

## Modeling bivalve diversification: the effect of interaction on a macroevolutionary system

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*Abstract.*—The global diversification of the class Bivalvia has historically received two conflicting interpretations. One is that a major upturn in diversification was associated with, and a consequence of, the Late Permian mass extinction. The other is that mass extinctions have had little influence and that bivalves have experienced slow but nearly steady exponential diversification through most of their history, unaffected by interactions with other clades. We find that the most likely explanation lies between these two interpretations. Through most of the Phanerozoic, the diversity of bivalves did indeed exhibit slow growth, which was not substantially altered by mass extinctions. However, the presence of “hyperexponential bursts” in diversification during the initial Ordovician radiation and following the Late Permian and Late Cretaceous mass extinctions suggests a more complex history in which a higher characteristic diversification rate was dampened through most of the Phanerozoic. The observed pattern can be accounted for with a two-phase coupled (i.e., interactive) logistic model, where one phase is treated as the “bivalves” and the other phase is treated as a hypothetical group of clades with which the “bivalves” might have interacted. Results of this analysis suggest that interactions with other taxa have substantially affected bivalve global diversity through the Phanerozoic.

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Accepted: August 19, 1988

### Introduction

The global Phanerozoic diversification of the class Bivalvia has been a contentious subject among paleobiologists (e.g., Gould and Calloway 1980). While general attributes of the group's overall history are now reasonably well understood, the evolutionary underpinning of this diversification remains enigmatic.

Bivalves first appeared in the Early Cambrian (Runnegar and Pojeta 1974; Pojeta 1975), underwent an initial radiation in the Ordovician (Pojeta 1971, 1978), and then diversified slowly and somewhat irregularly through the balance of the Paleozoic. Following the Late Permian mass extinction, through which they fared better than most other Paleozoic faunal elements, bivalves increased greatly in taxonomic numbers through the Mesozoic and became one of the most diverse marine classes in the Cenozoic (Nevesskaya 1972; Newell and Boyd 1978; Hallam and Miller 1988). This post-Paleozoic expansion has received two conflicting interpretations. One view is that it was mainly a consequence of ecospace-

clearing by the Late Permian mass extinction, which permitted bivalves to increase their diversification rate with a kind of macroevolutionary opportunism (Steele-Petrović 1979; Gould and Calloway 1980). The other interpretation is that bivalves experienced a slow but nearly steady diversification throughout most of their history, little affected by the waxing and waning of other groups and only minimally affected by mass extinctions (Stanley 1977, 1979, 1985).

Both of these alternatives have figured prominently as examples in more general macroevolutionary debates. Gould (1985) has cited the first interpretation as an example of the central importance of mass extinctions in altering the direction of evolution. Stanley (1977, 1979, 1985), on the other hand, has favored the second interpretation as an illustration of how diversification of a higher taxon proceeds when interspecific competition is weak.

In this paper, we present a further evaluation of bivalve diversification and suggest that neither of these interpretations is entirely correct. An assessment of bivalve ge-

neric diversity through the Phanerozoic indicates that the class did diversify at an approximately exponential rate throughout much of the time since its initial radiation in the Ordovician. However, "hyperexponential bursts" of diversification during the Ordovician radiation and after the Late Permian and Late Cretaceous mass extinctions suggest that a simple exponential model does not adequately describe bivalve history. We show that a coupled logistic model better fits both the long-term exponential diversification and the short-term bursts. This leads to the conclusion that interactions with other taxa may have impeded the diversification of bivalves throughout most of the Phanerozoic.

### Bivalve Generic Diversity

The generic diversity of bivalves from the Ordovician to the present is illustrated in Fig. 1A. Data for this graph were taken from an unpublished compilation of the stratigraphic ranges of marine genera by Sepkoski (see Sepkoski 1986; diversity data used in construction of the graph are available upon request). These new data show that bivalve diversification was indeed limited through most of the Paleozoic, but experienced a substantial upturn in the Mesozoic and especially the Cenozoic. However, on semi-logarithmic coordinates, these same data show that bivalve diversification was much more continuous across the eras of the Phanerozoic, as illustrated in Fig. 1B. The slope of a diversity curve is proportional to the per-taxon rate of diversification on semi-logarithmic graphs. Thus, Fig. 1B indicates that the per-genus rate for bivalves remained virtually constant over long intervals of the Phanerozoic as emphasized by the dashed best-fit line. Hence, the per-genus rate established in the Paleozoic persisted into the post-Paleozoic, as argued previously by Stanley (1977, 1979, 1985). The post-Paleozoic increase in the total rate of diversification (Fig. 1A) is simply the expectation of an exponential diversification.

However, there are several features in Fig. 1B that suggest a more complex history for bivalves. In particular, there are three intervals in which bivalves exhibited markedly higher per-genus diversification rates: the

Ordovician during their initial radiation, the Early and Middle Triassic during their rebound from the Late Permian mass extinction, and the early Tertiary during their rebound from the terminal Cretaceous extinction. These accelerations of diversification all have approximately the same magnitude and indicate that the rate of long-term exponential diversification was lower than the maximum rate that bivalves potentially could display. Thus, a simple exponential model is misleading in this instance. But, as discussed below, it is possible to describe a pattern of intermittent "hyperexponential bursts" on a background of slower, exponential diversification with coupled (i.e., interactive) logistic models of the type used by Sepkoski (1979, 1984) and Kitchell and Carr (1985) to analyze total familial diversity through the Phanerozoic.

### Diversification Model

The basic premise of a coupled logistic model is that two or more components ("phases") in an evolutionary system are diversifying simultaneously. The coupled model assumes that each diversifying phase expands logistically, governed by a fundamental diversification rate and an equilibrium particular to the phase. It further assumes that the diversity of each phase negatively affects all others, dampening their realized rates of diversification.

The discrete-time equation for a single phase in the coupled logistic system, used in numerical solutions of diversification with respect to time, can be written as

$$D_t = D_{t-1} + [(k_s - aX_{t-1}) - (k_e + bX_{t-1})] * D_{t-1} \quad (1)$$

where  $D_t$  is the diversity of the phase at time  $t$ ,  $D_{t-1}$  is the diversity of the phase in the previous time unit,  $X_{t-1}$  is the summed diversity of all simultaneously diversifying phases in the solution,  $k_s$  is the phase's initial per-taxon rate of origination,  $k_e$  is the phase's initial per-taxon rate of extinction, and  $a$  and  $b$  are the slopes, respectively, of the phase's per-taxon origination and extinction functions (see Sepkoski 1979; Kitchell and Carr 1985). When the value  $X_{t-1}$  is low (for ex-

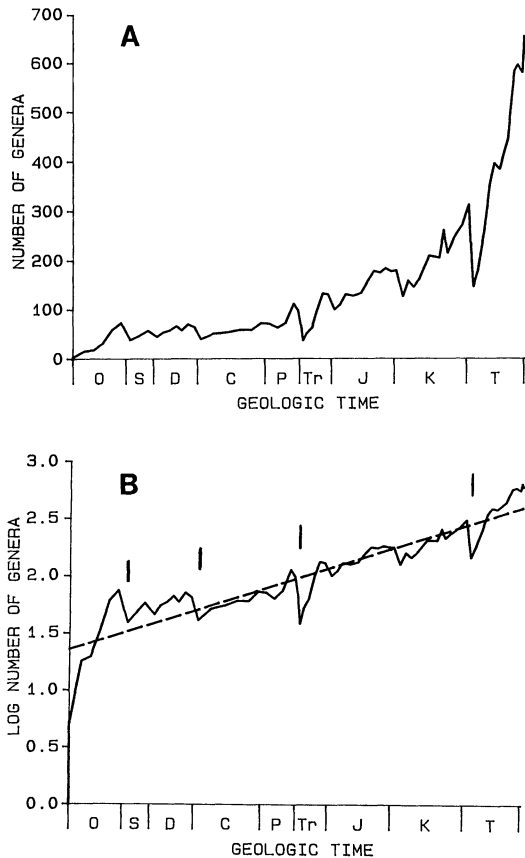


FIGURE 1. Diversity of bivalve genera from the Ordovician to the Recent. A, Diversity is plotted on an arithmetic ordinate, exhibiting dramatic increase in the post-Paleozoic and especially in the Tertiary. B, Diversity is plotted on a logarithmic ordinate, illustrating the approximately exponential nature of bivalve diversification in the post-Ordovician. The dashed line is a least-squares fit of a simple exponential function to all data. There are three intervals in this graph during which the per-genus rate of diversification was substantially greater than that suggested by the fitted line: the Ordovician, the Early and Middle Triassic, and the early Tertiary; slopes of exponential fits to diversity during these intervals are 0.021, 0.029, and 0.020 genera per genus-million years, respectively. The slope of the best-fit line to the entire curve is 0.0025, nearly an order of magnitude smaller. All data are resolved to the level of stratigraphic stage. Vertical tick marks delineate the four intervals of mass extinction discussed in the text.

ample, early in the solution or following a major "mass extinction"), diversification of a phase will not be substantially influenced by that of other phases. However, when summed diversity is high, origination rates may be markedly lower and extinction rates markedly higher than they would be in a non-

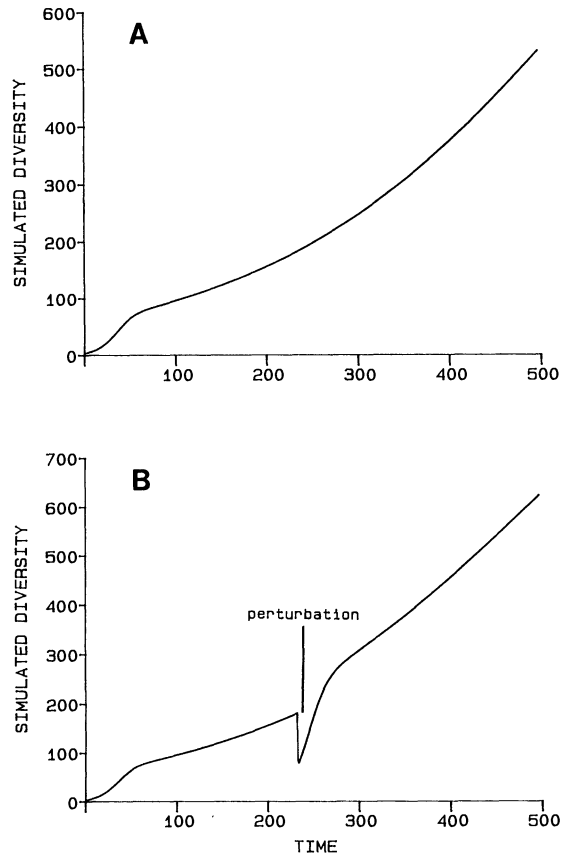


FIGURE 2. Solutions for one phase of a two-phase coupled (interactive) logistic model. A, Model without mass extinction. Note that the illustrated phase diversifies rapidly for 36 time units, but then drops off to a slower, approximately exponential increase that continues through the remainder of the simulation. B, Model with a mass extinction (perturbation) at 233 time units, resulting in a diversity decline of 56%. Diversity rapidly rebounds after the mass extinction and then continues its approximately exponential growth to the end of the simulation.

interactive system, thereby impeding or even reversing diversification.

Figure 2A displays part of a solution for a two-phase coupled logistic model in which the illustrated phase was treated as the "bivalves" and the other phase as a hypothetical group of clades with which they might have interacted. In this simulation, the following parameters were used (a similar pattern could potentially have been generated using other values; see Discussion):  $D_0 = 4$ ,  $k_s = 0.083$ ,  $k_e = 0.003$ , and  $a = b = 0.000035$  for the illustrated phase; and  $D_0 = 20$ ,  $k_s = 0.2$ ,  $k_e = 0.09$ , and  $a = b = 0.0000515$  for the second phase

(not shown). Thus, for time zero, the illustrated phase was assigned a lower per-taxon diversification rate, but higher equilibrium  $[= (k_s - k_e)/(a + b)]$ . The simulation was run through 496 time units, the approximate number of million-year increments from the Ordovician to the Recent.

Early in the solution, the illustrated phase diversified at a high rate, near what would be expected from its fundamental diversification rate. This expansion was soon impeded, however, because of the more rapid diversification of the other phase. The illustrated phase then continued to diversify, albeit much more slowly, as it gradually crowded out the second phase by virtue of its higher equilibrium. Thus, the overall pattern of the illustrated phase is one of initially rapid diversification, followed by slower, nearly exponential growth, which is notably reminiscent of the observed diversification for bivalves. The Ordovician was a time of rapid radiation, bivalves included, into a relatively low diversity world. By the time the Ordovician ended, the diversification rate of bivalves may have been dampened as marine habitats became more crowded with other taxa, and a slower, approximately exponential rate was maintained for most of the remaining Phanerozoic.

The interactive system can also describe the rapid recoveries of bivalve diversity after mass extinctions. Figure 2B illustrates a model with the same parameter values as in Fig. 2A, but with a major mass extinction simulated near the halfway mark in time, about where the Late Permian event would occur. The mass extinction was incorporated by increasing the slope of the extinction function of the illustrated phase to 0.000525 and that of the second phase to 0.000770 at 233 time units for a total of two time units (see Sepkoski 1984 and Kitchell and Carr 1985 for discussions concerning incorporation of mass extinctions). This perturbation caused both phases in the system to lose considerable diversity and to fall substantially below their respective equilibria. After the perturbation, both phases rediversified rapidly, again near their fundamental diversification rates, until the system again became crowded; thereafter, the illus-

trated phase once more began a slow, nearly exponential increase. Such a rapid recovery could not take place in a simple exponential system characterized by the slow diversification rate that bivalves exhibited through most of the Phanerozoic; a perturbation would merely displace the long-term exponential diversification downward.

In Fig. 2B, the diversity attained by the illustrated phase upon recovery from the perturbation is actually slightly above the track of the unperturbed solution in Fig. 2A. This discrepancy, however, is dependent solely on parameter values. By tuning the parameters and the time of perturbation, post-recovery diversity can be directed above, on, or even below the initial trajectory. A similar variety seems to occur in the observed diversification of bivalves (Fig. 1B): after both the Late Ordovician and the Late Devonian mass extinctions, bivalve diversity recovered to levels lower than expected from previous history, but after the end-Cretaceous mass extinction, it recovered to a level slightly higher than expected.

### Discussion

The coupled logistic model with perturbations accounts for many of the patterns seen in bivalve diversification, but it must be emphasized that the model presented here is strictly heuristic. We have not attempted to tune parameters precisely to what might be measured for bivalves, to simulate all extinction events, or to duplicate the exact path of bivalve diversification. Indeed, the apparent path may, in part, be the consequence of a poor fossil record. Most notably, because of spotty preservation in the Lower Triassic and Paleocene, diversity perturbations associated with the Late Permian and Late Cretaceous mass extinctions might not have been as severe as depicted in Fig. 1 (see Nakazawa and Runnegar 1973). Nevertheless, given the heightened overall percentages of generic extinction exhibited during these intervals (Sepkoski 1986), it is unlikely that the diversity perturbations would disappear entirely if the record were better. The diversity curve would almost certainly continue to exhibit some degree of decline and rebound at rates

exceeding "background" diversification. A coupled logistic model, based on the same principles and exhibiting the same features as before, could still be constructed to account for them. The purpose of the model was to evaluate particular patterns characteristic of the diversity curve; the absolute diversity values for both the real and simulated curves are not of major consequence in this instance. Similar patterns could have been developed using other values for model parameters, but the underlying necessity for a *coupled* logistic model would remain.

Furthermore, we do not mean to suggest that the second phase in the model represents any real, monophyletic group interacting with bivalves. What this exercise provides is a clearer understanding of patterns that cannot be explained by a simple exponential model that does not accommodate interaction. The superior fit of the interactive model, particularly to the "hyperexponential bursts," suggests that the observed pattern of bivalve diversification cannot be interpreted as evidence for unconstrained radiation into essentially unoccupied adaptive space. Rather, it appears that bivalves were interacting with other taxa in such a way that their realized diversification rate was constrained below the fundamental rate of their initial diversification.

An objection that could be offered to this analysis is that bivalve diversification was evaluated at the genus level rather than with species, the real units of evolution. This is of potential importance because a species-level curve, which cannot be constructed at the present time, might show neither a post-Ordovician inflection nor other attributes that we recognize as major features of this diversification. While the possible significance of this general objection cannot be denied, there is reason to believe that it is not of major consequence in this instance. Previous studies have demonstrated an underlying correspondence between patterns of global Phanerozoic diversification evaluated at the familial-, generic-, and species-levels (Sepkoski et al. 1981; Sepkoski 1984; however, see Signor 1985 for a counterexample). Moreover, analyses of diversification at higher taxonomic levels tend to dampen variation, especially

in mass extinction, recognized with species-level data (Sepkoski 1984). Coupled with recognition of a post-Ordovician inflection in the familial-level curve presented by Hallam and Miller (1988), these observations suggest that the inflection transcends the peculiarities associated with any single taxonomic level and, if anything, would be more pronounced for species. Thus, it is reasonable to infer that patterns described and evaluated in this study would be recognized with species-level data.

### Conclusions

On the basis of this analysis of bivalve global diversification, the following conclusions are offered:

1) The per-genus diversification rate established among bivalves in the Paleozoic was maintained in the Mesozoic, which indicates that the Late Permian mass extinction did not have a long-term impact on the global history of the class.

2) The diversification rate of bivalves was substantially higher than the normal "background" level during the early radiation of the group and immediately following mass extinctions, suggesting that bivalves have not undergone a simple, unencumbered exponential diversification through the Phanerozoic.

3) The success of the coupled logistic model in accounting for the observed characteristics of bivalve diversification suggests that interactions with other taxa have played important roles in the global history of the group.

### Acknowledgments

We thank J. A. Kitchell, D. L. Meyer, T. Oji, J. Pojeta, Jr., S. M. Stanley, and R. Terry for critiquing earlier versions of this manuscript. This research received partial support from NASA grant NAG 2-282 to JJS.

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