

The following resources related to this article are available online at www.sciencemag.org (this information is current as of November 16, 2009):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/cgi/content/full/314/5801/925f>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/cgi/content/full/314/5801/925f#related-content>

This article has been **cited by** 1 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/cgi/content/full/314/5801/925f#otherarticles>

Information about obtaining **reprints** of this article or about obtaining **permission to reproduce this article** in whole or in part can be found at:

<http://www.sciencemag.org/about/permissions.dtl>

Response to Comments on “Statistical Independence of Escalatory Ecological Trends in Phanerozoic Marine Invertebrates”

Joshua S. Madin,^{1*} John Alroy,¹ Martin Aberhan,² Franz T. Fürsich,³ Wolfgang Kiessling,² Matthew A. Kosnik,⁴ Peter J. Wagner⁵

Roopnarine *et al.* and Dietl and Vermeij do not challenge our results but argue that escalation can be seen only at fine scales. This claim diminishes the theory and needs to be tested, not asserted. Roopnarine *et al.* incorrectly presume that our data are dominated by carnivores. Dietl and Vermeij overlook the fact that in addition to having no effect on global diversity, escalation has no effect on occurrence frequency.

We thank Roopnarine *et al.* (1) and Dietl and Vermeij (2) for their comments on our time series analysis of ecological trends through the Phanerozoic eon (3), and although we agree that some scenarios may explain our results, we do not agree that large-scale analyses are irrelevant because we can assume that the world is too complex to demonstrate causal relations at the largest scales. The central argument of both comments is that escalation in one place or in one trophic or taxonomic group is always canceled out at larger scales by de-escalation in others, and therefore cannot be tested at these scales. This claim is an empirical induction, not a philosophical deduction, so it needs to be tested instead of asserted. Shielding escalation by redefining it as partially untestable may be tempting, but the use of such a strategy is the hallmark of a paradigm in retreat.

Not only does the escalation hypothesis make a clear and crucial prediction of a global-scale tradeoff between different ecological groups, but a longer time series may well have evidenced a weak statistical interdependency. We have conducted a power analysis showing that nontrivial but still unimpressive r^2 values of up to 0.24 could exist. Our point is not that there is no relationship whatsoever but that it is not important at the global scale that is of the greatest interest to biologists.

¹National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA 93101, USA.

²Museum für Naturkunde, Humboldt-Universität, 10115 Berlin, Germany. ³Institut für Paläontologie, Universität Würzburg, 97070 Würzburg, Germany. ⁴School of Marine Biology and Aquaculture, James Cook University, Townsville 4811, Australia. ⁵Department of Geology, Field Museum of Natural History, Chicago, IL 60605, USA.

*To whom correspondence should be addressed. E-mail: madin@nceas.ucsb.edu

Roopnarine *et al.* (1) misrepresent the motivation and implications of our time series analysis, which was intended to isolate correlations with possible causal significance from correlations with no such significance and only secondarily was meant to correct for taphonomic bias. Cross-correlations of auto-correlated time series are expected in the absence of even indirect causal connections; any two generally upward- or downward-trending time series will cross-correlate. Therefore, differencing is necessary to provide even the most basic evidence of a relationship.

Roopnarine *et al.* (1) state that a model of causality relating carnivore to noncarnivore frequency is flawed because of its simplicity, but escalation is just such a model, and its predictions are straightforward. More substantively, they argue that in marine ecosystems that are strongly dominated by carnivores, escalation may only be visible within carnivore guilds at different trophic levels. This seems plausible but not apropos of our data.

First, Roopnarine *et al.*'s evidence that long trophic chains exist in our data consists of citations to papers on terrestrial vertebrates, terrestrial plants and insects, predominantly nonbenthic marine organisms like fish, morphology, and theoretical models. The paleontological literature on escalation, however, almost entirely concerns benthic invertebrates such as gastropods, bivalves, and brachiopods. Second, our data show that the relative frequency and diversity of carnivorous invertebrates was rarely more than 10% throughout most of the Phanerozoic, and never more than 27%. Most of the few carnivores were likely to be primary consumers, and populations of high trophic-level predators were likely to have been too small to have had much of an effect. Third, the major groups comprising our noncarnivore

categories are mostly immobile or infaunal, so it is unlikely that we have scored them incorrectly. Fourth, we specifically excluded vertebrates from our analysis because their fossil record is poor relative to shelly invertebrates. Finally, the range of body masses within our major carnivore groups, like gastropods and ammonites, is rather narrow, so it is unlikely that many trophic levels were represented.

Roopnarine *et al.* present several scenarios that might explain why correlations might not emerge. None of these scenarios is testable in the absence of clear criteria for separating top and intermediate predators within benthic shelly invertebrates; an explanation for our results is not a criticism of them.

Dietl and Vermeij (2) object first to our having analyzed global data and second to our use of diversity data. They state that global data are not relevant to the trends they are trying to explain. However, they are the trends we are trying to explain, and global biodiversity is a topic of much discussion. Much of the literature on escalation is premised on the idea that it is a global phenomenon, and if it is not, then perhaps it is not such a key evolutionary process.

More specifically, they, like Roopnarine *et al.*, suggest that escalation might be more visible at local scales. We agree that it might be and hope that our results will encourage analyses at multiple scales that will explore the scale dependence of evolutionary processes instead of holding them back. Furthermore, as we stated, data on local areas and data spanning short time intervals are typically not open to the kind of rigorous time series analysis we performed. Although we strongly believe that local and global studies are complementary, we also hold that time series analysis is a good way to test for evolutionary processes, not just patterns.

Dietl and Vermeij (2) also state that diversity patterns are abstract epiphenomena that cannot yield information about selection or adaptation. The suggestion is that one should assume that all evolutionary processes operate at the population level. Again, the large amount of research on global diversity shows that researchers in such areas as systematics, macroevolution, macroecology, community ecology, and conservation biology hold other, less reductionistic views.

Dietl and Vermeij overlook the fact that our data did not just address diversity but also occurrence frequency, which we showed to capture the same temporal signals. Occurrence frequency is a product of ecological factors such as geographic range size, breadth of environmental distribution, and local abundance that are the focus of much research and presumably have some connection to evolution.

Dietl and Vermeij's main point is to assert that organisms do evolve through interactions, instead

of addressing our data, methods, or argumentation. This hypothesis is exactly what we tested and found not to be demonstrable at the scale that is amenable to proper time series analysis. Arguing that a hypothesis is untestable when it is contradicted does not provide evidence for it, and actually

showing that the causal emergence it predicts is not very strong does provide evidence against it.

References and Notes

1. P. D. Roopnarine, K. D. Angielczyk, R. Hertog, *Science* **314**, 925 (2006); www.sciencemag.org/cgi/content/full/314/5801/925d.

2. G. P. Dietl, G. J. Vermeij, *Science* **314**, 925 (2006); www.sciencemag.org/cgi/content/full/314/5801/925e.
3. J. S. Madin *et al.*, *Science* **312**, 897 (2006).

14 June 2006; accepted 19 October 2006
10.1126/science.1131363