Increase in evenness and sampled alpha diversity through the Phanerozoic: Comparison of early Paleozoic and Cenozoic marine fossil assemblages

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ABSTRACT

Existing reconstructions of the Phanerozoic history of biological diversity are based on occurrences of taxa and do not include abundance data. This study examines trends in the relative abundance of taxa and provides a new perspective on the Phanerozoic history of marine diversity. We compared the abundance versus diversity (AD) structure of early Paleozoic and Cenozoic samples of marine benthic genera compiled from the literature. The sample-standardized results indicate (1) a two-and-a-half–fold increase in sampled alpha diversity but, concurrently, (2) an increase in the evenness of fossil samples through time. The observed evenness trend may be due to taphonomic biases, time-averaging trends, differences in sampling techniques, or real changes in the structure of marine communities. Regardless of the underlying factors, the results indicate that the evenness of fossil samples increased through the Phanerozoic, largely owing to a decrease in the relative abundance of the most common taxa. Because sampling fossil sites of different evenness can result in different estimates of species richness even if their total alpha diversity is the same, the observed changes in evenness may have contributed to the Phanerozoic increase in sampled alpha diversity and, at least in part, to the increase in global diversity. The incorporation of taxon abundance data into future studies should produce a more robust, perhaps even different, interpretation of the Phanerozoic history of diversity.

Keywords: diversity, abundance, sampling, invertebrates, Phanerozoic.

INTRODUCTION

For decades, paleontologists have mined the fossil record to compile taxonomic databases and explore the Phanerozoic history of diversity (e.g., Newell, 1959; Valentine, 1969; Raup, 1976, 1978; Bambach, 1977, 1999; Sepkoski, 1978, 1981; Sepkoski et al., 1981; Benton, 1995; Alroy et al., 2001). Those studies used counts of taxa derived from range-based compilations (e.g., Newell, 1959; Valentine, 1969; Sepkoski, 1978, 1979, 1984), taxon occurrences in fossil collections (e.g., Alroy et al., 2001), and species richness at single fossil sites (e.g., Bambach, 1977). However, none of the previous projects incorporated abundance data to evaluate Phanerozoic trends in evenness (i.e., the abundance versus diversity [AD] structure of fossil assemblages).

Estimates of diversity are dependent on the underlying abundance distribution (Koch, 1978). Sampling the same number of individuals from two sites with the same total alpha diversity but different abundance distributions will produce different estimates of sampled alpha diversity. Alroy (2000) and Alroy et al. (2001) pointed out that this problem underlies all previous attempts at reconstructing the Phanerozoic history of diversity.

We use literature data to compare bulk samples of marine benthic macroinvertebrate genera collected from early Paleozoic (Cambrian-Silurian) and Cenozoic (Eocene-Miocene) sites. By including data on the abundance of taxa we aim to determine if the AD structure (i.e., evenness) of fossil samples has changed through time. Quantitative estimates of secular changes in relative abundance patterns at individual fossil sites are needed to properly reconstruct the Phanerozoic history of marine diversity.

DATA AND METHODS

A literature search yielded 147 bulk samples of marine benthic invertebrate genera or species (Table 1[1]) that include absolute specimen counts for all taxa in the samples. Each raw sample was randomly subsampled without replacement 1000 times down to a standardized abundance of 90 specimens. This value was selected to include as many sites as possible while maintaining a statistically reasonable sample size (analyses performed at various subsampling levels [$n = 45$, 190, and 290] yielded results consistent with those shown here). For each sample, 1000 random subsamples were used to compute a mean abundance versus diversity curve (MAD) (means were indistinguishable from medians [$r^2 > 0.99$] but resulted in smoother curves). These curves, generated by plotting mean cumulative abundance against mean cumulative diversity, are a variation of the dominance versus diversity curve of Whittaker (1975). Average MAD curves for groups of samples were computed as median abundance and diversity values calculated from MAD curves of individual samples. Traditionally, ecologists have used rank-ordered abundance distribution plots (RADs), generated by plotting logged abundance versus richness, with genera added in rank order (most common genera first); AD curves contain the same information—they are unlogged, cumulative RADs—but simplify calculation of MAD curves (RADs require integer values for ranked gen-

TABLE 1. SUMMARY OF DATA SETS

Type of data set	Total number of data sets	Median sample size	Median alpha diversity	Number of genus-level data sets	Number of species-level data sets
Carbonate samples					
Early Paleozoic	29	176.9	6.1	25	4
Cenozoic	4	118.0	12.8	4	0
Total	33	147.0	9.4	29	4
Siliciclastic samples					
Early Paleozoic (fine-grained)	30	321.1	11.3	19	11
Early Paleozoic (coarse-grained)	5	178.2	11.6	3	2
Early Paleozoic (total)	35	249.6	11.4	22	13
Cenozoic (fine-grained)	12	502.8	23.7	0	12
Cenozoic (coarse-grained)	21	768.8	36.0	0	21
Cenozoic (total)	33	635.8	29.8	11	22
Siliciclastic samples (total)	68	442.7	20.6	33	35

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[1] GSA Data Repository item 2002032, Raw data, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA, editing@geosociety.org, or at www.geosociety.org/pubs/ft2002.htm.

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era, which is not always possible when calculating a mean curve).

Because of the weaknesses of traditional diversity and evenness indices (Lande, 1996; Peters, 2001), we use the Kolmogorov-Smirnov D statistic (Zar, 1999) to measure the deviation of a standardized sample from a perfectly even sample of the same richness. This is conceptually based on the approach suggested by Tipper (1979) but applied to standardized samples; other workers (e.g., Bennington and Bambach, 1996; Peters and Bork, 1999) have used parametric chi-square tests to compare distributions. We use the evenness index D' ($D' = 1 - D$), which varies from 0 (maximum unevenness) to 1 (maximum evenness). Because D' statistic is a new metric with unknown theoretical properties, we also used for each fossil site a traditional evenness index J, which is calculated as the Shannon-Weaver diversity index divided by the natural log of the taxonomic richness and, like D', varies from 0 to 1 (Zar, 1999). Both J and D' performed consistently in our analysis, although D' appears to be more sensitive to changes in evenness than J: the differences between groups of samples were more notable when D' was used. Peters (2001) proposed a sum of squares metric (E_{ss}) and showed in simulations that E_{ss} outperforms other commonly used evenness metrics; we have found that D' correlates very highly with E_{ss}.

DATA SET EFFECTS

Because genus-level samples dominate our data ($n = 108$) and species-level data are more prone to taxonomic errors, we converted all data to the genus level (genus-level AD curves show nearly perfect overlap with the species-level curves from which they were derived). In addition, two unwanted sources of variation may affect the samples: differences in dominant higher taxa and facies.

Single higher taxa, which may have had an inherently distinct AD structure, commonly dominate paleontological bulk samples (as is the case here). After restricting our data by time interval and facies, the largest number of samples suitable for comparison of higher taxa was provided by Ordovician carbonates. Pairwise comparisons of Ordovician brachiopods ($n = 11$), corals ($n = 4$), and multiple higher taxa ($n = 14$) show that the curves do not differ notably (Fig. 1A) and are statistically indistinguishable (Kolmogorov-Smirnov test: multiple taxa vs. brachiopods: $D = 0.19$, $p = 0.08$; multiple taxa vs. corals: $D = 0.12$, $p = 0.52$; brachiopods vs. corals: $D = 0.08$, $p = 0.95$). This result is consistent with theoretical expectations (McKinney, 1996) and indicates that the inclusion of samples dominated by different higher taxa does not introduce any significant variation.

Because carbonates are typically limited to warm, shallow-marine environments far from clastic sediment sources, carbonate and siliciclastic samples may represent inherently distinct evenness structures with different AD curves. Moreover, lithology-specific fossil-extraction techniques may produce samples with different sampling biases. A comparison of carbonate ($n = 29$) and siliciclastic ($n = 23$) samples from the Ordovician time interval (Fig. 1B) (mixed carbonate-siliciclastic samples were excluded from analysis) shows that the two facies are indeed significantly different ($D = 0.23$, $p = 0.02$). Consequently, we restricted our temporal analyses to siliciclastic sites, which provide a well-balanced and reasonably large number of samples: 35 for the early Paleozoic and 33 for the Cenozoic. However, the siliciclastic facies still encompass a range of settings that may introduce unwanted variation. In particular, the Cenozoic and early Paleozoic samples differ in the proportion of fine-grained and coarse-grained deposits sampled; any systematic differences in evenness between the two settings may lead to a spurious temporal trend. For both time intervals, the two types of samples yield MAD curves that are similar in shape (Fig. 1, C and D) and statistically indistinguishable (early Paleozoic: $n = 35$, $D = 0.13$, $p = 0.41$; Cenozoic: $n = 33$, $D = 0.16$, $p = 0.17$). The limited variation in evenness across a wide range of siliciclastic settings from a given time interval justifies the inclusion of all siliciclastic samples in the final analysis. The observed limited variation is consistent with comparisons of present-day marine communities from mud and sand substrates (Wu and Shin, 1997).

RESULTS

The comparison of early Paleozoic ($n = 35$) and Cenozoic ($n = 33$) genus-level siliciclastic samples (Fig. 2) shows two significant differences in AD structure. First, sampled alpha diversity is higher in the Cenozoic than in the early Paleozoic. The median sampled alpha diversity for $n = 90$ is 7.8 genera in the early Paleozoic samples and 19.3 genera in the Ce-

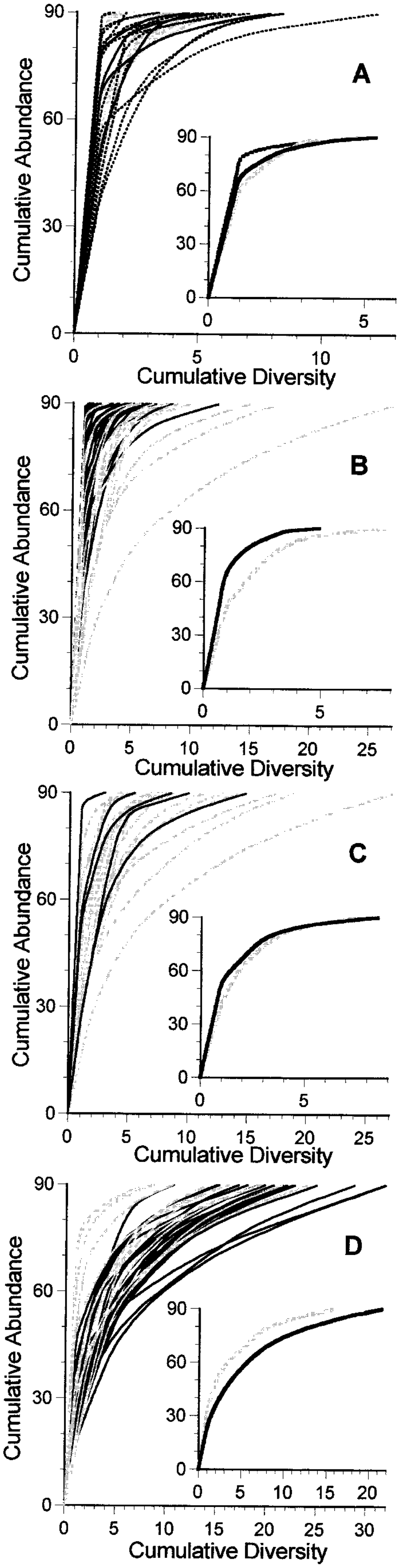

Figure 1. Mean abundance vs. diversity (MAD) curves showing sources of unwanted variation in data. All inset plots show median MAD curves for groups of samples. A: Ordovician carbonate brachiopod (gray lines), coral (black lines), and multiple taxa (dashed lines). B: Ordovician carbonate samples (black lines) and siliciclastic samples (gray lines). C: Early Paleozoic fine-grained samples (gray lines) and coarse-grained samples (black lines). D: Cenozoic fine-grained samples (gray lines) and coarse-grained samples (black lines).

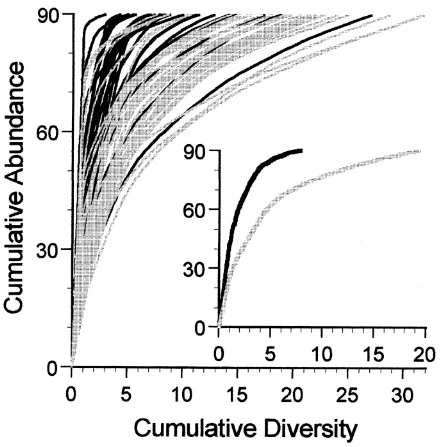

Figure 2. MAD curves for early Paleozoic (black lines) and Cenozoic (gray lines) genus-level siliciclastic samples. Inset shows median mean abundance vs. diversity curves for samples grouped by time interval.

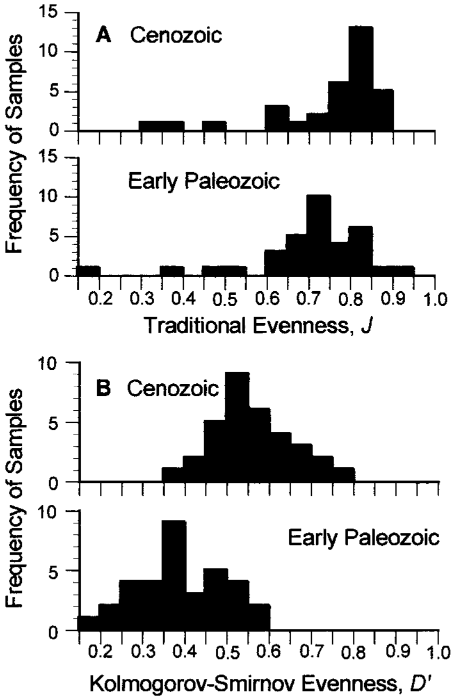

Figure 3. Sample-frequency distribution of evenness indices. A: Evenness index *J* for Cenozoic (top) and early Paleozoic (bottom). B: Evenness index *D′* for Cenozoic (top) and early Paleozoic (bottom).

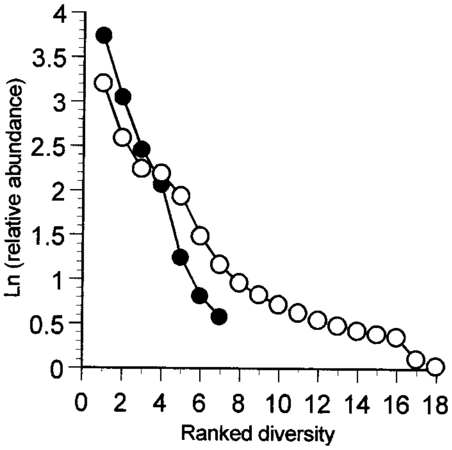

Figure 4. Rank-order abundance distributions of median mean abundance vs. diversity curves for early Paleozoic (closed circles) and Cenozoic (open circles).

nozoic samples, a factor of 2.47 increase in diversity.

Second, the Cenozoic samples display significantly higher evenness than the early Paleozoic samples (Fig. 2; $D = 0.31$, $p = 0.0004$). The early Paleozoic samples are dominated by few genera with relatively high abundance (75% of the abundance is represented on average by just 2.4 genera), whereas Cenozoic samples are less oligarchic in the partitioning of abundance across genera (75% of the abundance is represented on average by 5.7 genera). For both evenness indices used (Fig. 3), the difference is statistically significant (Wilcoxon test; $p = 0.01$ for J; $p < 0.0001$ for D'). Moreover, the difference between the two average curves (Fig. 2) is much larger than the differences observed across the two siliciclastic facies included in the analysis (Fig. 1, C and D) or across higher taxa (Fig. 1A).

A log plot of the median relative abundance of genera (RAD) shows that the relative abundance of the most common genera (ranked genera 1–3) is enriched in the early Paleozoic relative to the Cenozoic (Fig. 4). All other genera are enriched in the Cenozoic relative to the early Paleozoic. The difference between the RAD plots corresponds to a flatter shape (higher evenness) of the median Cenozoic MAD curve (Fig. 2).

DISCUSSION

Given that heterogeneities in facies and higher taxa cannot account for the observed differences in AD structure, our results suggest that the alpha diversity and evenness of fossil samples have increased through time.

The increase in sampled alpha diversity by a factor of 2.47 from the early Paleozoic to the Cenozoic is remarkably consistent with the estimates of Bambach (1977; see also Sepkoski, 1988). Over a comparable time interval, but using different literature data, Bambach found an increase in species-level alpha diversity by a factor of 2.44 in variable nearshore environments and by a factor of 2.48 in open-marine environments. However, sampled alpha diversity does not necessarily reflect the total alpha diversity because it is a combined function of the evenness of the underlying population and the sampling intensity (Koch, 1978; Alroy, 2000). Our samples are insufficient in size to evaluate the analyzed sites against theoretical abundance distribution models, and thus we cannot assess the biological legitimacy or fallacy of the observed increase in alpha diversity.

Several causes may underlie the observed increase in evenness. First, taphonomic megabiases may have distorted relative abundance of taxa in fossil assemblages. In particular, the diagenetic loss of aragonite fossils (e.g., Cherns and Wright, 2000) may have lowered the evenness of the early Paleozoic samples. Koch and Sohl (1983) explicitly compared collections with well-preserved aragonite and calcite to collections of poorer preservational quality and found significant differences in the number of taxa and makeup of the preserved fauna. Second, some authors have suggested that the levels of time-averaging may have increased through the Phanerozoic (e.g., Kidwell and Brenchley, 1996; Kowalewski, 1996). Time-averaging processes that mix communities of different taxonomic compositions can lower the relative abundance of dominant species, thereby increasing diversity and evenness. Third, Paleozoic fossils, which generally need to be extracted from lithified rocks, are more difficult to sample than Cenozoic fossils, which are typically sieved from unlithified sediment. The restriction of data to larger size fractions may result in the removal of some common taxa and an apparent decrease in evenness (see also Kidwell, 2001).

The observed trend may represent a real secular increase in the evenness of marine benthic invertebrate communities. This trend is expected, considering that habitat utilization, marine biomass, and rates of trophic flows may have increased significantly and systematically through time (Vermeij, 1977, 1995; Sepkoski, 1981; Bambach, 1983, 1999). In addition, as the dominant marine fauna changed through time (Sepkoski, 1981) and mass extinctions repeatedly altered ecological interactions and habitat resources (DiMichele and Phillips, 1996), new communities with different AD structures may have appeared.

One bias may work in the opposite direction. Paleozoic samples are more often tropical than Cenozoic samples (Allison and Briggs, 1993). This is the case here because most of our data are from North America or Europe. Because evenness and sampled alpha diversity tend to decrease toward high latitudes, the evenness of the Paleozoic sites may be overestimated relative to the Cenozoic ones. If the paleolatitudinal bias is a factor, it is clearly insufficient to overwhelm the other factors listed here.

The existing data are inadequate to evaluate which of the posed factors were the most important. Nevertheless, the observed trend is important because empirical paleontological data, including those used in previous studies of diversity, ultimately derive from fossil samples. This study demonstrates that fossil samples have changed AD structure through time.

IMPLICATIONS AND CONCLUSIONS

The increase in the evenness of fossil samples through the Phanerozoic, which primarily reflects the decrease in relative abundance of the most common taxa (Fig. 4), has two implications. First, the observed secular changes in evenness of the fossil samples may have contributed to the observed increase in alpha diversity. Fossil sites with the same total diversity but of different evenness may produce samples that yield different estimates of sampled diversity. Thus, it is theoretically possible that our results reflect only one change: the increase in evenness through time. Second, the change in evenness of fossil samples may be an important driver of the secular increase in global diversity. Because the relative abundance of the most common taxa has decreased through time, the likelihood of sampling less common taxa may have necessarily increased. Thus, higher diversity estimates can be expected for the Cenozoic simply because of the increase in evenness through time. However, the magnitude of the effect is difficult to assess because data based on taxonomic rather than bulk samples may be less prone to evenness changes (i.e., not all collections are random bulk samples: rare taxa may be better represented in taxonomic collections that aim to capture all taxa present in an outcrop).

Alroy et al. (2001) demonstrated that diversity estimates based on data standardized for multiple occurrences of taxa in faunal lists can depart notably from the traditional curve of Sepkoski, underscoring the sensitivity of diversity estimates to sampling issues. Our study echoes previous warnings (Alroy, 2000; Alroy et al., 2001) that studies of diversity should also incorporate abundance data to account for potential changes in evenness (a notable increase in evenness documented here may bias synoptic diversity curves even if sampling problems are otherwise accounted for analytically). Although the observed increase in sampled alpha diversity may or may not have biological significance (see preceding), the increase is real in a sampling sense by affecting any estimates of diversity based on empirical data. Ideally, many large bulk samples should be collected and compared against theoretical abundance distribution models, and necessary corrective methods (see especially Alroy, 2000; Alroy et al., 2001) should then be applied to improve our understanding of secular changes in diversity. Such efforts may ultimately give rise to a robust (and perhaps different) interpretation of the marine Phanerozoic history of diversity.

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REFERENCES CITED

Allison, P.A., and Briggs, D.E.G., 1993, Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction: Geology, v. 21, p. 65–68.

Alroy, J., 2000, New methods for quantifying macroevolutionary patterns and processes: Paleobiology, v. 26, p. 707–733.

Alroy, J., Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fürsich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J., Jr., Sommers, M.G., Wagner, P.J., and Webber, A., 2001, Effects of sampling standardization on estimates of Phanerozoic marine diversification: National Academy of Sciences Proceedings, v. 98, p. 6261–6266.

Bambach, R.K., 1977, Species richness in marine benthic habitats through the Phanerozoic: Paleobiology, v. 3, p. 152–167.

Bambach, R.K., 1983, Ecospace utilization and guilds in marine communities through the Phanerozoic, *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: New York, Plenum Press, p. 719–746.

Bambach, R.K., 1999, Energetics in the global marine fauna: A connection between terrestrial diversification and change in the marine biosphere: Geobios, v. 32, p. 131–144.

Bennington, J.B., and Bambach, R.K., 1996, Statistical testing for paleocommunity recurrence: Are similar fossil assemblages ever the same?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 127, p. 107–133.

Benton, M.J., 1995, Diversification and extinction in the history of life: Science, v. 268, p. 52–58.

Cherns, L., and Wright, V.P., 2000, Missing mollusks as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea: Geology, v. 28, p. 791–794.

DiMichele, W.A., and Phillips, T.L., 1996, Climate change, plant extinctions and vegetational recovery during the Middle-Late Pennsylvanian transition: The case of tropical peat-forming environments in North America, *in* Hart, M.B., ed., Biotic recovery from mass extinction events: Geological Society [London] Special Publication 102, p. 201–221.

Kidwell, S.M., 2001, Preservation of species abundance in marine death assemblages: Science, v. 294, p. 1091–1094.

Kidwell, S.M., and Brenchley, P.J., 1996, Evolution of the fossil record: Thickness trends in marine skeletal accumulations and their implications, *in* Jablonski, D., et al., eds., Evolutionary paleobiology: Chicago, University of Chicago Press, p. 290–336.

Koch, C.F., 1978, Bias in the published fossil record: Paleobiology, v. 4, p. 367–372.

Koch, C.F., and Sohl, N.F., 1983, Preservational effects in paleoecological studies: Cretaceous mollusc examples: Paleobiology, v. 9, p. 26–34.

Kowalewski, M., 1996, Time-averaging, overcompleteness, and the geological record: Journal of Geology, v. 104, p. 317–326.

Lande, R., 1996, Statistics and partitioning of species diversity, and similarity among multiple communities: Oikos, v. 76, p. 5–13.

McKinney, M.L., 1996, The biology of fossil abundance: Revista Española de Paleontologia, v. 11, p. 125–133.

Newell, N.D., 1959, Adequacy of the fossil record: Journal of Paleontology, v. 33, p. 488–499.

Peters, S.E., 2001, The evenness and richness components of taxonomic diversity: Geological Society of America Abstracts with Programs, v. 33, p. A141.

Peters, S.E., and Bork, K.B., 1999, Species-abundance models: An ecological approach to inferring paleoenvironment and resolving paleoecological change in the Waldron Shale (Silurian): Palaios, v. 14, p. 234–245.

Raup, D.M., 1976, Species diversity in the Phanerozoic: A tabulation: Paleobiology, v. 2, p. 279–288.

Raup, D.M., 1978, Cohort analysis of generic survivorship: Paleobiology, v. 4, p. 1–15.

Sepkoski, J.J., Jr., 1978, A kinetic model of Phanerozoic taxonomic diversity: I. Analysis of marine orders: Paleobiology, v. 4, p. 223–251.

Sepkoski, J.J., Jr., 1979, A kinetic model of Phanerozoic taxonomic diversity: II. Early Phanerozoic families and multiple equilibria: Paleobiology, v. 5, p. 222–251.

Sepkoski, J.J., Jr., 1981, A factor analytic description of the Phanerozoic marine fossil record: Paleobiology, v. 7, p. 36–53.

Sepkoski, J.J., Jr., 1984, A kinetic model of Phanerozoic taxonomic diversity: III. Post-Paleozoic families and mass extinctions: Paleobiology, v. 10, p. 246–267.

Sepkoski, J.J., Jr., 1988, Alpha, beta, or gamma: Where does all the diversity go?: Paleobiology, v. 14, p. 221–234.

Sepkoski, J.J., Jr., Bambach, R.K., Raup, D.M., and Valentine, J.W., 1981, Phanerozoic marine diversity and the fossil record: Nature, v. 293, p. 435–437.

Tipper, J.C., 1979, Rarefaction and rarefiction: The use and abuse of a method in paleoecology: Paleobiology, v. 5, p. 423–434.

Valentine, J.W., 1969, Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time: Palaeontology, v. 12, p. 684–709.

Vermeij, G.J., 1977, The Mesozoic marine revolution: Evidence from snails, predators, and grazers: Paleobiology, v. 3, p. 245–258.

Vermeij, G.J., 1995, Economics, volcanoes, and Phanerozoic revolutions: Paleobiology, v. 21, p. 125–152.

Whittaker, R.H., 1975, Communities and ecosystems: New York, Macmillan, 385 p.

Wu, R.S.S., and Shin, P.K.S., 1997, Sediment characteristics and colonization of soft-bottom benthos: A field manipulation experiment: Marine Biology, v. 128, p. 475–487.

Zar, J.H., 1999, Biostatistical analysis (fourth edition): Upper Saddle River, New Jersey, Prentice-Hall, 663 p.

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