

On the importance of global diversity trends and the viability of existing paleontological data

Arnold I. Miller

Department of Geology, Post Office Box 210013, University of Cincinnati, Cincinnati, Ohio 45221-0013.
E-mail: arnold.miller@uc.edu

Accepted: 25 July 2002

Does the History of Global Diversity Matter?

Regardless of the macroevolutionary issues at stake, most students of biodiversity would agree that there is value in calibrating global biodiversity trends through critical intervals. To cite one obvious example, given the overwhelming interest in mass extinctions, we would certainly like to know the extent to which diversity declined during these events. Just as significantly, if we are to argue that any mass extinction was truly a global phenomenon, we must demonstrate definitively that its biotic effects reached around the world. Clearly, “standard” global compendia (e.g., Sepkoski 1992, 2002) are insufficient for the latter objective, because they contain no geographic or environmental information. At the least, a database that compares biodiversity transitions among different regions or paleoenvironments is required. Such analyses have the added benefit of providing opportunities to evaluate geographic and environmental selectivity in extinctions, an important facet of any attempt to understand what caused them (e.g., Raup and Jablonski 1993; Jablonski and Raup 1995).

However, beyond the desire to assess mass extinctions and other globally mediated biotic events, does an accurate read of global diversity through a given stratigraphic interval really tell us anything that we could not learn about macroevolutionary processes simply by focusing on one or a few well-studied regions? After several decades of intense investigation, this question remains contentious. Even among the four authors who reached a landmark consensus about the trajectory of Phanerozoic global diversity (Sepkoski et al. 1981),

there was no consensus about what produced the pattern. On the one hand, Bambach (1977) suggested that Phanerozoic trends in median species richness *within* communities (a proxy for *alpha* diversity [see Sepkoski 1988]) paralleled trends exhibited in aggregate, global compilations of taxonomic richness. Further, in evaluating the ecological propensities of Sepkoski’s (1981) three evolutionary faunas, Bambach (1985) argued that increases in the level of global diversity achieved by successive faunas were tied directly to increases in ecospace utilization, a property that should be observable at the local level (see Aronson 1994 and Miller 2000 for other examples of possible scale-independence in long-term biodiversity trends). On the other hand, Valentine (e.g., Valentine et al. 1978) suggested that there was an intimate relationship between the major post-Paleozoic global marine diversity increase and a secular increase in the number of distinct faunal provinces.

If Valentine is correct, then we cannot hope to capture this important aspect of diversification by limiting our purview to one or a few regions. If Valentine is wrong, there are, nevertheless, strong indications that long-term diversity trends differed significantly among major regions around the world (e.g., Miller 1997; Jablonski 1998). Moreover, even if a consistent diversity trend is observed from region to region at the *alpha* level, this is no guarantee that we will observe the same overall pattern at the *beta* level (the degree of differentiation between communities [see Sepkoski 1988]) or higher (see Patzkowsky 1995; Miller and Mao 1998; Adrain et al. 2000). This decoupling of diversification at different hierarchical levels, whatever the cause, argues strongly for the existence of some set of evolutionary or ecolog-

ical processes confined to limited hierarchical scales.

It should be clear from the foregoing that, to determine what drives diversity at any scale, we must understand the similarities and differences in biodiversity trends among the major regions (e.g., paleocontinents) that constitute the world at any point in time. Limiting our analyses to just one or two regions simply will not suffice. This was illustrated cogently by Rosenzweig and McCord's (1991) classic analysis of the global replacement of turtles with inflexible necks by turtles with retractable, flexible necks. The fact that the transition was observed in several separate regions, but at different times, lends strong credence to the argument that the transition was not a random one, and that advent of a flexible neck was a key adaptation for the group. Without the regional comparison at the heart of this analysis, this definitive conclusion would not have been possible.

Have the Important Questions Already Been Asked and Answered?

Even if we grant that there is much to gain by assessing local and regional diversification in the light of global patterns, we could claim that we already know global patterns so well that we need not focus any additional effort at that scale. Although I think this is untrue because of continuing concerns about sampling effects (e.g., Miller and Foote 1996; Alroy et al. 2001; Peters and Foote 2001; Jackson and Johnson 2001), it is beside the point with respect to developing an agenda for future research and data collection. By definition, the kinds of data required for detailed assessments of diversification within and among regions are also precisely the kinds of data required to improve our calibrations of global diversity trajectories.

Beyond that, analyses at the global level continue to generate major hypotheses about the history of biodiversity. For example, Michael Foote has been working extensively with Sepkoski's (2002) genus-level compendium to develop improved estimates of global origination and extinction rates. From this research, he has recognized that changes in global marine diversity are more strongly cor-

related with changes in extinction rate than with changes in origination rate during the Paleozoic, but the reverse is true in the post-Paleozoic (Foote 2000). There was nothing in previous global studies that hinted remotely at this pattern, nor would its discovery have been possible by confining attention to a small set of regions during a few stratigraphic intervals.

Are We Going about It the Right Way?

The assembly of extensive, multifaceted databases such as the Paleobiology Database (PBDB; see Alroy et al. 2001) springs from the recognition that, after a generation of research that has left us with a rich collection of hypotheses about diversification at all scales, a geographically and environmentally resolved global database is essential if we are to continue moving forward in the study of Phanerozoic biodiversity. But are we collecting the data in the right way? Recently, Jackson and Johnson (2001) suggested that any effort to assess the history of biodiversity by cataloging information already published about ancient taxa is doomed to failure, because previous paleontological efforts have not captured the richness of diversity in important regions, particularly in the Tropics. As partial evidence, Jackson and Johnson assessed the level of Pliocene genus richness recognized in a remarkable, field-based effort to assess the Neogene Marine Biota of Tropical America (NMI-TA; see Budd et al. 2001), a major facet of which has been the Panama Paleontology Project (PPP). The number of Pliocene genera documented in aggregate for several higher taxa in this small region constitutes, in terms of raw numbers, an appreciable percentage of the richness for the *entire globe* documented in Sepkoski's genus-level compendium, as well as in the collections cataloged thus far by the Phanerozoic Marine Paleofaunal Diversity (PMPD) working group in the PBDB. Given these numbers, and because the localities where the majority of paleontological research has historically been conducted were not located in the tropics during the Cenozoic, Jackson and Johnson argued that a treasure trove of diversity from the tropical Cenozoic remains woefully undersampled. Further, rec-

ognizing this shortcoming, they offered the provocative suggestion that, rather than overestimating the global Cenozoic diversity increase (see Alroy et al. 2001), raw estimates of the Phanerozoic diversity trajectory (e.g., Sepkoski 1997) significantly *underestimate* the increase. To assess the Phanerozoic history of biodiversity definitively, Jackson and Johnson therefore advocated replicating the PPP approach in about 20 well-chosen regions arrayed stratigraphically throughout the column.

Although regional studies like the PPP are obviously of great value (see below), there are several reasons to be skeptical of Jackson and Johnson's conclusions. First, the PMPD working group has made no pretense of having yet captured a global-scale sample for the Pliocene or most other Phanerozoic intervals (in fact, the initial sampling was purposely limited [see Alroy et al. 2001]). Thus, for the moment, it is not appropriate to use the current PMPD data set as a basis for determining the state of accumulated paleontological knowledge about aggregate global genus richness for any interval. As the PBDB continues to grow, the number of unique genera cataloged for the Pliocene and other intervals will increase significantly.

Second, the poor representation that Jackson and Johnson documented for the tropical Cenozoic may well extend to the rest of the geologic column. Arguably, a modern, PPP-quality project conducted anywhere in the Phanerozoic record—even in venues that have seemingly been well-studied previously—would enhance greatly the richness of genera known from those regions. If this is the case, there is no compelling reason, at least by this measure, to expect that the published fossil record is significantly *biased* against the depiction of relative taxonomic richness for the Cenozoic.

Third, it is not clear that the published Cenozoic fossil record is skewed disproportionately to nontropical regions. For one thing, several major regions now classified as temperate (e.g., the east coast of North America) were decidedly more tropical or subtropical earlier in the Cenozoic. Perhaps more significantly, Walker et al. (2002) showed that the

Phanerozoic record exhibits a secular decline in the area and volume of shallow-marine carbonate rocks, likely tied to an actual net decline in the global expanse of shallow-marine carbonate environments. Thus, if there is a paucity of Cenozoic data from tropical, carbonate venues relative, say, to the Paleozoic, this probably reflects a real transition, the biotic effects of which we would do well to investigate!

Finally, as suggested earlier, to make sense of biodiversity transitions during any interval, we need to compare and contrast patterns among several regions, rather than just one or two. Jackson and Johnson's proposed approach necessarily limits the geographic coverage possible during any given interval.

That said, regional studies like the PPP, and other efforts to understand biotic transitions with extensive new field data, clearly provide a level of stratigraphic resolution and taxonomic rigor not available in previous literature. For example, a host of detailed, regional investigations have been conducted over the past few years that have affected dramatically our view of the Ordovician Radiation (e.g., Li and Droser 1999; Patzkowsky and Holland 1999; Waisfeld et al. 1999; Adrain et al. 2000). These studies provide opportunities to consider the nature and rate of biotic response to regional perturbations, which are far more common in the history of life than the global perturbations that characterized mass extinctions (Miller 1998; Patzkowsky 1999). In that sense, field-based studies are pivotal additions to what can be gathered from the literature, but they are not wholesale replacements. In the short run (i.e., the next decade), it is neither possible nor necessary to re-collect most of the fossil record.

Acknowledgments

I thank R. Bambach, M. Foote, and S. Wing for valuable feedback on an earlier draft of this essay. My research on global biodiversity has been facilitated by grants from the National Aeronautics and Space Administration's Program in Exobiology (grants NAGW-3307, NAG5-6946, and NAG5-9418) and the National Science Foundation's Program in Biocom-

plexity (grant DEB-0083983). This is Paleobiology Database Publication No. 14.

Literature Cited

- Adrain, J. M., S. R. Westrop, B. D. E. Chatterton, and L. Ramskold. 2000. Silurian trilobite alpha diversity and the end-Ordovician mass extinction. *Paleobiology* 26:625–646.
- Alroy, J., et al. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences USA* 98:6261–6266.
- Aronson, R. B. 1994. Scale-independent biological interactions in the marine environment. *Oceanography and Marine Biology: An Annual Review* 32:435–460.
- Bambach, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology* 3:152–167.
- . 1985. Classes and adaptive variety: the ecology of diversification in marine faunas through the Phanerozoic. Pp. 191–253 in J. W. Valentine, ed. *Phanerozoic diversity patterns: profiles in macroevolution*. Princeton University Press, Princeton, NJ.
- Budd, A. F., C. T. Foster, J. P. Dawson, and K. G. Johnson. 2001. The Neogene Marine Biota of Tropical America (“NMITA”) database: accounting for biodiversity in paleontology. *Journal of Paleontology* 75:743–751.
- Foote, M. 2000. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology* 26:578–605.
- Jablonski, D. 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. *Science* 279:1327–1330.
- Jablonski, D., and D. M. Raup. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. *Science* 268:389–391.
- Jackson, J. B. C., and K. G. Johnson. 2001. Measuring past biodiversity. *Science* 293:2401–2404.
- Li, X., and M. L. Droser. 1999. Lower and Middle Ordovician shell beds from the Basin and Range province of the western United States (California, Nevada, and Utah). *Palaaios* 14:215–233.
- Miller, A. I. 1997. Comparative diversification dynamics among palaeocontinents during the Ordovician Radiation. *Geobios Mémoire Spécial* 20:397–406.
- . 1998. Biotic transitions in global marine diversity. *Science* 281:1157–1160.
- . 2000. Conversations about Phanerozoic global diversity. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):53–73.
- Miller, A. I., and M. Foote. 1996. Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* 22:304–309.
- Miller, A. I., and S. Mao. 1998. Scales of diversification and the Ordovician radiation. Pp. 288–310 in M. L. McKinney and J. A. Drake, eds. *Biodiversity dynamics: turnover of populations, taxa, and communities*. Columbia University Press, New York.
- Patzkowsky, M. E. 1995. Ecological aspects of the Ordovician radiation of articulate brachiopods. Pp. 413–414 in J. D. Cooper, M. L. Droser and S. C. Finney, eds. *Ordovician odyssey*. Short Papers for the Seventh International Symposium on the Ordovician System. Pacific Section of the Society for Sedimentary Geology (SEPM), Fullerton, Calif.
- . 1999. A new agenda for evolutionary paleoecology—or would you in the background please step forward. *Palaaios* 14:195–197.
- Patzkowsky, M. E., and S. M. Holland. 1999. Biofacies replacement in a sequence stratigraphic framework: Middle and Upper Ordovician of the Nashville Dome, Tennessee, USA. *Palaaios* 14:301–323.
- Peters, S. E., and M. Foote. 2002 (for 2001). Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* 27:583–601.
- Raup, D. M., and D. Jablonski. 1993. Geography of end-Cretaceous marine bivalve extinctions. *Science* 260:971–973.
- Rosenzweig, M. L., and R. D. McCord. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology* 17:202–213.
- Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53.
- . 1988. Alpha, beta, or gamma: where does all the diversity go? *Paleobiology* 14:221–234.
- . 1992. A compendium of fossil marine animal families. Milwaukee Public Museum, Milwaukee.
- . 1997. Biodiversity: past, present, and future. *Journal of Paleontology* 71:533–539.
- . 2002. A compendium of fossil marine animal genera. *Bulletin of American Paleontology* No. 363.
- Sepkoski, J. J., Jr., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293:435–437.
- Valentine, J. W., T. C. Foin, and D. Peart. 1978. A provincial model of Phanerozoic marine diversity. *Paleobiology* 4:55–66.
- Waisfeld, B. G., T. M. Sanchez, and M. G. Carrera. 1999. Biodiversification patterns in the Early Ordovician of Argentina. *Palaaios* 14:198–214.
- Walker, L. J., B. H. Wilkinson, and L. C. Ivany. 2002. Continental drift and Phanerozoic carbonate accumulation in shallow-shelf and deep-marine settings. *Journal of Geology* 110:75–87.