An Exponential Pattern for Diversification of Marine Animal Taxa Since Early Paleozoic Time

Steven M. Stanley

University of Hawaii Department of Geology and Geophysics

Since early Paleozoic time, rates of diversification for marine animal taxa have not generally declined as diversity has increased. Even exceptionally high rates during the initial Ordovician evolutionary radiation and following Paleozoic mass extinctions were uncorrelated with diversity after Early Ordovician time. In fact, diversity has risen exponentially for half a billion years, except during biotic crises. This pattern accords with evidence that disturbances, including predation, rather than competitive interactions, typically limit population sizes of species on the modern seafloor. Exponential diversification of marine taxa will continue long into the future unless interrupted by natural or human-induced environmental perturbations.

Changes in global marine animal diversity through time, as documented by fossil occurrences (Fig. 1A, B), have been extensively studied in efforts to investigate the structure and history of the marine ecosystem (*1-13*). Through application of the logistic equation of population biology, the general pattern of diversification has often been modeled as exponential increase damped by crowding that intensifies as the multiplying entities approach some imputed carrying capacity of the environment (*4,5,11-13*); mass extinctions are incorporated as events that set back diversification (Fig. 1C). The so-called "Paleozoic plateau" for diversity has been cited as evidence of a carrying capacity, but this feature is only evident when diversity is plotted at the family level (Fig. 1A). When genus-level data are used instead (*14*), the plateau configuration gives way to a jagged pattern; diversification proceeds at a high rate, except when disrupted by a major pulse of extinction (Fig. 1B). I show here that, when realistic values are employed for basic parameters, the logistic model fails to depict the observed pattern of diversity change. Furthermore, after the first few million years of the initial evolutionary radiation of marine animal life, there was no significant relationship between total diversity and rate of diversification during the Paleozoic Era. On the other hand, an empirically parameterized model that entails simple exponential increase punctuated by mass extinctions replicates the observed pattern of diversity change with remarkable fidelity. The implication is that interspecific competition has failed to damp marine animal diversification significantly during the past half billion years. Unbridled diversification has been set back only by episodic catastrophes.

It has been suggested that the post-Paleozoic increase displayed by empirical plots of marine global diversity may actually be at least in part an artifact of an inverse relationship between the quality of the known fossil record and the age of fossil faunas (*1,15,16*). However, arguments have recently been advanced that such an artifact is weak or even nonexistent. For example, there is evidence that diversities recorded for relatively young intervals are not greatly inflated artificially by the so-called "pull of the Recent" (assignment of taxa to intervals, even though they have never been found within them, because they are known from some previous time and are alive today) (*9*). Furthermore, whereas most well-studied fossil faunas of Paleozoic age represent tropical paleoenvironments, most of those of Cenozoic age represent temperate paleoenvironments, where diversities are relatively low (*17*). Similarly, the proportion of studied faunas that inhabited nearshore settings, characterized by high environmental stress and relatively low diversity, is much greater for the Cenozoic than for the Paleozoic (*18*). In addition, the fossil record of benthic foraminifera, for which virtually all species of life assemblages are normally preserved in unlithified sediments, shows a marked increase for within-habitat diversity during Cenozoic time (*19*). The observation reported here that a simple model of exponential increase closely resembles the empirical diversity curve supports the view the latter depicts the actual pattern of change for global diversity.

In the logistic model, as the number of taxa (N) increases from its initial value (N_o) over time (t), the rate of increase (r), measured as the fractional increase of N per unit time, declines linearly from its original value (r_o); r reaches zero when N reaches the imputed carrying capacity for the marine ecosystem (K):

$$N = N_o \, {}_{\mathrm{exp}} r_o[(K\text{-}N)/K]t \qquad (1)$$

In some diversification models, following Sepkoski (*4*), higher taxa (largely orders, subclasses, and classes) have been segregated into three large groups, the Cambrian, Paleozoic, and Modern Faunas, according to when these taxa attained high diversity; a coupled logistic model has then been adopted, in which the sum of the numbers of taxa in the three groups is treated as the *N* for each group (*5,11*) (Fig. 1). In these models, the Modern Fauna was assigned such a high *K*-value that it eventually depressed the diversity of the Paleozoic Fauna: *r* for the latter became negative when *N* exceeded its relatively low *K*-value (Fig. 1C).

The linear decline of *r* during logistic increase provides a means of testing the logistic model. Fig. 2 is a genus-level plot of *r* for the Paleozoic Fauna against total recorded marine diversity for intervals of the Paleozoic Era, when this fauna was numerically dominant (*20*). Intervals marked by mass extinction are excluded. Plotted data are divided into two groups: (I) those representing either the initial (Ordovician) radiation of marine animals or recoveries following the Late Ordovician and Late Devonian mass extinctions, and (II) those representing all other intervals, which can be considered normal intervals. The plot fails to display a decrease in *r* for Group II intervals. Thus, the pattern of diversification was not logistic during normal times; more generally, diversification was not stifled by ecological crowding.

In Fig. 2 rates for Group I intervals form an array of points that barely overlaps the array representing normal intervals. This pattern implies that a distinctive kind of marine ecosystem existed during the initial marine radiation and recovery intervals. Here too, for intervals with diversities above 600 genera, there is no relationship between *r* and diversity. Values of *r* were exceptionally high during the first two (Arenig) intervals of the initial radiation, which constituted a unique time in the history of life, when morphogenetic plasticity favored very rapid evolutionary diversification. Few phyla of marine animals arose after Cambrian time, and few classes after Ordovician time (*7*). If competitive interactions failed to brake the diversification of existing taxa, as indicated by Fig. 2, they should not have stifled evolutionary innovations in the form of new phyla and classes; subtaxa of the latter would, on average, have been ecologically less similar to existing taxa than members of existing taxa were to each other. Instead, it appears to have been difficult for evolution to produce distinctive new body plans after the establishment, early in metazoan history, of complex regulatory gene networks that were fundamental to animal development but evolutionarily inflexible (*21*).

The relatively high *r*-value for the post-Devonian recovery may reflect the fact that the Late Devonian biotic crisis altered the marine ecosystem more profoundly than the terminal Ordovician mass extinction (*22*). Although weak ecological crowding cannot account for rapid evolutionary radiation during Group I intervals, a dearth of predatory taxa may have permitted unusually rampant speciation. For example, crinoids, which radiated dramatically in early Mississippian time (*23*), may have benefited from the disappearance of marine placoderm fishes at the end of the Devonian.

Sepkoski did not use empirically based values of *r* in his logistic modeling of marine diversification (Fig. 1C), but values that produced the best fit to the empirical plot (Fig. 1A). As *K* for the Paleozoic Fauna, he employed the maximum diversity within the "Paleozoic plateau." As *K* for the Modern Fauna, he employed the empirical value of *N* for Plio-Pleistocene time, although recorded diversity had been rising persistently up to that time for millions of years. Empirically based values of *r* (Fig. 3A-B) were instead used to parameterize the new coupled logistic curves presented here (Fig. 3C-F). In addition, whereas previous workers (*4,5,11-13*) have conducted logistic simulations at the family level (see Fig. 1C), the simulations depicted in Fig. 3 are based on data for genera, which provide better resolution because, as evident in a comparison of Figs. 1A and 1B, generic diversity is more labile than family diversity: extinction entails loss of all species, and an average genus contains fewer species than an average family.

The value of *K* employed for the Paleozoic Fauna (K_{P1} = 1,300 genera) to produce the simulations in Fig. 3 approximates total diversity (sum for all three faunas) at the end of early Ashgill time, its highest level for a Paleozoic interval boundary. In the absence of evidence that a particular *K*-value might exist for the Modern Fauna, four different values were employed. One hypothetical value (K_{M2} = 4500) approximates the highest recorded diversity (Plio-Pleistocene). The maximum value is arbitrarily set at K_{M3} = 10,000. The lowest value (K_{M1} = 1,300) is included to represent the hypothetical condition in which the apparent post-Paleozoic rise in diversity is the artificial result of progressive improvement of the fossil record toward the present.

The Cambrian Fauna is included in the simulations shown in Fig. 3 only through stipulation of its empirical diversity. One reason for this for this procedure is that this fauna declined in diversity so rapidly that it could have had little impact on the other two faunas after early Paleozoic time. In addition, the Cambrian Fauna declined rapidly in Sepkoski's coupled logistic simulation (Fig. 1C) only because it attained maximum family-level diversity in Late Cambrian time, when total marine family-level diversity remained low. However, its generic diversity continued to rise into Ordovician time, when *N* for the total fauna was quite high. Thus, an empirically based value of *K* assigned to the Cambrian Fauna for a genus-level logistic simulation would be so high that the simulation would fail mimic this fauna's rapid early Paleozoic decline.

In an empirically parameterized simulation that excludes the Cambrian Fauna, the Modern Fauna quickly dominates total diversity, even if it is assigned a *K*-value well below its recorded Plio-Pleistocene diversity (Fig. 3D). The Modern Fauna failed to dominate in this way in the simulations of Sepkoski because, to force the simulation to resemble the empirical pattern, he assigned this fauna a value of r_o only 21% as high as the one he assigned the Paleozoic Fauna (*6*). Empirical estimates at the genus level, however, make it about 65% as high (Fig. 3A, B). Even if the Modern Fauna is assigned a *K*-value as low as that of the Paleozoic Fauna, the resulting simulation looks nothing like the empirical pattern (Fig. 3E).

In contrast to the empirically based logistic simulations, one that depicts the pattern of diversity change as simple exponential increase punctuated by mass extinctions mimics the empirical pattern quite well (Fig. 4). In order to illustrate the overall simplicity of the empirical pattern, only a few *r*-values are used in this simulation, each being the mean for a large set of stratigraphic intervals (Fig. 4A). For the Modern Fauna, a single *r*-value was used for the initial Ordovician radiation and post-extinction intervals, and another *r*-value was used for normal intervals. For the Paleozoic Fauna, two *r*-values were employed for each of these sets of intervals. To depict diversification during the late Paleozoic ice age, when a unique state of the marine ecosystem existed and evolutionary turnover was sluggish (*24*), a very low value was assigned to each fauna (the empirical mean for the entire interval).

Unbridled exponential increase in taxonomic diversity, except at times of crisis, is consistent with marine ecological theory, which recognizes from predator-exclusion experiments that population densities of marine animals are generally limited by predation and other forms of disturbance rather than by interspecific competition for resources (*25*,*26*). Notably, aquaculturists can grow bivalve mollusks in predator-free cages on the seafloor at densities of $10^3/m^2$ without supplemental feeding (*27*).

Previous authors have assumed that the marked post-Paleozoic rise for recorded marine animal diversity (Figs. 1, 4B) requires a special explanation: They have, for example, attributed this rise to increased nutrient supply (*28*), decreased nutrient supply (*29*), or a proliferation of biogeographic provinces (*3*). These interpretations, however, reflect an arithmetic view of the post-Paleozoic diversification. For the Modern Fauna, which was largely responsible for this diversification, the mean value of *r* for intervals not marked by mass extinction was virtually the same for Paleozoic time and Mesozoic time (~ 0.011/m.y.). The principle of parsimony supports the conclusion that the empirical pattern depicted in Fig. 4A approximates the actual history of animal diversification in the ocean. It is highly unlikely that the simple exponential pattern exhibited by the empirically based diversity curve would be the fortuitous product of some combination of unrelated external factors.

Thus, the post-Paleozoic expansion of total diversity requires no special explanation. It was the inevitable result of the inherent rate of diversification of the Modern Fauna. Abiotic environmental changes have had only a minor impact on average rates of diversification, except during the late Paleozoic ice age (*24*) and, episodically, when major pulses of extinction have occurred. It follows that exponential taxonomic diversification of marine life will continue far into the future, unless terminated by a large-scale natural or human-induced disruption of the marine ecosystem.

Notes and References

1. D. M. Raup, *Science* **177**, 1065 (1972).
2. R. K. Bambach, *Paleobiology* **3**, 152 (1977).
3. J. W. Valentine, T. C. Foin, D. Peart, *Paleobiology* **4**, 55 (1978).
4. J. J. Sepkoski, *Paleobiology* **7**, 36 (1981).
5. J. J. Sepkoski, *Paleobiology* **10**, 246 (1984).
6. J. J. Sepkoski, R. K. Bambach, D. M. Raup, J. M. Valentine, *Nature* **293**, 435 (1981).
7. D. H. Erwin, J. W. Valentine, J. J. Sepkoski, *Evolution* **4**, 1177 (1987).
8. A. I. Miller, M. Foote, *Paleobiology* **22**, 304 (1996).
9. D. W. Jablonski, K. Roy, J. W. Valentine, R. M. Price, P. S. Anderson, *Science* **300**, 1133 (2003).
10. A. M. Bush, M. J. Markey, C. R. Marshall, *Paleobiology* **30**, 666 (2004).
11. J. A. Kitchell, T. R. Carr, in *Phanerozoic diversity patterns: profiles in macroevolution* J. W. Valentine, Ed. (Princeton Univ. Press, Princeton, NJ, 1985), pp. 277-309.
12. V. Courtillot, Y. Gaudemer, *Nature* **381**, 146 (1996).
13. A. Lane, Benton, M. E., *American Naturalist* **162**, 265 (2003).
14. Generic data employed here are from J. J. Sepkoski, *Bulletins of American Paleontology* **363** (2002).
15. S. E. Peters, M. Foote, *Paleobiology* **27**, 583 (2001).
16. J. Alroy *et al.*, *Proceedings of the National Academy of Sciences* **98**, 6261 (2001).
17. P. A. Allison, D.E.G. Briggs, *Geology*, **21**, 65 (1993)

18. A.M. Bush, R.K. Bambach, *Journal of Geology* **112**, 625 (2004).

19. M. A. Buzas, L. S. Collins, S. J. Culver, *Proceedings of the National Academy of Sciences* **99**, 7841 (2002).

20. The time scale employed in Figs. 1B, 3, and 4, and in all calculations is from F. Gradstein and J. Ogg. 1999. Geological Timescale. Purdue University, West Lafayette, Indiana.

21. E. H. Davidson, D. E. Erwin, *Science* **311**, 796 (2006).

22. M. L. Droser, D. L. Bottjer, P. M. Sheehan, *Geology* **25**, 167 (1997).

23. T. W. Kammer, W. I. Ausich, *Palaios* **21**, no. 3, 238 (2006).

24. S. M. Stanley, M. G. Powell, *Geology* **31**, 877 (2003).

25. R. T. Paine, *American Naturalist* **100**, 65 (1996).

26. D. K. Young, M. A. Buzas, M. W. Young, *Journal of Marine Research* **34**, 577 (1976).

27. E. M. Fernandez, J. Lin, J. Scarpa, *Journal of Shellfish Research* **18**, 77 (1999).

28. G. J. Vermeij, *Paleobiology* **21**:125 (1995).

29. J. W. Valentine, *Systematic Zoology* **20**, 253 (1971).

30. J. J. Sepkoski, *Journal of Paleontology* **71**, 533 (1997).

Figure Captions

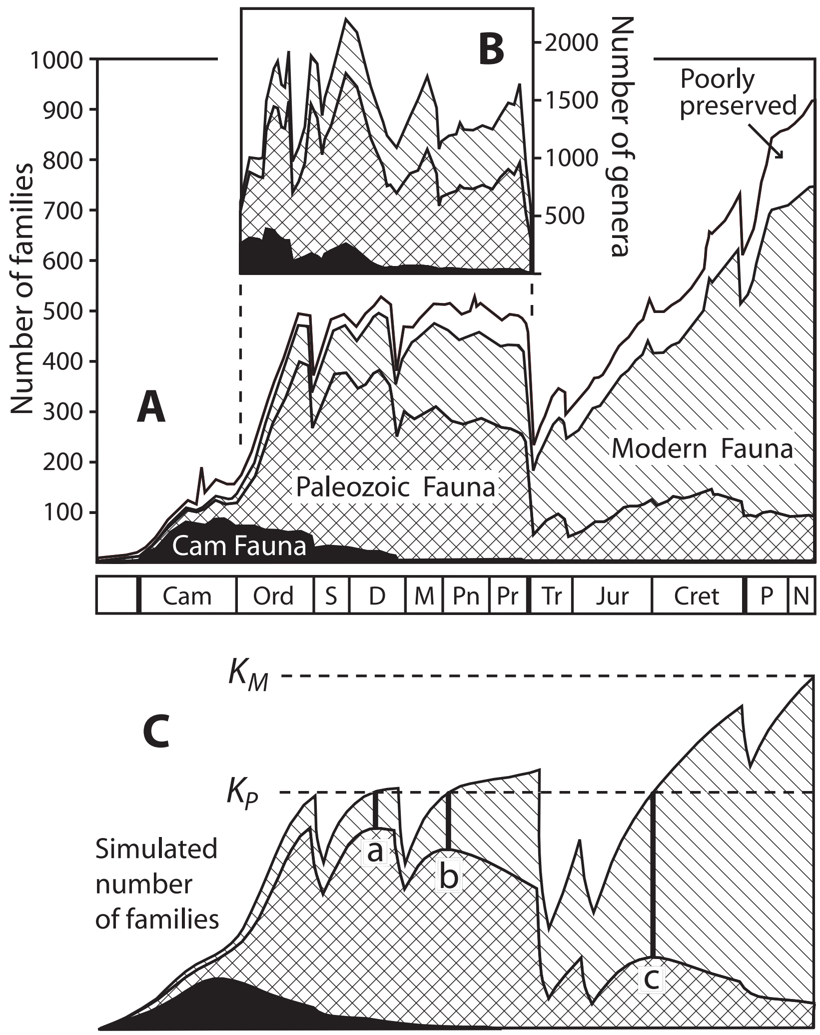
Fig. 1. Taxonomic diversity for the Cambrian, Paleozoic, and Modern marine faunas for intervals of Phanerozoic time, based on fossil occurrences of families (*5*,*30*) (**A**) and of genera at the time of the "Paleozoic plateau" (*14*,*20*) (**B**) and depicted by a simulation at the family level (**C)** that employed the coupled logistic model (*5*); a-c are points at which the simulated rate of diversification for the Paleozoic Fauna declines to zero because total diversity reaches the *K*-value assigned to this fauna (K_p), while the Modern Fauna is continuing to diversify toward its imputed saturation level (K_M).

Fig. 2. A test of the coupled logistic model. Fractional rate of increase in generic diversity for the Paleozoic Fauna (r) is plotted against total marine diversity for all Paleozoic intervals (N = average of the diversity at the start and end of each interval), beginning with the early Arenig. Six intervals in which a mass extinction occurred (see Fig. 4B) are excluded. Solid symbols represent Group I intervals, characterized by unusually rapid radiation. Hollow circles represent normal (Group II) intervals, for which there is a positive, rather than negative (though statistically insignificant), correlation, ($R = 0.084$).

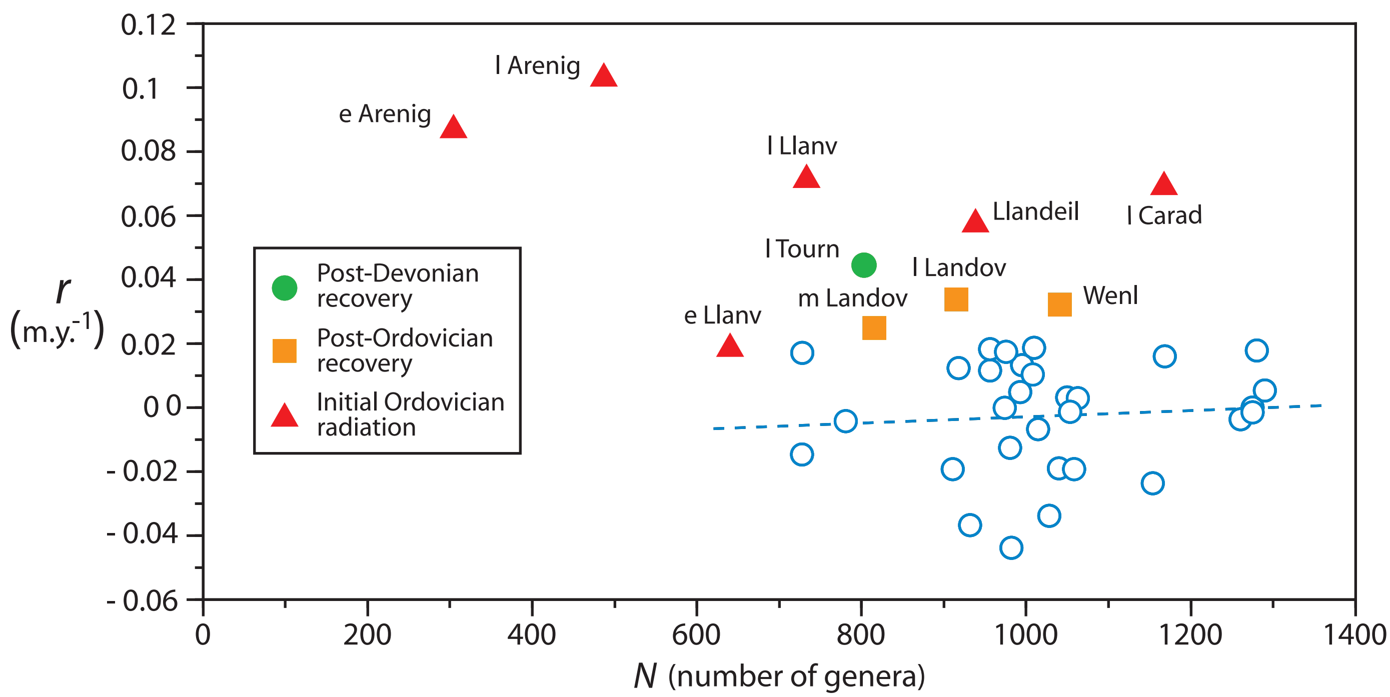
Fig. 3. Empirically parameterized, coupled logistic simulations for the Paleozoic and Modern faunas from early Arenig through Plio-Pleistocene time. Estimation of the intrinsic rate of increase (r_o) for genera of the Paleozoic and Modern faunas (**A, B**) is based on the assumption that their diversification followed a logistic pattern. For each fauna, the highest average *r*-value

for three contiguous intervals (hollow circles), calculated from the database of Sepkoski (*14*), occurred very early (Trempeleau through Arenig for the Paleozoic Fauna and late Arenig through late Llanvern for the Modern Fauna); this rate is assumed to be nearly exponential and to lie close to the linear path between r_o and $r = 0$ that would represent logistic increase from $N = 1$ to $N = K$. The straight line through the point representing this highest *r*-value and the point representing $r = 0$ is therefore taken to intersect the y-axis at r_o. In the four simulations (**C**-**F**), each of which employs a different *K*-value for the Modern Fauna, damped rates of increase (*r*) produce diversity increments from each interval boundary to the next by way of a single step via Eq. 1. Mean interval length is 5.4 m.y. The Cambrian Fauna is represented by its empirical values and contributes only modestly to total diversity. Simulated diversification is interrupted by 8 mass extinctions, in which diversity is lowered by the amount indicated by empirical data (see Fig. 4B).

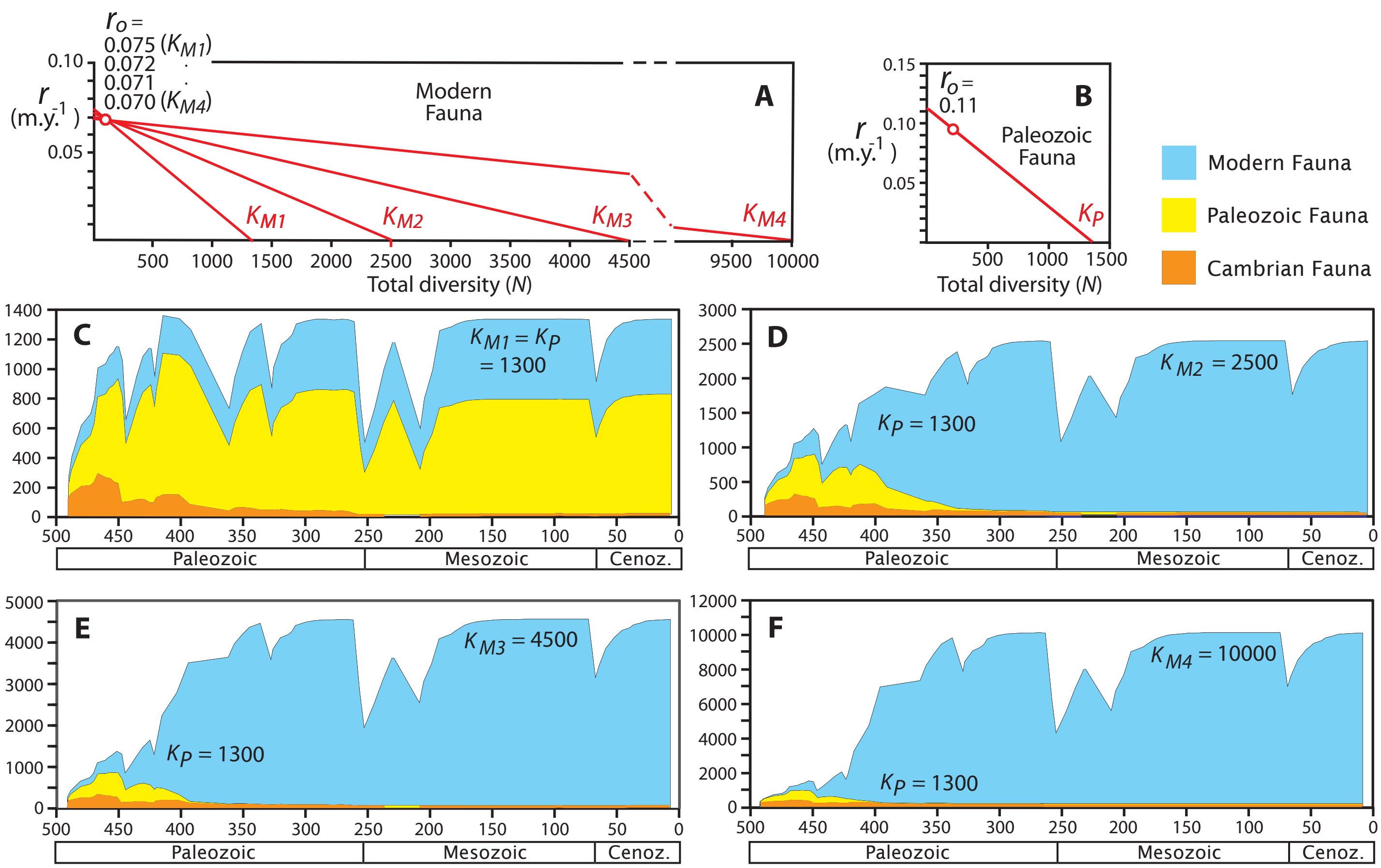
Fig. 4. Similarity between an empirically parameterized exponential simulation of generic diversity (**A)** and actual generic diversity (*14*) (**B)** of marine animals at interval boundaries from early Arenig through Plio-Pleistocene time. Mean interval length is 5.4 m.y. Dotted and dashed lines in **A** depict *r*-values employed to produce exponential increase for the Paleozoic and Modern Faunas, respectively; arrows indicate rates that continue to the end of the simulation. Vertical dashed lines in **B** indicate mass extinctions that were incorporated into the simulation as sudden drops in diversity; the lower and upper percentages represent losses of genera for the Paleozoic and Modern Fauna, respectively.



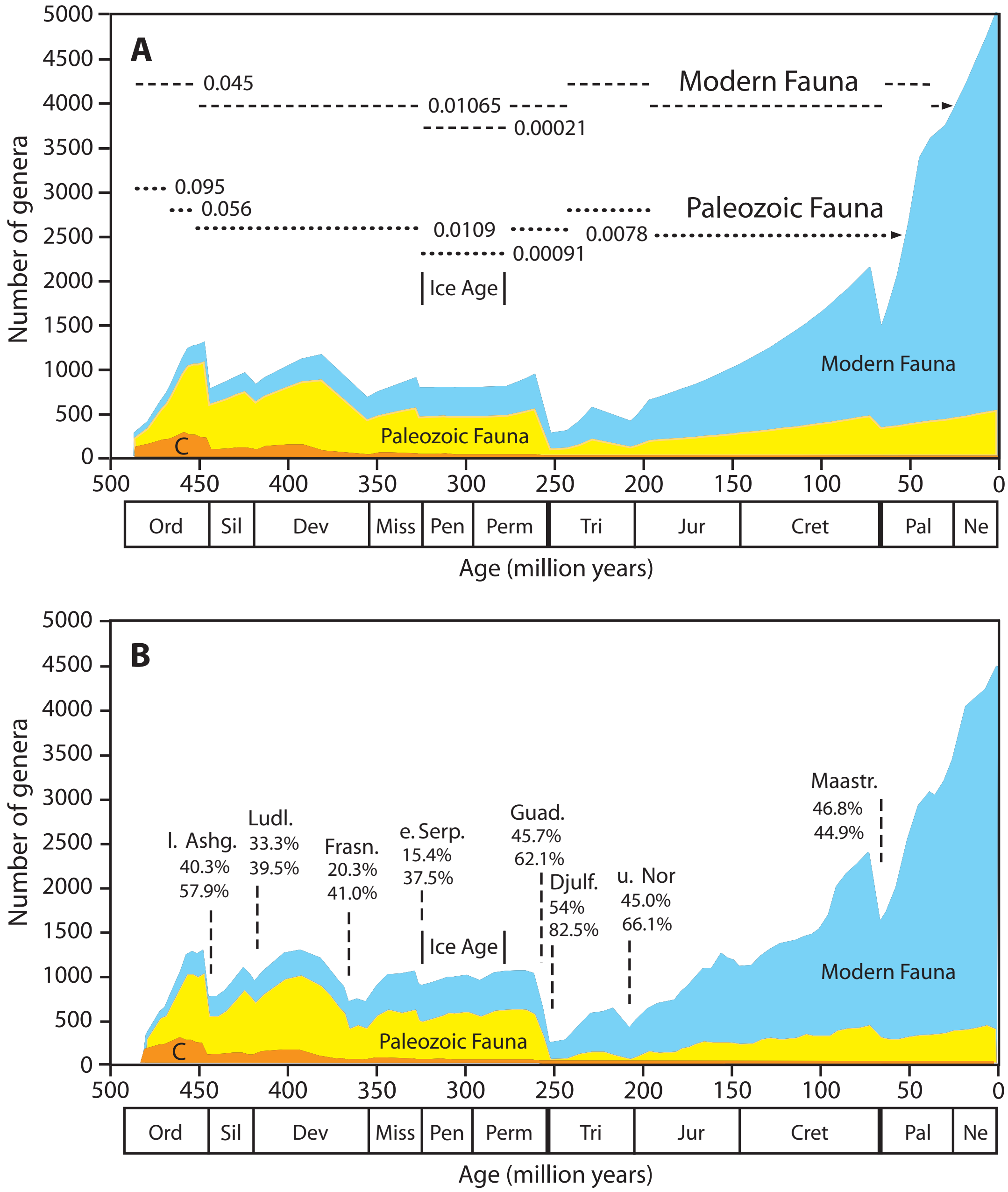
A
B
C
Number of families
1000
900
800
700
600
500
400
300
200
100
2000
1500
1000
500
Number of genera
Poorly preserved
Modern Fauna
Paleozoic Fauna
Cam Fauna
Cam
Ord
S
D
M
Pn
Pr
Tr
Jur
Cret
P
N
K_M
K_P
a
b
c
Simulated number of families



0.12
0.1
0.08
0.06
0.04
0.02
0 0
- 0.02
- 0.04
- 0.06
r
(m.y.-1)
0
200
400
600
800
1000
1200
1400
N (number of genera)
l Arenig
e Arenig
l Llanv
Llandeil
l Carad
l Tourn
l Landov
m Landov
Wenl
e Llanv
Post-Devonian recovery
Post-Ordovician recovery
Initial Ordovician radiation


r_o =
0.075 (K_{M1})
0.072
0.071
0.070 (K_{M4})
0.10
r
(m.y.$^{-1}$)
0.05
Modern Fauna
A
K_{M1}
K_{M2}
K_{M3}
K_{M4}
500 1000 1500 2000 2500 3000 3500 4000 4500 9500 10000
Total diversity (N)
0.15
r_o =
0.11
B
0.10
Paleozoic Fauna
0.05
K_P
500 1000 1500
Total diversity (N)
Modern Fauna
Paleozoic Fauna
Cambrian Fauna
C
K_{M1} = K_P = 1300
D
K_{M2} = 2500
K_P = 1300
E
K_{M3} = 4500
K_P = 1300
F
K_{M4} = 10000
K_P = 1300
500 450 400 350 300 250 200 150 100 50 0
Paleozoic
Mesozoic
Cenoz.

Stanley - Fig. 4



SUPPORTING ONLINE MATERIAL for Stanley Manuscript

Taxa for each of the three major Phanerozoic faunas for which generic data from Sepkoski (2002) are included in this study.

CAMBRIAN FAUNA	PALEOZOIC FAUNA	MODERN FAUNA
Archaeocyatha	Foraminifera	Protista
Cnidaria	Fusulinida	Acantharia
Trilobozoa	Chitinozoa	Ciliata
Cyclozoa	Porifera	Insertae sedis
Medusae insertae sedis	Stromatoporoidea	Modern Foraminifera
Hydroconozoa	Chaetetidae	Radiolaria
?Petalonamae	Calcarea	“Tintinea”
insertae sedis	Cnidaria	Porifera
Brachiopoda	Scyphozoa	Demospongia (include
Inarticulata	Hydrozoa	post-Devonian
Mollusca	Tabulata	“Stromatoporoidea")
Tergomya	Rugosa	Axinellida
Helcionelloida	Incertae sedis	Hexactinellida
Rostroconchia	Bryozoa	Cnidaria
?Stenothecoidea	Stenolaemata	Scleractinia
?Hyolithomorpha	Brachiopoda	Bryozoa
Arthropoda	Articulata	Gymnolaemata
Incertae sedis	Mollusca	Mollusca
Myriopoda	Nautiloidea	Gastropoda
Onycophora	Ammonoidea	Bivalvia
Trilobita	Polyplacophora	Scaphopoda
“Paratrilobita”	?Crioconarida	Coleoidea
Echinodermata	(= tentaculitids)	Arthropoda
Camptostromoidea	Incertae sedis	Brachyopoda
Helicoplacoidea	Arthropoda	Branchiopoda
Eocrinoidea	Ostracoda	Cirrepedia
Ctenocystoidea	Chelicerata	Copepoda

Homostelea	Pycnogonidae	Crustacea
	Echinodermata	Malacostraca
	Edrioasteroidea	Remipedia
	Blastoidea	Thylacocephala
	Parablastoidea	Insertae sedis
	Cystoidea	Echinodermata
	Stelleroidea	Echinoidea
	Crinoidea	Holothuria
	Graptolithina	