correlated with changes in d^{34}S or ocean acidification (Fig. 4b, Table S4b), or displayed any specific trend through time (Fig. 1b).

Discussion

Our meta-analysis reveals remarkable consistency in the link between geographic range and extinction selectivity throughout the past 500 million years. On aver-



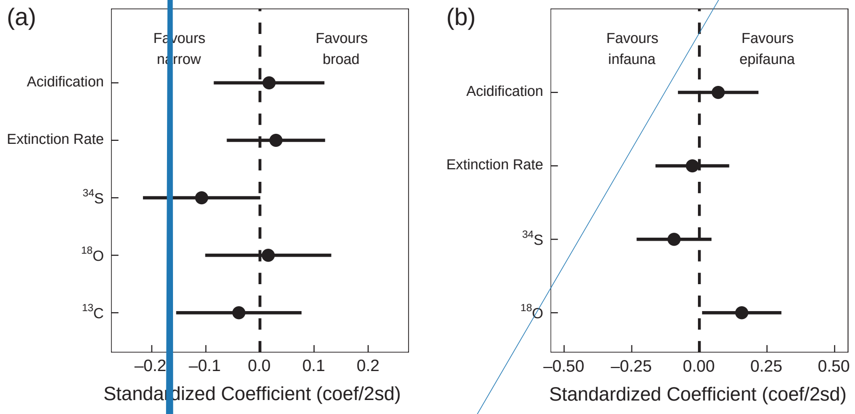


Fig. 4 Coefficients relating environmental proxies to extinction selectivity according to geographic range size (a) and life habit (b). Points represent standardized regression coefficient estimates and lines represent 95% CI. We standardized the regression coefficients by subtracting the mean and dividing by two standard deviations for all continuous variables (i.e., 'coef/2sd'), making the magnitude of the coefficients approximately comparable (Gelman, 2008). We provide unstandardized coefficients and CI in Table S4.

1994; Foote, 1997), the pattern of extinction selectivity documented here is unlikely to result from such sampling artifacts. Several individual studies have attempted to control for sampling and preservational biases, but all still report a strong correlation between geographic range and extinction selectivity (Payne & Finnegan, 2007; Rivadeneira & Marquet, 2007; Crampton et al., 2010; Harnik, 2011).

The absence of any discernable links between geographic range extinction selectivity and global environmental state may suggest that environmental changes influencing the proxies we examined exert little effect on extinction selectivity related to geographic range. If all taxa are affected equally by an environmental change without regard to geographic range, this would not alter the preexisting ratio of extinction probabilities. Alternatively, this pattern may be the result of more complex causal relationships. For example, an interval of warming could drive sea-level rise, thereby opening more habitat and potentially reducing the extinction of spatially restricted endemics. However, endemic taxa restricted to high latitudes may be effectively trapped, unable to shift range when biogeographic boundaries migrate (Parmesan, 2006; Cheung et al., 2009). Direct and indirect effects of climate change, therefore, may not additively drive extinction selectivity in any one direction and the strength of selectivity may change in different regions.

Associations between fossil diversity and environmental conditions are frequently assessed using globally averaged environmental proxies (Peters & Foote, 2002; Mayhew et al., 2008; Hannisdal & Peters, 2011; Peters et al., 2013), although the residence times and expected geographic and environmental variability of the relevant proxies vary considerably. In this study, extinction selectivity data are drawn from spatially regional to global and temporally discrete to averaged extinction events, whereas all environmental proxy data are global (or low latitude in distribution) and averaged over millions of years within each geologic stage. It is therefore possible that our finding that geographic range selectivity does not vary with environmental conditions may reflect some mismatch of temporal and spatial scale between our extinction and environmental proxy data. We found no evidence that either geographic scope (i.e., regional vs. global studies) or temporal resolution (i.e., single vs. multi-stage studies) significantly affected geographic range effect size in our meta-analysis. Nevertheless, it is important to bear in mind that our spatially and temporally averaged could address this by contrasting in detail the physiological responses of infaunal and epifaunal bivalves to different environmental regimes.

Several of the data points that display low residual log-odds ratios and low $\delta^{18}O$ values (i.e., that anchor the lowest left quadrant of Fig. 5a) are derived from the Knoll et al.'s (2007) study of the Late Permian time interval. When this study is removed from the analysis, the relationship between $\delta^{18}O$ and selectivity weakens (Fig. S1, compare to Fig. 4b). Although a link between CO_2 tolerance and infaunality is often referred to in the literature (Knoll et al., 1996, 2007), few empirical studies exist to support it (Widdicombe et al., 2011). In fact, Clapham & Payne's (2011) work on the Changhsingian (End Permian) extinction suggests that infaunal bivalves may have experienced greater extinction during the latest Permian than epifaunal bivalves. Despite this, the inclusion of the Knoll et al. (2007) study in this meta-analysis is warranted because (i) it is one of the few studies focusing on the intervals before and during a particularly catastrophic event and (ii) the studies targeting the time interval that follows (Triassic; McRoberts & Newton, 1995; Hautmann et al., 2008) yield similar results. Until we have a better understanding of the physiological response of mollusks living below and above the sediment–water interface, especially to hypercapnia vs. anoxia, it may be difficult to interpret these results in detail.

When extinction selectivity is tracked across the Phanerozoic, our meta-analysis reveals no statistically significant trend in selectivity according to life habit. There is, however, a slight tendency for extinction selectivity to shift from preferential survivorship of infaunal taxa in the late Paleozoic to preferential survivorship of epifaunal taxa in the early Mesozoic and then back to preferential survivorship of infaunal taxa in the late Mesozoic or Cenozoic. The timing of this second shift may coincide with the Mesozoic marine revolution (Vermeij, 1977, 1987), a radiation of shell-crushing and boring predators that begins in the Late Triassic and is purported to lead to a decrease in the ratio of epifaunal relative to infaunal prey species by the Cretaceous (Thayer, 1979; Aberhan et al., 2006; Bush et al., 2007; Tackett & Bottjer, 2012). Epifaunal bivalves, along with brachiopods, crinoids, and gastropods, are thought to have been heavily preyed upon throughout the Mesozoic marine revolution, driving the bivalves to invade deeper burrowing niches (Tackett & Bottjer, 2012). Unfortunately, the lack of extinction selectivity studies focusing on the mid-Jurassic to the Late Cretaceous makes this impossible to test using our current dataset.

Despite large differences in spatial and temporal scaling of extinction in ancient and modern oceans, our meta-analysis demonstrates that the predictors of selectivity can be effectively gleaned from 500 million years of earth history. Many of the environmental changes that are predicted to occur in the near future (e.g., ocean acidification, global climate change) have occurred multiple times in the past. The record of these past events provides conservation and global change biologists with opportunities to observe biotic responses and, in particular, patterns of extinction selectivity. The extent to which these patterns vary with environmental conditions provides useful data for models seeking to predict which organisms will go extinct in response to specific environmental changes. The crucial role that geographic range plays in survivorship of fossil marine organisms, regardless of environmental state, emphasizes that the preservation of range size should be a key priority in conservation (Mace et al., 2010). As nations struggle to support marine protected areas (MPAs) that cross international borders, the maintenance of overall range size, and connectivity among ranges, will only increase in importance (Wells & Day, 2004; Moffitt et al., 2011; Berumen et al., 2012; Day & Dobbs, 2013). The fact that geographic range is an accurate predictor of extinction over geologic time, regardless of environmental conditions, also supports its widespread use as a proxy for extinction selectivity by agencies such as the International Union for the Conservation of Nature (IUCN, 2014; see for example Cassini, 2011) and stresses the importance of targeting narrow-ranging taxa in conservation policymaking.

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