

Extinction: bad genes or bad luck?

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SUMMARY

Extinction of species and higher taxa is generally seen as a constructive force in evolution because it is assumed that the better adapted organisms are most likely to survive. It is possible, however, that most extinction is non-selective and that changes observed in the taxonomic composition of the biota are the result of random effects. Two scenarios for non-selective extinction are evaluated: one uses a time homogeneous birth-death model and the other postulates intermittent, catastrophic extermination of large numbers of species. In the present state of knowledge, neither scenario is mathematically plausible. This may be because extinction is, in fact, selective or it may be that our estimates of past diversities and evolutionary turnover rates are faulty. If extinction is selective, the time homogeneous model suggests that trilobites had species durations 14 to 28 percent shorter than normal for Paleozoic marine invertebrates.

RESUMEN

La extinción de especies y taxones superiores se ve generalmente como una fuerza constructiva en evolución, ya que se supone que los organismos mejor adaptados sobreviven más fácilmente. Es posible, sin embargo, que gran parte de la extinción no sea selectiva y que los cambios observados en la composición taxonómica de la biota sean el resultado de efectos aleatorios. En este trabajo se evalúan dos guiones para la extinción no selectiva: uno utiliza un modelo de tiempo de nacimiento-muerte homogéneo y el otro postula exterminaciones intermitentes, catastróficas de gran número de especies. En el estado actual de nuestros conocimientos, ninguno de estos dos guiones es matemáticamente plausible. Esto podría ser debido a que la extinción es, de hecho, selectiva, o bien podría ser que nuestras estimaciones de las diversidades del pasado y las tasas de avance evolutivo fueran erróneas.

Si la extinción es selectiva, el modelo de tiempo homogéneo sugiere que los Trilobites abarcan especies con duraciones del 14 al 28 por ciento más cortas que lo normal para los invertebrados marinos del Paleozoico.

RESUM

L'extinció d'espècies i taxons superiors es veu generalment com una força constructiva en l'evolució, puix que suposa que els organismes millor adaptats sobreviuen més fàcilment. És possible, tanmateix, que gran part de l'extinció no sigui selectiva i que els canvis observats en la composició taxonòmica de la biota siguin el resultat d'efectes aleatoris. En aquest treball s'avaluen dos guions per a l'extinció no selectiva: un utilitza un model de temps de naixement-mort homogeni i l'altre postula exterminacions intermitents, catastròfiques de gran quantitat d'espècies. En l'estat actual dels nostres coneixements, cap d'ambdós guions és matemàticament plausible. Això podria ésser degut a que l'extinció és, de fet, selectiva, o bé podria ser que les nostres estimacions de les diversitats del passat i les taxes d'avenç evolutiu són errònies.

Si l'extinció és selectiva, el model de temps homogeni suggereix que dintre els Trilòbits es troben espècies amb durades del 14 al 28 per cent més curtes que el normal en els invertebrats marins del Paleozoic.

INTRODUCTION

In the fossil record, extinction of species and higher taxa is so common that extinction must play a significant role in the evolutionary process. Virtually all species that have ever lived are now extinct. The paleontological literature contains a variety of estimates of species extinction rates but most fall within a fairly narrow range. Most observed or calculated mean durations are less than 10 million years: Simpson (1952) suggested that the means for all fossil groups range from one-half to five million years; Valentine (1970) estimated five to ten million years for marine invertebrates; and Raup (1978 a) calculated an average of 11.1 million years for mean species duration of marine invertebrates. Most analyses based on single taxonomic groups also yield estimates within this range: six million years for echinoderm species (Durham, 1971); 1.9 million years for Silurian graptolites (Rickards, 1977); and 1.2 to 2 million years for Mesozoic ammonoids (Kennedy, 1977).

With nearly 600 hundred million years of high diversity in the Phanerozoic record, it is clear that species turnover is relatively rapid. Because the number of living species is large, the net rate of species formation must have exceeded the net extinction rate but when speciation and extinction rates are expressed on a per lineage per million years basis, the two rates are, to a first approximation, the same.

Extinction rates at higher taxonomic levels are also substantial: mean durations of genera, families, and orders are short relative to the length of the Phanerozoic. Raup (1978 a) estimated the mean duration for marine invertebrate genera at 28.4 million years. Because the frequency distribution of durations is skewed, the median duration (half-life) for the same genera is only 10.6 million years.

Extinction is generally seen as a positive or constructive force in evolution. The differential survival of species over evolutionary time (species selection of Stanley, 1975) is thought by most evolutionary paleobiologists to lead to adaptation at generic and higher taxonomic levels. Even the most spectacular of the group extinctions, such as the trilobites, ammonoids, and dinosaurs, are seen by most as positive events in the sense of representing the replacement of less well adapted types by better adapted types.

But what do we really know about the extinction process? I submit that evolutionary theory is currently dominated by a strong conventional wisdom (attributable to Darwin and Lyell) to the effect that extinction is «easy», given time on a geologic scale. It is generally agreed that interspecific and intergroup competition, predation (including disease), and gradual habitat alteration (through climatic and/or tectonic changes) provide ample mechanisms for the extinctions observed in the fossil record. Although this model is certainly plausible, and may well be correct, proof in individual cases has been elusive. Well documented cases of competitive exclusion or competitive replacement in the fossil record are rare and the adaptive superiority of the new taxa or faunas is seldom compelling. It is simple to construct plausible scenarios but not simple to prove them beyond reasonable doubt.

In this paper, I will play the devil's advocate and explore a different interpretation. I will ask: if the conventional darwinian model is not correct, what alternatives on extinction are available and can they be rejected on the basis of logic or paleontologic data? The main alternative I will explore is that extinctions are randomly distributed with respect to overall fitness (or adaptiveness of the organism) and that extinction of a given species or higher group is more bad luck than bad genes. The conclusions I will reach are not definitive but I hope the exercise will stimulate further exploration of the problem from fresh points of view and with fresh methodologies.

THE NATURE OF FOSSIL DATA ON EXTINCTION

Stratigraphic ranges of species and higher taxa constitute the data base for the analysis of extinction. These ranges are subject to a host of biases and uncertainties, all of which detract from the rigor with which the extinction phenomenon can be studied (for discussion, see Newell, 1959a, b; Simpson, 1960; Raup, 1972, 1979a). Virtually all observed ranges are truncated simply because non-preservation can shorten the range but there is no analogous mechanism to lengthen the range (except for reworking by bioturbation or erosion and re-deposition of fossils). All too often, a species is known only from a single horizon and is thus just a point occurrence in time.

On the other hand, incomplete preservation of anatomy, physiology, and behavior may often mean that what paleontologists call species are actually composites of several (or many) biological species. When this is true, actual species duration may be shorter than what appears in the stratigraphic record (Schopf, 1979).

At higher taxonomic levels, stratigraphic range data are prone to additional uncertainty because of difficulties in the underlying taxonomy.

In spite of the problems, paleontologists have an enviably large data base and it should be hoped that broadly applied statistical analyses should yield meaningful answers to basic questions about extinction. In the context of this paper, however, it is important to exclude two types of extinction — types which do not represent the true death of a taxon. These are *pseudoextinction* and *monographic extinction*.

Pseudoextinction is the situation where a single species lineage is transformed by phyletic evolution into a new species. The new species would presumably have been reproductively isolated from the ancestral species had they lived together at the same time but the process is totally different from speciation as studied by the evolutionary

biologist. Because pseudoextinction does not represent death without issue, instances of pseudoextinction should be eliminated from the data before extinction is analysed. This is difficult because it is usually impossible to determine whether a species that is lost from the record actually died out or whether it was simply transformed. In view of the growing consensus in favor of the punctuated equilibrium model of Eldredge and Gould (1972), one could argue that pseudoextinction is not a dominant phenomenon — but good numerical estimates of its frequency are not available. Pseudoextinction at supraspecific levels cannot logically occur unless the higher taxon is monotypic and thus the problem is serious only at the species level.

Monographic extinction refers to the not uncommon practice among taxonomists whereby species or higher taxa are terminated arbitrarily at major stratigraphic boundaries even though morphological evidence for the break is lacking. This practice has much in common with the practice among some biologists of declining to place in the same species identical organisms that occur on widely separated continents. Both practices are based on theoretical evolutionary considerations rather than good morphological or genetic data. When fossil groups are subjected to monographic extinction, it has the unfortunate effects of shortening ranges and multiplying the extinctions at major boundaries. Fortunately, monographic extinction is becoming less common in taxonomy and many of the existing cases are being eliminated by monographic revisions. But the data on extinction still contain an unknown bias caused by this effect.

EXTINCTION AS A BIOLOGICAL PROCESS

The actual mechanisms of extinction are little understood and surprisingly little attention has been devoted to the problem by population biologists. Cases of extermination of species by human activities are celebrated and well known: the extinction may occur directly by human predation (hunting, etc.) or indirectly through the effects of other species introduced by man. The existence of a few particularly spectacular cases has led the general public to the view that ecosystems are more fragile than is probably the case and has also led to the idea (shared by many biologists) that the survival of any species is precarious and, in turn, that extinction is an almost trivial phenomenon. Yet there are relatively few cases (if any) of widespread species becoming completely extinct in historic times *without* human influence.

Local extinction (especially on small islands) is a commonly observed phenomenon and large amounts of quantitative information on frequencies have been amassed by ecologists (especially MacArthur and Wilson, 1967, and Simberloff, 1974). Unless a species is endemic to the local area, these extinctions are not extinctions in the global sense although the processes involved are presumably comparable. But even in local extinction, it is rarely possible to document causes. It is generally assumed that the classically darwinian mechanisms of competition and predation apply but verification has proven to be difficult.

The basic model subscribed to by most ecologists is that local extinction results when population size is drastically cut down by natural physical disaster, by competition from other species, or by predation by other species. Given very small populations, random sampling error in reproduction can lead to complete extinction. If a population's growth rate (births minus deaths) is approximately zero, population size will

behave as a random walk with an absorbing boundary at zero (extinction). Thus, below a certain population size, extinction becomes probable as a purely stochastic phenomenon. The critical population size varies with the species, of course, but is generally very small.

The classic mechanisms of competition and predation have been challenged. MacArthur (1972), for example, wrote:

«On the mainland... the degree of synchrony and orderliness of the predation needed to cause complete extinction can probably only be regularly achieved by man...».

Simberloff (1981) has raised serious doubts about the presumed effects of competition by species introduced into an area occupied by an established community.

Part of the problem may be that ecologists and population biologists operating as they must on a human time scale, are not able to observe a relatively rare and slow phenomenon. Yule (1924) estimated that an angiosperm speciation event occurs naturally somewhere in the world every 10 to 50 years. If this estimate is the right order of magnitude, and if the angiosperm extinction rate is comparable, the extinction process is certainly a difficult one for the biologist to study. A similar conclusion may be reached by another route. If we take five million years as the average duration for all species and if there are 1.5 million species of organisms living today, the following logic obtains. The extinction rate is approximately the reciprocal of the mean duration (assuming a linear survivorship curve for species, *à la* Van Valen, 1973) and thus is 0.2 per lineage per million years. Multiplying this rate by 1.5 million yields 300,000 extinctions per million years or one extinction of some plant or animal species somewhere in the world every 3 and 1/3 years. In terms of human life spans, this is indeed a rare phenomenon.

But, as already noted, extinction in geological time not only happens but is extremely common. Thus, mechanisms must exist. We cannot conclude that competition, predation, and gradual environmental change are not effective just because they are difficult to authenticate but the extinction phenomenon does appear to be open to alternate interpretations.

THE HOMOGENEOUS BIRTH-DEATH MODEL

Yule (1924) developed a mathematical model of evolution that treated speciation and extinction as random events with constant (though not necessarily equal) probabilities. He was arguing, in effect, that the processes of speciation and extinction are so multi-factorial that they are best treated formally as random variables. Yule claimed considerable success in applications of his model to actual data. This approach has been used more recently in Monte Carlo simulation (Raup, *et al.*, 1973; Raup and Gould, 1974; Gould, *et al.*, 1977) and by analytical methods (Raup, 1978a, 1978b) but the breadth of its applicability to the fossil record is yet to be demonstrated.

If we treat evolution as a branching process wherein each branch (species lineage) has a stochastically constant probability of dividing to form a new branch (speciation) and a stochastically constant probability of terminating (extinction), we are using what is known as a time homogeneous birth-death model. The time homogeneity refers to the supposition that the probabilities of speciation and extinction do not change systematically through time. The time homo-

geneous model has been applied to problems of epidemics, genetic drift, colonization of small islands, and a host of non-biologic problems. In an evolutionary context, the model implies that all species have the same probability of extinction.

For each species in the time homogeneous model, ultimate extinction is inevitable although the time of extinction cannot be predicted except probabilistically. The duration of a species is descriptively identical to the life span of an atom of a radioactive isotope and the survivorship curve for species is log-linear.

Of greater interest in a paleontological context are the implications of the time homogeneous model for monophyletic groups of species. If we define a «group» as all those species in an evolutionary tree which are descended from a single ancestor, then rigorous predictions can be made about the probable life span of the group. If the probabilities of extinction and speciation are equal, ultimate extinction of the group is assured although the expected length of time to extinction will depend greatly on the probabilities themselves and on the number of coexisting species at some time = 0. The lower the probabilities and the larger the «standing crop», the longer the expected life span of the group. Even if the speciation probability exceeds the extinction probability, there is a finite probability of extinction of the group and this probability depends on the difference between the two probabilities.

It is conceivable that groups of organisms can, over geological time, drift to extinction just because of an accidental excess of extinctions over speciations. If this were the case, a search for causes of extinction in the conventional sense would be meaningless. The workings of the time homogeneous model have been suggested as a general explanation for some clade extinctions (Raup, 1978b).

Extinction of large groups of organisms by sampling accident of the sort just described may be called *Galton extinction* because of Francis Galton's classic use of birth-death models to explain extinction rates in human surnames (Galton and Watson, 1875) For Galton extinction to be viable on a broad scale in the evolutionary record, it must be shown that major extinctions such as those of trilobites, ammonoids, and dinosaurs were probable events in terms of the time homogeneous model.

We can use the geologic record of trilobites as a testing ground (Figure 1). In the Cambrian, most major marine invertebrate groups were present but the fossil record is dominated by trilobites: about 75 % of all fossil species described from Cambrian rocks are trilobites; the other 25 % are distributed among about nine other major groups (Raup, 1976). By the end of the Permian, 350 million years after the start of the Cambrian, the trilobites were extinct. Could this have been a matter of Galton extinction without the need to postulate an adaptive disadvantage for trilobites? As will be shown, the probability of simple Galton extinction in this case is quite low unless our knowledge of marine invertebrate diversity and extinction rates is faulty.

To take the simplest possible approach to the trilobite problem, let us assume that speciation probability (λ) was equal to extinction probability (μ) and that this value was the same as that for other Phanerozoic invertebrates. If we assume that μ is the reciprocal of mean species duration, we can use $1/11.1 = .09$ as the value for λ and μ (from Raup, 1978a). Using the time homogeneous model, the probability of extinction of a group at or before time = t is:

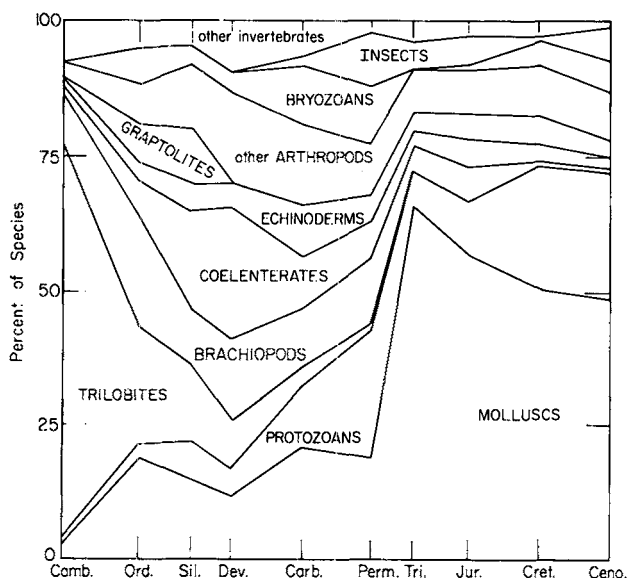


Fig. 1. - Variation in the taxonomic composition of the invertebrate fossil record (from RAUP, 1976). Large fluctuations in composition occurred but only two groups (trilobites and graptolites) went extinct. The trilobites constituted about 75 % of the Cambrian standing diversity.

$$P_0 = \left[\frac{\mu t}{1 + \mu t} \right]^a \quad (1)$$

where a is the number of coexisting species at time = 0. It is difficult to estimate a for Cambrian trilobites. The total number of Cambrian trilobite species described is known (Raup, 1976) but this is of little help because (1) it is a composite of all Cambrian forms and thus does not represent standing diversity at a point in time and (2) the number found and described is surely less than the number that actually lived. One approach is to use estimates of total marine invertebrate standing diversity for the Cambrian and calculate the trilobite fraction from this. Valentine, *et al.*, (1978) calculated a standing diversity for fossilizable shelf invertebrates for the Cambrian of about 8,000 species. If 75 % were trilobites (above), we have an estimate of 6,000 for a in equation (1). Thus:

$$P_0(t = 350) = \left[\frac{(.09)(350)}{1 + (.09)(350)} \right]^{6,000} = 4 \times 10^{-82}$$

This result is so near zero that we can conclude with confidence that the time homogeneous model used in this way with these values will *not* explain the trilobite extinction. That is, the probability is negligible that the trilobites drifted to extinction. Furthermore, the value of $P_0(t)$ is so low that minor alterations in the constants (such as reducing Cambrian diversity estimate) will not significantly affect the result.

It is instructive, however, to investigate how much the numerical situation would have to be changed to produce a P_0

(t) in a reasonable range. Table 1 explores this. Equation (1) was solved for several values of μ (expressed as its reciprocal, mean duration) and several values of a . The time estimate of 350 million years was used throughout. The underlined values of $P_0(t)$ are those that lie in a reasonable probability range. Values at or near 1.0 (upper right) are excluded in view of the fact that nine other groups were present in the Cambrian in lower diversity and did not go extinct in the Paleozoic. The reader is free to interpret Table 1. It appears to indicate that the time homogeneous model will explain the trilobite extinction only if standing diversity were much lower than has been estimated and/or mean duration of invertebrate species was much less than has been estimated. Both alternatives are conceivable but unlikely in the present state of knowledge.

TABLE 1. Probability of Galton extinction in 350 million years as a function of the number of coexisting species at the start and mean species duration. Equation (1) was used on the assumption of equal probabilities of speciation and extinction (each being the reciprocal of mean duration).

NUMBER OF SPECIES AT TIME = 0	MEAN DURATION (MILLIONS OF YEARS)				
	10	1	0.1	0.01	0.001
1	0.97	~1.00	~1.00	~1.00	~1.00
10	0.75	0.97	~1.00	~1.00	~1.00
100	0.06	0.75	0.97	~1.00	~1.00
1000	<u>10⁻¹²</u>	0.06	0.75	0.97	~1.00
6000	10 ⁻⁷⁴	10 ⁻⁸	0.18	0.84	0.98

If we accept that trilobite extinction was not the result of the simple form of Galton extinction just presented, then we can entertain more seriously the possibility that trilobites were in fact selected against compared with other marine invertebrates of the Paleozoic. The most likely expression of such selection would be a higher than normal extinction probability (μ). Let us assume, therefore, that the trilobite speciation rate was the same as for other organisms ($\lambda = .09$) but that the trilobite μ was higher. How much higher would it have to have been for selective extinction to be a viable hypothesis? The time homogeneous model can be used to investigate this using the following equation for group extinction probability:

$$P_0(t) = \left[\frac{\mu (e^{(\lambda-\mu)t} - 1)}{\lambda e^{(\lambda-\mu)t} - \mu} \right]^a \quad (2)$$

This equation is solved for several values of μ in Table 2, using the value of a and t employed in the initial calculations (above). The results shown in Table 2 indicate that if the extinction probability for trilobite species was between about 0.105 and 0.125, extinction of the whole group would be plausible. This corresponds to an average species duration which is 14 to 28 percent less than for other Phanerozoic invertebrates. It was noted in earlier analyses (Raup, 1978a) that generic durations in the Cambrian cohort were less than that of other geologic periods and this may be because of the dominance of trilobites in this cohort.

TABLE 2. Probability of Galton extinction in 350 million years as a function of species duration. Equation (2) was used with a standing diversity at the start of 6,000 and a speciation probability (λ) of 0.09.

EXTINCTION PROBABILITY (μ)	EQUIVALENT SPECIES DURATION	P_0 (t)
0.095	10.5 my	10^{-39}
0.10	10.0	10^{-8}
0.105	9.5	0.01
0.11	9.1	0.37
0.115	8.7	0.81
0.12	8.3	0.96
0.125	8.0	0.99
0.13	7.7	~ 1.00

The exercise just presented (table 2) illustrates how the time homogeneous model can be used to evaluate the possibility of inter-group differences in extinction probabilities. Table 2 suggests that the trilobite extinction was «caused» by a higher than average species extinction probability for trilobites. The extinction is still a Galton extinction if one considers the trilobites as a distinct entity with its own value of μ . It should be emphasized that the results shown in Table 2 do not prove that the trilobite extinction occurred in this manner. The calculations only tell us how much the extinction rate for trilobites would have to depart from the Paleozoic norm for the extinction to be explained by the model. It remains an open question whether the size of the required departure is biologically reasonable.

EPISODIC EXTINCTION

The Yule model discussed in the preceding section makes the tacit assumption that extinction is geologically continuous: all species risk extinction at all times and a short or long duration is a matter of chance. Conventional wisdom in paleobiology implies continuous extinction although most people accept that the frequency changes through time to produce occasional periods of mass extinction. But what if extinction is not a continuous process but is limited to brief episodes of geologically negligible duration? What effects would such an extinction regime have on paleontological extinction patterns?

Yule (1924) explored the mathematical implications of episodic extinction but did not reach definitive conclusions relevant to the present context. Episodic extinction has, of course, been suggested by many authors in the context of mass extinction. Cloud (1959) argued that catastrophic copper poisoning of the oceans may have been responsible for the Permo-Triassic extinctions. Schindewolf (1962) suggested that mass extinctions may result from isolated catastrophes of extraterrestrial origin. McLaren (1970) suggested a meteorite impact as the cause of the late Devonian extinctions. Urey (1973) correlated teklite ages with series boundaries in the Tertiary and thereby related meteorite impact and extinction. The most recent proposal for catastrophic mass extinction comes from Alvarez, *et al.* (1980) who claim to have hard geochemical evidence for a collision at the end of the Cretaceous between Earth and a 10-kilometer meteorite. Although this event is yet to be firmly documented, it has considerable credibility.

With the possible exception of the Alvarez, *et al.*, proposal, suggestions of catastrophic extinction through extra-terrestrial phenomena have been discarded quickly by most paleobiologists as being intractable or untestable. Indeed,

catastrophic explanations seem to be anathema to most students of evolution. However, it does appear that collisions between Earth and large extra-terrestrial objects are a fact of Earth history and the frequencies estimated by astronomers (Öpik, 1958, 1973, for example) are such that the biologic effects must be considered (see Dietz, 1961, for further discussion). It is appropriate, therefore, to explore the mathematical implications of episodic extinction.

It has been argued (Raup, 1979b) that catastrophic killing off of species would, if sufficiently extreme, cause a change in the composition of the Earth's biota even in the absence of selective survival. If the number of survivors were very small, pure chance would favor some biologic groups over others: that is, the percentage of a given group among the survivors might be higher or lower than in the pre-extinction biota. Furthermore, the re-population process following the mass extinction event would be by branching and thus subject to group-to-group stochastic variation. This could further enhance the differences between the pre and post-extinction biotic composition—all in the absence of conventional darwinian selection between species. Valentine, *et al.* (1978) estimated that the Permo-Triassic mass extinction killed off 77 % of the standing diversity of marine invertebrates. Raup (1979b), using rarefaction methodology, calculated that the reduction could have been as great as 96 %. But the quantitative implications of these estimates in terms of the effects on biotic composition and on extinction probabilities for large groups were not worked out.

Episodic extinction could occur in at least two forms: (1) catastrophic extinction of all species in a single geographic region or (2) extinction of a fraction of all species on a world-wide basis. The first scenario, biogeographic extinction, probably dates from Cuvier but more recently, Yule (1924) wrote:

«... the species exterminated would be killed out not because of any inherent defects but simply because they had the ill-luck to stand in the path of the cataclysm.»

Clearly, this provides a mechanism for non-selective, episodic extinction if levels of biogeographic endemism are high enough in relation to the frequency of catastrophes of a given size. Although catastrophes of extra-terrestrial origin are not required by this model, they are the most likely cause of total, non-selective destruction of all life in a region.

TABLE 3. Estimates by Öpik (1973) of frequencies and biological effects of collisions with extra-terrestrial bodies. Lethal area is defined as that area subject to surface temperatures of at least 900° F and ash thickness of at least 70 cm; semi-lethal area defined as temperatures of at least 160° F and ash thickness of 7 cm.

Minimum diameter of body (km)	2.1	4.2	8.5	17	34	73
Average spacing in time (my)	13	62	260	1100	4500	22000
Lethal area (radius, km)	160	420	1100	2500	5500	global
Semi-lethal area (radius, km)	480	1300	3300	7500	global	global
	(France)	(USA)	(Africa)			

Öpik (1958, 1973) made estimates of the frequency of collisions; he expressed size not only in terms of the diameter of the body (comet nucleus or meteorite) but also in terms of the area he considered would be lethal to all land life. A portion of his results is reproduced here in Table 3. It should

be noted that the Alvarez, *et al.* (1980) estimate of 10 km for the diameter of the postulated Cretaceous-Tertiary meteorite is within the probability of Öpik's values if one assumes an event occurring only two or three times in the Phanerozoic.

I have tested the plausibility of Öpik's estimates as a cause of biogeographic extinction by simulating collisions with the modern biogeography of all families of land mammals, birds, reptiles, amphibians, and fresh water fish. Targets were selected at random on the Earth's surface and for each target and each of several lethal areas, the number of endemic families was counted. In general, the results of this analysis do not support the generality of biogeographic extinction. Table 4 shows some of the data and one can see, for example, that a lethal area equal to about half the Earth's surface (10,000 km radius) produces extinction of an average of only about 12 % of the terrestrial vertebrate families. Table 3 indicates an average spacing in time of more than 4 1/2 billion years for impacts with this lethal radius. The number of family extinctions is thus too low and the spacing in time too great to provide a plausible explanation for the several mass extinctions affecting land life in the Phanerozoic.

TABLE 4. Results of simulation of biogeographic extinction. Extinctions are of presently living families of land birds, reptiles, mammals, amphibians, and fresh water fish. Each computer run represented a randomly chosen impact point having an assigned lethal area.

LETHAL RADIUS (KM)	NUMBER OF RUNS	MAXIMUM EXTINCTION (%)	MEAN EXTINCTION (%)
0	—	(0)	(0)
3,000	30	1.8	0.2
6,000	30	7.9	1.7
10,000	30	23.9	12.0
(hemisphere)			
15,000	15	48.1	34.4
20,000	—	(100)	(100)
(world)			

Thus, if Öpik's estimates of lethal area are correct, extinction of endemics alone will not explain mass extinctions. This is probably a conservative conclusion because endemism at the present time is almost certainly higher than during most of the geologic past.

We can now consider the second scenario (above): occasional events that kill off a fraction of the existing species on a global basis. We will assume (as a null hypothesis) that the species extinctions are non-selective with respect to fitness. To do so is to contemplate a sudden stress that is beyond the experience of all organisms and thus one for which none are adapted. Survival could be a matter of chance in the sense that certain species have characteristics that enable them to survive but are not advantageous in normal existence. Non-selective survival could also be a fluke of geographic distribution (biogeographic extinction in reverse). The basic question is whether this kind of episodic extinction produces a significantly different extinction pattern from that observed in the real world.

The extinction scenario just described was investigated by computer simulation, using numbers scaled as closely as possible to real world data and time scales. Table 5 shows data on the major extinctions of marine invertebrate families during the Phanerozoic (from Newell, 1967). For each geologic series, Newell tabulated the percent of families going extinct and these are presented as a cumulative frequency distribution in Table 5. They are converted to species extinctions by the rarefaction method of Raup (1979b): for example, a 30 % family extinction is approximately equiva-

lent to an 87 % species extinction. Also, the frequency data are converted to a probability of occurrence (per million years) by dividing the number of extinctions by the length of the Phanerozoic.

TABLE 5. Frequency of extinctions of marine invertebrates and the magnitude of these extinctions. Family extinction data from Newell (1967); species equivalents calculated using the method of Raup (1979b). Values of α for equation (3) are calculated from the probability and species columns.

FAMILIES DYING	PHANEROZOIC FREQUENCY	EQUIVALENT SPECIES KILL	PROBABILITY PER MY	α
≥ 5 %	28	32 %	0.0475	0.095
≥ 10 %	20	52 %	0.0339	0.065
≥ 15 %	12	68 %	0.0203	0.057
≥ 20 %	10	76 %	0.0169	0.054
≥ 25 %	7	80 %	0.0119	0.055
≥ 30 %	4	87 %	0.0068	0.057
≥ 35 %	3	91 %	0.0051	0.058
≥ 40 %	2	93 %	0.0034	0.061
≥ 45 %	2	95 %	0.0034	0.060
≥ 50 %	2	96 %	0.0034	0.059
≥ 55 %	0	—	—	—

At this point, we can use a mathematical model that is employed commonly in the study of other rare events: floods (Gumbel, 1958) and earthquakes (Howell, 1979), among others. The model assumes that the frequency of a rare event decreases exponentially with increasing magnitude of the event. In the present context, this can be expressed by the equation:

$$y = e^{-\alpha x}, \quad (3)$$

where y is the probability of an event occurring which is equal to or greater than the magnitude x and α is a constant. In this application, y is the probability per million years and x as the percent species extinction. For each entry in Table 5, an estimate of α can be made by entering the frequency and magnitude values in equation (3) and solving for α . (Thus, α is the negative of the natural log of the probability divided by the percent species extinction.) The several estimates of α are included in Table 5.

In Table 5, all values for α , except the first, cluster around 0.06 suggesting reasonable conformity to the exponential model of equation (3), at least for the larger extinctions. We can thus use the mean of these estimates (0.058, excluding the first value in Table 5) as a trial value of α in equation (3). With this value, 5 % of all extinction events kill off 50 % or more of the existing species and about 1 % of extinctions kill off 80 % or more species. The probability of 100 % extinction is 0.003 per million years and thus might be expected to occur about twice during the Phanerozoic (0.003 + 590 = 1.8). We know that total extinction has not occurred during this time but the expected number of such events is low enough that equation (3) and its α value are credible.

Equation (3) has been used as the basis for a monte carlo computer simulation, as follows. The simulation starts with a standing diversity of species that is distributed among ten higher taxonomic groups. One of the groups is given 75 % of the species and the remaining 25 % are divided evenly between the other nine groups. This array was inspired by the Cambrian fossil record dominated by trilobites (Figure 1). The total number of species in the starting array can be varied from run to run. The program then moves iteratively through time with one iteration per million years for 590 steps. At each iteration, a y value between 0.0 and 1.0 is chosen from a uniform random distribution and the percentage of species to

go extinct (x) is calculated from equation (3). Any value of x greater than 96 is arbitrarily reduced to 96. This percentage of species is then «killed»: each species is given a chance of extinction equal to the kill percentage (x). The probability of extinction of a given species is, of course, independent of its membership in a taxonomic group. The actual killing is done probabilistically (using a random number generator) in order to introduce natural sampling error.

After all extinctions are accomplished for a given iteration (an extinction event), the hypothetical fauna is re-populated by a random branching process. Each of the surviving species is given an opportunity to branch, with the probability being determined by the post-extinction number of species. That is, a branching probability is computed for each iteration which is that probability necessary to bring the total number of species back up to the number at the beginning of the run. As a result of this procedure, total diversity drops but returns approximately to the starting diversity after each iteration.

A large number of simulation runs were made using several values of initial species diversity (from 1,000 to 50,000) and several values of α in addition to the calculated value of 0.058. The basic questions to be asked of the results are: (1) Is the typical record of group extinctions significantly different from that predicted by the time homogeneous model? and (2) Do the simulations replicate the general pattern of change in Phanerozoic biotic composition (Figure 1)?

It should be emphasized that this kind of simulation is dangerous: when one has the possibility of varying several input parameters (starting diversity, initial distribution of species among groups, and extinction probability), one may be able to devise a combination of parameters that will reproduce real world patterns spuriously. The results must therefore be interpreted with great caution.

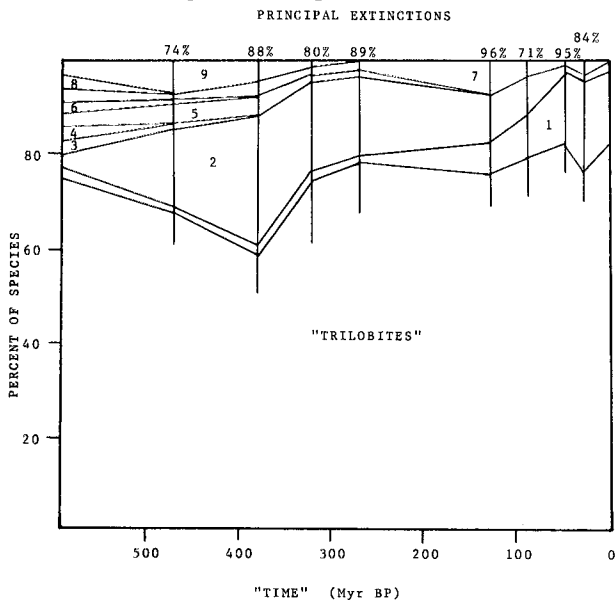


Fig. 2. - Example of simulation output. Starting diversity was 1,000 species (750 «trilobites» and 27 in each of the other nine groups). Only three of the smaller groups survived and the size of the large group fluctuated fairly widely.

The results of simulations will not be described in detail here. It will suffice to show two examples of output and present some qualitative generalizations. Figure 2 shows one run where the starting diversity was set at 1,000 species:

«trilobites» had 750 species and the other nine groups had 27 species each. The graph shows changing group composition through time. Extinction events involving greater than 70 % kill are indicated. Figure 3 shows a run with identical starting conditions except that initial diversity was 10,000.

From these and other runs, several general conclusions can be drawn. By far the most important in terms of the original objectives of the simulations is that *when properly scaled, the simulations do not satisfactorily replicate the sort of pattern seen in the real fossil record (Figure 1)*. When diversity is large (such as the «trilobites» starting with 7,500 species in Figure 3), the number of species is far more stable through time than in the actual fossil record. Even where the initial diversity of «trilobites» was lowered to 750 species (as in Figure 2), the group did not go completely extinct in any run although there were some where other groups developed dominance. Therefore, if our estimates of standing diversity of major fossil groups are reasonably accurate (6,000 Cam-

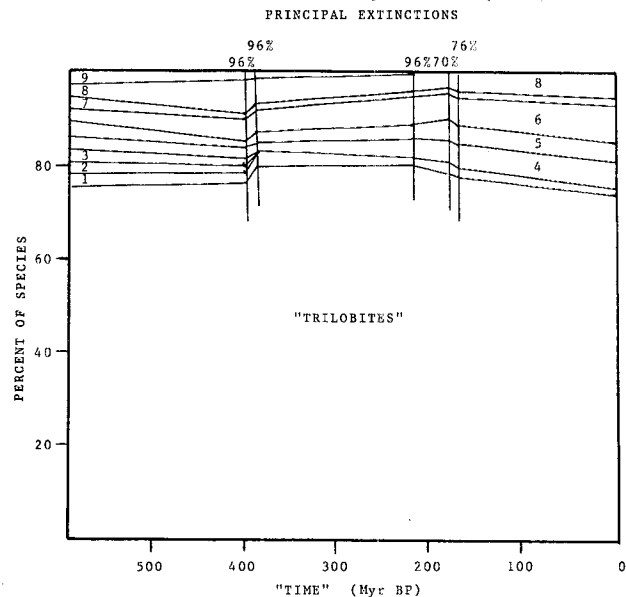


Fig. 3. - Example of simulation output. Starting diversity was 10,000 species (7,500 «trilobites» and 277 in each of the other nine groups). Three of the smaller groups went extinct and the size of the larger group was stable.

brian trilobites species, as used above, for example), then the simple episodic extinction model will not explain the actual evolutionary record in the absence of selective survival of species in certain higher groups.

In spite of the primary failure of the simulations to replicate the Phanerozoic record, a number of generalizations can be developed from the computer results which are useful and applicable to real world problems of extinction. The most important of these are listed below.

(1) *The average speciation rate (branches per lineage per million years) is higher than the mean extinction rate even though mean diversity remains level.* The reason for this is that if an extinction reduces diversity by 20 %, for example, re-population must be at a 25 % rate to bring diversity back to the original level. With a value of α of 0.058, the mean extinction probability is about 0.17 but the corresponding branching probability necessary to regain original diversity is about 0.20.

(2) *The number of groups going extinct is much higher than the number predicted by the time homogeneous model.* This is most striking in the higher diversity runs. In Figure 3, for example, three of the nine small groups went extinct. But if the probabilities are calculated using equation (2), with $\lambda = .17$, $\mu = .20$, $a = 277$, and $t = 590$, the probability of any one group going extinct is $3 + 10^{-20}$ and the probability of as many as three groups going extinct is essentially zero. One could argue, of course, that equation (1) should be used with $\lambda = \mu = 0.17$ because if extinction had not been episodic the species extinction and branching rates would have been the same. But in the case of Figure 3, equation (1) yields a $P_0(t)$ of 0.064 and the probability of at least three of the nine groups going extinct is only 0.002.

(3) *It is not uncommon for a group to linger for several million years after a mass extinction event.* This was seen in several runs: a particularly large extinction event greatly reduced the number of species in a group but did not eliminate the group completely. Rather, subsequent smaller extinctions «finished the job» even though the mass extinction was the primary cause. This can be illustrated by two examples from the run shown in Figure 2. Group 6 was cut down sharply by the 74 % extinction from 18 to 6 species but the group did not go extinct for another 18 «million years» and its demise was caused by a relatively minor extinction event. Group 5 was reduced from 32 to 8 species by the 80 % extinction at 322 Myr B. P. but it survived at low diversity past the 89 % extinction at 272 Myr B. P. and finally went extinct at 253 Myr B. P.

This general situation is undoubtedly analogous to cases in local extinction of species (discussed above) where a disaster of some sort reduced population size to the point where smaller chance factors can complete the extinction. This factor may also be involved in those cases in the fossil record where taxa linger beyond a mass extinction.

(4) *Many major extinctions cannot be seen in the simulated fossil record.* In figures 2 and 3, some of the mass extinctions are noticeable (after the fact) by the changes in group sizes that they produced. But since the changes in group sizes (and therefore relative taxonomic composition) are the result of variable sampling error in extinction and re-population, the effect may be negligible in a given case. This is especially true where groups have many species. In the Phanerozoic record, we recognize mass extinctions only by their effects. The simulations suggest that the effects of mass extinctions are not always obvious and may, in the general case, be seen only in groups already small. The effect for a given group may be either an increase or decrease in numbers relative to other groups.

(5) *The stability of a group through time depends on its size.* It is clear from comparisons of the «trilobites» and other, smaller groups in Figures 2 and 3 and from overall comparison of the two runs that the larger the group, the less fluctuation is experienced in number of species. This is simply a matter of scale and confirms the argument made by Stanley, *et al.* (1981) regarding monte carlo simulations of evolutionary patterns. In the simulations performed in this study, with an α of 0.058, a group having a standing diversity of more than 750 species is virtually immune from extinction and one with several thousand species shows virtually no significant change in diversity through time.

(6) *If one group dominates the fauna, it has a tendency to take over completely.* In situations where groups are small enough to experience size fluctuation, extinction is common (as in Figure 2). This produces an inevitable increase in

relative dominance of one or more large groups and may, depending on groups sizes, lead to the extinction of all but the largest group.

CONCLUSIONS

The darwinian model of selective extinction remains a plausible hypothesis. The time homogeneous birth-death model, which assumes that all species have the same probability of extinction regardless of fitness, is insufficient to explain the extinction of major biologic groups that have once attained high species diversity. A model based on episodic extinction followed by random re-population predicts an extinction pattern closer to the observed record but still falls short of being mathematically plausible. The extinction of once successful groups such as the trilobites is thus most reasonably explained on the basis of bad genes rather than bad luck, at least in the present state of knowledge. If this conclusion holds, both the time homogeneous model and the episodic extinction model can be used to measure the selective disadvantage of groups such as trilobites. In the case of the time homogeneous model, mean duration of species would have to have been 14 to 28 percent shorter for trilobites than for other marine invertebrates for the extinction of the group to be a mathematically plausible event.

The foregoing assumes that our knowledge of species diversities and average species durations in the geologic past is reasonably accurate. If either were an order of magnitude lower than we now think, the alternative models presented here would become viable.

The conclusions reached in this paper apply only to consideration of the behavior of species as members of phylum and class groups. To say that stochastic models do not apply at one scale says little about their applicability at other scales. It may be, for example, that models based on non-selective extinction are appropriate and valid when applied to the behavior of genera within orders of a single biologic group (such as the analysis of Cenozoic mammal genera by Raup and Marshall, 1980). In other words, evolution may be treated deterministically at some scales and probabilistically at other scales.

REFERENCES

- ALVAREZ, L. W., ALVAREZ, W., ASARO, F., & MICHEL, H. V. 1980: «Extraterrestrial cause for the Cretaceous-Tertiary extinction.» *Science* 208: 1095-1108.
- CLOUD, P. E. Jr. 1959: «Paleoecology - retrospect and prospect.» *J. Paleont.* 33: 926-962.
- DIETZ, R. S., 1961: «Astroblemes.» *Scientif. Amer.* August, 1961. pp. 50-58.
- DURHAM, J. W. (1971): «The fossil record and the origin of the Deuterostomata.» *North Amer. Paleont. Conv., Chicago, 1969 Proc.* (H) 1104-1132.
- EILDREDGE, N. & GOULD, S. J. (1972): «Punctuated equilibria: an alternative to phyletic gradualism.» *In: SCHOPIF, T. J. M., ed. Models in Paleobiology.* pp. 82-115. Freeman, Cooper & Co., San Francisco.
- GALTON, F. & WATSON, H. W. (1875): «On the problem of the extinction of families.» *J. Anthropol. Soc. London.* 4: 138-144.
- GOULD, S. J., RAUP, D. M., SEPKOSKI, J. J. Jr., SCHIOPF, T. J. M., & SIMBERLOFF, D. S. (1977): «The shape of evolution: a comparison of real and random clades.» *Paleobiol.* 3: 23-40.
- GUMBEL, E. J. (1958): «Statistics of Extremes.» Columbia Univ. Press, New York, 375 p.
- HOWELL, B. F. Jr. (1979): «Earthquake risk in eastern Pennsylvania.» *Earth and Mineral Sci.* 48: 57, 63-64.
- KENNEDY, W. J. (1977): Ammonite evolution. *In: HALLAM, A., ed. Patterns of Evolution,* 251-304. Elsevier Scient. Publ. Co., Amsterdam.
- MACARTHUR, R. H. (1972): «Geographical Ecology.» Harper & Row Publ., New York, 269 p.

- MACARTHUR, R. H. & WILSON, E. O. (1967): «*The Theory of Island Biogeography*.» Princeton Univ. Press, Princeton, N. J. 203 p.
- MCLAREN, D. J. (1970): «Presidential address: Time, life and boundaries.» *J. Paleont.* 44: 801-815.
- NEWELL, N. D. (1959a): «Adequacy of the fossil record.» *J. Paleont.* 33: 488-499.
- NEWELL, N. D. (1959b): «The nature of the fossil record.» *Amer. Philos. Soc. Proc.* 103: 264-285.
- NEWELL, N. D. (1967): «Revolution in the history of life.» In: ALBRITTON, C. C., ed. *Uniformity and Simplicity*. pp. 63-91. Geol. Soc. Amer. Spec. Paper 89.
- ÖPIK, E. J. (1958): «On the catastrophic effects of collisions with terrestrial bodies.» *Irish Astron. J.* 5: 34-36.
- ÖPIK, E. J. (1973): «Our cosmic destiny.» *Irish Astron. J.* 11: 113-124.
- RAUP, D. M. (1972): «Taxonomic diversity during the Phanerozoic.» *Science*. 177: 1065-1071.
- RAUP, D. M. (1976): «Species diversity in the Phanerozoic: a tabulation.» *Paleobiol.* 2: 279-288.
- RAUP, D. M. (1978a): «Cohort analysis of generic survivorship.» *Paleobiol.* 4: 1-15.
- RAUP, D. M. (1978b): «Approaches to the extinction problem.» *J. Paleont.* 52: 517-523.
- RAUP, D. M. (1979a): «Biases in the fossil record of species and genera.» *Carnegie Mus. Nat. Hist. Bull.* 13: 85-91.
- RAUP, D. M. (1979b): «Size of the Permo-Triassic bottleneck and its evolutionary implications.» *Science* 206: 217-218.
- RAUP, D. M. & GOULD, S. J. (1974): «Stochastic simulation and evolution of morphology-towards a nomothetic paleontology.» *System. Zool.* 23: 305-322.
- RAUP, D. M., GOULD, S. J., SCHOPF, T. J. M., & SIMBERLOFF, D. S. (1973): «Stochastic models of phylogeny and the evolution of diversity.» *J. Geol.* 81: 525-542.
- RAUP, D. M. & MARSHALL, L. G. (1980): «Variation between groups in evolutionary rates: a statistical test of significance.» *Paleobiol.* 6: 9-23.
- RICKARDS, R. B. (1977): «Patterns of evolution in the graptolites.» In: HALLAM, A., ed. *Patterns of Evolution*. Elsevier Sci. Publ. Co., Amsterdam. 333-358.
- SCHINDEWOLF, O. H. (1962): «Neokatastrophismus?» *Deut. Geol. Ges. Z.* 114: 430-445.
- SCHOPF, T. J. M. (1979): «Evolving paleontological views on deterministic and stochastic approaches.» *Paleobiol.* 5: 337-352.
- SIMBERLOFF, D. S. (1974): «Equilibrium theory of island biogeography and ecology.» *Ann. Rev. Ecol. Syst.* 5: 161-182.
- SIMBERLOFF, D. S. (1981): «Community effects of introduced species.» In: NITECKI, M. H., ed. *Biotic Crises in Ecological and Evolutionary Time*. Academic Press, New York 58-81.
- SIMPSON, G. G. (1952): «How many species?» *Evolution.* 6: 342.
- SIMPSON, G. G. (1960): «The history of life.» In: TAX, S. ed. *Evolution After Darwin*, vol. 1. 117-180. Univ. of Chicago Press, Chicago.
- STANLEY, S. M. (1975): «A theory of evolution above the species level.» *Nat. Acad. Sci. Proc.* 72: 646-650.
- STANLEY, S. M., SIGNOR, P. W., & LIDGARD, S. (1981): «Scaling and stability of simulated clades.» *Paleobiol.* 7 (in press).
- UREY, H. C. (1973): «Cometary collisions and geological periods.» *Nature*. 242: 32-33.
- VALENTINE, J. W. (1970): «How many marine invertebrate fossil species?» *J. Paleont.* 44: 410-415.
- VALENTINE, J. W., FOIN, T. C. & PEART, D. (1978): «A provincial model of Phanerozoic marine diversity.» *Paleobiol.* 4: 55-66.
- VAN VALEN, L. (1973): «A new evolutionary law.» *Evol. Theory.* 1: 1-30.
- YULE, G. U. (1924): «A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, FRS.» *Roy. Soc. London. Philos. Trans (B)*. 213: 21-87.