Coupling of predation intensity and global diversity over geologic time

Steven M. Holland*
Department of Geology, University of Georgia, Athens, GA 30602-2501

The geologic history of earth's biodiversity, and the origins of this pattern, are central problems in paleobiology and evolutionary biology. The basic picture for marine organisms was outlined in 1860 (1) but was considerably refined in the 1980s and 1990s by the late Jack Sepkoski. His databases of marine animal families and genera produced an iconic pattern of an early Paleozoic rise in diversity, followed by a late Paleozoic plateau or slow decline, a low after the end-Permian extinction, and a final protracted rise through the Mesozoic and Cenozoic (2, 3). The explanation for this pattern has been an active area of research, with interpretations ranging from preservational artifacts to a host of biologically mediated processes (4–7). Predation has been regarded as potentially important, but the data to establish its significance have been limited in scope (8–11). The work of Huntley and Kowalewski (12) in this issue of PNAS demonstrates for the first time a strong correlation between predation intensity and marine biodiversity throughout the Phanerozoic Eon. Their results are particularly compelling because the data are independent of the global-scale taxonomic lists used to generate diversity curves, making a spurious correlation between the two unlikely. The authors' evidence strongly suggests that predation and biodiversity are highly correlated in the marine realm, although which is cause and which is effect remains an open question.

Testing the relationship between diversity and predation quantitatively has proven difficult until recently. Previous studies have concluded that predator–prey interactions played a role in Phanerozoic diversity, based on parallel increases in shell strength and the diversity of shell-crushing and drilling predators in the Late Mesozoic (8) and mid-Paleozoic (9). Several previous studies (10, 13) obtained quantitative measures of predation intensity, but in limited numbers of samples over limited spans of geologic time. Other studies (7) compared the diversity trajectories of known predators and prey through time and concluded that diversities of predator and prey were not correlated.

Huntley and Kowalewski (12) have compiled an ambitious, collection-scale database that records the percentage of each species in each collection displaying predatory drill holes or healed repair scars, which are thought to reflect failed predation attempts. Their data cover most of the Phanerozoic, providing the first comprehensive, quantitative view of the intensity of predation in marine communities through time. Most importantly, they show that predation intensity correlates strongly with previous estimates of Phanerozoic marine diversity. This is unlikely to be a spurious correlation of two time series because first-differences are also strongly correlated. Similarly, the correlations are robust to different measures of predation intensity and to different approaches to estimating biodiversity.

Testing the relationship between diversity and predation quantitatively has proven difficult until recently.

New Insights

The predation pattern that Huntley and Kowalewski (12) present contrasts with previous portrayals. Instead of a mid-Paleozoic rise (9), predation frequency increased dramatically some 70 million years earlier and remained relatively static through the remainder of the Paleozoic. The postulated late Mesozoic rise in predation pressure occurred somewhat later than previously thought (8) and continued to rise into the latest Cenozoic. Huntley and Kowalewski also document substantially higher predation intensities than previously reported: up to 40% in the Silurian and, remarkably, as high as 22% in the Ediacaran. These high percentages underscore the importance of predation as an ecological process, even early in the history of complex marine life.

An important aspect of Huntley and Kowalewski's (12) data is that it is based on collection-level estimates of the frequency of predatory drill holes and healed predation scars. These data are fundamentally different from fossil ranges based on the geologically oldest and youngest global occurrences of genera and families in Sepkoski's data. Such different origins for these two data sets greatly diminish the possibility that the correlation reflects the overall quality of the fossil record, a concern previously leveled at global diversity compilations (5, 6, 14). Furthermore, Huntley and Kowalewski use proportions of shells displaying predation damage, rather than raw counts of shells, which makes their data robust to the effects of uneven sampling through time.

In addition to the possibility of a spurious correlation driven by the quality of the fossil record, Huntley and Kowalewski (12) raise two possible biological explanations for their results. The first is that changes in predation frequency over time may modulate evolutionary rates by opening new ecological niches and increasing ecological specialization, a view that many previous researchers have considered (8, 11, 15–17). The second view turns the first on its head, suggesting that evolutionary diversification may simply allow more opportunities for the evolution of complex predatory strategies such as drilling and shell breakage.

Questions and Prospects

The main challenges awaiting paleobiologists involve evaluating these two biological hypotheses and assessing the extent to which changes in preservation rate influence the correlation. To some degree, definitive testing will require an expanded data set that will increase the temporal resolution beyond that of the geological period. It is also plausible that both of these biological processes may be involved in a positive feedback loop, with diversification increasing the likelihood that complex predatory strategies will evolve in a greater number of clades and with increased predation driving faster evolutionary rates as prey species diversify through specialized re-

Author contributions: S.M.H. wrote the paper.

The author declares no conflict of interest.

See companion article on page 15006.

*E-mail: stratum@uga.edu.

sponses to increased predation. It may also be that diversity and predation are responding jointly to some other driving factor (11).

Other questions are raised by this study. For example, given the tight coupling of predation and diversity, why do recent analyses of the diversity histories of potential predators and prey fail to show any correlation (7)? Within collections, what are the relationships among estimates of predation pressure, the abundance of predators, the diversity of predators, and overall community diversity? What effect will sample-standardized diversity histories, now under development (14), have on the correlation between diversity and predation? Does the record of predation intensity through time correlate with measures of the quality of the fossil record (18)? Do predation-resistant morphologies correlate with predation intensity through time, or is there a measurable lag in the morphological response to increased predation?

Regardless of the answers to these questions, the work of Huntley and Kowalewski (12) is an important development for studies of Phanerozoic diversity. Their work demonstrates that the fossil record provides important data not only on changes in diversity over time but also on the changing importance of ecological interactions (19). Studies like this one, which present new methods for assessing the relationship of ecology to evolution, promise to expand the reach of paleobiology into exciting new dimensions that address fundamental questions about the history of life.

1. Phillips J (1860) *Life on the Earth: Its Origin and Succession* (Macmillan, Cambridge, UK).
2. Sepkoski JJ, Jr (1981) *Paleobiology* 7:36–53.
3. Sepkoski JJ, Jr (1997) *J Paleontol* 71:533–539.
4. Miller AI (2000) in *Deep Time*, eds Erwin DH, Wing SL (Paleontol Soc, Lawrence, KS), pp 53–73.
5. Smith AB (2001) *Philos Trans R Soc London Ser B* 356:1–17.
6. Peters SE, Foote M (2001) *Paleobiology* 27:583–601.
7. Madin JS, Alroy J, Aberhan M, Fürsich FT, Kiessling W, Kosnik MA, Wagner PJ (2006) *Science* 312:897–900.
8. Vermeij GJ (1977) *Paleobiology* 3:245–258.
9. Signor PW, III, Brett CE (1984) *Paleobiology* 10:229–245.
10. Kowalewski M, Hoffmeister AP, Baumiller TK, Bambach RK (2005) *Science* 308:1774–1777.
11. Bambach RK (1993) *Paleobiology* 19:372–397.
12. Huntley JW, Kowalewski M (2007) *Proc Natl Acad Sci USA* 104:15006–15010.
13. Kowalewski M, Dulai A, Fürsich F (1998) *Geology* 26:1091–1094.
14. Alroy J, Marshall CR, Bambach RK, Bezusko K, Foote M, Fürsich FT, Hansen TA, Holland SM, Ivany LC, Jablonski D, *et al.* (2001) *Proc Natl Acad Sci USA* 98:6261–6266.
15. Van Valen L (1973) *Evol Theory* 1:1–30.
16. Stanley SM (1973) *Proc Natl Acad Sci USA* 70:1486–1489.
17. Bambach RK (1983) in *Biotic Interactions in Recent and Fossil Benthic Communities*, eds Tevesz MJS, McCall PL (Plenum, New York), pp 719–746.
18. Foote M (2003) *J Geol* 111:125–148.
19. Labandeira CC (2002) in *Plant–Animal Interactions: An Evolutionary Approach*, eds Herrera C, Pellmyr O (Blackwell Scientific, Oxford), pp 26–74, 248–261.