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Are Sepkoski's evolutionary faunas dynamically coherent?

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ABSTRACT

For more than two decades, Jack Sepkoski's hypothesis of three great 'evolutionary faunas' has dominated thinking about the Phanerozoic evolution of marine animals. This theory combines pattern description with process modelling: diversity trajectories of major taxonomic groups are sorted into three categories, and the trajectories are predicted by coupled logistic equations. Here I use a re-creation of Sepkoski's classic three-phase coupled logistic model and an empirical analysis of his genus-level compendium to re-examine his claims about diversity dynamics. I employ a 'focal-group' variant of the proportional volatility G-statistic to determine whether variation in turnover rates of focal taxonomic groups can be explained by the average rates for each group through time combined with average rates across all groups within each temporal bin. If growth is exponential and ecological interactions between pairs of groups are always similarly strong, then groups will wax and wane very predictably, and these statistics will always be insignificant. If instead growth is density-dependent and there are no interactions, significant volatility should be confined to periods of rapid radiations, such as those following major mass extinctions. Finally, if unusually strong pairwise interactions directly cause certain groups to succeed or fail, then significant volatility in each competing group should be present during replacement episodes that are not tied to overall radiations or extinctions. Additionally, if clustering groups into faunas is informative, then summed faunal diversity histories will replicate the observed volatility of all groups treated separately. To illustrate the focal-group method, I apply it to diversity data for the major groups of Cenozoic North American mammals. Surprisingly, the tests show that although some orders experience significant radiations and extinctions, orders with visually similar trajectories such as archaic, mostly Paleocene mammals fail to share dynamic properties. Volatility is far greater in Sepkoski's marine data, with almost every class showing significant and strong deviations from background turnover rates. However, Sepkoski's three-phase model predicts these patterns inconsistently. As expected, the Cambrian and Paleozoic faunas show high volatility during the hand-off between them. However, the hypothesized twin late Paleozoic and Jurassic/early Cretaceous hand-offs between the Paleozoic and Modern faunas are not marked by excessively rapid declines and increases. Instead, the Modern evolutionary fauna shows highly unusual dynamic behaviour starting in the mid-Cretaceous, coincident with the Mesozoic marine revolution and well after the Paleozoic fauna's decline. Sepkoski's categorization also generally fails to summarize overall volatility during long stretches of the Paleozoic and Mesozoic.

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Finally, a multivariate statistical analysis shows that Sepkoski's model imperfectly summarizes volatility. The three great faunas can be distinguished, but some minor classes fall in different clusters than one would expect (e.g. Polychaeta; Malacostraca), and the diversity dynamics of Crinoidea are distinct from those of other Paleozoic classes. Thus, the results provide only partial confirmation of Sepkoski's model. The most important problem is the delayed radiation of the Modern classes, a pattern that implicates evolutionary innovation and/or environmental change instead of temporally invariant dynamic laws operating across the Phanerozoic.

Keywords: diversity dynamics, evolutionary faunas, extinction, macroevolution, mammals, marine invertebrates, paleontology.

INTRODUCTION

A reliable indicator of a scientist's success is the smoke and fire of debates surrounding his or her work. By that standard and many others, Jack Sepkoski's research on taxonomic diversification and extinction in the fossil record succeeded impressively. For example, Sepkoski temporarily finessed the ongoing dispute over the impact of sampling artifacts on Phanerozoic diversity curves (Valentine, 1969, 1970; Raup, 1972, 1976; Bambach, 1977) by getting the major participants to agree on a truce – and to accept Sepkoski's own family-level data as the standard (Sepkoski *et al.*, 1981; see also Miller, 2000; Alroy *et al.*, 2001; Smith, 2001). In collaboration with Dave Raup, Sepkoski discovered a gradual decline in background rates through the Phanerozoic (Raup and Sepkoski, 1982), a profound result that still remains the subject of considerable discussion (e.g. Flessa and Jablonski, 1985; Van Valen, 1985; Sepkoski, 1991; Gilinsky, 1994; Alroy, 1998; Newman and Eble, 1999). Soon after, Raup and Sepkoski (1984) presented startling evidence of a 26 million year long periodic cycle in extinction rates, which led to frenzied research throughout the Earth and planetary sciences (e.g. Courtillot and Besse, 1987; Hut *et al.*, 1987; Rampino and Stothers, 1988; Jetsu and Pelt, 2000; Alroy, 2003) in addition to paleobiology (e.g. Kitchell and Pena, 1984; Jablonski, 1986; Patterson and Smith, 1987; Sepkoski, 1987; Stanley, 1990).

Above all of this stood Sepkoski's orchestrated body of work on what he called the three great Phanerozoic marine evolutionary faunas (Sepkoski, 1978, 1979, 1981, 1984, 1991, 1996). The gist of his theory was that the major taxonomic groups of marine animals could be sorted into three general categories on the basis of their shared ecologies and diversity histories. Each of these evolutionary faunas could be recognized by similar distributions in geological time and environmental space. Indeed, Sepkoski (1981) marshalled impressive descriptive evidence (specifically, a factor analysis of diversity trajectories) that the taxonomic richness of each Linnean class in each fauna increased and decreased at roughly the same time (see also Flessa and Imbrie, 1973). He also showed that within the Paleozoic, members of each fauna shared a common paleoenvironmental distribution along an onshore–offshore gradient (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985). Specifically, his 'Paleozoic' fauna, or evolutionary fauna 2, first diversified onshore, then captured offshore habitats from the collapsing 'Cambrian' evolutionary fauna 1, and by the end of the Paleozoic itself was pushed away from onshore environments by the 'Modern' evolutionary fauna 3. Sepkoski (1991) even demonstrated that one could account for much of this complex Paleozoic pattern with a simple, semi-stochastic model of evolutionary diffusion between onshore and offshore habitats.

More importantly, Sepkoski (1979, 1984) tried to explain the shared temporal and spatial distributions of the evolutionary faunas by arguing that each of them was macroevolutionarily coherent. Thus, each could be characterized by a single, uniform set of equation parameters – essentially, a carrying capacity and an intrinsic rate of diversification – that governed its history through the Phanerozoic. Furthermore, evolutionary interactions among the three faunas could be described using coupled logistic equations, with the competitive impact on a fauna of all other faunas being a simple function of their diversity. This model implied that although families and genera within a fauna did subtly interfere with each other's evolutionary success, the degree of interference caused by taxa in different faunas could be even greater by virtue of their large numbers. Replacement occurred because equilibria differed, so growth was faster in some faunas. Thus, a fauna could be seen not so much as an alliance, but as a set of individuals happening to share a certain tolerance for competition. In addition to modelling the Phanerozoic macrofossil record in general, Sepkoski also argued that coupled logistic equations could explain apparent evolutionary interactions among specific, ecologically similar pairs of groups (Miller and Sepkoski, 1988; Sepkoski, 1996; Sepkoski *et al.*, 2000).

Sepkoski's evolutionary fauna paradigm has been a smashing success. Virtually every discussion of large-scale trends in the marine fossil record over the past two decades has invoked it (e.g. Ausich and Bottjer, 1982; Valentine and Jablonski, 1983; Bambach, 1985, 1999; Van Valen, 1985; Erwin *et al.*, 1987; Miller and Sepkoski, 1988; Gilinsky and Good, 1991; Gilinsky, 1994; Benton, 1995; Sprinkle and Guensburg, 1995; Brett *et al.*, 1996; Foote, 1996; Sheehan, 1996, 2001; Adrain *et al.*, 1998; Miller, 1998; Droser *et al.*, 2000; Sepkoski, 2000; Droser and Finnegan, 2003). Most authors have accepted the deterministic, causal aspects of Sepkoski's theory with surprisingly little scepticism (but see Miller, 1998, 2000). Instead, concerted replacement of evolutionary faunas typically has been accepted as a background assumption in discussions of long-term trends in turnover rates (Gilinsky and Good, 1991), ecological (as opposed to taxonomic) transitions (Droser *et al.*, 2000), relatively short-term patterns of community stability and reorganization (Brett *et al.*, 1996; Sheehan, 1996, 2001) and evolutionary trajectories of particular groups (Sprinkle and Guensburg, 1995; Adrain *et al.*, 1998; Sepkoski, 2000).

There have been some critiques of Sepkoski's work on coupled logistic dynamics. However, these discussions mostly have focused on side-issues (but see Miller, 1998, 2000): the philosophy and quality of the underlying taxonomy (Patterson and Smith, 1987; Sepkoski, 1987; Sepkoski and Kendrick, 1993; Wagner, 1995; Adrain and Westrop, 2000); the fact that ecological and taxonomic transitions may differ considerably (McKinney *et al.*, 1998; Droser *et al.*, 2000); and the general evidence for a three-fauna pattern in diversity curves (Bambach, 1985; Kitchell and MacLeod, 1988) or for logistic dynamics (Signor, 1978, 1985; Hoffman, 1985; Benton, 1995, 2001), regardless of how these patterns might be broken down using coupled equations. No-one other than Sepkoski himself has directly tested Sepkoski's process-based assumptions that marine classes within each fauna have similar dynamic properties and that negative interactions among faunas cause replacements.

In this paper, I provide just such a test by applying a simple and broad statistical technique to Sepkoski's own data. The method is detailed first. The basic idea is to determine whether all of the temporal variation in origination and extinction rates of each class can be explained by the average rate of turnover within that class through time, combined with averages across all classes in each time interval. The next section is an outline of this 'proportional volatility' statistical test, followed by an illustration of its performance with an empirical example concerning the record of North American Cenozoic mammals. The mammal data are unusually ripe for this kind of an analysis because bias factors are minimized, and there are strong ecological reasons to suspect that non-random replacement has occurred.

The rest of the paper takes three very different approaches to the problem of assessing the three-fauna hypothesis. First, I re-create Sepkoski's classic simulation model and use it to show exactly what it would predict with respect to proportional volatility. A series of interrelated predictions are derived. Second, I apply the volatility test directly to Sepkoski's classic compendium of marine genera, showing whether classes arranged into his three evolutionary faunas depart from background turnover rates when the model would expect them to, and whether the three-fauna classification generally does a good job of summarizing class-level volatility. Finally, I illustrate volatility time series for key individual classes and then summarize these complex data by means of multivariate correspondence analysis. The resulting patterns define sets of marine classes with similar diversity dynamics. To the extent that Sepkoski's model truly gets at overarching evolutionary processes and not just historical contingencies such as mass extinctions, these dynamic sets should correspond to the three great faunas.

METHODS

Previous work

Paleobiologists have sought for many years to test whether origination and extinction rates vary significantly. Typically, these tests have focused on showing whether rates vary either through time or among taxonomic groups, without looking for interactions. For example, Flessa and Levinton (1975) used a runs test to show that origination rates are temporally clumped, and a chi-square test to show that the frequency distribution of these rates is significantly variable. Prothero (1985) also used a chi-square approach to study temporal variation, but followed Raup and Marshall (1980) by testing counts of events in temporal bins directly instead of examining overall frequencies of such counts as Flessa and Levinton (1975) had done. Barry *et al.* (1990, 1995) did much the same thing as Prothero (1985), except that their null model assumed a temporally uniform distribution of extinction events, not extinction rates.

Many other authors have sought to avoid the parametric assumptions and power problems of the chi-square method in studies of temporal variation. Hubbard and Gilinsky (1992) developed a bootstrap test to reject the null model of constant turnover through time, drawing with replacement from extinction counts for order-by-time-interval cells to simulate total extinction rates across all orders. Maas *et al.* (1995) also used randomization, but shuffled entire age-ranges of species instead of drawing extinction counts. Wagner (1995) computed exact probabilities of observing extinction counts given average turnover rates through time. Alroy (1996) employed the variance of rates through time as a test statistic, determining significance by means of a Monte Carlo simulation that assumed a constant underlying turnover rate. Finally, Stucky (1990) took the completely different approach of comparing observed per-taxon rates to expected values given a non-linear regression of rates against standing diversity.

The question of whether taxonomic groups vary in their turnover rates has attracted somewhat less attention. Raup and Marshall (1980) used a chi-square test to show that orders of mammals have different per-genus origination rates. Their analyses focused on one temporal interval at a time. The general characteristics of each order were then inferred by tallying up significant departures from randomness for that order through all the time intervals. Crick (1981) employed the same method without modification, whereas Ward and Signor (1983) examined geometric means of genus durations within families instead of extinction rates *per se*, and Holman (1989) tested for variation among orders within classes and phyla using a randomization approach. Importantly, all of these authors ignored the question of whether ordinal turnover rates in particular intervals were high relative to the background turnover rates of those same groups, not just the average turnover rate of all groups through all time or within particular time intervals.

The focal-group proportional volatility test

In this paper, I adapt a recently proposed method (Alroy, 2000) that tests for episodes of faunal replacement, a question not addressed by any of the other studies. It simply assumes that there is in fact substantial variation in rates, not only through time but among groups, and then tries to control for the variation and look for excesses that might indicate rapid, non-random replacements. It employs a very simple 'proportional volatility *G*-statistic' that quantifies the departure of observed turnover rates from rates predicted by the averages for each group and for each time interval (Alroy, 2000, eqn. 19). The equation produces a single number for each time interval that essentially is a sum of logged ratios between observed and expected turnover rates for each group in that interval. High numbers indicate that observed rates are either unusually high or unusually low. The *G*-statistics are distributed as chi-square, so significance can be determined by consulting a table of critical values. Sums for extinction and origination rates can be computed separately; adding them yields the overall volatility.

The general idea of the equation goes back to the chi-square test of Raup and Marshall (1980). It differs because the *G*-statistic is used instead of the less robust chi-square statistic (Sokal and Rohlf, 1995); because of the way the individual cell values are predicted simultaneously from temporal bin and taxonomic group averages, instead of either just averages across groups for each temporal bin (Raup and Marshall, 1980) or averages through time with all groups lumped (Prothero, 1985); and because the turnover rates themselves are computed using the exponential decay equations of Foote (1999) instead of more traditional raw turnover counts or turnover percentages.

Initially, the proportional volatility test was used to show simply whether there was or wasn't significant replacement among all groups in each temporal bin (Alroy, 2000). Because just one *G*-value was computed for each bin, there was no indication of which group or groups might be responsible for the variation. Hence, the original test could have shown significant values if just one group diversified or declined while all other groups showed random change; if exactly one group replaced exactly one other group; if a single selective extinction episode caused most of the non-random change in taxonomic composition; or if one large ensemble of groups replaced some other ensemble. To distinguish these biologically interesting scenarios, it is necessary to show whether turnover in each individual group is non-random relative to all other turnover at a time, and relative to its own background turnover rate.

The solution to this problem is very simple: instead of computing a vector of group averages and using it to predict turnover rates separately for each group at each time, just two averages are computed, one for a focal group and one for all other groups lumped together. These two rates are used in combination with the temporal bin averages to compute expected counts of focal group and non-focal group turnover events in each bin. The observed and expected counts are then compared to produce *G*-statistics. The resulting time series shows whether the focal group has diversified at random relative to its own average exponential rate of diversification. The hypothesis that an evolutionary fauna behaves as a dynamic entity can be tested by lumping all of that fauna's component orders or classes as one large focal group, and then comparing the focal group's turnover to the rates for all other groups combined.

In its original application (Alroy, 2000), the proportional volatility *G*-statistic was computed only using data for major taxonomic groups (i.e. mammalian orders). Data for groups that were too taxonomically depauperate to yield their own distinct taxonomic rates were simply discarded. However, the focal group *G*-statistic contrasts data for one major group against combined data for all other groups, whether large or small.

To save space, here I only illustrate combined *G*-statistics for origination and extinction rates, even though I discuss the relative contribution of each kind of rate in a few places. Because the index combines separate *G*-values for each kind of rate by simple addition (Alroy, 2000, eqn. 19), each *G*-statistic curve actually summarizes two separate curves, one for each kind of rate.

The focal-group *G*-statistics are potentially sensitive to the choice of turnover rate metrics (Foote, 1994, 2000). In this paper, I consistently employ the instantaneous rate equations of Foote (1999), which assume that turnover is a steady exponential process within each temporal bin and have numerous robust properties (Alroy, 2000; Foote, 2000). Analyses of Sepkoski's genus-level compendium standardize the rates for the elapsed amount of time in each bin, with interval lengths based directly on the time scale used by Sepkoski (2002). Standardization is irrelevant to the analyses of mammalian data and simulated Phanerozoic evolutionary faunas because interval lengths are constant in those cases.

The focal-group proportional volatility test should be able to detect differential episodes of taxonomic replacement in several ways:

1. If a taxonomic group suddenly diversifies in the wake of a key innovation (e.g. Hunter and Jernvall, 1995), that one group and no others should show elevated turnover rates soon after the innovation evolves.
2. If ecological release mediated by geographic invasion or mass extinction is important (e.g. Erwin *et al.*, 1987; Foote, 1996; Alroy, 1999a), that should register with elevated rates during the diversification of one or more successful groups, with unremarkable rates for all groups before the perturbation.
3. If two particular groups are engaged in a *pas de deux* replacement episode (e.g. Miller and Sepkoski, 1988; McKinney *et al.*, 1998), those two groups alone should exhibit alternatively elevated and depressed rates that complement each other precisely during the hypothesized interval of replacement.
4. If groups suffer differentially from a mass extinction in ways that cannot be predicted from background rates (Jablonski, 1986; Miller, 1998, 2000), the overall *G*-statistic should be significant for intervals surrounding the extinction event, but group-wise statistics need not be unless differential survivorship very strongly affects just a few groups.

5. Most importantly, if evolutionary faunas are coherent, *G*-statistics for those faunas lumped as focal groups should show just as much variation as overall *G*-statistics computed by treating each group separately; each taxonomic group within a fauna should show roughly the same *G*-statistic patterns; and a replacement between two faunas should register with simultaneous runs of significant rates during the replacement interval.

VOLATILITY OF MAMMALIAN EVOLUTIONARY FAUNAS

Data and context

The fossil record of North American Cenozoic mammals provides an excellent opportunity to test the *G*-statistic approach. Thanks to the use of appearance event ordination (Alroy, 1992, 1994, 1996, 1998, 2000), the data can be split into 65 uniform, 1.0 million year long temporal intervals. This approach side-steps the imprecise, typological and subjectively defined North American land-mammal age time scale, and thereby circumvents problems with defining turnover rates when interval lengths vary (Raup, 1972; Foote, 1994). The raw data are species-level and taxonomically standardized; effects of temporal variation in the amount of data have been corrected using standardized random subsampling (Alroy, 1996, 1998, 2000); and turnover rates are defined using instantaneous rate equations that have robust properties (Foote, 1999, 2000; Alroy, 2000). Potential problems with unrecognized junior synonyms or otherwise taxonomically invalid species are not dealt with here because this bias has almost no demonstrable effect on turnover rates, despite strongly influencing absolute diversity (Alroy, 2002).

The time series begins with the great Paleocene radiation of mammals (Archibald, 1993; Alroy, 1999a) and spans several large shifts in taxonomic composition, with the most pronounced turnover occurring around the Paleocene–Eocene boundary (Clyde and Gingerich, 1998) and in the mid-Eocene (Alroy, 2000). These transitions can be attributed neither to global climate change (Alroy *et al.*, 2000) nor to extra-terrestrial bolide impacts (Alroy, 2003), so they are likely to represent biotic interactions of the kind that concerned Sepkoski (1979, 1984). The data also are advantageous because ecological roles in mammals are tightly constrained at the ordinal level (Eisenberg, 1981): body sizes within orders are uniform, most orders are either predominantly faunivorous or herbivorous, and although many mammals have generalized locomotor strategies, most species within several important orders are either arboreal (e.g. Primates) or ground-dwelling (e.g. Artiodactyla and Perissodactyla).

Thus, changes in the proportional diversity of mammalian orders should communicate large ecological shifts if any actually occur. Indeed, the overall turnover rates already have been shown to be much more variable through time than one would expect at random (Alroy, 1996), and similarly the *G*-statistic approach already has been used to show that orders replace each other non-randomly (Alroy, 2000). Specifically, at least three major replacement episodes already have been suggested (Alroy *et al.*, 2000). The Cretaceous–Tertiary boundary is marked by the total (if temporary) extirpation of endemic marsupials and the first appearance of numerous placental groups, which results through immigration, cladogenesis and anagenesis in a massive increase in average body size (Alroy, 1999a) and a significant increase in the range of dental morphologies (Jernvall *et al.*, 1996). The Paleocene–Eocene transition is coincident with the immigration of true primates, advanced carnivorans, artiodactyls and perissodactyls, which increases alpha diversity and average body mass (Clyde and Gingerich, 1998) and renders the distribution far more unimodal because so many species are added to the middle size range (Alroy, 2000). Finally, in the mid-Eocene the relative diversity of ground-dwelling ungulates seems to increase at the expense of arboreal primates, which translates into an abrupt shift to a bimodal size distribution (Alroy, 2000).

Evolutionary faunas

The existence of so much evolutionary turbulence suggests reasonably good prospects for finding coherent suites of orders arranged as 'evolutionary faunas'. A simple visual inspection of a proportional diversity plot (Alroy, 2000, figure 8) would suggest at least two and arguably three faunas (Fig. 1). The first, characteristically 'Paleocene' fauna would include the primitive, rodent-like Multituberculata; the largely insectivorous marsupials; the extinct, arboreal order Plesiadapiformes (which is likely paraphyletic to the Primates: Silcox, 2001; Bloch and Boyer, 2002); and the paraphyletic assemblage of primitive, mostly medium-sized herbivores known as the 'condylarths'. This archaic evolutionary fauna is dominant throughout the Paleocene, steadily declines during the Eocene, and is almost extinct by the Oligocene. The second, 'Modern' fauna, including the six dominant modern orders Insectivora, Rodentia, Lagomorpha, Carnivora, Artiodactyla and Perissodactyla, rises to prominence around the Paleocene–Eocene transition. A third, much smaller 'Eocene' fauna could be created by splitting off two orders (Creodonta, Primates) that diversified in the early Eocene but went extinct in North America before the end of that epoch.

Focal-group *G*-statistic curves for the three nominal faunas are surprisingly flat (Fig. 2A), and lumping the data into three faunal categories removes all of the significant variation that is seen in the ordinal data when they are treated separately (Fig. 2B). The lack of volatility is particularly remarkable because the Modern fauna experiences such a steady and dramatic increase in proportional diversity during the Paleogene, rising from less than 6% of the fauna in the basal Paleocene to nearly 90% by the end of the Eocene. Almost all of this increase is at the expense of the Paleocene fauna, which nosedives from over 80% of

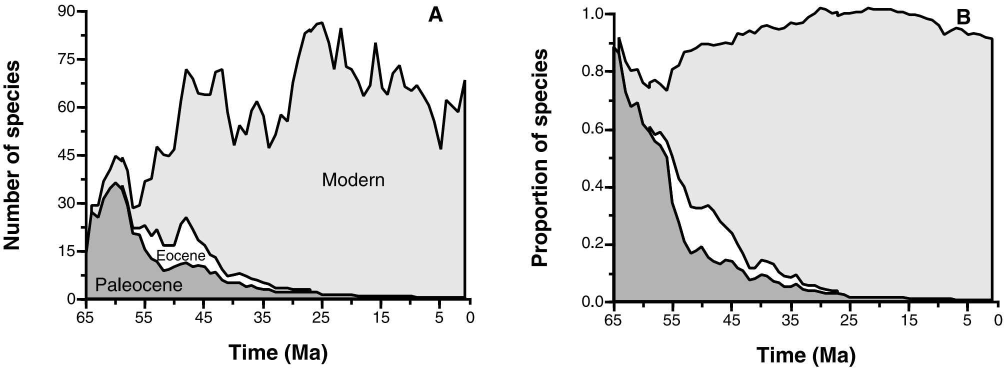


Fig. 1. Sampling-standardized, species-level diversity of North American mammalian evolutionary faunas. (A) Boundary-crosser diversity. (B) Proportional diversity. Some small orders (e.g. Xenarthra) are not placed in faunas, so proportions do not sum to unity.

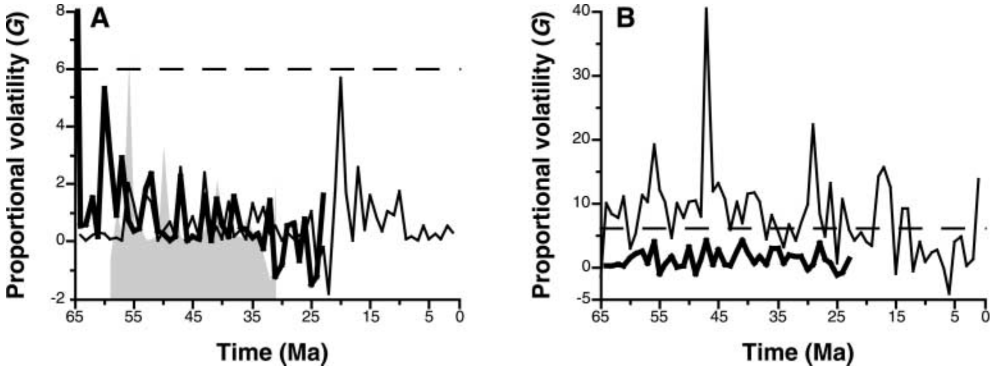


Fig. 2. Proportional volatility of Cenozoic North American mammals. (A) Focal-group volatility of three hypothesized evolutionary faunas. Bold line = Paleocene fauna; shaded area = Eocene fauna; thin line = Modern fauna; dashed line = upper 95% confidence interval for *G*-statistic with two degrees of freedom. (B) Total volatility of orders. Bold line = volatility of 12 orders after grouping them into evolutionary faunas; thin line = volatility of 12 major orders treated separately. Latter curve differs from earlier version (Alroy, 2000, figure 9b) due to correction of minor algorithm errors and calculation of average turnover rates for orders based only on data for the last 65 million years (as opposed to the last 70 million years). However, the new curve confirms that there are major replacement episodes at the Paleocene–Eocene boundary (56–55 Ma bin), in the mid-Eocene (47–46 Ma bin) and in the mid-Oligocene (29–28 Ma bin).

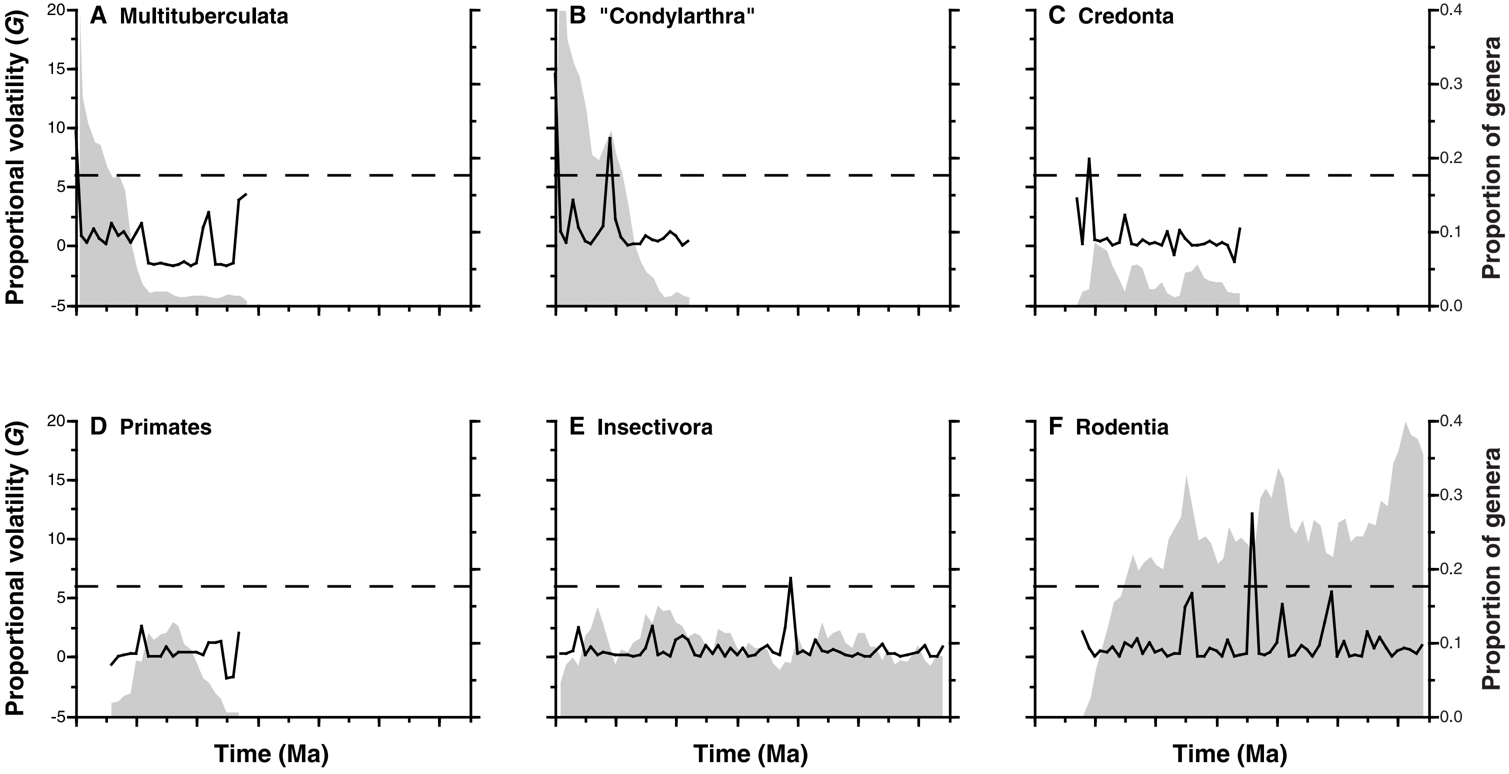
the biota in the early Paleocene to less than 10% by the mid-Eocene, and indeed goes entirely extinct by the beginning of the Miocene. Essentially, the results suggest that the Modern fauna's gradual rise was simply an epiphemonenon of the group's relatively favourable balance of background origination and extinction rates.

Nonetheless, the focal-group statistics do suggest one possibly interesting pattern: a spike in volatility for the nominal Eocene fauna at the Paleocene–Eocene boundary. This spike represents the combined group's sudden rise in diversity from about 5% to 16%, a level that is approximately maintained for nearly another 10 million years. Unsurprisingly, almost all of the *G*-value for the critical 56–55 Ma bin is due to the fauna's extremely high origination rate.

The impact of the Paleocene–Eocene transition is made slightly more visible by lumping the two Eocene orders Creodonta and Primates in with the Modern fauna. This rearrangement yields a significant *G*-value of 8.43 for the 56–55 Ma bin, across which the combined Eocene–Modern fauna doubles its diversity from 23% to 46%. However, instead combining the Eocene orders with the Paleocene fauna does obliterate the pattern, reducing the *G*-value to the insignificant level of 0.11. The reason is that the increase of the Eocene orders comes almost entirely at the expense of the Paleocene orders, whose diversity drops from 50% to 34% across this temporal bin.

Ordinal patterns

Individual analyses of the major orders (Fig. 3) explain the almost complete failure of the three-fauna model, because they show that the orders have largely independent, unintegrated dynamics. The two most important Paleocene groups (Multituberculata and 'condylarths') both seem to have rapidly changing but essentially stochastic diversity


A Multituberculata
B "Condylarthra"
C Credonta
D Primates
E Insectivora
F Rodentia
Proportional volatility (G)
20
15
10
5
0
-5
Proportion of genera
0.4
0.3
0.2
0.1
0.0
Time (Ma)

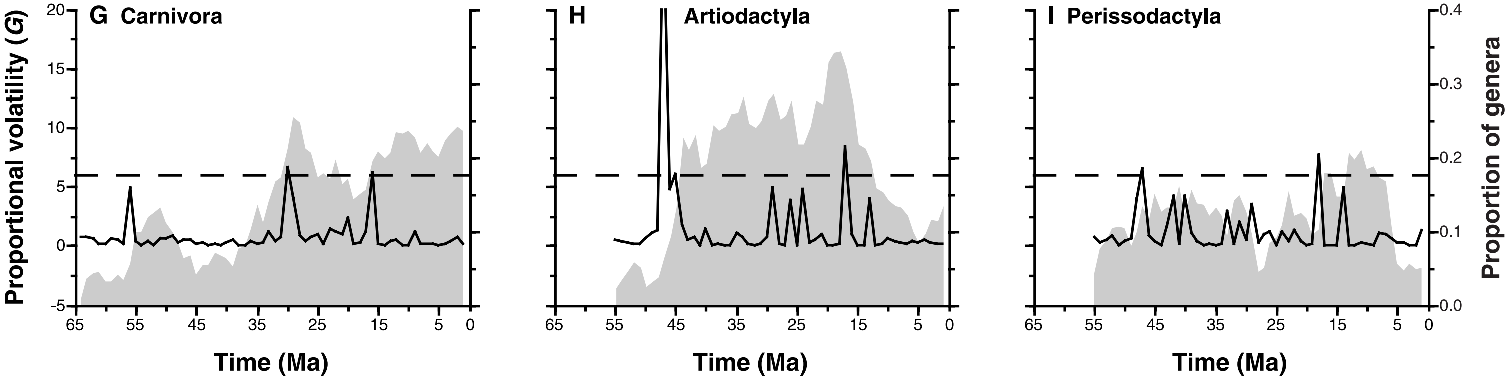


Fig. 3. Proportional volatility of selected North American mammal orders. Thin black lines = focal-group proportional volatility *G*-statistics; shaded areas = proportional genus-level diversity derived from a sampling standardization analysis of faunal data (see Alroy, 2000, figure 8); dashed lines = 95% confidence intervals. (A) Multituberculata, (B) 'Condylarthra', (C) Creodonta, (D) Primates, (E) Insectivora, (F) Rodentia, (G) Carnivora, (H) Artiodactyla, (I) Perissodactyla.

dynamics, with a single pulse of significant volatility for 'Condylarthra' corresponding to its drop in diversity at the Paleocene–Eocene boundary (Fig. 3A,B).

The Primates, the more diverse of the two orders comprising the Eocene evolutionary fauna, show no significant volatility at all (Fig. 3D), and instead the one excursion in the *G*-statistic curve for this fauna (Fig. 2) turns out to be driven entirely by a large *G*-value of 6.84 for the origination rate of creodonts (Fig. 3C). In other words, the properties of the 'Eocene fauna' actually seem to be properties of the Creodonta.

The modern orders are eclectic in the extreme. In proportional terms, the Insectivora (Fig. 3E) show a remarkably static diversity trajectory. As a result, the *G*-statistic is virtually flat throughout the Cenozoic, implying that the group never experienced a true pulse of origination or extinction. The pattern for Rodentia (Fig. 3F) is dramatically different, with a highly variable but essentially directionless trend after a massive initial radiation. Nonetheless, there is one interval (29–28 Ma bin) that marks an abrupt increase in proportional diversity from the relatively low Eocene and early Oligocene levels; the overall *G*-value here is largely a function of the origination rate value of 12.06. The Carnivora (Fig. 3G) exhibit a large diversification event at 30–29 Ma. Although not exactly coincident, both pulses are part of a biota-wide mid-Oligocene radiation that increased overall taxonomic diversity by about 50% and ranks as one of the half dozen most important transitions of the Cenozoic (Alroy *et al.*, 2000).

Interestingly, another, more marginally significant pulse of carnivoran diversification occurred at the Paleocene–Eocene boundary (56–55 Ma bin). This pattern strengthens the argument that the massive biotic reorganization at this boundary, which also is reflected by high overall turnover rates and shifts in body mass distributions (Clyde and Gingerich, 1998; Alroy *et al.*, 2000), was driven by rapid diversification in certain key groups following an immigration pulse. It also reinforces the idea that although multiple groups may make up the winning side in a game of taxonomic replacement, such groups need not continue to share their diversity trajectories. Indeed, after the Eocene the fates of the Creodonta and Carnivora were entirely different.

The pattern for the Artiodactyla (Fig. 3H) is perhaps the most interesting of all. Multiple pulses of turnover volatility are evident, the most impressive being a string of high values that mark the group's mid-Eocene (47–44 Ma) rise to dominance. This increase is a key component of the mid-Eocene biotic transition (Alroy *et al.*, 2000), which also coincides with a shift from unimodal to bimodal size distributions and a subtle decrease in the diversity of middle-sized, arboreal herbivores belonging to the Plesiadapiforms, Primates and 'condylarths'. The decline of the Artiodactyla is punctuated by a series of significantly low origination rates, for example in the mid-Miocene (17–16 and 13–12 Ma bins). These declines are not matched by those seen for any of the other groups.

The Perissodactyla present yet another pattern (Fig. 3I). The group also diversifies significantly through the mid-Eocene. However, its other impressive turnover pulses are two widely separated Miocene diversification events (18–17 Ma, 14–13 Ma) that record the radiation of horses (MacFadden and Hulbert, 1988) and fail to correspond to major changes in other groups. Interestingly, the group's decline around the Mio-Pliocene boundary seems to be stochastic, perhaps a side-effect of generally high extinction rates for large mammals during this interval (Webb, 1983; Alroy, 1999b; Alroy *et al.*, 2000).

In summary, the *G*-statistic analyses reveal a complicated dance of taxonomic replacement. Groups wax and wane at multiple points during the Cenozoic, often at times of generally high turnover across the biota. However, some major turnover episodes such as the one at the Mio-Pliocene boundary have strong effects on taxonomic composition that appear to be essentially stochastic. More importantly, increases in one group do not always mirror decreases in other groups; cases in which two or more groups radiate simultaneously – such as the Paleocene–Eocene and mid-Oligocene – are the exception rather than the rule; and attempting to summarize taxonomic diversity trajectories by constructing evolutionary faunas simply fails, because groups with similar overall trends typically do not show strong, fine-scale similarities in diversity dynamics. All of this is consistent with earlier evidence that although diversification across the class Mammalia is density-dependent (Alroy, 1996, 1998), these controls are weaker at the ordinal level, permitting largely random taxonomic replacement (Alroy, 1996).

SEPKOSKI'S MODEL

Any statistical method can fail to find a pattern of interest simply because the method lacks power. In light of this fact, the preceding results for Cenozoic mammals raise a red flag: could the real problem be with the method, not with the data? It is therefore important to show that the *G*-statistic approach really would find evidence of Sepkoski's three great faunas if these faunas actually were dynamically coherent. Here I test this hypothesis by analysing data generated from Sepkoski's original three-phase numerical simulation model, just as he illustrated it (Sepkoski, 1984). I specifically focus on a version of the model he seemed to favour, which included 'perturbations' meant to mimic the Permo-Triassic and end-Triassic mass extinction events (Sepkoski, 1984, figure 8b). In addition to recreating this classic model (Fig. 4A), I also present a version of the model in which each fauna experiences independent logistic growth and there is no competitive interference among them whatsoever (Fig. 4B). This exercise shows that several key features of Sepkoski's model depend crucially on competition: the slow initial radiation of the Modern fauna, and the steady declines of the other two faunas from their respective peaks.

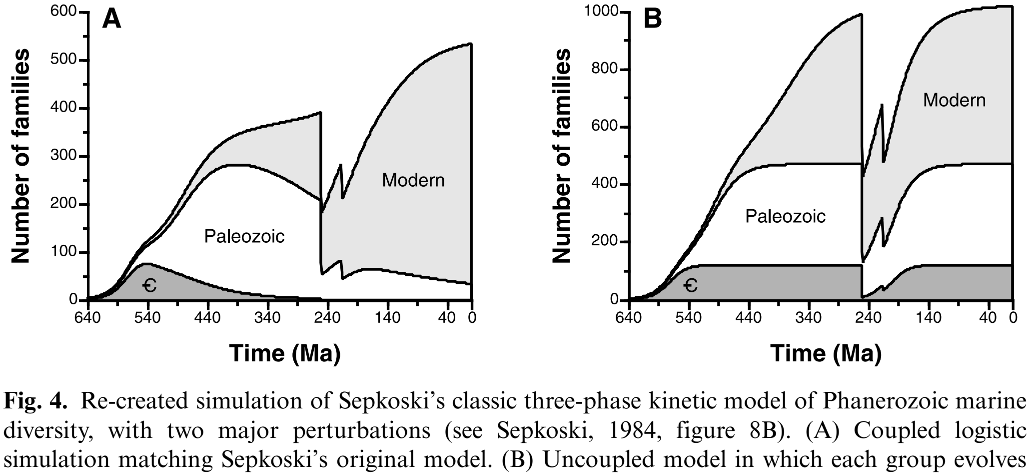


Fig. 4. Re-created simulation of Sepkoski's classic three-phase kinetic model of Phanerozoic marine diversity, with two major perturbations (see Sepkoski, 1984, figure 8B). (A) Coupled logistic simulation matching Sepkoski's original model. (B) Uncoupled model in which each group evolves logistically but independently, with other parameters unchanged.

Parameters and equations

Unfortunately, Sepkoski (1984) never stated all of the parameters and exact algorithmic steps for this key version of the simulation model. Certain assumptions therefore had to be made.

1. It appears that the simulations employed relatively short and uniform time steps. Therefore, the model was run with discrete, 1.0 million year long steps.
2. Sepkoski (1984, figures 3, 8) began his simulation runs at about 640 Ma, sometime during the Vendian and well before the Cambrian, which he illustrates beginning at 590 Ma (Sepkoski, 1984, figure 1). This estimate is based on measurements of his figure 8A and the assumptions that the Permo-Triassic extinction begins around 250 Ma, again as illustrated, and that the illustrated simulation continues until 0 Ma.
3. Sepkoski (1984, table 2) only gave intrinsic increase and carrying capacity parameters for each fauna fitted separately to the data, without regard for the effect of competing faunas (i.e. the uncoupled model assuming each fauna grows according to a simple logistic equation). Back-estimating the parameters for the coupled model is extremely difficult. The key starting assumption is that the Paleozoic fauna goes into decline when the total diversity of all three faunas is at the fauna's own stated equilibrium level of 350 families, a point reached at around 420 Ma. If so, then the Paleozoic fauna declines to about 200 families just before the Permo-Triassic event and 45 families just after, and following a brief rebound declines back to this same low level by the Recent. The Cambrian fauna goes into decline at 530 Ma when total diversity is around 120 families, which indicates its equilibrium level equals this count and is not 85, as given in the table. The fauna's own actual diversity at this time is just 70 families; it goes completely extinct around 290 Ma. Meanwhile, the Modern fauna expands to about 40 families at 420 Ma, 180 before the Permo-Triassic perturbation and 485 by the Recent. The best back-estimate of its equilibrium diversity level is 550 families, much lower than the stated figure of 850 (Sepkoski, 1984, table 2).
4. The reported intrinsic rates of increase (Sepkoski, 1984, table 2) are 0.127, 0.0627 and 0.0133 families per family per million years for the three faunas. Much lower rates for the Cambrian and Paleozoic faunas and a much higher rate for the Modern fauna are needed to reproduce the illustrated trajectories. A reasonable fit is obtained with rates of 0.07, 0.042 and 0.235 families per family per million years.
5. If the Permo-Triassic event is at 250 Ma, then the end-Triassic perturbation appears to start about 215 Ma (Sepkoski, 1984, figure 8B), which also is the illustrated date of the Triassic–Jurassic boundary (Sepkoski, 1984, figure 1). Sepkoski (1984, pp. 260–261) stated that during the two extinction episodes, carrying capacities would be reduced to 7% (Permo-Triassic) and 10% (end-Triassic) of original values by varying the strength of the density dependence coefficient for extinction. The illustrated figure very roughly indicates Permo-Triassic diversity crashes of 78% for the Paleozoic fauna (from 200 to 45) and 39% for the Modern fauna (from 180 to 110). Although Sepkoski did not state exactly how long his 'perturbations' were supposed to last, in a similar analysis of bivalve diversification, Miller and Sepkoski (1988) imposed a 2 million year perturbation to simulate the Permo-Triassic extinction. Perturbations of the stated intensity and of this duration combined with the back-estimated rates of increase yield apparently appropriate diversity crashes (Fig. 4 *vs* Sepkoski, 1984, figure 8B), with respective Permo-Triassic drops of 75% and 30% for the Paleozoic and Modern faunas (Fig. 4).

6. Although one could try to run the model using only net diversification rates, it seems clear that Sepkoski (1984) actually computed separate origination and extinction rates for each fauna at each time interval. This turns out to be potentially important because Sepkoski (1979, 1984) used linear per-taxon turnover rate equations that implied negative origination rates at very high diversity levels. Negative rates being impossible, he assumed arbitarily that origination rates would be exactly zero at these diversity levels. This rate truncation caused a sudden kink in the linear function relating net diversification rate to diversity, with the slope becoming much more shallow at the hinge point. In other words, rates of diversity decline at very high diversity levels were ameliorated by what is essentially an algorithmic artifact. In practice, this unusual assumption has very little impact on the observed dynamics, because the requisite high diversity levels are rarely achieved.

7. However, these complications make it necessary to assume some arbitrary decomposition of diversification rates into origination and extinction rates. I assumed that extinction rates would approach zero as diversity declined to zero because Sepkoski illustrated essentially such a case in his paper on the three evolutionary faunas (Sepkoski, 1984, figure 5A). Sepkoski repeatedly illustrated the ratio of the slopes of the two density dependence lines being roughly equal, with the slope for origination being slightly higher (Sepkoski, 1978, figure 7A; Sepkoski, 1979, figure 8; Sepkoski, 1984, figure 5A). However, I could not repeat the illustrated slow declines of the Cambrian and Paleozoic faunas with subequal slopes and, therefore, had to assume strongly asymmetrical density dependence, with the slope being 12.5 times higher for origination.

Predicted patterns

Although not perfect, the recreated version of Sepkoski's favoured model (Fig. 4) does capture all of the key patterns he emphasized (Sepkoski, 1984): the succession of three faunas with respective diversity peaks in the Cambrian, mid-Paleozoic and Recent; a mid-Paleozoic diversity plateau created by the slow decline of the Paleozoic fauna being matched by the slow rise of the Modern fauna; differential extinction of these two faunas at the Permo-Triassic boundary; a relatively substantial diversity rebound for the Paleozoic fauna in the Triassic; and, following a second mid-Mesozoic peak, a slow decline for that fauna that still leaves it with substantial diversity at the end of the Phanerozoic.

With the simulated origination and extinction rates in hand, the next step was to compute the *G*-statistic for each fauna's rates, as compared to the summed rates of the other two faunas (Fig. 5). The raw data for 1.0 million year long bins were lumped into 7.0 million year long bins so as to approximate the 77 temporal intervals for the 543 million year long Phanerozoic (average 6.96 million years) that Sepkoski employed in his own empirical work (Sepkoski, 2002). Diversity, origination and extinction counts were rounded to the nearest integer at this step to enhance realism and avoid computational problems involving very small fractional counts.

The *G*-statistic curves for the coupled logistic version of the model (Fig. 5A) reveal several extremely striking patterns, all of which can be seen solely in the data for the Paleozoic fauna. The Cambrian fauna's initial, explosive radiation does not register as a significant departure from background rates, because the other two faunas are so small during the Vendian and early Cambrian that the overall turnover rates essentially are determined by the Cambrian fauna. However, this fauna's decline throughout the second half of the Cambrian and the Ordovician does register with virtually identical and consistently highly

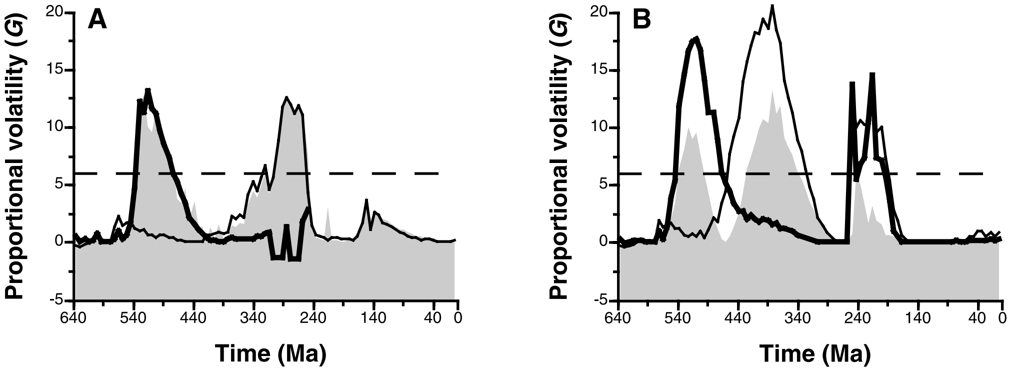


Fig. 5. Proportional volatility of the three marine evolutionary faunas, as predicted by coupled and uncoupled versions of Sepkoski's three-phase model. Bold line = Cambrian fauna; shaded area = Paleozoic fauna; thin line = Modern fauna; dashed line = 95% confidence interval. (A) Predicted volatility given coupled logistic dynamics. High volatility in the late Paleozoic and late Mesozoic marks replacement episodes. (B) Predicted volatility given uncoupled logistic dynamics. High volatility occurs during initial radiations and the rebound from the Permo-Triassic mass extinction.

significant values for both the Cambrian and Paleozoic faunas. Thus, the *G*-statistic data clearly show that Sepkoski's model predicts an extended, dynamically non-random replacement episode during the Ordovician.

Later patterns in the Paleozoic fauna's curve are entirely mirrored by the data for the Modern fauna (Fig. 5A), which is sensible because only those two faunas are diverse enough to generate a signal after the Silurian. Importantly, the Paleozoic fauna's initial decline generates a long string of highly significant values in the Permian, just before the mass extinction. This pattern again shows that the *G*-statistic is sensitive enough to detect a faunal replacement in progress. However, there is relatively low volatility at the Permo-Triassic boundary, and hardly any volatility during the Triassic recovery.

One final episode of replacement is indicated by some marginally elevated, insignificant values during the latest Jurassic and early Cretaceous (Fig. 5A). These values illustrate the final decline of the Paleozoic fauna from its relatively small, short-lived peak in diversity during the late Jurassic. After this point the Modern fauna entirely dominates, so there is no real difference between average rates for each interval and the Modern fauna's own rate, and the *G*-statistic therefore always is nearly zero.

The uncoupled version of the model yields strikingly different predictions (Fig. 5B). Each fauna experiences higher-than-background volatility only during the major initial radiations and the rebounds from the two mass extinctions. Because the faunas all first appear at the same time and all suffer greatly during the same two extinction events, their volatility curves are largely synchronized. Thus, temporal overlap of volatility episodes is not prima facie evidence for dynamic interactions driven by ecological competition.

However, there are crucial differences between this pattern and the one predicted by logistic coupling: high volatility comes only when groups are in the peak phase of logistic diversification, which here happens shortly after the groups first appear in the Cambrian (~500 Ma), then again during the Modern fauna's peak diversification pulse (~400 Ma) and, finally, right after the Permo-Triassic mass extinction (~200 Ma). Thus, there are high volatility peaks in the mid-Paleozoic and early Mesozoic, which completely fail to match the large late Paleozoic (~250 Ma) peak and small late Mesozoic peak (~150 Ma) predicted by the coupled model. Additionally, peaks in *G*-values have different heights for different faunas (Fig. 5B), instead of matching perfectly during two clearly demarcated Paleozoic replacement episodes (Fig. 5A).

These simulated results make it very clear what Sepkoski would have predicted. (1) The replacement of the Cambrian fauna by the Paleozoic fauna should register with significant turnover volatility for both groups throughout the late Cambrian and Ordovician. This, however, might not say anything about dynamic interactions *per se*. (2) The Paleozoic-to-Modern handover also should result in high volatility for a long stretch of late Paleozoic time, after each group already has attained substantial diversity. (3) There need not be a short-term volatility spike around the Permo-Triassic mass extinction, or at the end of the Triassic. Indeed, Sepkoski (1996, p. 243) did say specifically that the rise of the Modern fauna was 'a process accelerated by, but not contingent upon, the end-Permian mass extinction'. (4) There should be a subtle elevation of turnover rates for both the Modern and Paleozoic faunas during the Jurassic and early Cretaceous – that is, somewhat before or overlapping with the Mesozoic marine revolution, which affected Modern groups starting in the Cretaceous (Vermeij, 1977; Bambach, 1999). Thus, Sepkoski's model arguably predicts that changes in the late Mesozoic were not a true revolution, but instead resulted from the long-term unfolding of fixed dynamic laws.

VOLATILITY OF MARINE EVOLUTIONARY FAUNAS

Composition of evolutionary faunas

To test the key predictions of the three-phase model, it is necessary to assemble sets of marine classes as stand-ins for Sepkoski's three evolutionary faunas. Sepkoski (1984) eventually did just that, but originally (Sepkoski, 1981) he treated his data in a completely different way. He first defined the three faunas on the basis of a factor analysis, and then estimated the diversity of each fauna by weighting his total family-level diversity curve by the appropriate factor scores. Although Sepkoski (1981, figure 5) listed the major classes constituting each fauna in his famous family-level curve, what each faunal curve actually represented was a linear combination of the diversity of every single class, with classes 'belonging to' a fauna merely being the classes whose diversity counts were most heavily weighted in this linear equation. In other words, this illustration – possibly the most widely reproduced figure ever published by a quantitative paleobiologist – started out as a mathematical abstraction.

Indeed, Sepkoski was very clear on the point that certain classes adhered to faunas more strongly than others, and that classes might even 'belong' to multiple faunas. For example, Bivalvia and Gastropoda are the two dominant members of the Modern fauna, but both of them also are minor constituents of the Paleozoic fauna (Sepkoski, 1981, table 1). On the flip side, some classes – each having very meagre diversity – are never more than minor elements in the first place. Obvious examples are Conodonta and Graptolithina, each of which belongs very weakly to both the Cambrian and Paleozoic faunas.

Despite the statistical ambiguity that Sepkoski justifiably favoured, there is no feasible alternative to treating evolutionary faunas as simple summations of class-level data sets. The reason is that although diversity *per se* can be estimated from factor scores, origination and extinction rates cannot; and the *G*-statistic depends on having exact estimates of turnover rates. I therefore computed joint diversity histories for the three faunas (Fig. 6) by following Sepkoski's favoured assignments of classes (Sepkoski, 1981, figure 5). This is exactly the procedure allowed by Sepkoski in his later papers (e.g. Sepkoski, 1984, 1997).

Sepkoski (1981, figure 5) appeared to list classes with factor scores >0.1 (Sepkoski, 1981, table 1), but left two groups out of the figure, presumably for artistic reasons. These groups are 'Hyolitha' (Cambrian fauna) and Hexactinellida (Modern fauna). Some groups listed as classes by Sepkoski (1981) are treated as phyla or otherwise redefined in the most recent version of his compendium (Sepkoski, 2002), but are analysed as 'classes' in this paper. These are 'Hyolitha' (Orthothecimorpha + Hyolithomorpha + several orders that are *incertae sedis*), 'Monoplacophora' (Tergomya + Helcionelloida + *incertae sedis* orders), 'Inarticulata' (Lingulata + Inarticulata + *incertae sedis* orders) and 'Stelleroidea' (= Asterozoa = Somasteroidea + Asteroidea + Ophiuroidea).

To maximize the statistical power of the results and the biological realism of the operative taxonomic units, I employed the latest genus-level version of the compendium (Sepkoski, 2002) instead of the original family-level version (Sepkoski, 1982). The new version employs an updated time scale that differs from that of Sepkoski (1981) most radically in the early Paleozoic. Admittedly, the genus- and family-level curves are distinct, with a much more pronounced Meso-Cenozoic radiation and higher variability overall in the genus-level data set (Sepkoski, 1997), However, both data sets qualitatively capture the same major transitions among taxonomic groups in relative diversity, and the use of genus-level data allows precise evaluations of minor classes such as the Hexactinellida that otherwise would have to be set aside.

To minimize possible impacts of short-term fluctuations in sampling regimes, I computed boundary-crosser diversity counts (Carr and Kitchell, 1980; Alroy, 1996; Alroy *et al.*, 2001) instead of the more conventional total counts of genera sampled in each bin. Concerns about biases in sampling (Raup, 1972; Sepkoski *et al.*, 1981) have returned to the forefront of paleobiological research in recent years, but Sepkoski's data lack the contextual information needed to standardize sampling intensity and restrict the data to particular environments and geographical regions (e.g. Alroy, 1996; Miller and Foote, 1996; Miller,

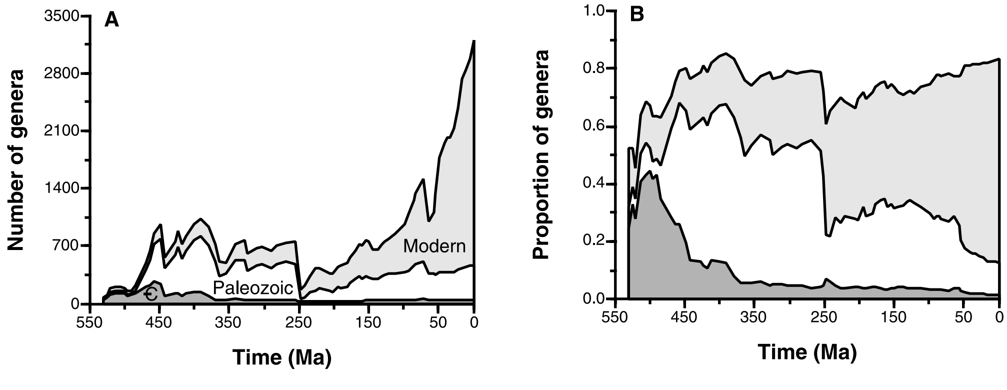


Fig. 6. Genus-level diversity of marine evolutionary faunas based on the latest version of Sepkoski's compendium (Sepkoski, 2002). (A) Boundary-crosser diversity, (B) proportional diversity. Microfossil classes (e.g. Radiolaria) and some small macrofossil classes are not placed in faunas, so proportions do not sum to unity.

1998; Alroy *et al.*, 2001; Smith, 2001; Crampton *et al.*, 2003). However, sampling biases are less likely to affect the proportional data used in this study than the absolute counts figuring in most macroevolutionary research. Key patterns found in this study also are at too great a temporal scale (i.e. comparisons of entire geological periods) to be dismissed easily as sampling artifacts.

The 21 groups placed by Sepkoski (1981) into the three faunas comprise 25,301 genera, 81.7% of the compendium's total of 30,984. These groups range in known diversity between 146 genera ('Hyolitha') and 3597 genera (Cephalopoda). Because the computation of turnover rates involves excluding singletons, only 13,093 genera out of 15,988 non-singleton genera (i.e. 81.9%) actually bore on the analysis.

Results

The focal-group *G*-statistic trends for the three evolutionary faunas show a series of clear and important patterns (Fig. 7A).

1. The Cambrian fauna exhibits very high volatility during its Cambrian increase, with much lower *G*-values during its largely Ordovician decline.
2. The Cambrian data are not mirrored by high *G*-values for the Paleozoic fauna, which exhibits high volatility only once its own massive radiation begins in the Ordovician.
3. Most of the Paleozoic and Mesozoic witnesses only sporadic volatility for any of the faunas, with no important surge during the Permian.

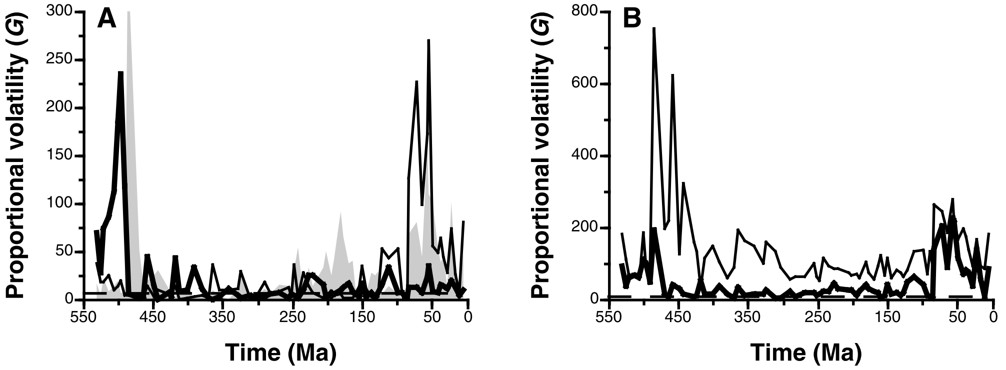


Fig. 7. Proportional volatility of the three marine evolutionary faunas, as computed from Sepkoski's genus-level compendium (Sepkoski, 2002). Data for each fauna are based on summed boundary-crosser diversities and turnover counts for classes composing it, as follows: Cambrian fauna = Trilobita, Polychaeta, 'Monoplacophora', 'Inarticulata', 'Hyolitha'; Paleozoic fauna = Articulata, Crinoidea, Ostracoda, Cephalopoda, Anthozoa, Stenolaemata, 'Stelleroidea'; Modern fauna = Gastropoda, Bivalvia, Osteichthyes, Malacostraca, Echinoidea, Gymnolaemata, Demospongia, Chondrichthyes, Hexactinellida. (A) Focal-group volatility of Sepkoski's three evolutionary faunas. Bold line = Paleozoic fauna; shaded area = Paleozoic fauna; thin line = Modern fauna; dashed line = upper 95% confidence interval for *G*-statistic with two degrees of freedom. (B) Total volatility of marine classes. Bold line = volatility of 21 classes after grouping them into evolutionary faunas; thin line = volatility of 21 major orders treated separately.

4. Volatility also is relatively low right around the Permo-Triassic extinction, suggesting that this event was not strongly selective at the level of evolutionary faunas.
5. The Paleozoic fauna experiences high volatility throughout the Triassic and Jurassic, but not the Cretaceous, and the pattern is not mirrored by the one seen for the Modern fauna.
6. Both faunas are volatile in the very late Cretaceous and Paleogene.
7. The Modern fauna generally has lower volatility than the Paleozoic fauna, but starting in the late Cretaceous it shows persistently very high volatility.

Similar problems are revealed by a separate analysis that contrasts overall class-level volatility with volatility of the three evolutionary faunas when considered simultaneously (Fig. 7B). Although the three-fauna scheme captures the initial Cambrian radiation, it consistently under-represents volatility throughout the rest of the Paleozoic and most of the Mesozoic. Indeed, it suggests that nearly nothing important was happening during that long stretch of time, when in fact very high class-level volatility was present during such intervals as the Carboniferous. Only the elevated class-level turnover during the latest Cretaceous and Cenozoic (<100 Ma) is captured by the three-way scheme. Indeed, *G*-values for the three-fauna data are so low that they even fail to exhibit the mid-Paleozoic and early Mesozoic spurts of volatility predicted by a model in which each fauna undergoes independent, but strongly constrained, logistic diversification (Fig. 5B).

These patterns are not very encouraging. Some of them are broadly consistent with the three-phase model: early Paleozoic volatility of the Cambrian and Paleozoic faunas, and coincident volatility of the Paleozoic and Modern faunas during certain intervals. However, the Cambrian and Paleozoic volatility bursts are non-overlapping; the clearly predicted spurt of volatility shortly before the Permo-Triassic extinction (Fig. 5A) is not seen at all; and if any 'replacement' of the Paleozoic fauna by the Modern fauna occurred, it seems to have been delayed all the way into the Cenozoic (<65 Ma).

All of these patterns differ considerably from the mirror-image volatility curves for pairs of competing groups that were predicted (Fig. 5A) by Sepkoski (1984). Unless Sepkoski's coupled model somehow could be reformulated to predict asymmetrical volatility responses to replacement episodes, it makes more sense to interpret the data as reflecting episodic evolutionary innovations and/or environmental shifts that favoured radiating groups but had little impact on decoupled holdover groups. Specifically, the Cretaceous–Cenozoic radiation of Modern classes came much later than Sepkoski's model would predict, and it was greatly offset from any major mass extinction. Thus, the Mesozoic marine revolution (Vermeij, 1977) seems to have resulted from a basic alteration of the underlying dynamical regime, not just from the gradual operation of constant laws. In any case, the generally ambiguous results prompt an obvious question: is there any dynamic coherence at all to the classes that make up the evolutionary faunas?

VOLATILITY OF INDIVIDUAL MARINE CLASSES

Time series data for marine classes

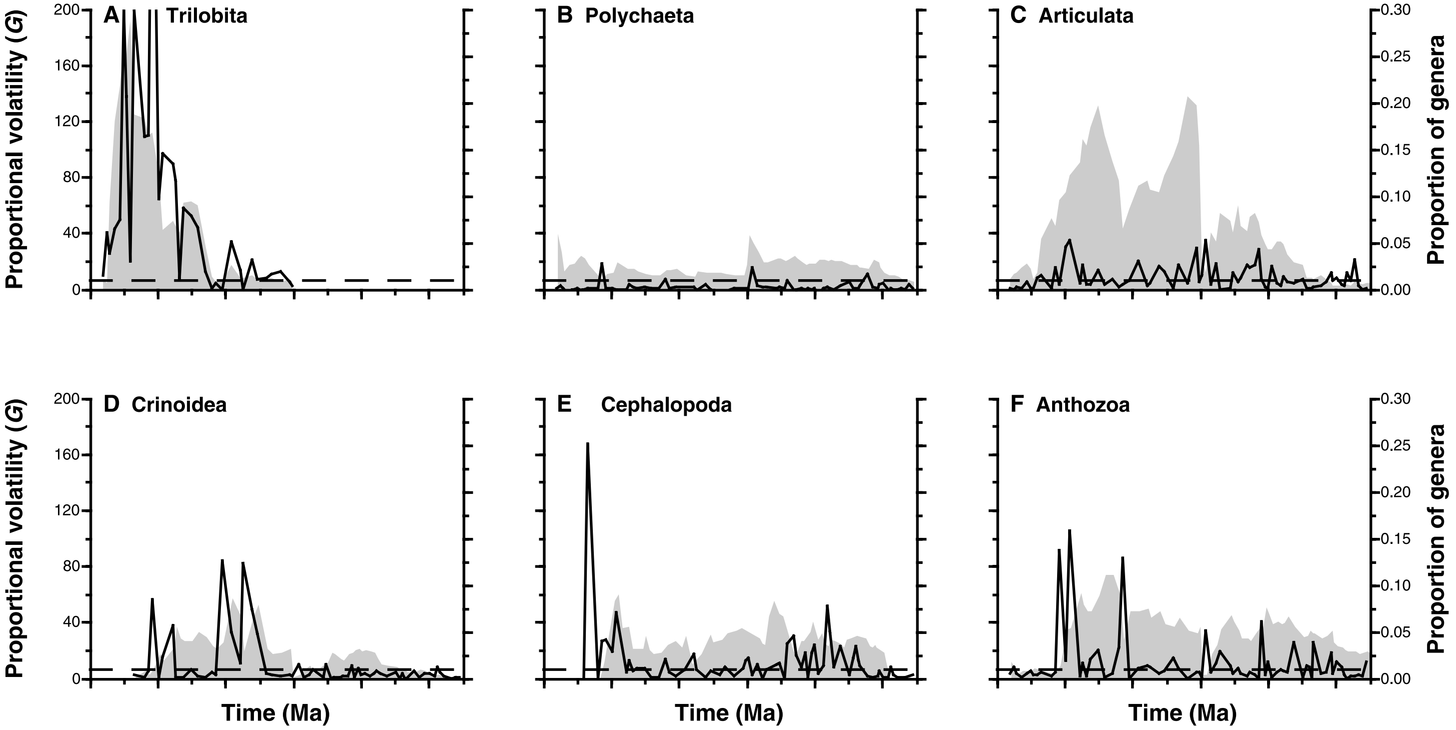
Separate focal-group volatility analyses of the major classes constituting the evolutionary faunas (Fig. 8) show a surprising range of patterns. Pronounced volatility for the Trilobita (Fig. 8A) is not mirrored by the Polychaeta (Fig. 8B), even though both belong to the Cambrian fauna. Within the Paleozoic fauna, several groups do show high volatility during the Ordovician radiation, including the Crinoidea, Cephalopoda, Anthozoa and Stenolaemata (Fig. 8D–G). However, volatility for the Articulata, the key component of this fauna, is remarkably low during this same interval (Fig. 8C). Thus, the volatility analysis suggests that the Cambrian-to-Paleozoic replacement episode mainly involved Trilobita and several secondary Cambrian and Paleozoic groups. Meanwhile, it is hard to discern a clear signature of the predicted late Paleozoic hand-off between the Paleozoic and Modern faunas. Volatility is generally low for all groups during the last 100 million years before the Permo-Triassic extinction, and peak volatility in all of the Modern classes comes much later. Importantly, as with the summed Modern fauna data (Fig. 7A), almost all of the Modern classes (Fig. 8H–L) exhibit high volatility during the late Cretaceous and Cenozoic, not only much later than the predicted Permian replacement, but shortly after Sepkoski's predicted second wave of replacement during the late Jurassic and early Cretaceous (Fig. 5). Finally, some idiosyncratic patterns are highly visible, such as pronounced volatility of the Crinoidea during its Carboniferous diversity peak.

Multivariate analytical methods

The results to this point may seem ambiguous as a critique of Sepkoski's three-fauna scheme. First, it is possible that placing classes into faunas strictly by following Sepkoski (1981) has somehow obscured the predicted dynamic pattern (Fig. 5A), which might have appeared with slightly different assignments. Second, visual inspection of individual volatility curves (Fig. 8) is not a rigorous way to show whether these patterns sort easily into three broader categories. The best way to address these concerns is to use multivariate analysis to illustrate broad dynamic themes and variations across the classes.

Numerous multivariate methods could be employed for this purpose. Sepkoski himself might have favoured factor analysis (e.g. Sepkoski, 1981). However, factor analysis and related methods assume linear responses of variables to underlying gradients (ter Braak, 1995), whereas we might reasonably expect temporally non-linear, modal responses as episodes of replacement affect the marine biota. For example, a hand-off between two evolutionary faunas might be marked by a temporary elevation in volatility, with low volatility before and after. These sorts of modal responses are best summarized with the widely used method of correspondence analysis, which I implement here by applying standard reciprocal averaging algorithms (Hill, 1973; ter Braak, 1995) to a full matrix of focal-group *G*-statistic values.

Another plausible approach would be to apply correspondence analysis directly to the turnover rate data, instead of the *G*-statistics. This might seem appealing because (1) the *G*-statistic is distributed as chi-square (Sokal and Rohlf, 1995, p. 691) and (2) correspondence analysis is a special case of generic multidimensional scaling in which the implicit dissimilarity metric is the chi-square distance (ter Braak, 1995, p. 152). Hence, it may seem that applying correspondence analysis to a matrix of *G*-statistics is redundant. Nonetheless, there are several reasons to take this approach. First, the *G*-statistics are a joint function of separately predicted origination and extinction rates (Alroy, 2000, eqn. 19), but correspondence analysis of a raw turnover rate matrix would require predicting a single, summed turnover rate, thereby obscuring the difference between high turnover in general and specific episodes of not merely high but unpredictable origination or extinction rates. Second, a direct correspondence analysis of the turnover rates would involve predicting the cell



A Trilobita
B Polychaeta
C Articulata
D Crinoidea
E Cephalopoda
F Anthozoa
Proportional volatility (*G*)
0
40
80
120
160
200
Proportion of genera
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Time (Ma)

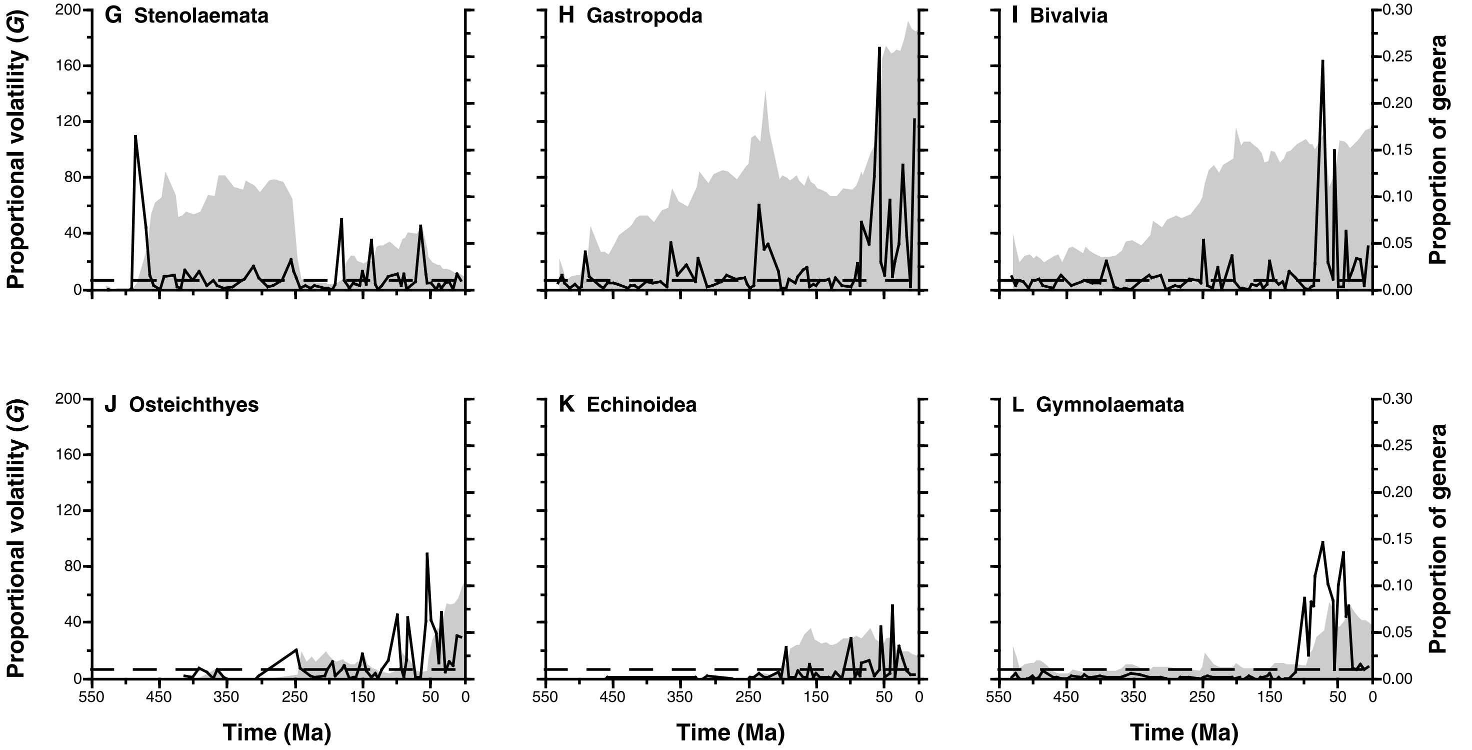


Fig. 8. Proportional volatility of selected marine classes. Thin black lines show focal-group proportional volatility *G*-statistics; shaded areas show proportional genus-level diversity derived from the final version of Sepkoski's compendium (Sepkoski, 2002). (A) Trilobita, (B) Polychaeta, (C) Articulata, (D) Crinoidea, (E) Cephalopoda, (F) Anthozoa, (G) Stenolaemata, (H) Gastropoda, (I) Bivalvia, (J) Osteichthyes, (K) Echinoidea, (L) Gymnolaemata.

values based on the unweighted arithmetic means of the row (temporal interval) and column (taxon) totals – but within a temporal interval, the overall turnover rate should be a weighted function of the diversities of each taxon, as with the *G*-statistic used here. Third, the question at hand is to summarize the individual *G*-statistic patterns (Fig. 8), so it is more sensible to analyse those patterns directly.

One minor complication is the presence of 217 missing values in the data matrix, which includes 1554 cells overall because there are 74 time intervals and 21 taxa. These missing values denote times when groups either already were extinct or had not yet appeared. By default, correspondence analysis treats missing values as if they were zero, which could generate spurious results because taxa sharing many identical, missing values will tend to group strongly. Therefore, the reciprocal averaging algorithm was modified to downweight rows or columns with missing data, rescaling the sums of products obtained in each averaging cycle by the factor $(n + 1 - m)/(n + 1)$, where $n =$ the number of rows or columns and $m =$ the number of missing cells in the column or row. Similar results were obtained by excluding combinations of time intervals and taxonomic groups that were responsible for large numbers of missing cell values, or by substituting missing values with 1.39, the median expected value of the *G*-statistic given two degrees of freedom.

Results of correspondence analysis

A scree plot (Fig. 9) suggests that only the first two axes are definitely meaningful, although the next five stand out a bit. By contrast, three axes were interpeted by Sepkoski (1981, figure 2) in his principal components analysis of raw diversity counts. Furthermore, the marine classes were much better separated on Sepkoski's first axis than on the one obtained here, and the exact meaning of the correspondence analysis axes is substantively different. Axis 1 (Fig. 10) does seem to separate key members of the three faunas in rough succession: the Cambrian group 'Inarticulata' has the lowest score by a large margin, all of the other Cambrian and Paleozoic fauna members apart from Polychaeta and 'Stelleroidea' have strongly negative scores, and six of the nine Modern classes have strongly positive scores.

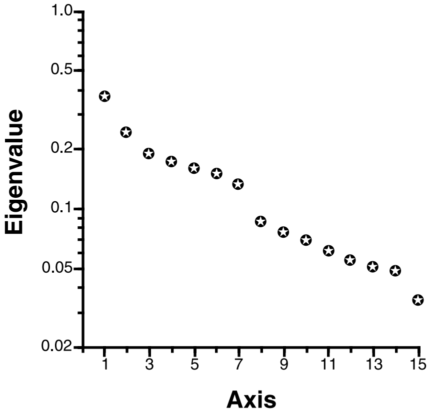


Fig. 9. Eigenvalues of the first 15 axes derived by correspondence analysis of proportional volatility data for marine classes.

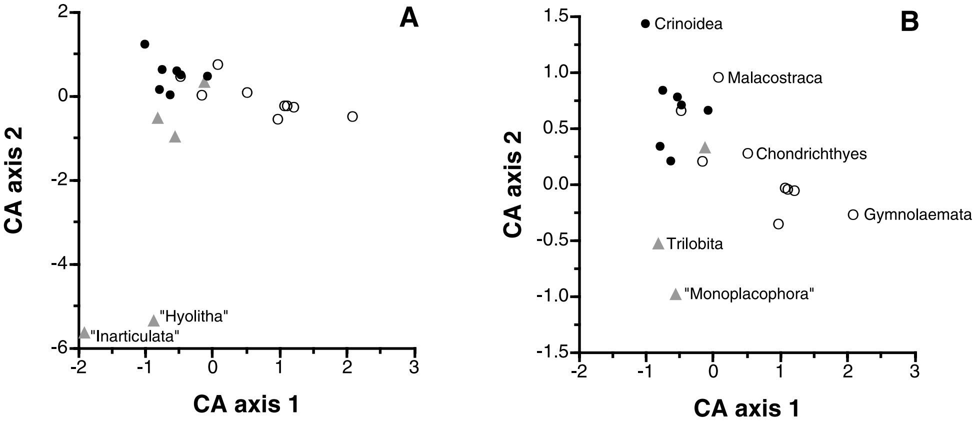


Fig. 10. Correspondence analysis of proportional volatility data for marine classes, based on Sepkoski's genus-level compendium. Grey triangles = Cambrian fauna; solid circles = Paleozoic fauna; open circles = Modern fauna. Classes with outlying axis scores are labelled. (A) Plot of all points. (B) Plot with expanded y-axis, omitting two Cambrian classes.

Axis 2 seems primarily to emphasize the distinctness of Sepkoski's Cambrian evolutionary fauna, with two Cambrian classes (Lingulata and 'Hyolitha') receiving very negative scores, while most others cluster in a relatively narrow range (Fig. 10A). The axis also increases the separation of several Cambrian groups (e.g. Trilobita and 'Monoplacophora') and Modern groups from the central cluster that includes most of the Paleozoic classes. There is, however, a clear warning sign: the Cambrian class Polychaeta and the supposed Modern classes Malacostraca, Demospongia and Hexactinellida all fall squarely in the same small region as the Paleozoic classes, while the Modern class Chondrichthyes falls in between the Paleozoic and Modern clusters (Fig. 10B). Axis 2 also pulls Crinoidea far out from the Paleozoic region, which makes sense given its unusually high Devonian and Carboniferous volatility (Fig. 8D).

The remaining axes typically serve to pick out small sets of contrasting groups: Crinoidea *vs* Cephalopoda and Stenolaemata (axis 3), Crinoidea *vs* Anthozoa, Demospongia and Hexactinellida (axis 4), Gastropoda *vs* Echinoidea and 'Stelleroidea' (axis 5), Trilobita *vs* 'Hyolitha' (axis 6), or Bivalvia *vs* Gymnolaemata (axis 7). Some of these axes are likely to represent taphonomic or monographic signals, with easily preservable groups such as molluscs being contrasted against fragile or taxonomically complex groups such as bryozoans or echinoderms.

In summary, the correspondence analysis of turnover volatility broadly confirms the three-fauna model. However, there are many difficulties. Most of the Cambrian classes are dynamically distinct, not just from the other classes but to a large extent from each other (see also Miller, 1998, 2000). Polychaeta is closer to the Paleozoic than Cambrian faunal elements, and separation of minor Modern classes such as Malacostraca from the Paleozoic fauna also is not very clear. Finally, Crinoidea demonstrates such a distinct pattern that it may not be very helpful to include it with so many other classes in the central Paleozoic cluster. All of this fine-scale variation simply is not addressed by the fundamentally typological three-phase model, and it suggests that crafting rigid deductive hypotheses about discrete faunal categories may not be the most helpful way to conceptualize macro-evolutionary processes. Instead, it may be more fruitful to discuss continuous gradients of dynamical behaviour, with most groups having intermediate patterns.

CONCLUSIONS

This paper's results do strongly reinforce Jack Sepkoski's core argument that macro-evolutionary patterns at high taxonomic levels are just not random (e.g. Sepkoski, 1978, 1979, 1981, 1984). Specifically, there is good evidence for protracted radiations and declines of major groups, such as the dramatic Cambro-Ordovician rise and fall of the trilobites, and the marked proportional diversification of the Modern fauna that erupted in the late Cretaceous and Cenozoic. This general result strongly confirms the utility of Sepkoski's general approach, which broke ground by tying the idea of taxonomic replacement to the dynamic methodology of coupled logistic equations (Sepkoski, 1979, 1984; Miller and Sepkoski, 1988; Sepkoski *et al.*, 2000). To put this point in perspective, one should note that when Sepkoski began his research in the wake of the classic simulation model of Raup *et al.* (1973), completely random macro-evolutionary processes were greatly in vogue. Indeed, the classic factor analysis of Flessa and Imbrie (1973) was dismissed by some critics (Smith, 1977) exactly because of this sceptical, stochastic mindset.

However, general confirmation of Sepkoski's ideas does not translate into specific support for the three-phase kinetic model. It is not true that turnover rates for individual classes sort easily into three common patterns (Sepkoski, 1981); instead, several classes exhibit idiosyncratic trajectories (Fig. 8), and classes are best thought of as falling on a continuous gradient between Paleozoic and Modern dynamic syndromes (Fig. 10). It is not true that major episodes of turnover volatility are confined to a few periods of time (Sepkoski, 1984); instead, steady replacement is seen in almost every period, and much of this pattern is poorly described by assigning classes to just three clusters (Fig. 7B). It is not true that the Ordovician stands out as an interval of consistently high volatility in both Cambrian and Paleozoic groups (Fig. 7A), which casts doubt on the existence of separate Cambrian and Paleozoic faunas (Sepkoski, 1978) and on the hypothesis that replacements of faunas often are mediated by mass extinctions (Miller, 1998, 2000). And it is not true that either the Permian or mid-Mesozoic witnessed high volatility of classes belonging both to the Paleozoic or Modern faunas (Fig. 7A), these being the two key periods in which most of the replacement supposedly occurred (Sepkoski, 1984).

However, the largest problem with the three-phase model presented by the volatility data is the permanent elevation in turnover rates of Modern classes (Figs. 7, 8), which began in the Cretaceous (Bambach, 1999) and corresponded to the Mesozoic marine revolution (Vermeij, 1977). This dramatic pattern has little to do with the replacement of nominal Paleozoic classes, and was not predicted directly by any of the specific models or analyses that Sepkoski originally presented (Sepkoski, 1981, 1984, 1996; Miller and Sepkoski, 1988; Sepkoski *et al.*, 2000; see Fig. 5A).

By default, the results strongly imply that the Mesozoic marine revolution must have involved a fundamental change in the rules of Sepkoski's great game – a major evolutionary innovation, a major shift in biogeographic or environmental circumstances, a sampling artifact, or a combination of the three. A case for sampling could be made by noting that global sampling improves dramatically during the Cretaceous and Cenozoic (Raup, 1976; Alroy *et al.*, 2001; Crampton *et al.*, 2003; but see Smith, 2001). If rare species tend to have high extinction rates (Cheetham and Jackson, 1996; Jones *et al.*, 2003), then one would expect higher apparent turnover at such times of improved sampling.

Sepkoski, in fact, was well aware of Vermeij's hypothesis, but thought it was 'consistent with the formal structure of the three-phase kinetic model' (Sepkoski, 1984, p. 253; see also Sepkoski, 1981, p. 51), which after all did predict rapid diversification of Modern groups during the Cretaceous. The only indication that Sepkoski recognized a potential conflict came years later, when he failed to model high mid-Cretaceous diversification rates in cyclostome bryozoans, but then dismissed this single anomaly as a possible sampling artifact (Sepkoski *et al.*, 2000, p. 14). In retrospect, Sepkoski's position is entirely understandable given the limitations of analysing diversity patterns without controlling for variance in turnover rates among groups and among time intervals, as the proportional volatility statistic now permits.

The mismatch between Sepkoski's evolutionary fauna model and his own empirical data still may seem startling. However, Sepkoski himself might not have been surprised by it, because his style of science was to keep evolutionary models at a healthy distance from the vagaries of the fossil record. Indeed, he repeatedly cautioned against fitting models directly to fossil data, arguing that sampling problems and other statistical artifacts could create spurious 'significance' and erroneous parameters (Sepkoski, 1978, 1979); he intentionally made his onshore–offshore diversification model as schematic as possible, because his main goal was to prove the concept, not to fit some set of data (Sepkoski, 1991); and he repeatedly brought up the point that his coupled logistic equations could take on many different parameters and still accurately predict qualitative trends (Sepkoski, 1979, 1984, 1996; Miller and Sepkoski, 1988).

Indeed, the real importance of Sepkoski's work was to present a new paradigm: diversity dynamics, a field of study that would not have come into existence without Sepkoski's trail-blazing work. In light of that accomplishment, Sepkoski's classic papers on the three evolutionary faunas now seem most important because of the way they used data not to prove specific empirical hypotheses, but to illustrate mathematically grounded concepts of process and causality: density dependence of turnover rates, which may cause logistic diversification (Sepkoski, 1978); coupling of dynamic equations, which may cause long-term taxonomic replacements (Sepkoski, 1979) and unexpected patterns in recoveries from mass extinctions (Miller and Sepkoski, 1988; Sepkoski, 1996); differences in r- and K-values, which may cause temporally staggered diversity peaks and superficial diversity plateaus (Sepkoski, 1984); hand-offs between dynamically distinct groups (e.g. Miller and Sepkoski, 1988; Sepkoski *et al.*, 2000), which may cause non-linear density dependence patterns (Sepkoski, 1979) and long-term extinction rate declines (Sepkoski, 1984); and short-term excursions in equilibrium diversity levels, which may cause mass extinctions (Sepkoski, 1984). The three great evolutionary faunas may lack distinct and cohesive diversity dynamics and, therefore, may largely be epiphenomena of mass extinctions. Nonetheless, Sepkoski's dynamic approach to macro-evolution will stand forever as one of the most important advances in the theory of paleobiology.

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