

ARTICLES

Did Alpha Diversity Increase during the Phanerozoic? Lifting the Veils of Taphonomic, Latitudinal, and Environmental Biases

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ABSTRACT

We estimate the effects of three biases on the observed alpha diversity of paleocommunities from the Middle Paleozoic and Late Cenozoic. The first bias results from the preferential dissolution of aragonite relative to calcite; this bias can lower the relative abundance and preserved diversity of aragonitic taxa, potentially lowering the rarefied diversity of an entire fossil assemblage. We model the effects of this bias by analytically reinserting aragonitic specimens and taxa into Paleozoic assemblages that have been described in the literature. The aragonitic specimens are inserted using a wide range of reasonable assumptions about the original local paleocommunity composition. Although the dissolution bias is probably not as severe as has been argued by some, our analytical modeling indicates that the average Paleozoic assemblage may have lost up to 29% of its total diversity. The second bias results from the higher diversity of the tropics relative to temperate latitudes, but the Late Cenozoic collections we analyzed from the literature represent temperate assemblages whereas the Paleozoic collections were tropical in origin (the northward drift of North America and Europe through time caused this difference). On the basis of latitudinal diversity gradients in the Late Cenozoic, the diversity of the temperate Late Cenozoic samples should be at least doubled for an accurate comparison to the tropical Paleozoic samples. The third bias is environmental: our Late Cenozoic samples tend to come from more onshore, stressed habitats than the Paleozoic samples. In our study, this factor should reduce the apparent diversity of Late Cenozoic paleocommunities by about 9%. After correcting for these biases, standardized alpha diversity appears to increase by a factor of 3.0–3.7 from the Middle Paleozoic to the Late Cenozoic. Previous studies that did not correct for these biases suggested that alpha diversity increased by a factor of 2.5 times; the earlier studies produced approximately correct results because (by chance) the effects of the biases largely cancel out. In the “consensus” article on marine diversity history, an observed increase in alpha diversity was taken as powerful support for an increase in global diversity from the Paleozoic to the Cenozoic. Although we do not test all conflating factors, this study provides new rigor to this longstanding view on alpha diversity change in the Phanerozoic.

Online enhancement: appendix.

Introduction

Community paleoecology is, ultimately, the analysis of which taxa co-occur and at what relative abundances. Paleocommunities have proved useful, for example, in mapping environmental patterns and gradients (Ziegler 1970; McGhee and Sutton 1981; Springer and Bambach 1985; Bambach and Benning-

ton 1996; Holland et al. 2001). Also, analyses of paleocommunity (or alpha) diversity (Seilacher 1974, 1977; Bambach 1977) provided key support for the “consensus” model of Phanerozoic marine diversity (Sepkoski et al. 1981) because they were not biased by variations in rock availability (Raup 1972; Peters and Foote 2001; Smith 2001) or paleontological interest (Sheehan 1977), two biases that plague global compilations of diversity (for other current opinions on Phanerozoic diversity history, see Miller 2000; Alroy et al. 2001; Foote 2001; Jackson and Johnson 2001; Bush et al. 2004).

Manuscript received December 22, 2003; accepted May 27, 2004.

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Despite these successes, most analyses of paleocommunities have remained descriptive, and theoretical breakthroughs are generally lacking. As a result, Gould (1980, p. 108, 112) noted that community paleoecology received mixed reviews in an informal survey of "subjects of invertebrate paleontology that had been most fruitful or most disappointing since 1959." More recently, the debate over the coordinated stasis model of paleocommunity change has not resulted in a clear resolution (Miller 1997; Ivany 1999). At the theoretical and analytical level, community paleoecology has been a disappointing endeavor in part because many biological, chemical, and geological processes obscure the original taxonomic structure of a community. Here we present the first in a series of articles that we hope will place paleocommunity analysis on a more rigorous foundation.

Due to time averaging (the mixing of noncontemporaneous organisms), the assemblages in our database do not represent biological communities in the sense of groups of organisms living and interacting in single places at single instants. However, they do represent paleocommunities—groups of organisms that lived in single places through a period of time (Bambach and Bennington 1996). Typically, the interval of time averaging in such assemblages is on the order of hundreds to thousands of years (Kowalewski and Bambach 2003). Since the analysis is restricted to untransported fossil assemblages, these assemblages reflect the general makeup of the fossilizable portion of the living community as it accumulated over time (Kidwell 2001, 2002) and, therefore, they do carry an ecological signal, which is not necessarily true of every fossil assemblage. We use the term paleocommunity to emphasize the strong ecologic signal borne by these fossil assemblages.

In this article we test the effects of several biases on the measurement of local paleocommunity diversity. Previous studies showed that marine alpha diversity increased by a factor of 2.5 from the Paleozoic to the Cenozoic (Bambach 1977; Powell and Kowalewski 2002). Powell and Kowalewski's (2002) study is particularly noteworthy because these authors corrected for variations in sample size using rarefaction (Hurlbert 1971; Raup 1975; Tipper 1979), an important first step toward the rigorous comparison of paleocommunities. However, no corrections for preservational or collecting biases were applied in either of these alpha diversity studies, although Powell and Kowalewski explicitly discussed biases. After correcting for biases of preservation and collection, will Cenozoic paleocom-

munities still appear more diverse than Paleozoic ones?

The first bias addressed here, the inhomogeneous preservation of aragonitic and calcitic shells, was recently discussed by Cherns and Wright (2000). Aragonite and calcite are both forms of calcium carbonate, but aragonite is less stable under earth-surface and near-surface conditions and, therefore, aragonitic shells are more likely to dissolve before permanent burial. Cherns and Wright compared Silurian fossil assemblages with "normal" preservation to assemblages in which silica had replaced many fossils (calcitic and aragonitic) before dissolution. (For purposes of this article, "normally" preserved assemblages are not silicified, phosphatized, or preserved in a fossil lagerstätten. They consist of original or recrystallized shell material, casts, and molds.) Cherns and Wright claimed a 100-fold to 150-fold reduction in the abundance of aragonitic bivalves relative to calcitic brachiopods in the non-silicified assemblages they studied and suggested that such shortfalls might typify Paleozoic faunas and lead to significant underestimates of species richness. Wright et al. (2003) reached similar conclusions about Mesozoic faunas. These studies implied that "missing molluscs" may cripple local paleocommunity reconstruction and the analysis of alpha diversity in the Paleozoic and Mesozoic.

To test the effects of aragonite dissolution on observed patterns of change in alpha diversity, we compiled a data set from the literature on Middle Paleozoic and Late Cenozoic fossil assemblages. We then analytically model the potential original (i.e., predissolution) diversities of the Paleozoic paleocommunities by reinserting aragonitic specimens and taxa under a range of reasonable parameters.

We also examine two additional biases that may affect studies of alpha diversity—paleolatitudinal and paleobathymetric setting. Many paleontological samples are collected from North America and Europe, which were near the equator during the Paleozoic but shifted to temperate latitudes by the Cenozoic (Ziegler et al. 1979; Scotese 1997). Because diversity typically increases from the poles to the tropics (Fischer 1960; Roy et al. 1996, 1998; Crame 2001, 2002), comparing tropical Paleozoic assemblages to temperate Cenozoic assemblages should bias against the recognition of a diversity increase from the Paleozoic to the Late Cenozoic (Allison and Briggs 1993; Jackson and Johnson 2001). Also, local diversity tends to increase from stressed inshore habitats to more stable offshore habitats (Bambach 1977), thus introducing yet another bias in recognizing diversity trends if samples

are not similarly distributed among environments over time.

In their study of alpha diversity, Powell and Kowalewski (2002) suggested that the observed increase in rarefied diversity from the Paleozoic to the Cenozoic might reflect an increase in taxonomic evenness rather than taxonomic richness (see also Peters 2001); we discuss this problem briefly at the end of the article. We conclude by assessing the combined effects of the three biases and offering an answer to the question, did alpha diversity increase from the Paleozoic to the Cenozoic?

Data Compilation

Criteria for Selecting Data. Our literature-based data set contains 79 fossil assemblages from the Late Ordovician through Frasnian (Late Devonian) and 47 from the Miocene through Pleistocene (see the online-only appendix, also available from the *Journal's* Data Depository in the *Journal of Geology* office upon request, for sources). The Paleozoic data sets postdate the Ordovician radiation but precede the ecological reorganizations of the later Paleozoic (sensu Bambach 1999; Droser et al. 2000). The Late Cenozoic was chosen for comparison to maximize the chance of finding a diversity change because genus richness does not convincingly rise above Paleozoic levels until the mid-Cenozoic in some treatments of Sepkoski's global compendium (Alroy et al. 2001, their fig. 1). Late Cenozoic samples were used instead of recent ones because fossil faunas from the Miocene to Pleistocene have passed through the filters of taphonomy and preservation, maximizing their potential similarity to Paleozoic collections. Important differences in preservational state certainly remain between Paleozoic and Late Cenozoic faunas, especially the degree of lithification of the enclosing rock. However, the use of sampling-standardization counteracts biases introduced by the ease of recovering large samples from unlithified Late Cenozoic locales (but see Kowalewski and Hoffmeister 2003 on sieve-size effects).

The samples were drawn from those used by Bambach (1977), Powell and Kowalewski (2002), the Paleobiology Database (<http://www.paleodb.org>), and our own literature searches (appendix). In all cases, we examined the original publication to determine whether it met our criteria for inclusion. Abundance counts were necessary for quantitative analysis, and each assemblage had to contain at least 100 specimens, with 37 Paleozoic and 38 Late Cenozoic collections containing more than 200 specimens. Each Paleozoic sample had to include all

macrofauna present; that is, no sample excluded some higher taxa. Because many quantitative studies of Late Cenozoic assemblages report only mollusks, we were forced, like Bambach (1977), to use a number of exclusively molluscan samples. However, many Late Cenozoic fossil assemblages are heavily dominated by mollusks anyway.

Most samples were single collections from single beds and thus represent local paleocommunities sensu Bennington and Bambach (1996). A few samples represent a set of replicate collections from the same paleocommunity type, that is, collections from the same facies that contain the same general fauna. Bennington and Bambach (1996) restricted the use of the term paleocommunity to sets of local paleocommunities that cannot be statistically distinguished; because we have not statistically compared any of the collections in our database, this term does not strictly apply to any part of our analysis. When we use the term paleocommunity in this article without the modifiers "local" or "type," we are referring to the general concept of ecological affiliation and its analyzable features at the local habitat level, which are accessible in the fossil record.

All samples represent level-bottom environments (i.e., no reefs or bioherms), and these environments were classified in an onshore-offshore gradient, to be discussed later. Analyses were performed at the genus level for comparability with other studies of Phanerozoic-scale diversity trends. Powell and Kowalewski (2002) found that genera were good proxies for species in analyses of alpha diversity patterns.

Raw Data and Diversity Patterns. Figure 1 shows the rarefaction curves for the raw Paleozoic and Late Cenozoic data, and table 1 summarizes the genus richness expected at several sampling levels. The average curve for the Late Cenozoic is well above that of the Paleozoic; at 100 specimens, the average Late Cenozoic sample has 1.84 times as many genera as the Paleozoic, and at 200 specimens, this ratio equals 1.92 (table 1). (We use means, not medians, because the total diversity in a region is a multiplicative function of the mean diversity of local assemblages, e.g., Whittaker 1960.) The apparent diversity increase is less than that observed by Bambach (1977) and Powell and Kowalewski (2002), who found a rise in alpha diversity of about 2.5 times. We had hoped to run analyses at the 400-specimen level, but our sampling of large Late Cenozoic collections was biased toward less diverse, inshore habitats (discussed subsequently). Since diverse offshore collections were not large enough to include in the rarefaction at

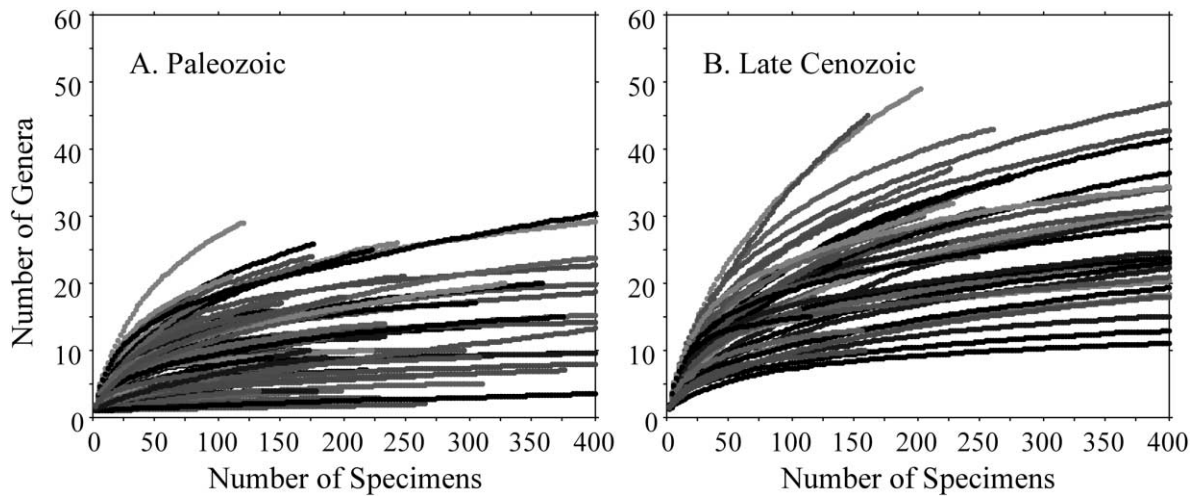


Figure 1. Rarefaction of raw data for the (A) Paleozoic and (B) Late Cenozoic samples. Lines are shaded to help distinguish different samples.

the 400-specimen level, the median collection richness of Late Cenozoic samples in our data set actually drops between 200 and 400 specimens (table 1). (Even so, at 400 specimens these Late Cenozoic samples are again half as diverse as the Paleozoic samples.) The lack of large, offshore Late Cenozoic collections is interesting because there is a common impression that Cenozoic samples are generally larger than Paleozoic samples. Large Late Cenozoic samples certainly exist, but the ones we found tabulated in the literature were primarily restricted to the least diverse habitats. Because results were similar when analyses were run at sample sizes of 100 and 200 specimens, we present the results at the 200-specimen level, over twice the sample size at which Powell and Kowalewski (2002) did their analyses.

Bias 1: The Early Dissolution of Aragonite in the Paleozoic

Dissolution and Preservation of Aragonitic Fossils. Aragonite dissolves more rapidly than calcite in seawater (Canfield and Raiswell 1991; Smith et al. 1992; Brachert and Dullo 2000; Morse and Arvidson 2002), although both can be destroyed easily by dissolution if not removed from hostile near-surface conditions (Driscoll 1970; Davies et al. 1989; Callender et al. 2002; Powell et al. 2002). Thus, aragonitic shell material often has a lower probability of entering the fossil record than calcitic material. Studies by Palmer et al. (1988) and Cherns and Wright (2000) for the Paleozoic; Palmer et al. (1988), Sanders (2001), and Wright et al. (2003) for the Me-

sozoic; and Smith et al. (1992) and Brachert and Dullo (2000) for the Cenozoic document the preferential dissolution of aragonite throughout the Phanerozoic. The strength of this bias may have fluctuated between aragonite and calcite seas (Stanley and Hardie 1998), but the bias has always existed.

However, fossils of aragonitic taxa do remain in many Paleozoic rocks despite the loss of their shells by dissolution. In cohesive sediments, the inner and outer surfaces of the void left by a dissolved shell often are pressed together and superimposed as the void closes during sediment compaction, forming a composite mold (McAlester 1962). This composite surface will remain during lithification, but because no open void is left, composite molds are not visible (except on bedding planes) unless the rock is split. In the Paleozoic, composite molds of aragonitic fossils are common in unreworkeed beds deposited in environments that supported mollusk-rich faunas. For example, the Silurian mudstones of Arisaig, Nova Scotia, contain abun-

Table 1. Average Diversity of the Raw Paleozoic and Late Cenozoic Samples Rarefied to 100, 200, and 400 Specimens^a

| Number of specimens | 100 | 200 | 400 |
|----------------------|-------|-------|-------|
| Late Cenozoic mean | 18.40 | 24.20 | 26.23 |
| Late Cenozoic median | 19.00 | 23.80 | 23.59 |
| Paleozoic mean | 9.99 | 12.62 | 16.75 |
| Paleozoic median | 9.52 | 12.39 | 15.11 |
| LC/Pz mean | 1.84 | 1.92 | 1.57 |
| LC/Pz median | 2.00 | 1.92 | 1.56 |

^a Also listed is the ratio of Late Cenozoic to Paleozoic diversity (LC/Pz).

dant, well-preserved composite molds of aragonitic mollusks, even though no shell material remains (Bambach 1969), whereas calcitic brachiopods from the same location retain their original shell material (Harper 1973). However, mollusks did not thrive in all Paleozoic marine habitats, as has been extensively documented (Sepkoski and Miller 1985; Springer and Bambach 1985; Miller 1988; Novack-Gottshall and Miller 2003). Another indication that infaunal bivalves were not more common in many Paleozoic habitats is the shallow depth of bioturbation in many Paleozoic sediments (Sepkoski et al. 1991). If abundant infaunal bivalves had been present, more Paleozoic sediments would be homogenized in the manner of most Cenozoic deposits.

In many unreworked Paleozoic sediments, the shallowness of bioturbation and the preservational redundancy provided by composite molds often allow most of the original shelly fauna to be collected despite the taphonomic loss of the original aragonitic shell material. However, composite molds are generally destroyed in Cenozoic sediments by the deeper and more extensive bioturbation typical of the later Phanerozoic (Thayer 1983; Sepkoski et al. 1991; Droser and Bottjer 1993; Bottjer and Droser 1994); more extensive bioturbation also irrigates the sediments, facilitating carbonate dissolution (Canfield and Raiswell 1991; Green et al. 1992). Even if composite molds were present in a Cenozoic deposit, they could not easily be collected from unlithified sediments.

Most Paleozoic collections come from shell concentrations because sampling is easier and more efficient than splitting lithified rocks to find individual specimens. Shell beds form by the reworking and concentration of shells while sediments are still unlithified (Kreisa 1981; Kreisa and Bambach 1982); undissolved shells can be reworked and re-deposited into shell beds, but physical or biological reworking destroys composite molds in unconsolidated sediments. Therefore, shell beds may contain a fossil assemblage in which the original proportions of taxa are skewed because remains of aragonitic individuals are preferentially lost during reworking compared with calcitic individuals.

Winnowing may also reduce the duration of time averaging of aragonitic forms in shell beds relative both to the calcitic shells in the shell bed and the composite molds of a nonwinnowed deposit. Only recently dead aragonitic shells should remain undissolved and available for reworking, whereas calcitic shells are more resistant to dissolution and may range more widely in age (cf. Kowalewski 1997; Kidwell 1998; but see Carroll et al. 2003).

Variations in the amount of time averaging can affect diversity estimates. For example, Kidwell (2002) found that time-averaged, modern molluscan death assemblages had on average 1.22 times more diversity than the non-time-averaged, living communities from which they were forming (when sampling intensity was standardized). Kowalewski et al. (2003) found similar results for mixed mollusk-brachiopod assemblages from the San Juan Islands, U.S.A. Two points suggest that the difference in time averaging between winnowed aragonitic faunas and calcitic or nonwinnowed aragonitic faunas in the Paleozoic should be less than the difference between grab samples of Recent life and death assemblages. First, time averaging is (if anything) more intense in the Recent than the Paleozoic (Kidwell and Brenchley 1994, 1996; Kidwell 1998; Kowalewski and Bambach 2003). Second, winnowed aragonitic faunas in the Paleozoic may be somewhat time-averaged, unlike living grab samples. Therefore, the calcitic and nonwinnowed aragonitic faunas should, on average, be no more than 1.22 times as diverse as winnowed aragonitic faunas, once sampling intensity is standardized.

By comparing winnowed and nonwinnowed bivalve faunas from the same paleocommunities from Arisaig, Nova Scotia (Bambach 1969), we find that winnowing reduces diversity by a range of factors. In some of Bambach's units, the winnowed and nonwinnowed samples of bivalves have equivalent standardized diversities. However, in one unit (faunal subdivision 20 of Bambach 1969), the nonwinnowed collections rise to be about 1.6 times as diverse as the nonwinnowed collections from the same paleocommunity setting (fig. 2). Figure 2 appears to represent a worst-case scenario.

Carbonate dissolution certainly occurs in the Cenozoic as well, but we do not test its effects on diversity. Although there is a differential loss of aragonite compared with calcite in the Cenozoic (Brachert and Dullo 2000), many Cenozoic mollusks have robust, organic-poor shells that make them more durable than Paleozoic shells, and Late Cenozoic shell beds contain an abundance of both calcitic and aragonitic skeletons (Kidwell and Brenchley 1994, 1996). Furthermore, Kidwell (2001, 2002) found that modern molluscan death assemblages record rather faithfully the rank abundances of taxa in the living community. Many Cenozoic collections may be biased instead by the failure to include nonmolluscan fossils in abundance counts, but again, we do not correct for this bias.

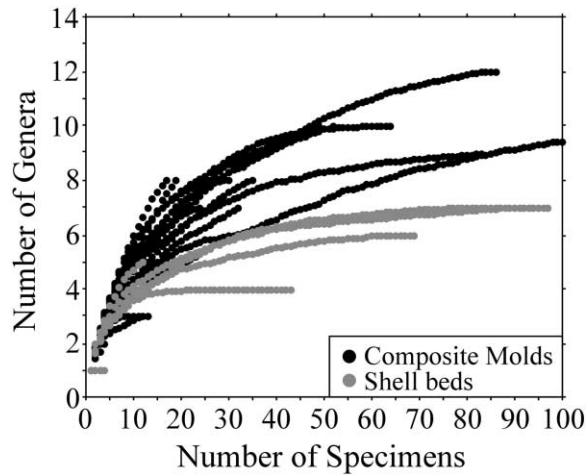


Figure 2. Rarefaction of bivalve faunas from shell beds (*gray*) and composite mold collections (*black*) from Bambach's (1969) unit 20 at Arisaig, Nova Scotia. This example is shown as a worst-case scenario; in other units from Arisaig, the bivalve faunas from shell beds are similar in diversity to composite mold faunas.

Previous Estimates of the Magnitude of the Aragonite Megabias. Cherns and Wright (2000) attempted to study the preferential loss of aragonitic fossils in the Silurian of Gotland, Sweden, by comparing a normally preserved fauna (as defined previously) to a silicified fauna. The silicified fauna was relatively immune to the bias of early aragonite dissolution because both calcitic and aragonitic shells were replaced by silica soon after burial, giving a glimpse of the original percentage of each mineralogy in that environment. In the silicified assemblage, the calcitic brachiopods were about one-third (36%) as abundant as were specimens of the aragonitic bivalves, whereas brachiopod specimens outnumbered bivalves 59 to 1 in the nonsilicified assemblage. Cherns and Wright (2000) concluded that the early dissolution bias underrepresented aragonitic fossils by a factor of 100–150 in the normally preserved assemblage. They also noted that only about half as many bivalve species were recovered from the nonsilicified assemblage as from the silicified assemblage. Wright et al. (2003) performed a similar study on Jurassic fossils. These studies imply that extreme losses of aragonitic forms might typify Paleozoic and Mesozoic faunas, but several aspects of the authors' methodology raise questions about the quantitative accuracy of their results. We will discuss the study of Cherns and Wright (2000) because it directly pertains to preservation in the Middle Paleozoic.

The drop in bivalve diversity from the silicified

to nonsilicified assemblages of Cherns and Wright (2000) gives the impression that the early dissolution of aragonite severely reduced the diversity of the fauna. However, the taxon counts of Cherns and Wright (2000) were compiled from raw samples with no correction for variations in sample size. The silicified fauna contained almost double the number of species of bivalves as the nonsilicified fauna, but it also contained 38 times more bivalve specimens (3421 vs. 89). Rarefying the original data presented by Liljedahl (1985) and Pojeta (1979), the two bivalve paleocommunities appear similarly diverse (at 89 specimens, there were seven species in the nonsilicified samples vs. 6.6 in the silicified samples). The apparent decrease in bivalve diversity observed by Cherns and Wright results primarily from collecting fewer bivalves from the nonsilicified fauna. It would have been interesting to look as well at the effects of early dissolution on the standardized diversity of the entire assemblage, an approach we use below. (Of course, if bivalves were lost from an assemblage, then standardization alone would not correct the ratio of bivalves to brachiopods.)

In addition, the two Silurian assemblages studied by Cherns and Wright (2000) were not collected from similar paleocommunity types, and there is no reason to expect them to be quantitatively comparable in terms of abundance or species-richness of bivalves. Although both assemblages came from the same general part of the spectrum of shelf habitats (Benthic Assemblage zone 2 of Boucot 1975), the assemblages were dominated by different taxonomic suites of both brachiopods and bivalves. These differences cannot be attributed to preservational differences. In addition to the taxonomic differences, the two bivalve faunas were dominated by species with different lifestyles: suspension feeders dominated the nonsilicified bivalve fauna, whereas 90% of the silicified bivalve fauna were burrowing deposit-feeders. As Cherns and Wright noted as an alternative hypothesis, some of the differences between samples in the relative abundances of bivalves and brachiopods could be ecologic, not taphonomic; although their nonsilicified assemblage doubtlessly suffers from an aragonite dissolution bias, the quantitative magnitude of the bias is not determined by comparing it with an entirely different taxonomic assemblage.

Koch and Sohl (1983) examined the effects of aragonite dissolution on the diversity of local molluscan paleocommunities from the Late Cretaceous of the Gulf of Mexico coast of the United States. They classified each of 83 collections into

one of six preservational categories based on the preservational quality of aragonite and calcite. They corrected for sample size variation using rarefaction and found that, at 200 specimens, 15%–20% of species-level diversity was lost between collections containing calcite and aragonite and those from which aragonite was leached, leaving molds. Their results are difficult to compare quantitatively with the model we develop below. Their analysis was performed at the species level, and they note that taxa identifiable to genus-level but not species-level occurred in their poorly preserved collections. This counted as missing diversity in their work, although it would not in our genus-level analysis. Also, Koch and Sohl studied the effects of aragonite dissolution throughout the history of a deposit, not just early, syndepositional dissolution. In one treatment, Koch and Sohl limited the analysis to assemblages collected from similar sediments, but it is not clear that the well-preserved and poorly preserved collections were derived from the same paleocommunity or paleocommunity type. As they recognized, some of the diversity difference they observed could be ecologic.

Although Bambach (1969) did not make exact counts of brachiopod specimens when breaking rock to collect composite mold bivalves, brachiopods generally outnumbered bivalves in the mudstones from which the composite mold samples were collected, but bivalves equaled or slightly exceeded brachiopods in some cases. The ratio of brachiopods to bivalves in the shell bed collections was clearly greater, however, with brachiopods outnumbering bivalves seven to one (determined from the average number of brachiopod specimens per collection from Harper [1973] compared with the number of bivalves from those same shell beds). Thus, bivalves in shell beds were 12.5% of the combined brachiopod-bivalve fauna rather than the 30%–60% fraction of specimens in interbedded mudrocks (composite mold collections). This is equivalent to a loss of aragonitic specimens by a factor of three to 10, far less than the factor of 100–150 suggested by Cherns and Wright (2000).

Because no available study documents precisely the actual loss of aragonite compared with calcite, we model the entire range of possible values for the strength of the aragonite dissolution bias in the model we develop below. We also model the loss of diversity due to reductions in time averaging using as a worst-case scenario the 1.6-fold difference in diversity between bivalves found as

composite molds and those found in shell beds in Bambach's (1969) unit 20.

Correcting Standardized Paleozoic Alpha Diversity: Modeling the Effects of Aragonite Dissolution

Modeling the Loss of Aragonite. How much does the preferential dissolution of aragonite affect measurements of alpha diversity? In particular, how much could the dissolution bias depress the diversity of entire assemblages, such as those studied by Bambach (1977) and Powell and Kowalewski (2002)? Could this bias cause the observed difference in alpha diversity between the Paleozoic and Late Cenozoic?

We test the effects of this bias in the context of standardized sampling to avoid the conflating factor of sample size. However, sample size is not the only factor that confounds the measurement of the true taxon richness of a sample. Most notably, evenness (a measure of the similarity of taxa in relative abundance) influences rarefied diversity at low sampling levels (Peters 2001; Powell and Kowalewski 2002). For now, we use rarefied diversity as a measure of the relative diversity of collections, and we reserve comment on evenness until the "Discussion."

When aragonite dissolves preferentially, the total percentage of aragonitic specimens in an assemblage drops, making aragonitic taxa more rare and lessening the likelihood of collecting them. Thus, altering the relative abundances of aragonitic taxa changes the rarefied diversity of the sample (often, but not necessarily, lowering it). The effect of the dissolution bias can be corrected by increasing the percentage of aragonitic specimens in a sample back to the level of the original local paleocommunity; as discussed previously, this level is not precisely known, so the analytical model developed below includes the full range of possible values. To increase the percentage of aragonitic specimens, we first classified each Paleozoic genus in the database as having a calcitic or aragonitic skeleton. Most bimineralic genera of mollusks were classed with the aragonitic taxa because, in our judgment, the calcitic shell layer of most bimineralic taxa in our database did not have a much higher preservation potential than aragonite alone (as in Kidwell and Brenchley 1994). For instance, prismatic layers generally have a high content of organic matrix, and the calcite prisms tend to disaggregate once these organics decay. The remaining calcite certainly would be more vulnerable to destruction in reworking than whole shells. Most mollusks were

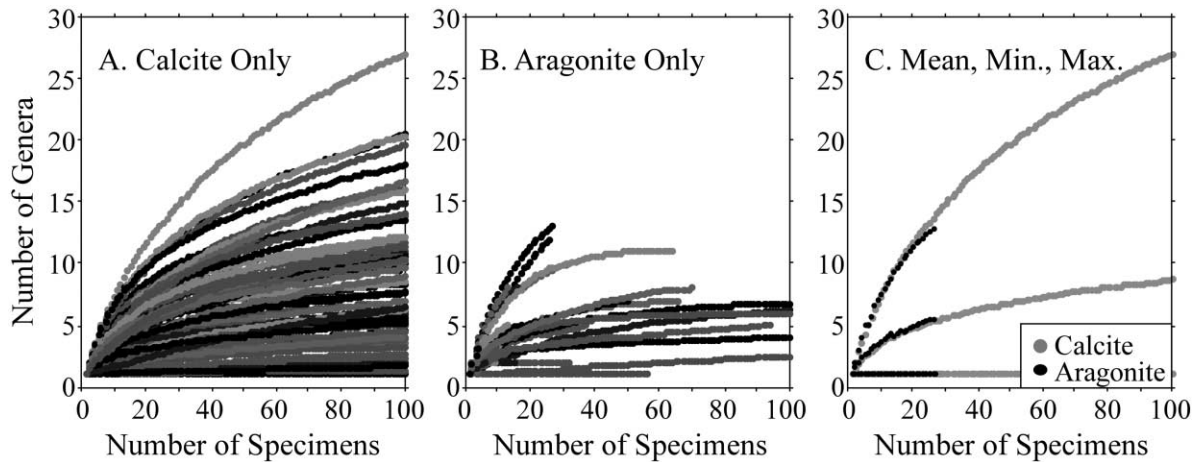


Figure 3. Rarefaction of Paleozoic samples, divided into (A) calcitic and (B) aragonitic fractions. In A and B, the lines are shaded to help distinguish different samples. C, Mean, minimum, and maximum rarefaction curves for calcitic (gray) and aragonitic (black) fractions.

thus classed as aragonitic, whereas other major taxa such as brachiopods, trilobites, and rugose and tabulate corals were classified as calcitic. Most samples in our Paleozoic data set had few aragonitic-shelled specimens: the mean percentage of aragonitic specimens was 7.8%, and the median was 1.5%.

The model estimates the rarefied diversity expected from the Paleozoic samples as the percentage of aragonite (p_a) varies from 0% to 100%. If the chosen p_a matches that of the original living assemblage, then the model estimates the standardized diversity of the original assemblage. Other values of p_a demonstrate the diversity expected by different magnitudes of the taphonomic bias between calcite and aragonite. Although calcitic and aragonitic taxa are assumed to have different preservation potentials, the model assumes that all calcitic taxa were equally preservable at one level and that all aragonitic taxa were equally preservable at a second, generally lower, level.

For a particular run of the model, the desired p_a and the sample size (n) are set. The number of aragonitic fossils in the modeled sample equals $np_a/100$, and the number of calcitic fossils equals $n(1 - p_a/100)$. Ideally, one would then rarify the aragonitic fraction of a test sample to $np_a/100$ specimens and the calcitic fraction to $n(1 - p_a/100)$ specimens and add the expected number of taxa in each to get the expected diversity of the sample at size n . However, many of the samples contained few aragonitic specimens (fig. 3B), and $np_a/100$ aragonitic specimens were not available for many runs of the model. To do this analysis, therefore, one

must estimate how many aragonitic taxa would have been present if the sampling intensity of the aragonitic fraction had been greater. Such estimations are generally taboo (rarefaction calculates the number of taxa expected if sampling intensity was lower, not higher), but we suggest a method that is a sufficient approximation in this case. Since we must approximate the number of aragonitic taxa that would have been present, the model does not calculate the exact diversity expected under various taphonomic regimes, but it provides a reasonable first-order approximation.

Figure 3A and 3B shows the rarefaction curves for the calcitic and aragonitic fractions of all Paleozoic samples. From the available data, the distribution of the aragonitic rarefaction curves appears quite similar to that of the calcitic curves. From one to 26 specimens, at which point many of the aragonitic samples run out of specimens, the minimum, maximum, and mean of the two distributions are quite similar (fig. 3C). Therefore, the model uses the rarefaction curves of the calcitic fractions as substitutes for the rarefaction curves of the aragonitic fractions. In the simplest case, the model estimates the rarefaction curve of the aragonitic fraction of a sample using a randomly drawn rarefaction curve from the calcitic fraction (fig. 3A). Specifically, the model draws a random calcitic fraction and a random aragonitic fraction, calculates the estimated diversity of each at $n(1 - p_a/100)$ specimens and $np_a/100$ specimens, respectively, and adds these to get the estimated total diversity. This procedure was run at 100,000 iterations for values of p_a ranging from 0% to 100%,

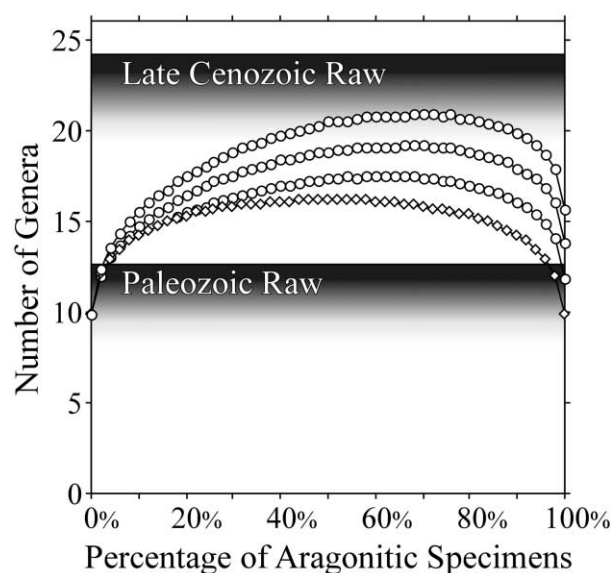


Figure 4. Modeled average genus richness of the Paleozoic samples rarified to 200 specimens when the percentage of aragonitic specimens is varied. In the lowest curve (*diamonds*), the aragonitic fractions of the samples are assumed to be similar to the calcitic fractions in abundance-diversity structure. In the next three curves (*circles*), the diversities of the aragonitic fractions are inflated relative to the calcitic fractions by factors of 1.2, 1.4, and 1.6, from lowest to highest. The number 1.2 is derived from Kidwell's (2002) meta-analysis, 1.6 is derived from Bambach's (1969) data from unit 20 (fig. 2), and 1.4 is shown as an intermediate value. The standardized diversities of the raw Late Cenozoic and Paleozoic samples are also shown; the shading is for aesthetic reasons.

thus estimating the diversity of samples at any original percentage of aragonitic specimens.

The model probably overestimates the effects of the dissolution bias because we model all local paleocommunities as having the same original percentage of aragonite. In reality, some paleocommunity types may not have originally had an abundant aragonitic fauna (Sepkoski and Miller 1985; Springer and Bambach 1985; Miller 1988; Novack-Gottshall and Miller 2003), but we model all as having the same original percentage as the other paleocommunity types more influenced by the bias. In this way, the analysis is biased against seeing an increase in diversity from the Paleozoic to the Cenozoic.

The lowest curve in figure 4 (*diamonds*) shows the average diversity expected for 200 specimens in the Paleozoic samples for varying p_a . Average diversity peaks when aragonitic and calcitic spec-

imens each make up 50% of the assemblage and decreases as either calcite or aragonite begins to dominate; the symmetry exists because of the assumption that the calcitic and aragonitic fractions have similar distributions of rarefaction curves. If all aragonite is lost from a set of such local paleocommunities, then a standardized sample loses 39% of its diversity. One might expect 50% of the diversity to be lost, but we are modeling sampling-standardized samples. Because we maintain a constant total number of specimens, if one loses 50 aragonitic specimens from a sample, one also gains 50 calcitic specimens, and these specimens will partly offset the diversity loss.

The retention of a fairly low amount of aragonite can greatly ameliorate the reduction in diversity—a loss of aragonite from 50% to 20% of a sample causes only a mild 6% loss in diversity. In fact, expected diversity changes little between 20% and 80% aragonitic specimens (fig. 4) because the calcitic and aragonitic fractions both contain sufficient specimens for their rarefaction curves to have flattened somewhat; gaining or losing a few specimens from either fraction has relatively little effect on diversity. However, with fewer than 20% aragonitic specimens, the expected diversity drops rapidly as aragonitic specimens are lost because there are few specimens in the aragonitic fraction and its rarefaction curve is steep. With this simple model, the maximum possible diversity loss in our Paleozoic samples (because they do have some aragonitic taxa still represented by fossils) is 22%, in which case the raw Late Cenozoic data still have a higher average alpha diversity than the Paleozoic data.

Modeling the Reduction in Time Averaging. More complex runs of the model were devised to counteract the possible effects of time averaging on diversity, which are twofold. First, the aragonitic fraction of an assemblage may not be as time averaged as the calcitic fraction, lowering aragonitic diversity, as discussed earlier. To counteract this bias, we scaled the rarefaction curves representing the aragonitic fraction of a sample upward by a range of factors—the aragonite inflation factors. (The entire rarefaction curve is not scaled upward by the amount of this factor; given one specimen, every rarefaction curve has one taxon. At the one-specimen sampling level, therefore, the inflation factor must be one. As sampling intensity increases, the scaling factor rises at a rate determined by the ratio between the rarefaction curves from the composite mold and shell bed collections in Bambach's unit 20. For example, an inflation factor of 1.6 indicates

that the inflation factor rises from 1.0 to 1.6 as sampling intensity increases.)

Given Kidwell's meta-analysis (Kidwell 2002), we expect the average aragonite inflation factor to be no more than 1.22. We also modeled inflation factors as high as 1.6, which was the maximum observed value for a single set of samples from Bambach's (1969) data from Arisaig (fig. 2). However, in many cases an inflation factor may not actually be needed—in figure 3C, the overlap between the mean, minimum, and maximum rarefaction curves of the calcitic and aragonitic sample fractions is quite striking. It would be quite a coincidence if the aragonitic rarefaction curves were higher before the loss of time averaging due to differential dissolution, only to lose exactly the right amount of diversity to equal the calcitic fractions. In any case, the use of the inflation factors makes this a conservative analysis.

Second, time averaging might influence the accuracy of these models if the intensity of time averaging changed through the Phanerozoic (Kowalewski and Bambach 2003), over-inflating the diversity of collections from geologic periods characterized by more time averaging. Many factors influence the intensity of time averaging; for example, Kidwell and Brenchley (1994, 1996) and Kidwell (1998) suggested an increase in time averaging because common Paleozoic taxa such as brachiopods have organic-rich shells presumed to disintegrate relatively rapidly as the organics decay, whereas most modern mollusks have organic-poor shells and very robust skeletons. However, Carroll et al. (2003) found that death assemblages of modern terebratulid brachiopods in Brazil were just as time averaged as modern bivalves. Also, Kowalewski and Flessa (1996) have noted that the preservation of organophosphatic lingulid brachiopods has decreased since the Paleozoic, probably because of increased bioturbation, implying that Paleozoic samples of such organic-rich shells are more time averaged than later. Thus, a secular trend in change in time averaging remains unproven, but our analyses include a broad range of scenarios that encompass the possible effects of a change in time averaging.

If we assume that calcitic Paleozoic faunas and Cenozoic mollusks are similarly time averaged (one possible interpretation of Carroll et al.'s [2003] work), then the inflation factor for aragonitic faunas in Paleozoic shell beds is at most 1.22 (it would be less if the aragonitic faunas are somewhat time averaged, as is likely). This is at the low end of the range we modeled (1.0–1.6). If Paleozoic faunas are less time averaged than Late Cenozoic ones, then

Paleozoic fossil assemblages should be less than 1.22 times as diverse as the living assemblages from which they formed. Thus, an aragonitic inflation factor above 1.22 is unlikely. In this case, the diversity of entire Paleozoic assemblages should be scaled upward by a factor no more than 1.22 to account for the lower amount of time averaging (on top of the aragonitic inflation factor). Since we have modeled aragonitic inflation factors greater than 1.22, the range of results we will show is large enough to accommodate both of these corrections. If, for some reason, the Paleozoic is more time averaged than the Late Cenozoic, then Paleozoic diversity values are already artifactually inflated and our analysis is biased against seeing a diversity increase.

In the runs of the model that make use of the aragonitic inflation factor, the estimated original diversity of the Paleozoic samples rises above that seen in the simpler version of the model (circles vs. diamonds in fig. 4). The aragonitic fractions now have steeper rarefaction curves than the calcitic fractions, destroying the symmetry seen when the aragonitic fractions were assumed to have the same diversity structure as the calcitic fractions. As the aragonitic inflation factor increases, so does the total possible diversity and the percentage of aragonitic specimens at which that diversity is achieved (about 60%–80%).

If no aragonitic inflation factor is needed in this analysis, then the maximum loss of diversity from Paleozoic communities was 22% at a sample size of 200. The preferred maximum value of the aragonite inflation factor is 1.2 because of Kidwell's (2002) meta-analytic results, in which case the total loss of diversity from local paleocommunities can be no more than 29% (fig. 4). This is our best upper estimate of diversity loss. If the aragonitic inflation factor is higher than expected, say 1.6, then the maximal average diversity loss could be as high as 40%. Even in this case, the original diversity of Paleozoic local paleocommunities still does not reach Late Cenozoic levels (fig. 4). In fact, in order to make Paleozoic assemblages equal the diversity of Late Cenozoic assemblages, the average aragonite inflation factor would have to achieve values not yet observed (2.0, whereas the greatest inflation factor yet observed is 1.6), and the original proportion of aragonitic specimens would commonly have to be about 70%–80%. We consider both of these conditions highly unlikely.

Bias 2: Latitude

If it is necessary to correct for the taphonomic bias of aragonite dissolution in Paleozoic assemblages,

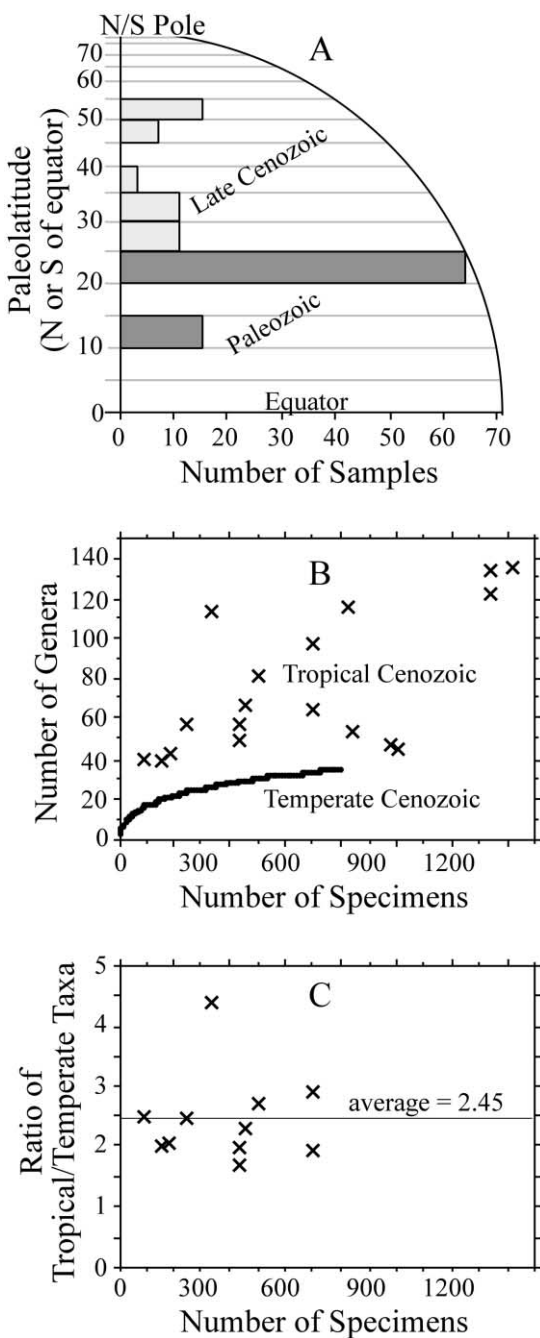


Figure 5. Latitudinal bias in comparing Paleozoic and Cenozoic samples. *A*, Paleolatitudes of Paleozoic (dark gray) and Late Cenozoic (light gray) samples. The Southern Hemisphere is reflected onto the Northern Hemisphere. *B*, Average rarefaction curve for the temperate Late Cenozoic samples (black curve) at the species level and the number of genera (x's) for tropical Late Cenozoic molluscan assemblages from the Panama Paleontological Project (Jackson et al. 1999). *C*, Ratio of tropical richness to average temperate richness at the same sampling intensity.

it is equally necessary to correct for geographic and environmental differences in the distribution of Paleozoic and Late Cenozoic samples. The diversity of many higher taxa increases from temperate to tropical climates in modern and fossil biotas (Fischer 1960; Roy et al. 1996, 1998; Crame 2001, 2002). Paleontological data (including the current data set) often overrepresent North America and Europe, which shifted from tropical latitudes in the Paleozoic to temperate latitudes in the Cenozoic (Ziegler et al. 1979; Scotese 1997). Comparing tropical Paleozoic biotas to temperate Cenozoic ones should bias against observing an increase in diversity (Allison and Briggs 1993; Jackson and Johnson 2001). This bias is apparent in our data set: the sampled Late Cenozoic faunas all lived between 28° and 55°N paleolatitude, whereas the Paleozoic faunas were confined to 10°–25°S paleolatitude (fig. 5A).

To correct for this bias, we could either adjust the Paleozoic data to estimate temperate Paleozoic alpha diversity, or we could adjust the Late Cenozoic data to estimate tropical Late Cenozoic alpha diversity. The former is difficult without better data on the strength of latitudinal diversity gradients in the Paleozoic, whereas the latter is straightforward given published data. Strictly speaking, the result is a comparison of alpha diversity between tropical environments of the Paleozoic and Late Cenozoic; a comparison of temperate samples might yield somewhat different quantitative results, although it would not negate or reverse our conclusions since temperate faunas in the Paleozoic were less diverse than tropical faunas, although the gradient may not have been as steep as in the Late Cenozoic (Crame 2001).

To test the effects of this latitudinal bias, we compared our temperate Late Cenozoic samples with published data on tropical molluscan assemblages studied by the Panama Paleontology Project (the Panama data included only mollusks, but the same is true of most of our temperate data). Jackson et al. (1999) listed the number of specimens and the number of taxa for a variety of Late Cenozoic (Miocene-Pleistocene) samples from the New World tropics; figure 5B compares these data to our Late Cenozoic data. Since Jackson et al. (1999) report results at the subgenus level, we ran the comparison with the temperate data tabulated at both the genus and species level, thus bracketing the subgenus level. The rarefaction curves of the temperate data were highly similar at the genus and species level; to be conservative, we show the results using species for the temperate data.

For samples with less than 800 specimens, the tropical samples average 2.45 times the diversity of

the temperate samples (fig. 5C). For larger numbers of specimens, this factor may even increase. Roy et al. (1996) found a similar pattern in the total bivalve genus richness along the modern eastern Pacific coast: the average diversity of 5°-wide bins doubles from about 300 genera between 25° and 55° latitude to about 600 genera between 10° and 25°. Thus, we estimate that the Late Cenozoic samples would have been 2–2.45 times as diverse had they been collected from tropical rather than temperate locales.

Bias 3: Environment

On the basis of paleocommunity compositions reported in the literature, Bambach (1977) found that species richness increased from stressed shoreline habitats to stable offshore settings throughout the Phanerozoic. Therefore, heterogeneous sampling among environmental zones through time may bias studies of alpha diversity. We tested for this possibility by classifying each sample on a five-category, onshore-offshore gradient: (*e1*) shoreline complex, (*e2*) nearshore shelf, (*e3*) open shelf, (*e4*) distal open shelf, and (*e5*) outer shelf margin. The environmental designations are those of the original authors or, in cases where environmental identification was not explicit, they are interpreted from the geological context of the strata collected. The shoreline complex includes estuarine, lagoonal, intertidal, and shoreface habitats. Nearshore shelf was assigned, when not specified, if a collection was clearly from a shallower, more nearshore setting than other, more open shelf collections from the same study. Distal open shelf was assigned, if not specified, if a collection was clearly from a deeper, more offshore or outer shelf habitat than other shelf collections from the same study. Outer shelf margin was assigned to collections identified as shelf margin or slope.

The Paleozoic and Late Cenozoic samples have obviously different environmental distributions (fig. 6A, 6B). The modal environment in the Paleozoic is the open shelf, and there is only one sample from the shoreline complex (fig. 6A); in contrast, the modal Late Cenozoic environment is the shoreline complex, and there are no outer shelf margin samples (fig. 6B). When the samples are rarefied to 100 or 200 specimens, alpha diversity in the Paleozoic stays rather constant from the nearshore shelf (*e2*) to the open shelf (*e3*), then increases further offshore (*e4–e5*; fig. 6C, 6E). At 100 and 200 specimens, Late Cenozoic alpha diversity increases from *e1* to *e2*, then remains constant or increases slightly through *e4* (fig. 6D, 6F).

What is the magnitude of the bias introduced by unequal sampling of the environmental zones in the two time intervals? In the average diversity values shown in table 1, each individual sample is weighted equally, so that each environmental zone is weighted by the number of samples assigned to it. Ideally, to eliminate any bias, one would like an equal number of samples in each environmental zone in each time interval. We can simulate this collection scheme by recalculating the average diversity of each time interval with each environmental zone weighted equally. Averaging the means of every environmental zone present in each time interval, the Late Cenozoic is 1.94 times as diverse as the Paleozoic at 100 specimens and 2.10 times as diverse at 200 specimens. This average is conservative because the Paleozoic data include samples from environmental zone *e5*, its highest diversity zone, whereas the Late Cenozoic average does not. Also, these figures include zone *e1* in the Paleozoic, even though there is only one data point. According to our Late Cenozoic data and the work of Bambach (1977), one would expect that faunas from the shoreline complex in the Paleozoic should be less diverse than more offshore faunas, so the one data point in *e1* may be high for the *e1* habitat. The ratios of Late Cenozoic to Paleozoic alpha diversity of 1.94 and 2.10 are slightly higher than those obtained for the raw data, for which the Late Cenozoic is 1.84 times as diverse as the Paleozoic at 100 specimens and 1.92 times as diverse at 200 specimens. The environmental distribution of the samples is biased slightly against seeing a diversity increase from the Paleozoic to Late Cenozoic, lowering the observed average diversity in the Late Cenozoic by 9% at 200 specimens.

This environmental bias may affect global studies of diversity change as well. Exposed Paleozoic rocks often represent shelf habitats, which are more easily preserved and more extensive than habitats in the shoreline complex, especially in intracratonic basins. Shoreline complex habitats exist only at the shoal margins of basins, so they are more subject to erosional loss during times of lowered sea level. In contrast, most exposed Late Cenozoic sediments represent onshore habitats because these sediments are all that is exposed of still flooded marine basins. (These onshore habitats, too, will be more subject to erosion in the future.)

Discussion

Cumulative Effects of Biases on Alpha Diversity. In the raw data shown in table 1, rarefied alpha diversity rose from the Paleozoic to Late Cenozoic

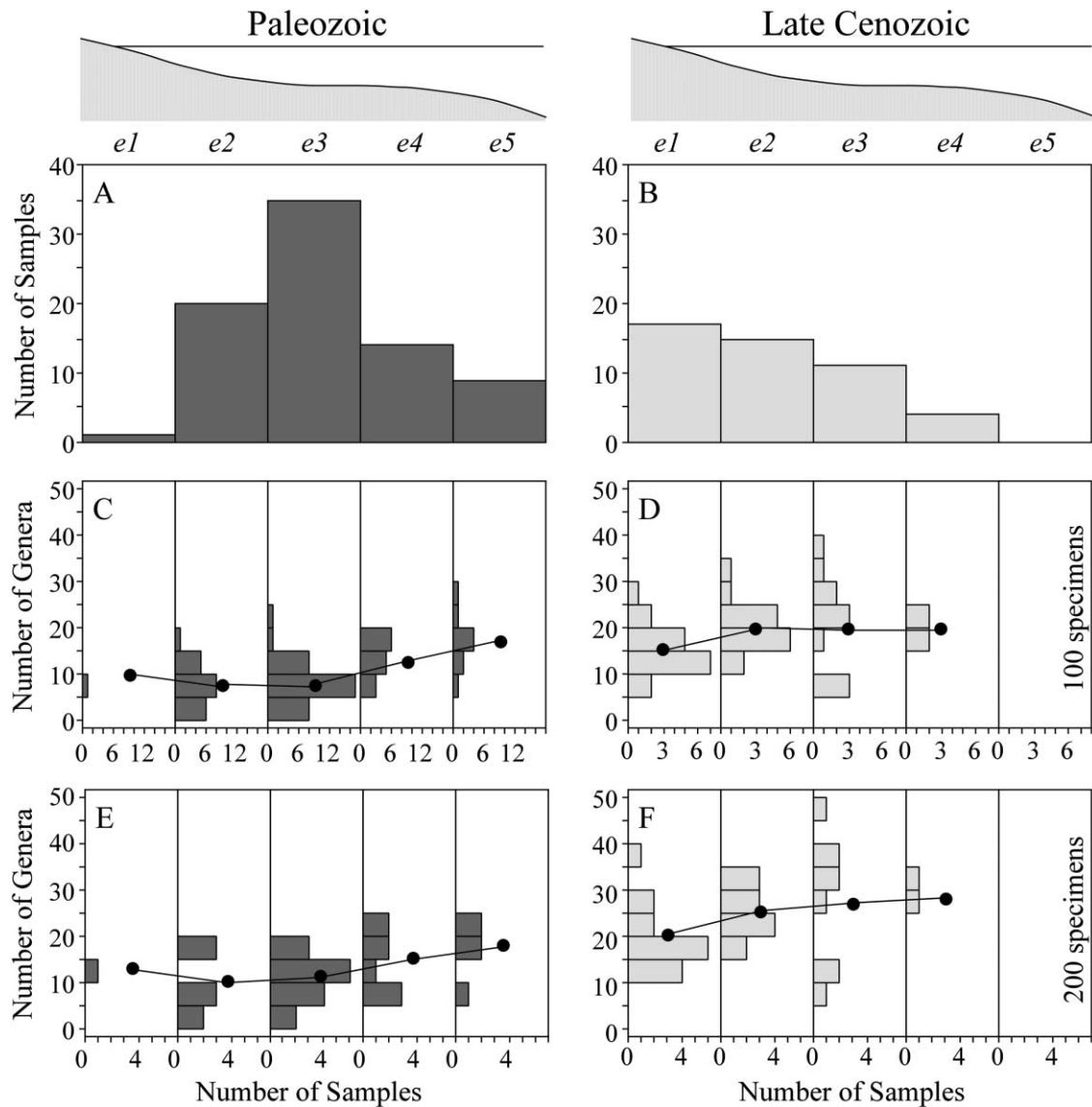


Figure 6. Environmental distributions of samples and sample diversity along an onshore-offshore transect. *A*, Environmental distribution of Paleozoic samples. *B*, Distribution of Late Cenozoic samples. *C*, *D*, Genus richness of Paleozoic (*C*) and Late Cenozoic (*D*) samples by environmental category, rarefied to 100 specimens. *E*, *F*, Genus richness of Paleozoic (*E*) and Late Cenozoic (*F*) samples by environmental category, rarefied to 200 specimens.

by a factor of about two. However, the analyses above show that this value is influenced by taphonomic, latitudinal, and environmental biases.

The exact magnitude of the aragonite dissolution bias on diversity cannot be gauged without knowing more about the aragonitic components of Paleozoic faunas. First, we do not know the original ratio of aragonitic to calcitic specimens in the studied assemblages, and second, we do not know the exact diversity structure of the aragonitic faunas (e.g., the shapes of their rarefaction

curves). Therefore, we modeled a range of plausible scenarios. To raise Paleozoic alpha diversity to levels found in the Late Cenozoic, one must assume that the average aragonitic sample fraction was twice as diverse as the average calcitic fraction, and aragonitic individuals must have made up 70%–80% of the original local paleocommunity. Experience with mollusk-rich Paleozoic assemblages demonstrates that the aragonitic sample fractions are not that diverse and that aragonitic specimens generally comprise only

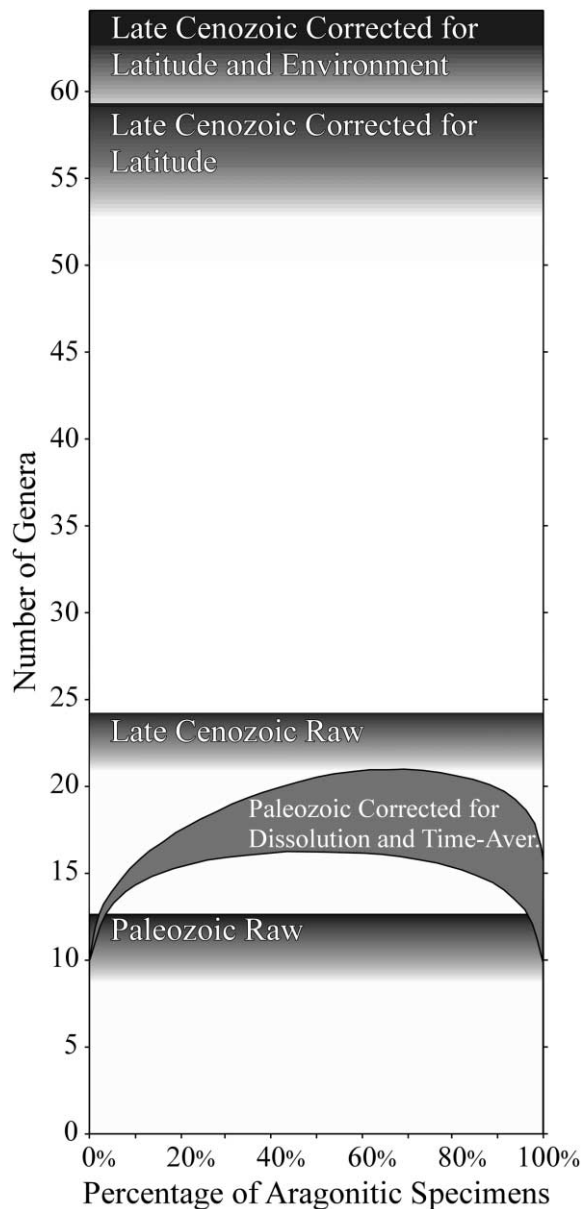


Figure 7. Paleozoic versus Late Cenozoic genus richness corrected for all biases considered. The shaded area (*Paleozoic Corrected for Dissolution and Time Averaging*) contains the results of figure 4 for reasonable estimates of the aragonitic inflation factor (1.0–1.6). The shading is for aesthetic reasons.

about one-third to one-half of the original local paleocommunity. With reasonable parameters, alpha diversity is only underestimated by 22%–40% (figs. 4, 7), with a preferred value of 29%.

Even if the taphonomic bias did account for the observed diversity difference between the raw Paleozoic and raw Late Cenozoic data (which it does

not), the Late Cenozoic data must be corrected for the other two biases for a proper comparison with the Paleozoic. In the raw data, Late Cenozoic alpha diversity is underestimated relative to Paleozoic alpha diversity because the Cenozoic data are from temperate settings whereas the Paleozoic data are tropical. Also, the difference in the environmental distribution of the samples from the two time intervals requires a further adjustment. After correcting for these two biases, Late Cenozoic paleocommunities are at least 3.0–3.7 times as diverse as Paleozoic ones (fig. 7).

In the end, the taphonomic, latitudinal, and environmental biases largely cancel out; by coincidence, our estimate of alpha diversity increase (3.0–3.7 times) is fairly close to the estimates of Bambach (1977) and Powell and Kowalewski (2002; 2.5 times) who made no corrections for these biases, though they recognized them.

Evenness and Alpha Diversity. When an assemblage is sampled, the number of taxa recovered is affected both by the total number of taxa in the assemblage and by the evenness of their relative abundances. Like Powell and Kowalewski (2002), we found an increase in evenness between the Paleozoic and Cenozoic (Bush and Bambach 2004). At greater sampling intensities than those attempted here, the standardized alpha diversity of Paleozoic paleocommunities could theoretically catch up to the standardized alpha diversity observed in the Late Cenozoic. However, this would require that rare species accumulate more slowly as sampling intensity increases in Late Cenozoic assemblages than in Paleozoic ones, and in our data, the Late Cenozoic rarefaction curves continue to rise more rapidly than the Paleozoic ones, even at 800 specimens (data to be published in Bush and Bambach 2004). Also, all observational data known to us indicate that Late Cenozoic and Recent faunas do not approach saturation, even when sampled at huge sample sizes (Williams 1964; Cobabe and Allmon 1994; Collins and Coates 1999; Daley and Kowalewski 2000; Bouchet et al. 2002). On the other hand, near-saturation of sampling in the Paleozoic has been observed in several instances (e.g., Bambach 1969 for Silurian bivalves; Tolmacheva et al. 2003 for Middle Ordovician brachiopods, ostracods, and conodonts). This suggests that Paleozoic alpha diversity is unlikely to “catch up” to Late Cenozoic alpha diversity at any practical sample size. In another article in preparation, we will address the evenness issue explicitly and link it to increases in ecospace use through the Phanerozoic (Bambach 1983, 1985).

Conclusions

The early dissolution of aragonitic shells distorts the fossil record, but some preservational windows, including silicification and composite mold preservation, ameliorate the bias. In their comparison of a silicified fauna with a nonsilicified fauna, Cherns and Wright (2000) estimated that aragonitic mollusks are underrepresented by a factor of 100–150 relative to brachiopods in the Silurian of Sweden. This value is questionable because Cherns and Wright did not compare the same paleocommunity type under different preservational regimes but compared samples from different paleocommunity types containing different taxa.

Modeling the effects of the preferential loss of aragonitic shells on rarefied diversity indicates that this bias could reduce the apparent diversity of Paleozoic assemblages by at most 22%–40%, with a best maximum estimate of 29%. Although it is possible to invent a scenario in which these assemblages lost half their original diversity, the necessary parameters for that level of diversity loss do not represent realistic average conditions.

Comparing temperate Late Cenozoic assemblages with tropical Paleozoic assemblages biases against finding an increase in diversity since the Paleozoic. The raw diversity of temperate Late Cenozoic assemblages must be more than doubled for an accurate comparison to tropical Paleozoic assemblages. Environmental biases underestimate the relative alpha diversity of the Late Cenozoic by 9%.

As a result of all three biases combined, Paleozoic alpha diversity is underestimated by no more than 22%–40%, and Late Cenozoic alpha diversity is un-

derestimated by more than half. After adjusting for all biases, average alpha diversity probably increased by a factor of 3.0–3.7 between the Middle Paleozoic and Late Cenozoic. This result supports the conclusions of Bambach (1977), which were used as support for the consensus model of Phanerozoic marine diversity (Sepkoski et al. 1981).

Coincidentally, taphonomic, latitudinal, and environmental biases approximately cancel out (although they may depress the relative diversity of the Late Cenozoic more), so earlier reports of changes in alpha diversity were of the correct magnitude.

ACKNOWLEDGMENTS

Alfred M. Ziegler was a pioneer in studying fossil assemblages as communities (e.g., Ziegler 1965). This article is dedicated to him on the occasion of his retirement from the faculty of the University of Chicago. In the data set used in this study, we include data from one of his best-known articles on paleocommunities (Ziegler et al. 1968) and from some of the collections he made for A. Boucot, his field camp mentor, from the Silurian section at Arisaig, Nova Scotia. We thank J. Parrish for inviting us to participate in the symposium held in honor of A. M. Ziegler and for spearheading the publication of articles from that event. Many thanks to S. M. Kidwell and M. Kowalewski for high quality reviews and to J. L. Payne for helpful comments. We especially thank A. M. Ziegler, whose careful and thoughtful approach to science has been a guiding approach to R. K. Bambach throughout his career. This is publication 25 of the Paleobiology Database Project.

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