Strong coupling of predation intensity and diversity in the Phanerozoic fossil record

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The importance of ecological interactions in driving the evolution of animals has been the focus of intense debate among paleontologists, evolutionary biologists, and macroecologists. To test whether the intensity of such interactions covaries with the secular evolutionary trend in global biodiversity, we compiled a species-level database of predation intensity, as measured by the frequency of common predation traces (drillings and repair scars ranging in age from Ediacaran to Holocene). The results indicate that the frequency of predation traces increased notably by the Ordovician, and not in the mid-Paleozoic as suggested by multiple previous studies. Importantly, these estimates of predation intensity and global diversity of marine metazoans correlate throughout the Phanerozoic fossil record regardless of corrections and methods applied. This concordance may represent (*i*) an ecological signal: long-term coupling of diversity and predation; (*ii*) a diversity-driven diffusion of predatory behaviors: an increased probability of more complex predatory strategies to appear at higher diversity levels; or (*iii*) a spurious concordance in signal capture: an artifact where rare species and less-frequent (e.g., trace-producing) predatory behaviors are both more detectable at times when sampling improves. The coupling of predation and diversity records suggests that macroevolutionary and macroecological patterns share common causative mechanisms that may reflect either historical processes or sampling artifacts.

macroecology | macroevolution

Congruencies and discordances between biologically relevant patterns extracted from the geological record offer key historical data about the processes that have governed the history of life. For example, correlations between secular changes in rock volume, sea level, and biodiversity (1, 2), ocean chemistry and types of biomineral skeletons (3), and local and global diversity levels (4) all opened major research avenues with broad historical relevance. More recently, key predictions of the important, and controversial, hypothesis of escalation (biotic systems have become more dangerous through the Phanerozoic, and organisms respond evolutionarily to their enemies) have been tested by using time series spanning the Phanerozoic (5). Madin *et al.* (5) suggest that, when the data are properly analyzed, there are no significant correlations between the long term patterns in the proportion of carnivorous marine invertebrates and the proportions of infaunal or mobile prey and between the proportion of bioturbators and the proportion of immobile epifauna. The results of Madin *et al.* and others did not support escalation as an important shaper in the history of Phanerozoic marine life, but the validity of their approach was subsequently debated (6–8). Here, by comparing secular changes in biodiversity (2, 4) with estimates of the intensity of predator–prey interactions, we offer a more direct test of this fundamental question shared by paleontologists, evolutionary biologists, and macroecologists: Do ecological interactions matter over evolutionary timescales (5–13)?

When evaluating the importance of ecological interactions in driving the Phanerozoic evolution of metazoans, predation has received particular attention, both because it has been invoked repeatedly as an evolutionary force (10, 14–16) and because quantitative data on the geological history of predator–prey interactions are accessible by studying trace fossils left on prey skeletons.

These trace fossils primarily include drill holes, generally interpreted as successful predation attempts, and repair scars, believed to represent failed durophagous predation attempts (12, 17, 18). Previous trace fossil studies centered on two approaches: literature- and museum-based compilations of long-term patterns at low taxonomic resolution (e.g., class-level data on occurrences of drilled prey fossils throughout the Phanerozoic) (12, 17) and quantitative studies based on bulk samples, but carried out at much finer temporal and taxonomic scales (e.g., repair scar and drilling frequencies in mollusk prey analyzed at family or genus level over geologically short time segments) (9, 18, 19). Although these studies provided important insights into the history of predation, none was sufficiently comprehensive to allow for a rigorous comparison with other secular trends such as biodiversity. In fact, the previous quantitative projects focused mainly on reconstructing predation records, but did not compare those records to long-term diversity patterns or, at best, addressed the issue marginally in qualitative and anecdotal terms. This may not be so surprising, when considering that the patterns revealed in those studies hinted at discordance rather than concordance between trends in diversity and predation intensity: mid Paleozoic spike in predation (12, 14, 17) occurred in the middle of the Paleozoic diversity plateau long after the Great Ordovician Radiation and the Mesozoic Marine Revolution took place in mid-late Mesozoic/early Cenozoic (16), while diversity may have continued to increase throughout the late Cenozoic (20–22) as well.

To test for correlation between diversity and predation intensity, we have assembled a predation database for marine invertebrates that (*i*) provides methodologically consistent species-level estimates of trace fossil frequencies; (*ii*) spans the entire recorded history of marine metazoans (Ediacaran–Holocene); and (*iii*) includes a sufficient number of estimates based on bulk samples to assemble a time series of predation intensity estimates that can be contrasted against the fossil record of diversity.

Results

The first-order pattern of the Phanerozoic history of species level predation intensity is partly consistent with previous studies by suggesting two intervals of increased predation: one in the Paleozoic, and the second, more prominent one, in the late Mesozoic/Cenozoic (Fig. 1). However, our Paleozoic estimates indicate that predation intensity increased already by the late Ordovician/early Silurian, predating notably (by ≈70 million years) the mid-Paleozoic Marine Revolution, an interval of intense escalation
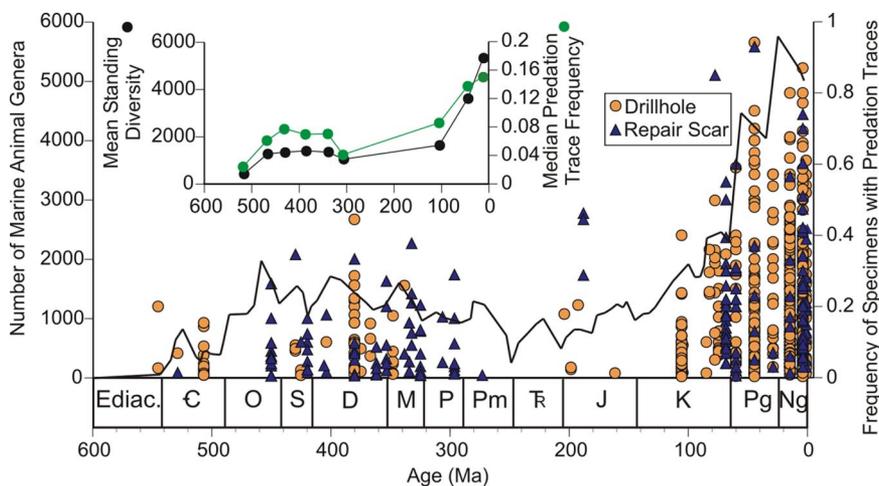
Fig. 1. Phanerozoic history of genus-level marine animal diversity (black line) (22) and predation trace frequency of marine invertebrates (orange circle, drillhole; blue triangle, repair scar). (*Inset*) Average diversity (black circles) and predation (green circles) values for each period with at least 10 predation occurrences.

postulated initially on the functional morphology of presumed predators and prey (14) and subsequently supported by trends in predation on brachiopods and sessile echinoderms (12, 23). Similarly, although the Mesozoic Marine Revolution was initially proposed as a period of intense escalation in the mid-to-late Mesozoic (16), our results highlight the dearth of species-level predation estimates until the late Mesozoic (12) [see supporting information (SI) *Text*] and also suggest that the further increase in predation intensity occurred throughout the late Cenozoic. This pattern is consistent with assemblage-level global compilations (12), but not with estimates based on functional morphology (16) or regional drill-hole data with finer time resolution (18, 24). Finally, predation intensities estimated here at the species level tend to be much higher than was suggested by previous calculations at coarser taxonomic resolution. For example, predation intensity reached as high as 22% in the Ediacaran and nearly 40% by the Silurian, which are levels observed in previous assemblage-level studies using different metrics only for the Cenozoic (12, 18, 24).

Predation intensity proxies compiled here and the previously assembled genus-level diversity estimates (21, 22) appear remarkably concordant (Fig. 1): frequencies of predation traces increase and decrease in concert with estimates of global biodiversity. The two patterns become nearly perfectly congruent when diversity and predation estimates are both binned by geological period: median species-level frequencies of predation traces and mean genus-level diversity track each other tightly across geological periods (Fig. 1 *Inset*). Given a good agreement between the family- and genus-level diversity curves (4, 21), we follow previous authors in assuming that the genus-level diversity curve approximates a species-level diversity curve (also, most of our predation estimates came from samples dominated by monospecific genera, so the species-level predation data are, to a large extent, synonymous with genus-level data). The strong congruence between diversity and predation intensity is observable regardless of metrics and corrections used: strong (and mostly significant) correlation coefficients persist for (*i*) the raw data ($r = 0.93$; $P = 0.0002$); (*ii*) the detrended data corrected for autocorrelation by first differencing ($r = 0.74$; $P = 0.037$) (Fig. 2); (*iii*) other measures of central tendency (see *SI Text*); and (*iv*) diversity estimates recalculated without singletons (Table 1). Also, the correlation cannot be attributed to binning artifacts (see SI Table 2). However, given that historical patterns are often scale-dependent, the period-level correlation observed here should not be extrapolated to finer time scales or used to refute patterns uncovered at sub-period resolution.

When grouped into higher taxa, the Phanerozoic distribution of prey species occurrences mirrors Sepkoski's three evolutionary faunas (20) (Fig. 3). This visual similarity is statistically significant when the data are binned by period (Fig. 3 inset). The proportion of standing diversity that belongs to the Paleozoic fauna correlates with the proportion of prey species occurrences that belong to the Paleozoic fauna (raw data: $r = 0.83$, $P = 0.0009$; first differences: $r = 0.73$, $P = 0.01$). Although this concordance may be quite trivial (i.e., predators prey on most common prey), multiple explanations of this pattern are possible, as shown below.

Discussion

The strong coupling of the fossil records of predation and diversity is remarkable considering that predation estimates are based on specimen-level data, whereas Sepkoski's diversity data contain no information about specimen abundance. This observation is consistent with the idea that diversity and abundance may correlate tightly (25). However, concurrent temporal shifts in diversity and abundance do not need to translate into a corresponding increase in predation intensity. Higher diversity and abundance do not necessarily imply higher predation rates: there are more predators, but there is also more prey. Thus, a correlation between predation and diversity implies that either key ecological parameters of the biosphere, such as evenness structure or predator–prey ratios, must have varied through time or that other mechanisms need to be invoked. To this end, we propose three end-member hypotheses (*Ecological Signal*, *Diversity-Driven Diffusion of Predatory Behaviors*,
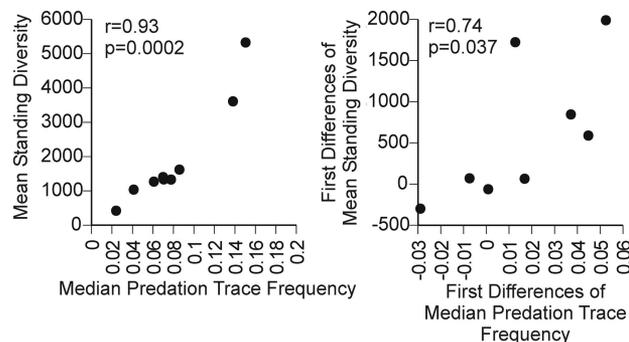

Fig. 2. Scatter plots of average diversity and average predation trace frequency for periods with at least 10 predation occurrences. *r*, Spearman correlation coefficient, calculated in SAS 9.1.

Table 1. Spearman correlation of mean taxonomic diversity and median predation trace frequency for data binned at the resolution of a geological period

	Raw data		First differences	
	r	P	r	P
Standing diversity	0.93	0.0002	0.74	0.037
Standing diversity minus singletons	0.95	<0.0001	0.71	0.047
Bottom boundary crossers	0.97	<0.0001	0.67	0.071
Top boundary crossers	0.88	0.0016	0.69	0.058

Only periods with at least 10 predation occurrences were included. r, Spearman correlation coefficient; P, a two-tailed probability of r = 0. Correlation analyses were performed with SAS 9.1.

and *Spurious Concordance in Signal Capture*) that can explain the strong coupling of global diversity and diversity structure with predation intensity observed throughout the Phanerozoic fossil record of marine invertebrates.

Fig. 3. Relationship between Sepkoski's three evolutionary faunas and prey-species occurrences. (*Upper*) Sepkoski's genus-level diversity data classified by evolutionary fauna and averaged by period. (*Lower*) All pre-Holocene prey species occurrences from the predation database classified by evolutionary fauna and binned by period (n = 1,820). Scatter plots compare the proportion of species diversity and proportion of species in the predation database within a period that belong to the Paleozoic evolutionary fauna for raw data and first differences. Even though there are three evolutionary faunas, the ratio of the Paleozoic fauna to other two faunas is an effective way of summarizing all data. In the Cambrian, the metric measures the ratio of the Cambrian-to-Paleozoic faunas (only a small fraction of diversity belongs to modern evolutionary fauna). Conversely, after the Cambrian, the metric measures the ratio of modern-to-Paleozoic faunas (only a negligible fraction of diversity belongs to Cambrian evolutionary fauna). Thus, the proportion of the Paleozoic fauna is a simple metric that is applicable throughout the entire Phanerozoic. r, Spearman correlation coefficient. Images illustrate examples of prey from the three evolutionary faunas (from left to right): Trilobite with repaired bite mark: *Elrathia kingii* [Cambrian; Utah; reproduced with permission from ref. 37 (Copyright 1989, Macmillan Publishers Ltd.)]. Drilled brachiopods: *Stenocisma fabarium* and *Echinauris lateralis* [Permian; West Texas;

Ecological Signal: A Long-Term Coupling of Diversity and Predation. Multiple studies (10, 15, 16, 26) have suggested that ecological processes and macroevolutionary processes may be causally linked, and the correlation between predation intensity and diversity can be explained as a manifestation of a strong relationship between the two. Van Valen's Red Queen hypothesis (27), Stanley's explanation for the rapid evolution of multicellularity (15), Vermeij's escalation model (10), and Bambach's postulation of increased ecospace utilization (26) are all examples of studies that are consistent with the idea that ecological interactions can either influence or respond to processes that happen over evolutionary time scales. The mirroring of evolutionary faunas by prey species occurrences is not inconsistent with this explanation, interpreted as a reflection of predators switching favored prey items over evolutionary time by preferentially targeting the diverse (and likely also abundant) prey groups (but see hypothesis III, *Spurious Concordance in Signal Capture*, below).

Consistent with the ecological hypothesis, recent quantitative studies suggest that evenness and other aspects of diversity-abundance structures, which all could influence the intensity of predation on abundant prey taxa analyzed here, may have changed through the Phanerozoic (28, 29). Even more important, substantial changes in relative abundance of organisms representing different trophic levels and modes of life may have occurred in the late Mesozoic and/or Cenozoic (30, 31), although the biological veracity of those pattern is still viewed as inconclusive by some authors (30). Nevertheless, these changes, which included a decrease in relative abundance of sessile, suspension-feeding epifaunal organisms, and concurrent increase in relative abundance of mobile, predatory, and infaunal forms (30, 31), took place after the Jurassic (30) and could account for the concordant increase in frequency of predation traces.

Diversity-Driven Diffusion of Predatory Behaviors: An Increased Probability of More Complex Predatory Strategies to Appear at Higher Diversity Levels. Vermeij suggested that the whole ingestion of marine benthic prey is a primitive behavior in comparison to more derived predatory strategies like drilling and peeling (10). From a purely stochastic standpoint, such relatively more advanced predatory strategies are more likely to occur during
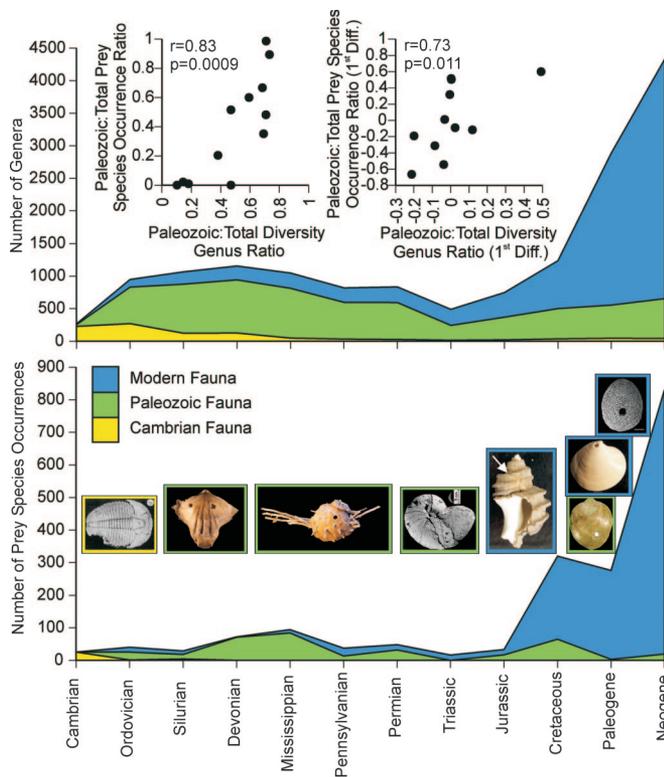
Smithsonian Institution National Museum of Natural History (NMNH), photo courtesy of Finnegan Marsh, NMNH]. Nautiloid with bite marks: *Argonautilus catarinae* [Cretaceous; California; reproduced with permission from ref. 38 (Copyright 2004, SEPM (Society for Sedimentary Geology))]. Gastropod with repair scar: *Ecphora* [Miocene; Maryland; Virginia Polytechnic Institute and State University (VPI&SU) Geosciences collection]. Drilled brachiopod: *Bouchardia rosea* (Holocene; Brazil; photo courtesy of Marcello G. Simões and Sabrina Rodriguez, São Paulo State University, São Paulo, Brazil). Drilled bivalve: *Dosinia* (Holocene; Sanibel Island, FL; VPI&SU Geosciences collection). Drilled echinoid: *Fibularia* sp. (Oligocene; New Zealand; photo courtesy of James H. Nebelsick, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany).

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times of high taxonomic diversity. This phenomenon can be described as a passive diffusion of realized behaviors resulting from a true biological signal of increasing taxonomic diversity: trace-producing predatory strategies, such as drilling and peeling, become more common when taxonomic diversity increases. This explanation fits well with the proliferation of drilling predation and repair scars concurrent with the Ordovician radiation and the subsequent diversity high of the Paleozoic Plateau (14). Similarly, this model can explain why the Mesozoic Marine Revolution (16) coincided with the post-Jurassic taxonomic diversification of the marine metazoans. Moreover, the scarcity of predation traces in the early Mesozoic is also consistent given that the largest setback of metazoan diversity in Earth's history occurred at the end of the Permian. As with hypothesis I (*Ecological Signal*), the mirroring of Evolutionary Faunas by prey species occurrences (Fig. 3) could be a reflection of predators consuming the most diverse and, presumably, most abundant groups at any given time.

Spurious Concordance in Signal Capture: A Sampling Artifact Where Rare Species and Less-Frequent Predatory Behaviors (Such As Trace-Producing Attack Strategies) Are Both Captured More Efficiently at Times When Sampling Accessibility/Intensity Is Improved. The two hypotheses above both assume implicitly that Sepkoski's genus-level diversity curve and related patterns represent true biological signals. However, correlations between temporal changes in rock volume, sea level, and biodiversity (1, 2, 32), secular trends in diagenesis and sampling methodology (30), and sample-standardization efforts (33) suggest that Phanerozoic diversity curves may be, at least partly, a sampling artifact. Although standardization efforts may have overcompensated for sampling problems, and other biases may be less important than previously thought (30, 31, 34, 35), recent regional analyses (36) and ambiguous tests of diagenesis-related biases (30) suggest that sampling and preservational issues should not be ignored just as yet. Consequently, the idea of spurious concordance should be considered: trace producing behaviors may be easier to detect during time intervals when sampling or preservation is improved (whereas the frequency of traces in any given sample is independent from how many samples total are available for study, the probability of finding samples with high frequencies of traces increases when more samples and/or better preserved samples are available). Thus, the correlation between predation intensity and diversity may simply reflect the fact that, when sampling and preservation improve, both the diversity appears to increase and, concurrently, more records of intense predation become available. Likewise, the mirroring of Evolutionary Faunas by prey occurrences may simply reflect the fact that dominant prey taxa are more likely to provide examples of prey species with quantifiable evidence of predation.

The strong coupling of taxonomic diversity and predation intensity indicates that long-term (Phanerozoic) trends in the intensity of ecological interactions and global biodiversity are tightly linked. The three causative mechanisms for this concordance are proposed as testable hypotheses for future research. The issue can be tested in future research by meta analyses of modern benthic marine environments in search for correlatives between taxonomic diversity and predation intensity (hypothesis I, *Ecological Signal*) and between taxonomic diversity and diversity of predatory behaviors (hypothesis II, *Diversity-Driven Diffusion of Predatory Behaviors*). As important, determining the biological veracity of Sepkoski's curve, which has proven to be no trivial feat so far, would go a long way toward assessing the viability of hypothesis III (*Spurious Concordance in Signal Capture*). Our ability to address the importance of ecological interactions over evolutionary time scales relies, in large part, on our ability to reliably reconstruct the fossil record of global biodiversity.

Methods

Using literature data and previous data surveys (196 publications total), we compiled 2,292 occurrences of predation traces ranging in age from Ediacaran to Holocene. We restricted our analyses to species-level frequency data on predatorial drill holes and repair scars reported from bulk samples with $n \geq 10$ specimens per prey species. The restricted dataset includes a total of 904 species-level estimates of predation intensity, including 191 estimates of repair scars, interpreted as failed predation events, and 713 estimates of drilling, assumed to represent successful predation events.

The pooling of drill hole and repair scar data, a step that is necessary to retain reasonable sample size for a sufficient number of geological periods, may be debatable given that these two trace types estimate ecological interactions with different outcomes: those won by predators versus those won by prey. Arguably, both of these measures are proxies of the intensity of predator–prey interactions, regardless of the identity of the winner. More importantly, however, when each type of trace is analyzed separately, significant positive correlations with diversity persist for raw data. These correlations cease to be significant after first differencing, which may simply reflect a further loss of power (see *SI Text*), but they are invariably positive, and thus qualitatively consistent with the pattern recovered for pooled data.

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