Science AAAS

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Science **314**, 925d (2006);
DOI: 10.1126/science.1130073

Comment on "Statistical Independence of Escalatory Ecological Trends in Phanerozoic Marine Invertebrates"

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The analysis of Madin *et al*. (Reports, 12 May 2006, p. 897) of Phanerozoic diversity failed to support expected correlations between carnivores and noncarnivores, leading the authors to reject escalation as an important macroevolutionary process. The test, however, is based on a flawed model of causality, and the ecological groups are improperly delineated with regard to the hypothesis.

Madin *et al*. (*1*) present a hypothesis predicting that because of escalating interactions, changes in the diversity of an ecologically defined set of carnivores will cause changes of composition in noncarnivore sets, substantiating the claim that predators act as important agents of selection. Their examination of such trophically delineated groups in the Phanerozoic fossil record yielded significant rank correlations between an ecological set comprising carnivores and other sets comprising the proportions of noncarnivores of various habits, such as infaunal and mobile. Subsequent first-order differencing of diversity time series, presumably to correct for taphonomic bias and other factors such as clade-specific rates of origination and extinction (assuming that clades do not span more than one of the ecological sets), reduced most of the correlations to insignificance, leading the authors to reject escalation as a causative explanation. The absence of correlation, however, is insufficient confirmation of independence because the model of causality is inadequate.

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Division of the Phanerozoic fauna into carnivores and noncarnivores is inappropriate because if animals indeed evolve in response to their enemies, then the set of carnivores comprises relevant disjointed subsets of carnivores of various trophic levels, making the variance of the set itself a function of carnivore diversity. Consider the set of carnivores, for example, to comprise the exclusive subsets of top carnivores and intermediate carnivores. The true correlation between noncarnivores and carnivores therefore depends on the relative proportions of top and intermediate carnivores. These data were not presented by Madin *et al*. Several other factors that are expected to show temporal and geographic variation also influence the correlation, including (i) the strengths of the interactions between top and intermediate carnivores, because the latter may respond in escalatory fashion to predation; (ii) the intensity of escalation of intermediate carnivores in response to their predators and the phenotypic diversity of those responses; (iii) the strengths of interactions between top carnivores and their noncarnivore prey, as well as between intermediate carnivores and their noncarnivore prey; and (iv) the relative intensities of escalation of true noncarnivores to their top and intermediate predators. If the expression of variations in the intensities of the interactions is itself a nonstationary feature (e.g., escalated defenses of intermediate carnivores do not always result in enhanced predatory capabilities), then disparities in the relative ranks within carnivore and noncarnivore sets will increase, resulting in lower rank correlations between those sets. In other words, noncarnivore diversity may not reflect escalatory increases within the set of carnivores.

Three brief examples serve to highlight these issues. First, ammonites were important intermediate predators in Paleozoic and Mesozoic oceans, yet conflicting demands on the shell for both buoyancy and defense resulted in fluctuations in the degree of ammonite shell armor during the Mesozoic, even as the frequency of shell repair increased (*2*). Such variation in escalation is unmeasured in the Madin *et al*. analysis, and one wonders how this variation would drive escalation in noncarnivores. Second, examination of the trophic habits of carnivores in the eight middle Permian to middle Triassic terrestrial fossil assemblages from the Karoo Basin of South Africa (*3*) reveals significant fluctuations in the relative proportions of the number of genera of top and intermediate carnivores. Third, compilations of ancient and modern food webs reveal complex networks of trophic relationships among carnivores (including omnivores) (*4*–*6*), where the total evolutionary impact of predation on noncarnivores must be filtered through numerous intermediate species. These data suggest that the expectation of simple relationships between patterns of global Phanerozoic diversity and processes of biological interaction is an insufficient framework for testing macroevolutionary hypotheses. Instead, hypotheses of adaptation must be tested at relevant organismal scales.

References and Notes

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16 May 2006; accepted 17 October 2006
10.1126/science.1130073