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Chapter 18

The Geological History of Biodiversity

Michael Foote

At least for animals in the marine realm, a number of major features of biodiversity, measured as global genus or family richness, seem firmly established (Sepkoski 1981, 1997; Sepkoski et al. 1981; Raup and Sepkoski 1982; Bambach et al. 2004; Bambach 2006; Alroy et al. 2008):

1. Biodiversity has increased over the past half-billion years.
2. It has fluctuated markedly around its secular rise.
3. A number of drops in diversity are clearly associated with major mass extinction events, although others may be associated instead with reduced origination rates.
4. Superimposed on these secular patterns have been substantial changes in the faunal composition of the biosphere.

With the possible exception of the third point, all of these features were already known in Charles Darwin's day (Phillips 1860).

In attempting to narrow the history of biodiversity into a tractable scope, I will emphasize two topics that would probably have interested Darwin: (1) the imperfection of the geologic record and (2) the proposition that secular trends in biodiversity, at the largest scale, have been shaped by biotic interactions. I will focus on global taxonomic richness of readily fossilized marine invertebrates, which have the most extensively documented fossil record. Compared with other measures, such as morphological and ecological diversity, abundance, and evenness, richness is best understood dynamically, in relation to the underlying processes of origination and extinction.

The Imperfection of the Geological Record

Darwin (1859) devotes considerable space to the problem of geological and paleontological incompleteness, and he paints a picture that might make

a would-be paleontologist despair of ever hoping to document the evolution of life with data from the fossil record. One reasonable reading of this part of the text is not so much that Darwin felt he had solid evidence for the dismal state of the record, but rather that the spottiness of the record was required by natural selection, under the assumption that evolutionary change was insensibly gradual:

> ...*Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps, is the most obvious and gravest objection which can be urged against my theory. The explanation lies, as I believe, in the extreme imperfection of the geological record (Darwin 1859: 280).*

In addition to the paucity of intermediate forms, Darwin was troubled by the sudden appearance of major biologic groups early in the Phanerozoic geological record. Although taxonomic richness was not Darwin's main concern, an extremely spotty record would obviously hinder any attempt to document the history of richness.

As early as 1860, Darwin's pessimistic view of the quality of the geologic record had already been questioned. John Phillips, in a volume that documented secular trends in the composition of the global fauna over the course of the Phanerozoic, felt that the paleontological record was rather complete, provided that one looked in the right places. In direct response to Darwin (1859), Phillips wrote:

> *Surely this imperfection of the geological record is overrated. With the exceptions of the two great breaks at the close of the Palaeozoic and Mesozoic periods, the series of strata is nearly if not quite complete, the series of life almost equally so. Not indeed in one small tract or in one section; but on a comparison of different tracts and several sections. For example, the marine series of Devonian life cannot be found in the districts of Wales or Scotland, but must be collected in Devonshire, Bohemia, Russia and America. When so gathered it fills very nearly if not entirely the whole interval between the Upper Silurian and the Carboniferous Fauna. So in England the marine intermediaries of the Oolitic and Cretaceous ages are not given: but the Neocomian Strata supply the want. We have no Meiocene Strata in England, but their place is marked in France and America (Phillips 1860: 207).*

So, we have Darwin seeing a glass perhaps 99% empty and Phillips seeing it more like half full. Rather than trying to resolve the issue based on the data available 150 years ago, we will jump forward to the twenty-first century and consider some of the major advances that allow researchers to cope with paleontological incompleteness. First, geologists simply know more about the fossil record than they did then. Many more regions have been explored, for example, and the record of pre-Cambrian and Cambrian

strata has been documented in great detail. Second, geological and paleontological data have been archived in ways that enable systematic retrieval and analysis. Finally, paleontologists and stratigraphers have developed tools for quantifying the degree of completeness of the record and for circumventing many of the biasing effects of incompleteness.

Although Phillips was more optimistic than Darwin about the quality of the fossil record, he recognized that this record could not be read literally, and his *model* of Phanerozoic marine diversity (Figure 18.1) was based in part on his attempts to correct for variation in the spatial and temporal coverage of the record (Miller 2000). His starting point was Morris's (1854) tabulation of British fossil species. Because different periods of geologic time are more or less completely represented in Britain, Phillips (1860) divided the raw count of species by the preserved thickness of strata to obtain an estimate of the number of species per unit time. Although there were earlier

FIGURE 18.1 Phillips's Model of Species Diversity (Abscissa) over Phanerozoic Time (Ordinate) (From Phillips 1860.)

and arguably more comprehensive compilations of fossil diversity than the Morris–Phillips combination (Bronn 1849), Phillips's treatment stands out for its clear attempt to deal with the effect that the size of a paleontological sample has on preserved diversity as well as for its quantitative depiction of long-term changes in faunal composition (Phillips 1860: Figure 6). Rudwick (2008) also credits Phillips with recognizing the global, rather than local or regional, significance of his proposed divisions of geological time and with other advances in thinking about geological history.

All depictions of the history of diversity are models, like that of Phillips, each involving different data and, more importantly, having different assumptions about how to convert the raw data to an estimate of diversity. At the one extreme, simply tabulating the number of taxa from an interval of time involves at least three assumptions: (1) Sampling is reasonably complete, so that the observed first and last appearances of taxa are good proxies for their true times of origination and extinction. If this is not the case, then rapid changes in diversity will be poorly resolved and will appear to be spread out over a longer span of time than was in fact the case. (2) Sampling is nearly uniform over time, so that long-term trends and short-term fluctuations are not dominated by changes in the ability to sample fossil taxa. (3) The best-sampled taxa, generally the numerically abundant and well-skeletonized forms, are, in terms of total diversity, representative of the global fauna as a whole. Various attempts

to adjust for incomplete and variable sampling generally reject the first two assumptions in favor of alternatives, but they must generally accept the third, *faute de mieux.*

Biotic Interaction

As has been amply pointed out, Darwin (1859: 62) saw the "Struggle for Existence in a large and metaphorical sense," far broader than the idea that organisms compete directly with each other. The principle of natural selection led him to conclude that if environmental conditions are roughly constant, there should be a discernible net improvement over time, so that species alive today should be better suited than their extinct counterparts:

> There has been much discussion whether recent forms are more highly developed than ancient. I will not here enter on this subject, for naturalists have not as yet defined to each other's satisfaction what is meant by high and low forms. But in one particular sense the more recent forms must, on my theory, be higher than the more ancient; for each new species is formed by having had some advantage in the struggle for life over other and preceding forms. If under a nearly similar climate, the eocene inhabitants of one quarter of the world were put into competition with the existing inhabitants of the same or some other quarter, the eocene fauna or flora would certainly be beaten and exterminated; as would a secondary fauna by an eocene, and a palæozoic fauna by a secondary fauna. I do not doubt that this process of improvement has affected in a marked and sensible manner the organisation of the more recent and victorious forms of life, in comparison with the ancient and beaten forms; but I can see no way of testing this sort of progress (Darwin 1859: 336–337).

Darwin does not suggest that he has evidence of "this sort of progress," only that it is a logical corollary of the theory of natural selection.

The geologic record of biodiversity provides evidence that large-scale diversity fluctuations (i.e., at the global scale, over tens of millions of years, and involving many major clades) are shaped in part by biotic interaction. Rates of origination and net diversification are negatively correlated with diversity, and rates of extinction may be positively correlated. This diversity dependence is hard to make sense of without biotic interaction. I am not referring, for the most part, to changes in the composition of the biota (e.g., mammals replacing dinosaurs), for which the removal of incumbent competitors by extinction is often an important prerequisite (Jablonski 2008a), but rather to the total level of diversity itself, whose relationship with rates of diversification is consistent with a diffuse biotic interaction that is not strongly clade-specific. The subject of wholesale displacement of one clade by another is a vast one that cannot be treated adequately here (Benton 1987, 1996; Sepkoski 1996; Jablonski 2008b), although I will briefly discuss one particularly interesting example.

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Incomplete Sampling

Paleontologists have made great progress in coping with the incompleteness of the fossil record, as reviewed recently by Kidwell and Holland (2002). One of the most powerful approaches has been to predict the expected direction of sampling bias, relative to an opposite effect suggesting little or no bias. For example, Jablonski et al. (2006) documented a strong tendency for fossil bivalve genera to appear first in tropical versus extratropical latitudes. Because there are reasons to think that the tropics are more poorly sampled, Jablonski et al. concluded that the pattern of tropical first appearances is unlikely to result from sampling bias. Similar arguments can be made for the origin of major evolutionary novelties (i.e., orders of marine invertebrates) in the tropics (Jablonski 1993) and in nearshore versus offshore environments (Jablonski and Bottjer 1991). Wagner (1997) showed that morphological transitions decreased in magnitude during the evolutionary radiation of rostroconch mollusks in the early Paleozoic. Spuriously larger transitions between sister taxa would be expected if the earlier representatives were more poorly sampled, since there would be more missing intermediates. But, Wagner was able to show that the earlier forms were in fact better sampled, and he therefore argued that the observed trend was unlikely to reflect sampling bias. Ruta et al. (2006) made a similar case regarding a temporal decline in the size of evolutionary transitions in early tetrapods. Peters (2006) showed that global origination and extinction rates of marine invertebrate genera within time intervals do not correlate well with the durations of stratigraphic gaps flanking these intervals. Because there should be a strong correlation if peaks in origination and extinction were artifacts of gaps in the record (Holland 1995), Peters reasoned that the patterns of origination and extinction were unlikely to be spurious.

Another general approach to assessing whether observed patterns may result from incomplete sampling is the use of *taphonomic control taxa*. If members of a taxon of interest are absent from a set of strata, whereas members of another taxon with similar environmental preferences and preservational properties are present, then the lack of the focal taxon may tentatively be interpreted as a genuine absence. In a phylogenetic analysis that combined morphological character data with information on stratigraphic occurrence, Bodenbender and Fisher (2001) used the presence of stalked crinoid echinoderms as evidence that ecologically similar blastoid echinoderms could have been preserved, if they had been present. Postulated evolutionary trees were regarded as relatively unparsimonious if they require the absence of blastoids in strata where they should have been found if they had in fact existed.

Methods have been developed recently that use explicit models of incomplete sampling, not just to predict the likely consequences of sampling, but also to obtain quantitative estimates of parameters, such as rates of

origination and extinction, which are important to an understanding of the dynamics of diversification. For example, Foote and Raup (1996) showed that, if sampling probability and extinction rate are uniform among species, then the frequency distribution of observed stratigraphic ranges can be used to develop a joint estimate of the sampling probability and average extinction rate (for refinements, see Solow and Smith 1997 and Foote 1997). They used this approach to argue that the shorter mean duration of mammal species compared with bivalve species (a classic comparison that goes back to Simpson 1944) is real, not an artifact of less complete sampling of mammals. Wagner (1997) also used this approach in the rostroconch example previously cited. Sampling models have been used to place confidence limits on the times of first and last appearance of individual taxa, which must necessarily be later and earlier, respectively, than their true times of origination and extinction. These models can either assume uniform sampling (Strauss and Sadler 1989; Marshall 1990) or can take empirically calibrated variation in sampling into account (Marshall 1997; Holland 2003). Such models have been applied, for example, to assess the likelihood that the disappearance of certain taxa is an artifact of reduced sampling of their preferred habitat (Holland 2003) and to determine whether gradual patterns of last appearance are consistent with a truly sudden extinction event (Marshall and Ward 1996).

Relaxing the assumption that rates of origination, extinction, and sampling are constant over time, Connolly and Miller (2001) and Foote (2001, 2003) considered the expected probability distribution of taxonomic first and last appearances resulting from a time series of these rates. They then used inverse methods, such as maximum-likelihood, to estimate rates from the observed first and last appearances of marine animal genera. Finally, a number of methods of sampling standardization have been developed, wherein an attempt is made to compensate for temporal variation in the completeness of the fossil record by subsampling a comparable amount of data from each time interval (e.g., Raup 1975; Miller and Foote 1996; Alroy et al. 2001, 2008; Bush et al. 2004). Here, the inverse procedure of Foote (2003) will be combined with sampling standardization to estimate temporal patterns of diversity, origination, and extinction.

Biotic Interaction

The role of biotic interactions in macroevolution has been reviewed recently by Jablonski (2008b), and I will not repeat his efforts. I will instead focus on some new analyses and two exemplary case studies that address the idea that biotic interaction may have influenced long-term changes in global biodiversity. The case for biotic interaction at this large scale derives mainly from the pioneering work of Sepkoski (1978, 1979, 1984, 1991, 1996; Miller and Sepkoski 1988), who extended population biology models, including

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In Sepkoski's extension of demographic models, species or higher taxa take the place of individuals; rates of taxonomic origination and extinction take the place of birth and death rates; and diversity dependence of taxonomic rates takes the place of density dependence of birth and death rates. Sepkoski often invoked the coupled logistic model, in which there are two or more phases with different parameters, namely, initial origination and extinction rates, strengths of diversity dependence of these rates, and carrying capacities (i.e., fixed, global diversity equilibria). In the model, the diversification rate of each phase at any point in time depends on its parameters as well as the total diversity of all phases. This particular model has been criticized for the fit between model and data, discrepancies between genus- and family-level patterns, and difficulty imagining why the global biota should have a fixed carrying capacity (Benton 1995; Courtillot and Gaudemer 1996; Benton and Emerson 2007; Erwin 2007, 2008; Stanley 2007, 2008). However, the general question of diversity dependent diversification—one of the principal *prima facie* lines of evidence for biotic interaction (Sepkoski 1996; Jablonski and Sepkoski 1996)—should be kept separate from the particular model of diversity dependence. Moreover, although Sepkoski argued that empirical diversity patterns were well described by the coupled logistic model, he arguably saw this model largely as a heuristic tool. Whether or not Sepkoski's particular model holds, there is no denying that he prompted paleobiologists to think about diversification in a new way, and 25 years after he presented a three-phase coupled model, his work is still the starting point for virtually all attempts to model global biodiversity over the Phanerozoic.

Not only does one need to separate the question of diversity dependence from the coupled logistic model, but it also is necessary to separate diversity dependence from the idea that there is an invariant equilibrial diversity—a fixed carrying capacity either for the biota as a whole or for some subset of it (Kitchell and Carr 1985; Benton and Emerson 2007; Erwin 2007). One reasonable interpretation of the results presented here is that the biota tracks a carrying capacity but that this capacity varies considerably over time.
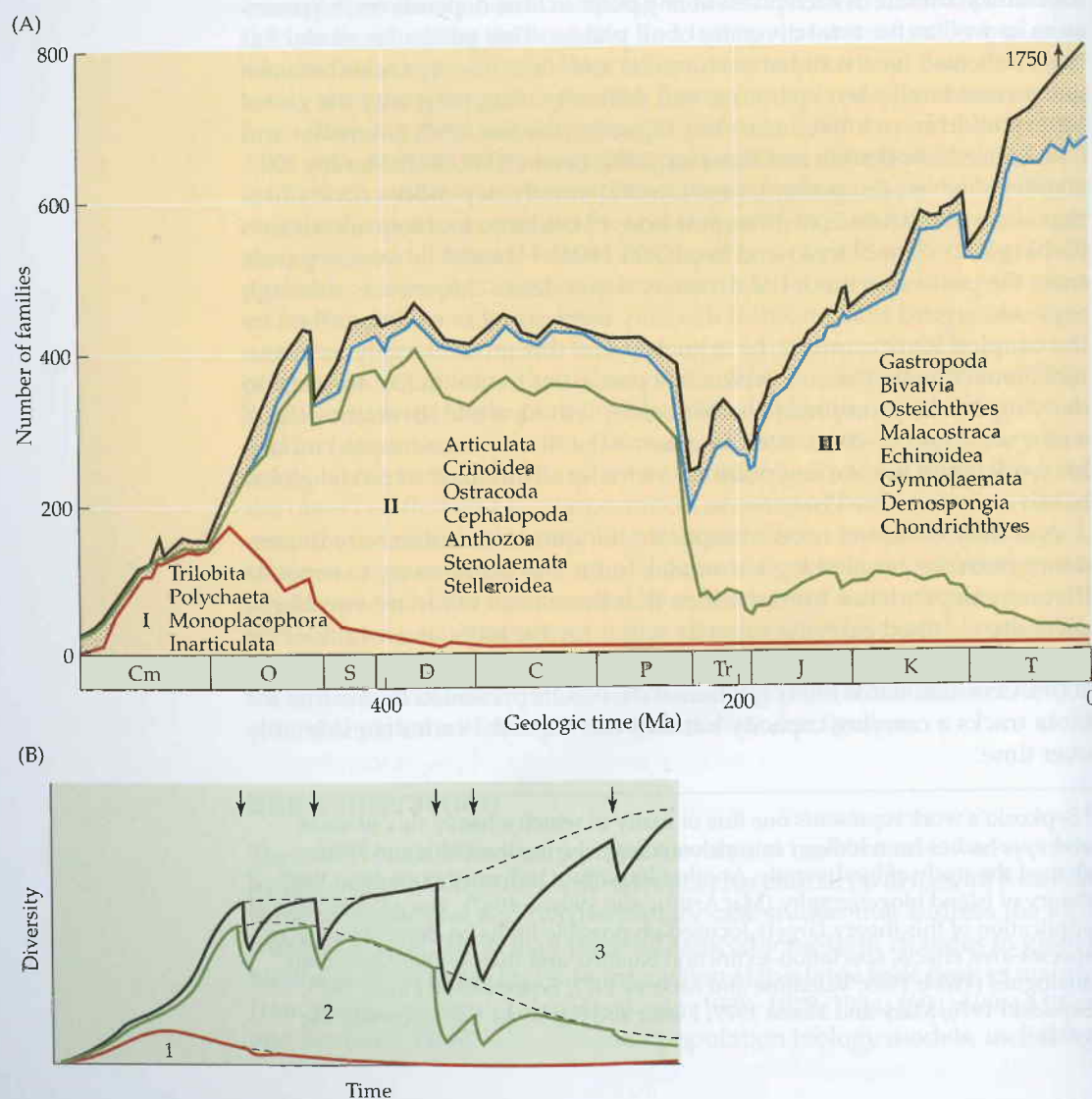
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[1] Sepkoski's work represents one line of many in which a heavy flux of ideas and approaches from biology into paleontology during the 1960s and 1970s shaped the study of biodiversity. Another important influence came from the theory of island biogeography (MacArthur and Wilson 1967). The paleobiological application of this theory largely focused on possible limits on diversity, such as species-area effects, speciation–extinction balance, and their higher-taxonomic analogues (Webb 1969; Valentine and Moores 1972; Schopf 1974; Flessa 1975; Sepkoski 1976; Mark and Flessa 1977; Flessa and Sepkoski 1978; Rosenzweig 1995).

Overview of Previous Work

History of Diversity

Figure 18.2A shows Sepkoski's classic depiction of family-level diversity of marine animals, along with the principal groups that contribute to his statistically delimited Cambrian, Paleozoic, and Modern evolutionary faunas (Sepkoski 1981), and Figure 18.2B illustrates the three-phase coupled logistic model that he used to represent this history of diversity (Sepkoski 1984). In this model, whose parameters are derived from the observed

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histories of origination, extinction, and diversity of the three evolutionary faunas, there are externally imposed perturbations corresponding to mass extinctions, but the ultimate fate of the three phases, at least in terms of numbers of taxa, is the same with or without such perturbations, as shown by the solid and dotted lines.

Figure 18.3 shows genus diversity over the Phanerozoic, based on the times of first and last appearance of about 31,000 marine animal genera from Sepkoski's (2002) compendium. With even a quick glance at this graph, it is not surprising that a number of workers (Benton 1995; Benton and Emerson 2007; Stanley 2007) have suggested long-term exponential growth in diversity as a better model than simple (Courtillot and Gaudemer 1996) or coupled (Sepkoski 1984) logistic growth. But, much of the apparent growth in diversity is concentrated in the last 10% or so of the Phanerozoic, and this increase may be exaggerated by an increase in the quality of sampling (Raup 1972, 1976; Smith 2001; Peters and Foote 2001) and by the fact that the presence of still-living taxa can be indirectly inferred for longer spans of time than that of extinct taxa, the "Pull of the Recent" (Raup 1979; but see Jablonski et al. 2003).

Sampling issues can be partly circumvented with comprehensive data that include not just the times of first and last appearance of each taxon, but also the intervening occurrences in the stratigraphic record. Miller developed a pioneering database for Ordovician marine invertebrates that compiled thousands of fossil assemblages from around the world, along with their geologic age and various contextual data, such as their paleoenvironment (Miller and Mao 1995; Miller 1997). The database enabled him to ask the question, how would a global diversity trajectory appear if the same amount of data were sampled from each time interval? The result (Miller and Foote 1996) was striking.[2] Whereas the raw data from Sepkoski suggest a rather steady increase in diversity throughout much of the Ordovician

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[2] Since I am a co-author of that paper, I should make it clear that my contribution was minor and that the conception of the project and the analyses of taxonomic diversity were entirely Miller's work.

◄ **FIGURE 18.2 Sepkoski's Early Representation of Marine Diversity** (A) Number of marine animal families over geologic time (Ma, millions of years ago). The taxonomic names within the three fields are the major groups that contribute to the three evolutionary faunas that Sepkoski delimited statistically. The stippled field represents families not attributed to any of these faunas, and the arrow points to present-day diversity. (Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary.) (B) Coupled logistic model based on data in (A), with perturbations corresponding to major mass extinctions. Solid and dashed lines indicate diversity trajectories with and without mass extinctions. (A from Sepkoski 1981; B from Sepkoski 1984.)
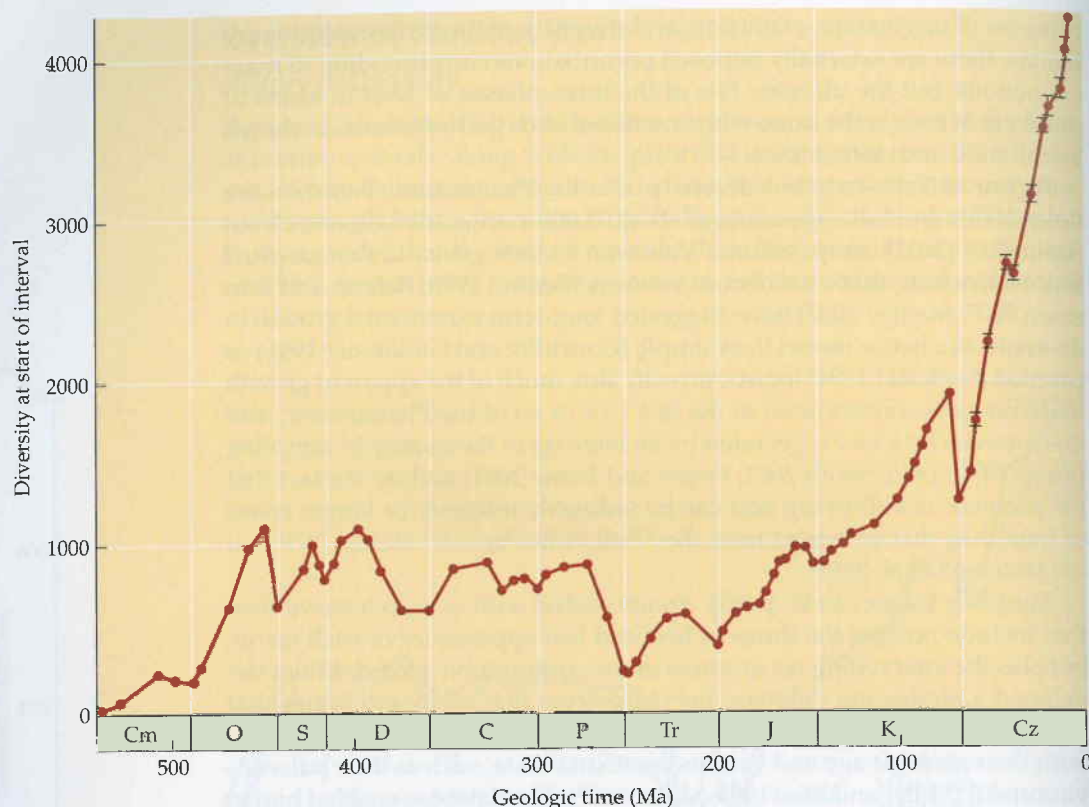
FIGURE 18.3 Diversity of Marine Animal Genera Diversity is plotted as the number of genera known to be extant at the start of each stratigraphic stage. Vertical error bars show ± one standard error, based on bootstrap resampling of the stratigraphic ranges of genera. (Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Cz, Cenozoic.) (Based on data in Sepkoski 2002.)

(see Figure 18.3), the "sampling-standardized" diversity trajectory suggested that diversity increased through the middle Ordovician and then leveled off. The obvious question arose: what would Phanerozoic diversity look like if one could do for each time period what Miller had done for the Ordovician? The quest to answer this was in large part responsible for the effort that ultimately led to the Paleobiology Database (http://paleodb.org), a digital archive of the published paleontological record, coupled with diverse analytical tools—effectively a GenBank for paleontology. Although methods of sampling standardization have evolved beyond Miller's initial efforts (Alroy et al. 2001, 2008; Bush et al. 2004; Alroy 2009), his work was seminal.

Dynamics of Diversification

If we are to understand the dynamics of diversification and not just describe its temporal trajectory, it is essential to relate diversity to its underlying evolutionary rates (Sepkoski 1978, 1984; Levinton 1979; Carr and Kitchell 1980; Stanley et al. 1981; Benton 1995; Foote 2000a,b, 2006; Benton and Emerson 2007; Alroy 2008). Some previous approaches to testing for diversity-dependent dynamics are potentially problematic. For example, Stanley (2007: Figure 11) compared average standing diversity in each time interval with the net diversification rate in the same interval. He did not find a significant negative correlation, and therefore concluded that diversity dependence was weak at best. But average diversity and net diversification rate are not logically independent, and their direction of forced dependence will lead, all else being equal, to a positive correlation between diversity and diversification rate, potentially obscuring any true negative correlation that may exist. Alroy (2008) avoided this problem by comparing total diversity in one time interval with rates of origination and extinction in the following interval, and he found a significant positive correlation between diversity and extinction rate. Total diversity in an interval may not be the most relevant figure, however, since much of the diversity generated could become extinct before the following time interval. I therefore suggest here a slight modification of Alroy's approach, namely to compare standing diversity at the start of a time interval with taxonomic rates in that interval. I also use finer temporal resolution than Alroy; average interval lengths are roughly 7 rather than 11 million years. Despite this and other analytical variations described in the following section, I follow the spirit of Alroy's (2008) analysis.

Materials, Methods, and Results

Data for the new results presented here were downloaded from the Paleobiology Database. Details of the download and vetting of data are described in Miller and Foote (2009). What matters for the present discussion is that the data are organized into *collections*, which are lists of co-occurring taxa with contextual information, such as geologic age. The taxonomic level used here is that of the genus, and the presence of a genus in a collection, irrespective of whether it is represented by one or more species, is referred to as an *occurrence*. Given such data, there are many ways to subsample in an effort to even out the temporal variation in the size of the sample (Alroy et al. 2001, 2008; Bush et al. 2004). I have opted for a simple approach known as by-list, *occurrence-weighted* (OW) subsampling (Alroy et al. 2001). In this approach, the basic unit of sampling is the collection, and collections are resampled at random, without replacement, until a given quota of occurrences is obtained for each time interval. This procedure is repeated a number of times (here, 100) and the results are averaged.
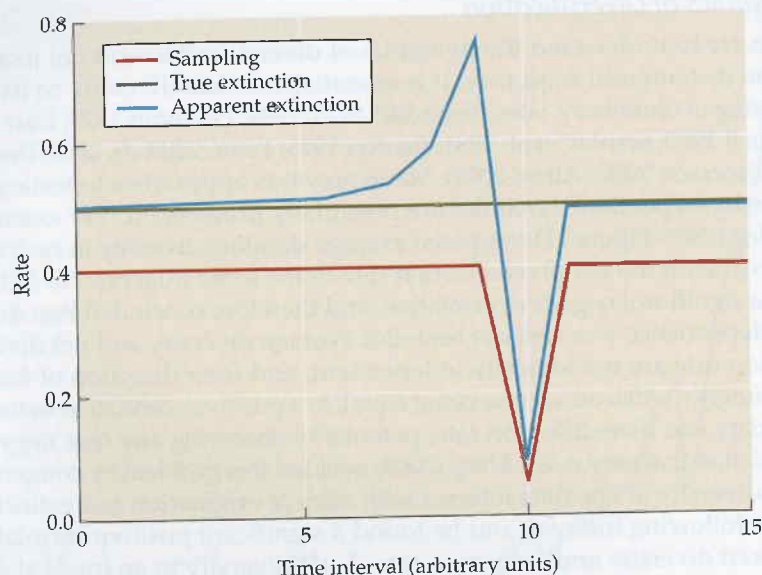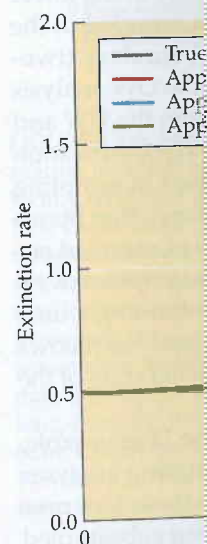
FIGURE 18.4 Model Showing the Per-Taxon Rate of Sampling, True Extinction, and Apparent Extinction A short-lived deficit in sampling in one time interval leads to a spuriously low extinction rate in that interval and spuriously high rates in the intervals leading up to it. Origination rate is affected similarly, with the effect propagating forward in time. (Based on equations in Foote 2000a.)

For each random subsample of the data, the temporal ranges of genera are recorded. The temporal ranges are used to tabulate a matrix **X**, in which the quantity X_{ij} is the number of sampled genera with first appearance in interval i and last appearance in interval j. Any genus that is sampled at least once before a given time interval and at least once during or after that time interval is credited as extant at the beginning of the interval (Foote 2000a); this count is designated X_b.

Incomplete sampling affects perceived rates of taxonomic origination and extinction as well as standing diversity, regardless of whether sampling is variable or constant. For example, suppose that true extinction rates were constant and there were a dearth of sampling in one time interval (Figure 18.4). Then many of the genera that would have made a last appearance in this interval, if sampling had been constant, will have last appearances in one of the previous time intervals. As a result, apparent extinction rate will be spuriously low in the interval in question and spuriously high in the previous intervals, with the effect decaying exponentially backward in time. If, by contrast, the interval in question is marked by better than average sampling, that interval will show spuriously high extinction and the preceding intervals will show spuriously low extinction. In the case of origination, the effect of incomplete sampling propagates forward in time.

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Even if sampling is constant, a true excursion in origination or extinction rate will be smeared out in time because not all of the excess first or last appearances will be captured in the interval of time in which the rate excursion occurs (Signor and Lipps 1982; Foote 2000a) (Figure 18.5). This smearing out of true rates is potentially quite important in assessing diversity dynamics. If, for example, a large decrease in diversity is quickly followed by an increase in the rate of origination, there may be a spurious delay before the acceleration in origination is seen in the fossil record (Foote 2000a, 2003; Lu et al. 2006). This fact may contribute to the apparent lag between extinction and biotic recovery on geologic timescales (Hallam 1991; Erwin 1998, 2001; Sepkoski 1998; Kirchner and Weil 2000).

The effects of incomplete and variable sampling shown schematically in Figures 18.4 and 18.5 can be modeled with some basic assumptions, namely that all taxa extant during an interval of time are characterized by the same rates of origination, extinction, and sampling in that interval, although these rates may vary from one interval to the next (Foote 2003). This model leads to a set of equations relating true rates to expected probabilities P_{ij} that a randomly chosen taxon will have an observed first appearance in interval i and last appearance in interval j (Foote 2003). Given the correspondence between model parameters and probabilities, a likelihood function can be
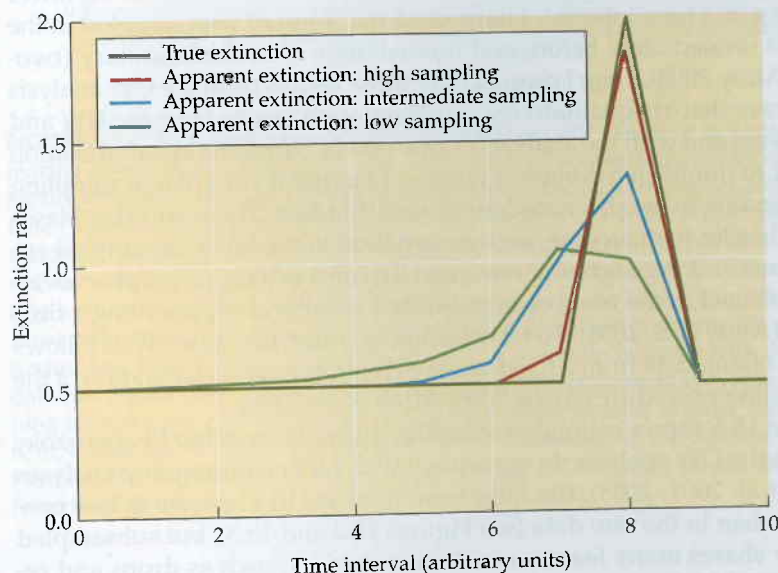
FIGURE 18.5 Model Showing the Effect of Incomplete Sampling on a True Increase in Extinction Rate The true extinction excursion is smeared backward in time, and lower average sampling rates lead to greater smearing. Origination rate is affected similarly, with the effect propagating forward in time. (Based on equations in Foote 2000a; see Signor and Lipps 1982.)

developed that incorporates these probabilities and the observed counts X_{ij}. This function is maximized numerically to obtain the best fitting set of origination, extinction, and sampling rates per interval.

Because the random subsampling of data includes multiple occurrences of genera within their stratigraphic ranges, these occurrences can be used to estimate the sampling probabilities for each time interval. The number of genera inferred to be extant during a time interval is the number sampled at least once before that interval and at least once afterwards. The proportion of these that are also sampled within the interval gives an estimate of the sampling probability for that interval (Paul 1982; Foote and Raup 1996). In the analyses presented, the numerical optimization is constrained to follow these sampling probabilities, hence only the origination and extinction rates are estimated by the inverse procedure. The model used here assumes that originations are clustered at the beginning of each time interval and that extinctions are clustered near the end, rather than being spread throughout the interval. This assumption is supported by previous analysis of data on Phanerozoic marine animals (Foote 2005; cf. Alroy 2008). All rates are converted to instantaneous per-capita rates, per time interval (Foote 2000a, 2003).
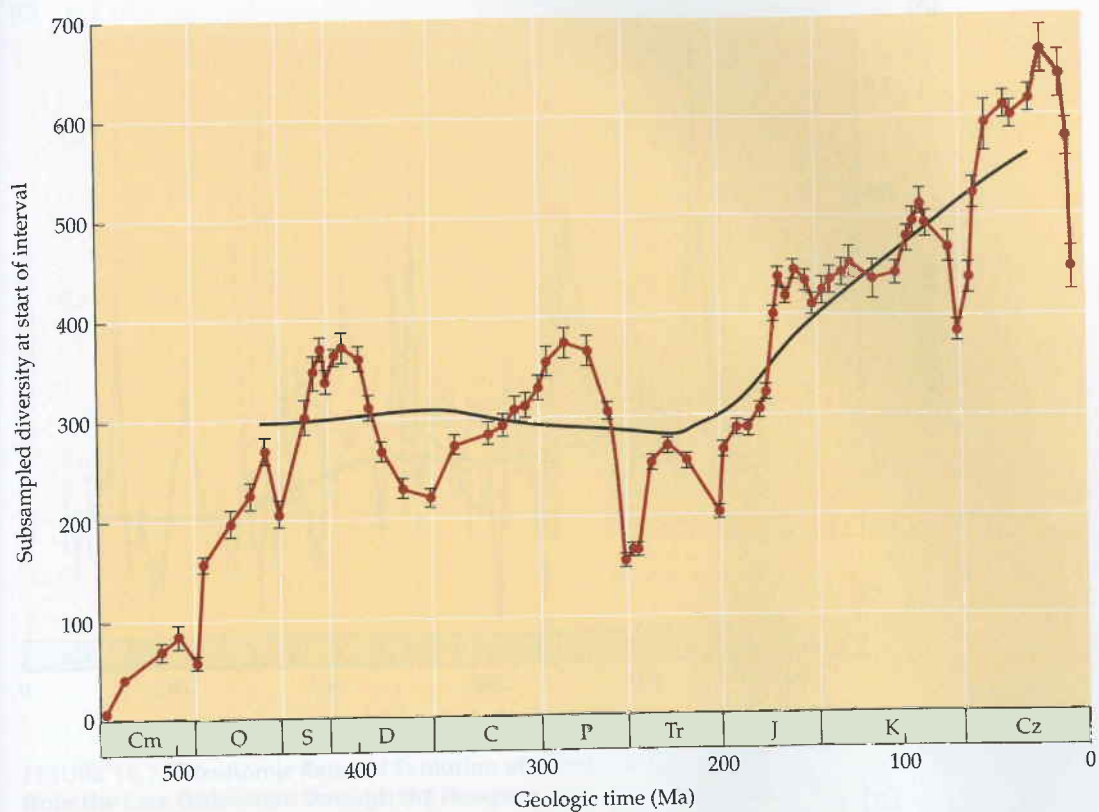
In addition to the OW method of subsampling, I have analyzed data using the *lists-unweighted* method (UW; Alroy et al. 2001) and the *shareholder-quorum* method (SQ; Alroy 2009). In addition to total diversity at the lower boundary of a time interval, I have used the count of taxa sampled in the intervals immediately before and immediately after the boundary (two-timers; Alroy 2008). Here I present only those results from the OW analysis of total taxa that are qualitatively consistent with results from the UW and SQ analyses and with the analysis of two-timers. Sampling standardization is meant to diminish the biasing effects of temporal variation in sampling corresponding to the sheer amount of available data. There are other biases that are harder to overcome, such as variation in the range of sampled environments and in geographic coverage. To some extent, geographic coverage is reflected in the number of published references representing a time interval (Alroy et al. 2008). To take this into account, the SQ analysis follows Alroy in taking data from a fixed quota of references at each iteration of the subsampling procedure (Alroy 2008; Alroy et al. 2008).

Figure 18.6 shows estimated standing diversity over the Phanerozoic, based on the OW analysis. In agreement with other subsampling analyses (Alroy et al. 2001, 2008), the long-term increase in diversity is less pronounced than in the raw data (see Figures 18.2 and 18.3), but subsampled diversity shares many features with the raw data, such as drops and rebounds surrounding major extinction events. To minimize possible edge effects (Foote 2000a, 2003) and the effects of sparse Cambrian data, I will focus on the stretch of time between the middle Ordovician Period (Caradoc Epoch, about 460 million years ago) and the Paleogene Period (Oligocene

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FIGURE 18.6 Sampling-Standardized Genus Diversity Analysis is limited to marine invertebrates. The heavy line in this and subsequent figures shows a locally weighted least squares regression through the focal timespan, from the Late Ordovician through the Paleogene. The method of by-list, occurrence-weighted sampling was used, with a quota of 1012 occurrences per time interval; this quota can be satisfied by all but two stages within the focal timespan (the Induan in the Early Triassic and the Coniacian in the Late Cretaceous). Error bars show ± one standard error (standard deviation of the results of 100 resampling trials). This model of diversity shares certain features with the raw data (see Figure 18.3), such as decreases at most major extinction events and a long-term secular rise, but the increase over the Phanerozoic is more subdued. (Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Cz, Cenozoic.) (Based on data from the Paleobiology Database, http://paleodb.org.)

Epoch, about 23 million years ago). Because the time series of diversity and taxonomic rates show temporal trends, it is important to detrend the data if the time series are to be compared to each other (Alroy 2008). Detrending is accomplished by fitting a locally weighted regression (LOWESS), with
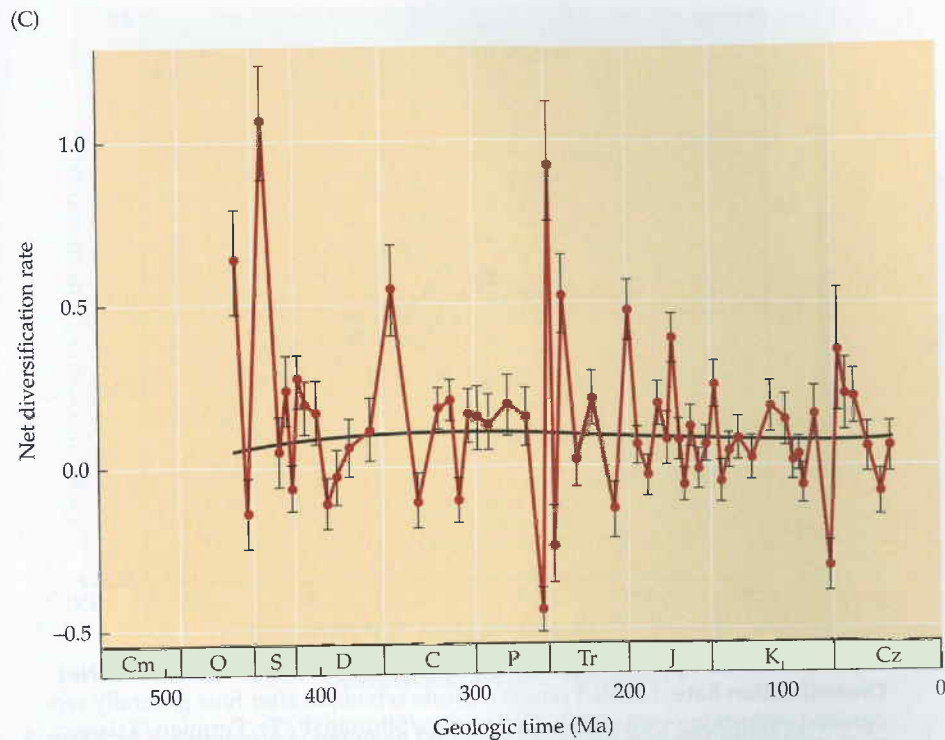
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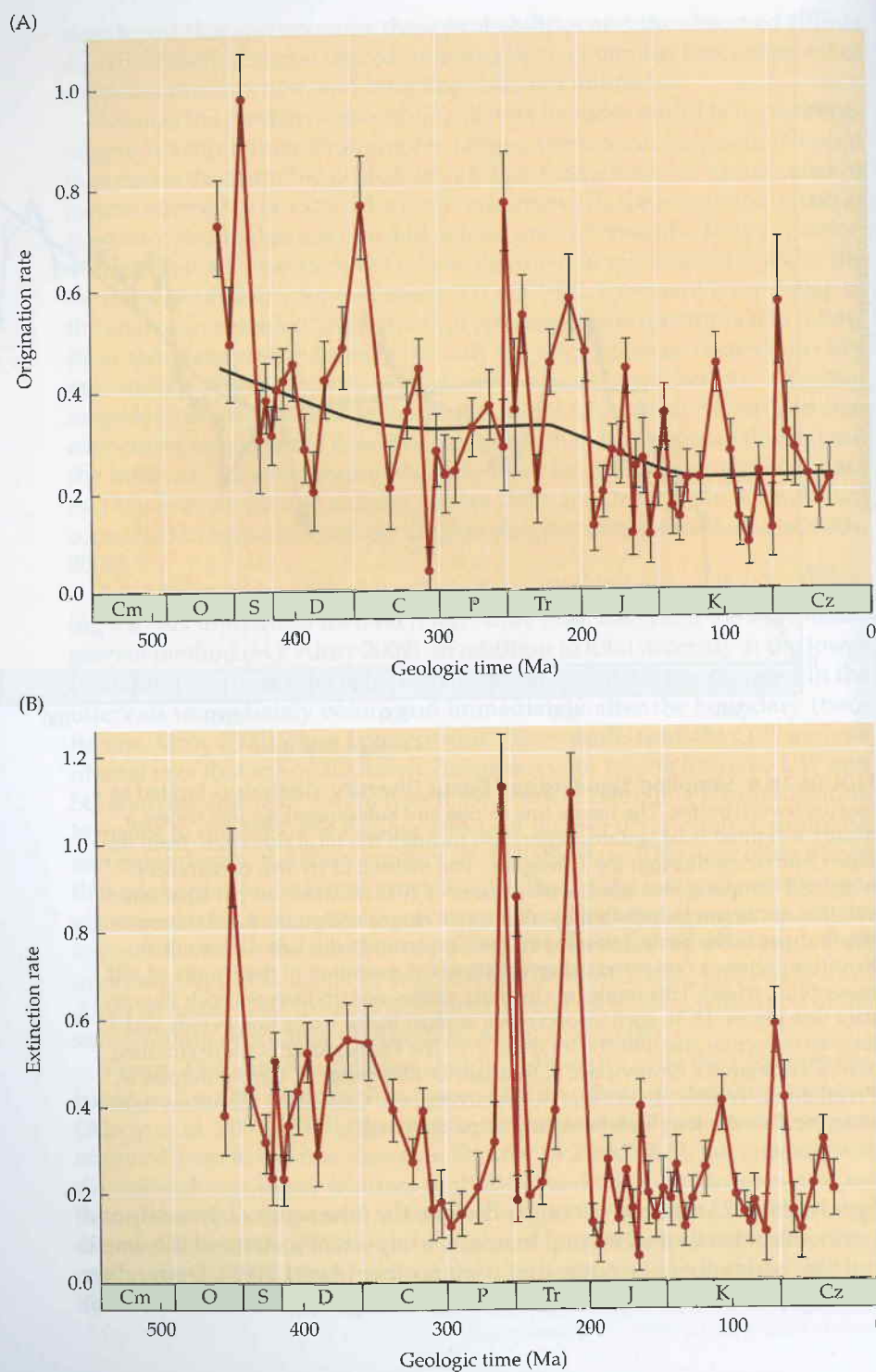
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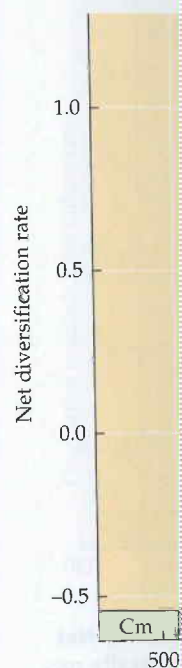
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FIGURE 18.7 **Taxonomic Rates of Evolution of Marine Invertebrate Genera from the Late Ordovician through the Neogene** (A) Origination. (B) Extinction. (C) Net diversification. (See Figure 18.6 for description of heavy lines and error bars.) (Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Cz, Cenozoic.)

a smoothing span of 50% of the data points, and analyzing the residuals. Figure 18.7A–C presents the estimated rates of origination, extinction, and net diversification. The black lines in Figures 18.6 and 18.7A–C show the LOWESS regression of each time-series against geologic time. Partly because of the diversity measure used here (Alroy et al. 2008), the time series of diversity is significantly autocorrelated, even if just the residuals from the regression are considered (Spearman rank-order correlation between successive diversity residuals: $r_s = 0.77$, $p < 0.001$). Therefore, I will report the correlations between the first differences in residuals of diversity and taxonomic rates. Results are qualitatively consistent if the raw residuals, rather than their first differences, are analyzed.

The residuals in diversity at the start of each time interval are negatively correlated with the residuals in net diversification rate within the interval (Figure 18.8; Spearman rank-order correlation $r_s = -0.53$, $p < 0.001$), and this correlation holds even if the intervals following the five major mass
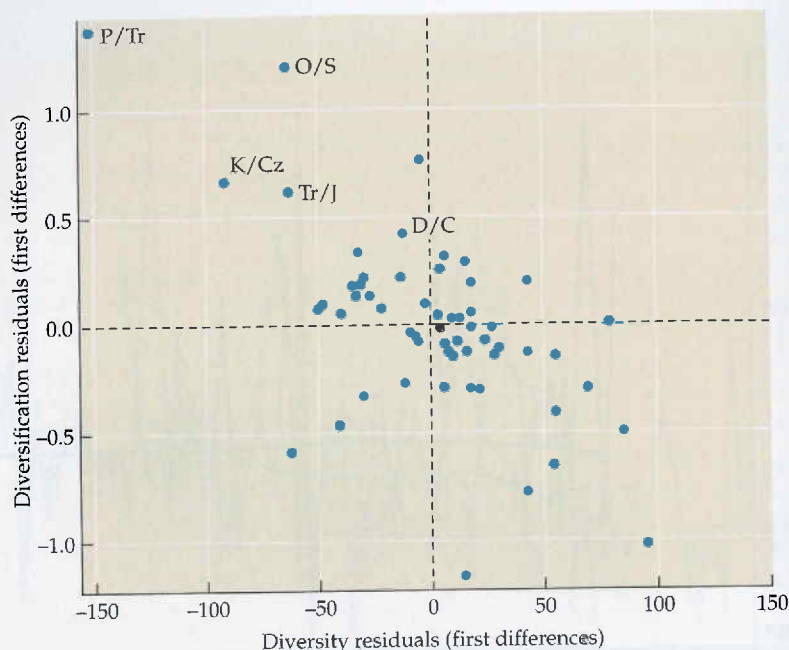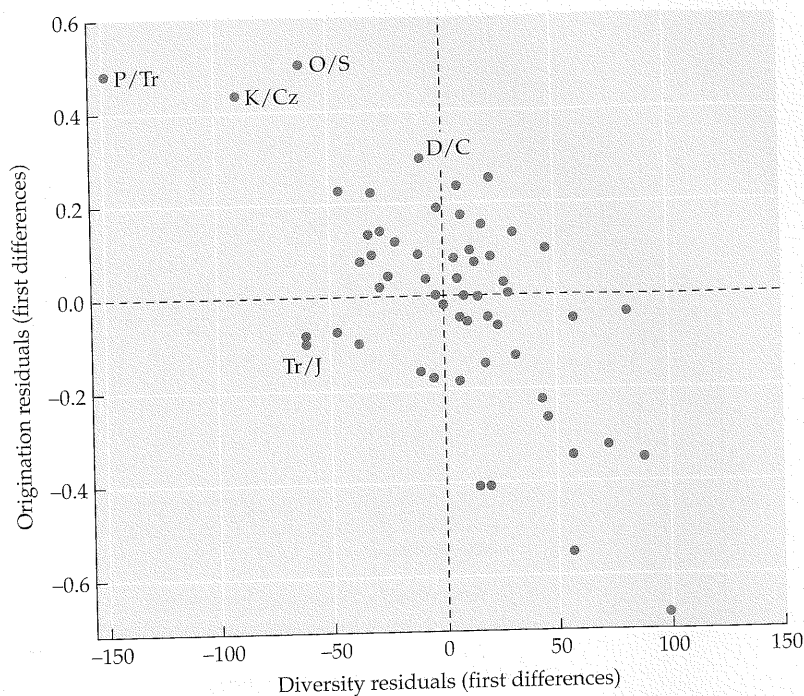
FIGURE 18.8 Comparison between Diversity Residuals and Residuals of Net Diversification Rate Labeled points indicate rebounds after four generally recognized extinction events (O/S, Ordovician/Silurian; P/Tr, Permian/Triassic; Tr/J, Triassic/Jurassic; K/Cz, Cretaceous/Cenozoic) and one additional event (D/C, Devonian/Carboniferous). Extinction rate is elevated in the final two stages of the Devonian: the Frasnian and the Famennian (Bambach 2006; Foote 2007), and the event is generally referred to as the Frasnian–Famennian extinction. For purposes of this paper, the Famennian extinction rate is taken to represent a single Late Devonian event. This usage agrees with some analyses (Foote 2007) that suggest a substantially higher extinction rate in the Famennian than in the preceding stage. Diversification rate is significantly and negatively correlated with diversity whether or not these five recovery intervals are included.

extinction episodes of the Phanerozoic are omitted ($r_s = -0.36$, $p < 0.01$). If the negative and positive diversity residuals are analyzed separately, there is still a pronounced negative correlation for the negative residuals ($r_s = -0.62$, $p < 0.001$), but not for the positive residuals ($r_s = -0.13$, $p = 0.49$). These results suggest that lower than average diversity enhances diversification, but that higher than average diversity does not suppress net diversification (Stanley 2007). This finding would be inconsistent with the canonical logistic model of Sepkoski.

On the whole, analysis of the origination and extinction components of net diversification agrees with previous results (Sepkoski 1978, 1979;
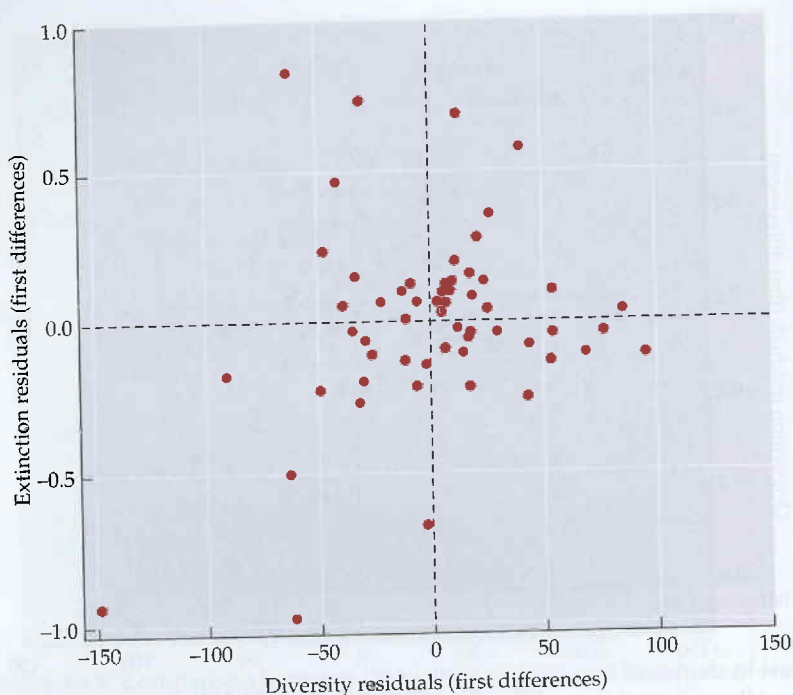
FIGURE 18.9 Comparison between Diversity Residuals and Residuals of Origination Rate Origination rate is significantly and negatively correlated with diversity whether or not the recovery intervals are included. (O/S, Ordovician/Silurian; D/C, Devonian/Carboniferous; P/Tr, Permian/Triassic; Tr/J, Triassic/Jurassic; K/Cz, Cretaceous/Cenozoic.)

Alroy 1998; Connolly and Miller 2002) that suggest substantial diversity dependence of origination (Figure 18.9; $r_s = -0.48$, $p = 0.0014$; $r_s = -0.34$, $p = 0.012$, with recoveries from major mass extinctions omitted), but little net diversity dependence of extinction (Figure 18.10; $r_s = 0.12$, $p = 0.37$). These results stand in contrast to some theoretical suggestions that extinction should be diversity dependent (Levinton 1979) and to the analyses of Alroy (2008), who found diversity in an interval to be significantly and positively correlated with extinction in the following interval but to be virtually uncorrelated with origination in the following interval. Because different approaches yield somewhat different results, the conclusion that can be most safely drawn is that net diversification rate is negatively diversity dependent, irrespective of how this relationship may break down into its origination and extinction components.

FIGURE 18.10 **Comparison between Diversity Residuals and Residuals of Extinction Rate** Extinction rate is positively but not significantly correlated with diversity.

Additional Case Studies

Bivalve Genera over the Phanerozoic

An interesting analysis of long-term diversity dynamics for a single major clade is Miller and Sepkoski's (1988) treatment of bivalve diversity at the genus level. After an initial radiation during the Ordovician, bivalve richness increased at a nearly constant average per-capita rate (Figure 18.11). This long-term increase was interrupted by a few negative excursions at extinction events, after which the rate of diversification was accelerated for a short time interval, bringing diversity back to the pre-extinction trajectory. Even though the long-term rate of diversification is roughly constant, the rebounds after perturbations suggest diversity dependence of the net diversification rate rather than simple exponential growth. Indeed, Miller and Sepkoski interpreted this diversity history as one phase of a coupled logistic system with time-homogeneous parameters and superimposed perturbations. The Ordovician increase in diversity, the long-term trend, and the rapid rebounds after extinction events are all accommodated by a single set of initial origination and extinction rates, carrying capacities, and damping coefficients.
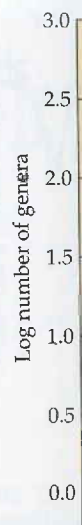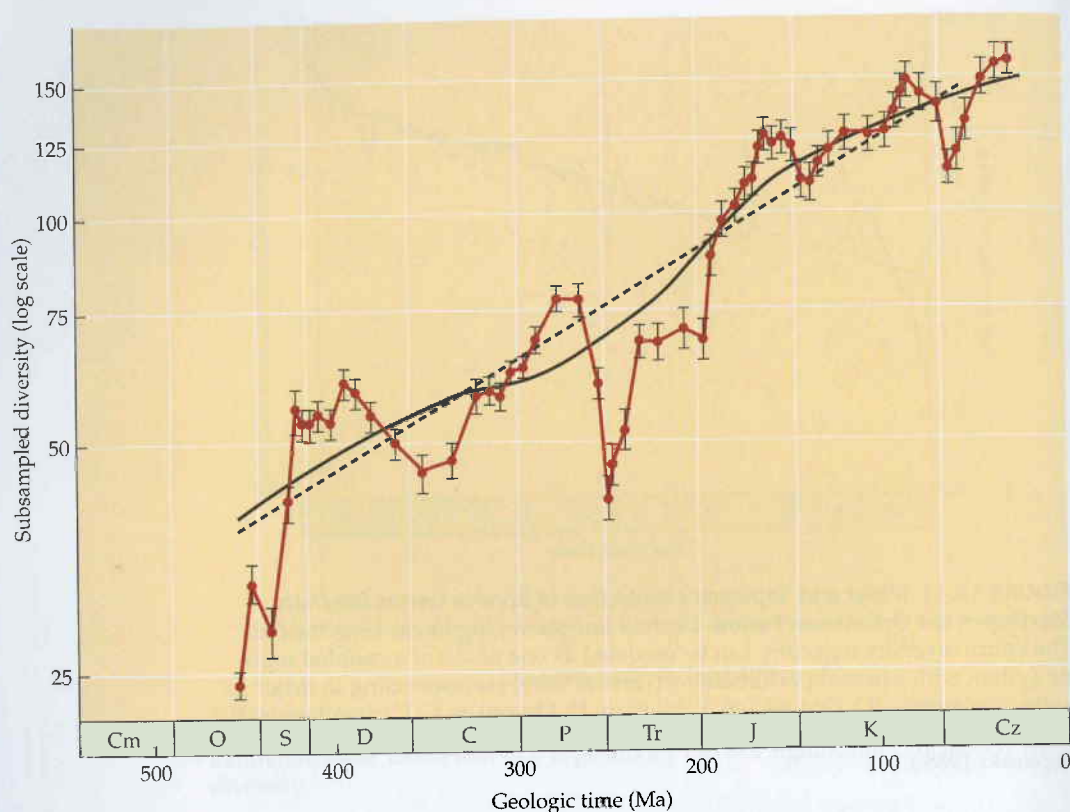

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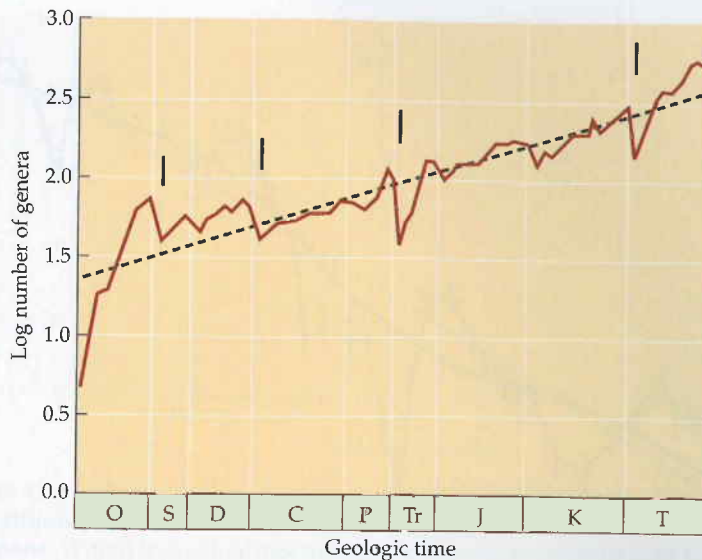
FIGURE 18.11 Miller and Sepkoski's Depiction of Bivalve Genus Diversity Starting in the Ordovician Period Dashed line shows log-linear fit to the data. The entire diversity trajectory can be modeled as one phase of a coupled logistic system with external perturbations (vertical lines) corresponding to major extinction events. (O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary.) (From Miller and Sepkoski 1988.)

Given the concerns with the quality of the fossil record, can the long-term pattern in bivalves be trusted? After all, analysis of the marine fauna as a whole suggests that attempts to standardize sampling have a considerable impact on the shape of the diversity curve (Alroy et al. 2001, 2008). Jablonski et al. (2003) documented that nearly all fossil bivalve genera in Sepkoski's compendium with living representatives also have fossil representatives in the Plio-Pleistocene (roughly the past 5 million years). They therefore concluded that the observed increase in bivalve diversity is not an artifact of the Pull of the Recent. Because the analysis by Jablonski et al. still leaves open the possibility of long-term changes in the quality of sampling, it is worth trying to correct for this directly with sampling standardization, as depicted in Figure 18.12. In this figure, a LOWESS regression is rather similar to a linear regression—in other words, the temporal pattern is reasonably close to that depicted by Miller and Sepkoski, although there is clearly more deviance than in their representation. In agreement with the raw data, however, there is little net change in the average rate of diversification over some 400 million years, and diversification accelerates greatly following many major drops in diversity, just as Miller and Sepkoski argued.
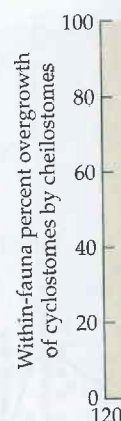
FIGURE 18.12 Sampling-Standardized Diversity of Bivalve Genera Analytical methods, heavy line, and error bars are the same as in Figure 18.6. Dashed line shows log-linear regression of the data points. A quota of 190 occurrences per interval was used; this quota can be satisfied by all but four intervals: Pragian in the Early Devonian; Eifelian in the Middle Devonian; Tournaisian in the Early Carboniferous; and Bashkirian in the Late Carboniferous. Nearly log-linear, long-term trend is consistent with Miller and Sepkoski's (1988) interpretation of the raw data (see Figure 18.11). (Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Cz, Cenozoic.) (Based on Data from the Paleobiology Database http://paleodb.org.)

Cheilostome and Cyclostome Bryozoans

While it is possible to establish a reasonable *prima facie* case for biotic interactions shaping large-scale biodiversity patterns (Sepkoski 1996; and results previously presented), there has been substantially less progress in establishing the details of how such patterns emerge. Here I will briefly summarize a case study that demonstrates a possible contributing factor at the finest level of organismic interactions, but still leaves questions unanswered.

McKinney (1992, 1995) has demonstrated that two major groups of bryozoans, the Cyclostomata and Cheilostomata, are not equal competitors for
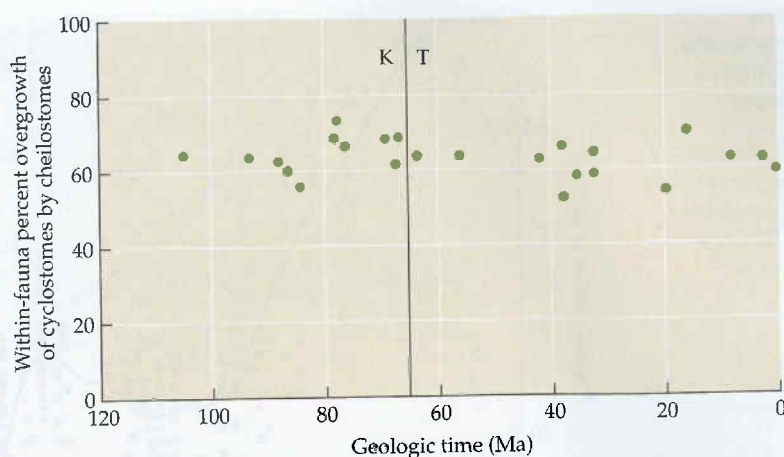

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FIGURE 18.13 **Geologic History of Overgrowth Relationships Involving Competition between Colonies of Cyclostome and Cheilostome Bryozoans** Within individual assemblages, cheilostome colonies tend to overgrow cyclostome colonies about two-thirds of the time, with no long-term trend. K/T marks the boundary between the Cretaceous and Tertiary periods. (From McKinney 1995.)

space on the marine floor. When colonies of the two groups come into contact on a hard substrate, cheilostomes manage to overgrow cyclostomes about two-thirds of the time, and this competitive edge has been roughly constant for the past 100 million years (Figure 18.13). Over the same span of time, the net rate of diversification of cheilostomes has exceeded that of cyclostomes; both clades diversified through the Cretaceous period, but cyclostomes never recovered from the loss of diversity at the end-Cretaceous extinction event (Figure 18.14). Local communities have also become increasingly dominated by cheilostomes, whether this is assessed by species richness (Figure 18.15A) or relative abundance (as skeletal mass; Figure 18.15B). The

FIGURE 18.14 **Global Genus Diversity of Cyclostome and Cheilostome Bryozoans** Both groups increased in diversity through the Late Cretaceous, but cyclostomes, in contrast to cheilostomes, failed to diversify following the end-Cretaceous extinction event. (J, Jurassic; K, Cretaceous.) (From Sepkoski et al. 2000.)
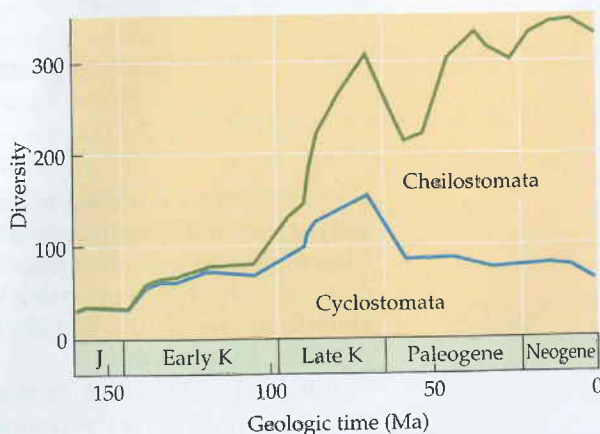
FIGURE 18.15 Comparative Representation of Cyclostome and Cheilostome Bryozoans Within Individual Fossil Assemblages
(A) Percent of species that are cyclostomes. (B) Percent of skeletal biomass belonging to cyclostome colonies. Curves fitted to data separately for Cretaceous and Tertiary periods. (From McKinney et al. 1998.)
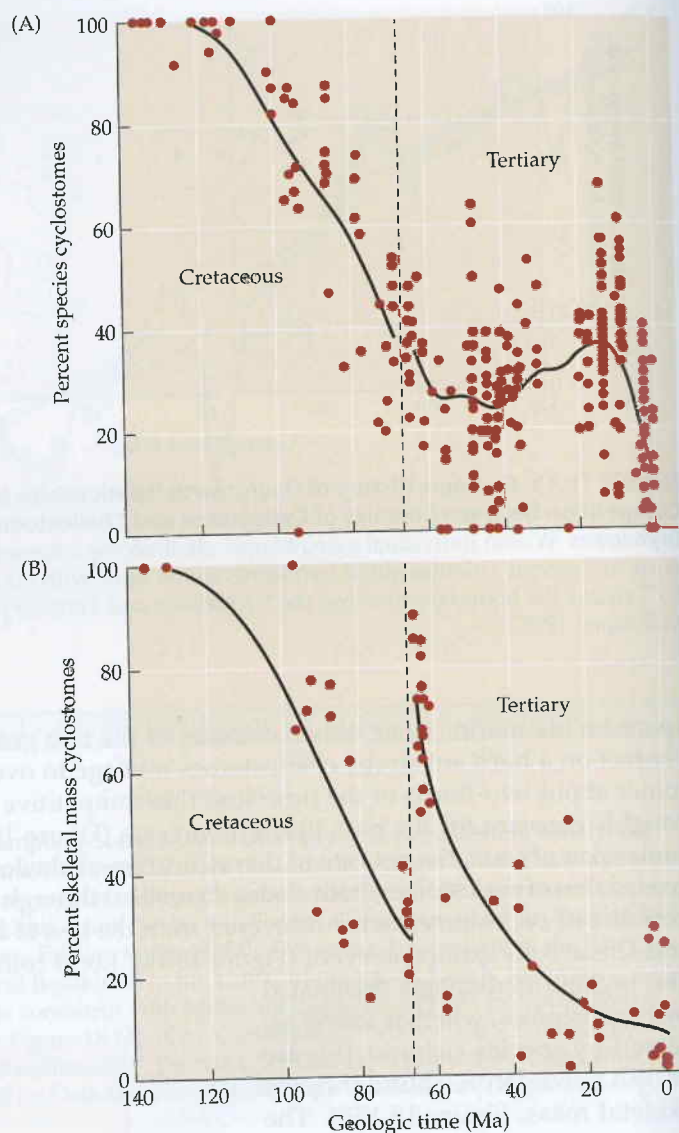
shift is more pronounced in the latter (McKinney et al. 2001). Based on the pattern of diversification alone, it would be hard to say much about competition between members of the two groups, but given the independent evidence for competitive interaction (see Figure 18.13) and relative abundance (see Figure 18.15B), it is irresistibly tempting to try to connect diversity and competition.

It is not hard to imagine that competitive superiority would lead to greater dominance at the community scale. But how might this translate
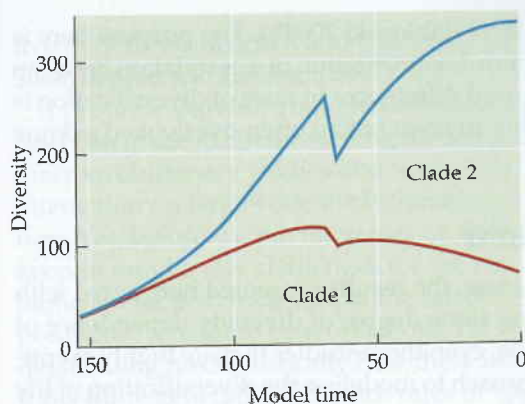
FIGURE 18.16 Two-Phase Coupled Logistic Model with Parameters Intended to Represent Cyclostomes (Clade 1) and Cheilostomes (Clade 2) The perturbation corresponds to the end-Cretaceous extinction event. (From Sepkoski et al. 2000.)

into greater global diversity? One obvious possibility is that it reduces the probability of extinction of the superior competitor. Data on stratigraphic ranges of bryozoan genera suggest that this is not the case, however. Over the past 100 million years (starting in the Cenomanian stage of the Late Cretaceous), the mean per-capita rate of extinction based on Sepkoski's (2002) data was 0.10 (± 0.017) in cheilostomes and 0.098 (± 0.010) in cyclostomes, a trivial difference. Over the same time span, however, cheilostome genera had much higher rates of origination: 0.31 (± 0.031) versus 0.092 (± 0.0095). Indeed, Sepkoski et al. (2000) modeled the cyclostome–cheilostome system with coupled logistic equations (Figure 18.16) and came to the conclusion that suppressed origination is what kept cyclostome diversity from growing following the perturbation of the Cretaceous/Tertiary extinction event.

But what exactly is the link, if any, between competition for space and rate of origination? Or is it just a coincidence? Do cheilostomes compete better for space and have higher rates of origination for other reasons that have nothing to do with competitive ability vis-à-vis cyclostomes? Here we come to one of the major gaps in the understanding of diversification: the causal relationship between organismic traits, on the one hand, and rates of origination and extinction, on the other (Jablonski 2008c). Even many of the clearest examples of a strong statistical correlation between traits and rates stop short of suggesting mechanisms connecting the two. There are important exceptions, of course. For example, the correlation between larval morphology and species-level extinction risk within gastropods evidently exists because larvae that can disperse farther allow species to have broader geographic ranges and therefore greater resistance to extinction (Hansen 1980; Jablonski 1986; Jablonski and Hunt 2006; and Crampton et al. 2010 for an alternative view). Although this particular case is not thought to be underlain by biotic interaction, some preliminary efforts have begun to model the relationship between interaction at the organismic level and dynamics

of diversification at the clade level (Jablonski 2008b). The purpose here is not to be negative—even the mere documentation of a correlation between differences in organismic traits and differences in rates of diversification is a major step forward—but rather to point out an often-overlooked avenue for future research.

Discussion and Conclusions

Despite methodological differences, the results presented here agree with many previous studies showing some degree of diversity dependence of taxonomic rates. At the very least, even those studies that are highly skeptical of Sepkoski's particular approach to modeling the diversification of life agree that rates of diversification accelerate after major extinction events (e.g., Benton and Emerson 2007; Erwin 2007, 2008; Stanley 2007, 2008), but it is shown here that diversification is still diversity dependent, if we ignore recoveries from the major mass extinctions.

In a prior study that also used sampling standardization to assess diversity dependence, Alroy (2008) found positive correlations between: (1) total diversity in a time interval and extinction rate in the following interval and (2) extinction rate in one interval and origination rate in the following interval. In contrast to the present study, Alroy did not detect diversity dependence of origination rates. This outcome could well be because, for origination rate in an interval of interest, total diversity in the previous interval—Alroy's measure—is less relevant than standing diversity at the start of the interval of interest. Alroy's correlation between extinction and subsequent origination is consistent with this suggestion, since standing diversity at the start of an interval is affected by origination and extinction rates in the previous interval.

Clearly, different analyses of the data lead to somewhat different interpretations of the details of diversity dynamics, and there is yet no consensus on the particular model that accommodates all these details. Nonetheless, there is clear support for feedback among diversity, origination, and extinction that is consistent with biotic interaction affecting the dynamics of the system. Release from competition is the most commonly invoked reason for the elevation of origination rates following declines in diversity, but Stanley (2007, 2008) instead argues that predation was the key to enhanced origination, as the extinction of predators allowed prey taxa to diversify. At a smaller geographic scale, it is often the case that provinces affected more strongly by an extinction event experience greater invasion in the wake of the extinction (Jablonski 2008a), but this is not always so (Krug and Patzkowsky 2007). Finally, it is important to reiterate that diversity dependence need not imply an equilibrial system. A model in which rates of origination and extinction respond on short time scales to changes in diversity, but in which the global carrying capacity varies, is certainly a

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Bambach, R. K. 2006⋯ Planet. Sci. 34: 127⋯

live hypothesis (Kitchell and Carr 1985; Hewzulla et al. 1999; Erwin 2007, 2008; Benton and Emerson 2007).

I presume Darwin would have been pleased to see how much progress has been made in circumventing the incompleteness of the fossil record in macroevolutionary studies and to see that the possible influence of biotic interaction on large-scale evolutionary trends has received serious attention. Yet, before we pat ourselves on the back too vigorously, we should keep in mind a few challenges for the coming decades: (1) The details of biotic interaction, for example the relative importance of competition and predation, remain to be worked out. (2) We are still a long way from understanding mechanistically how these interactions, as well as organismic traits more generally, influence rates of speciation and extinction. (3) Although there are a number of candidates for a detailed model of diversity dynamics, we have not determined which is best supported by the available data.

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