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MASS EXTINCTIONS, DIVERSIFICATION, AND THE NATURE OF PALEONTOLOY

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ABSTRACT

Patterns of extinction and diversification in the Phanerozoic can be accounted for by stochastic models. This result may suggest that these general patterns of biotic evolution represent a huge number of largely independent processes rather than singular processes. Therefore, paleontologists should focus on individual events and chains of events rather than on the general patterns.

Keywords: Mass extinctions. Diversification. Phanerozoic.

RESUMEN

Los modelos de extinción y de diversificación pueden referirse a modelos estocásticos. Este resultado puede sugerir que dichos comportamientos generales de la evolución orgánica representan a un gran número de procesos ampliamente independientes más que a fenómenos singulares. No obstante, los paleontólogos deberían fijarse en los fenómenos individuales o en los encadenados más que en los modelos generales.

Palabras clave: Extinción en masa. Diversificación taxonómica. Fanerozoico.

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MASS EXTINCTIONS

Paleontology is about history of the biosphere. Several paleontologists have recently undertaken to seek general laws of this history. Certainly, the most spectacular among these endeavors are the ones concerned with mass extinctions and taxonomic diversification in the Phanerozoic.

The history of the biosphere is punctuated with periods of extraordinarily high intensity of extinction. For example, the Late Permian is marked by the ultimate demise of a considerable proportion of the major groups of organisms which predominated in the marine environment during the previous several hundreds of millions of years. Trilobites and blastoids became extinct along with a number of minor groups; corals, brachiopods, cephalopods, crinoids, and bryozoans were decimated. The estimates of the number of marine animal species that died out at that time run up to the staggering 95% of the total marine fauna (Raup, 1979).

During the Maastrichtian, marine planktonic organisms, especially those with calcareous shells, were almost entirely wiped out. Ammonites, the major cephalopod group of the Mesozoic Era, disappeared at that time, and extinction affected also other mollusks, bryozoans, and echinoids. On land, dinosaurs became extinct.

Such periods of unusually high intensity of extinction traditionally are called mass extinctions. The distinction of mass extinctions as a separate class of biological phenomena, however, is largely arbitrary. Three other periods in the history of the biosphere also have traditionally been regarded as mass extinctions: the Late Ordovician, Late Devonian, and Late Triassic. A number of other periods have been considered to be major, perhaps mass, extinctions but there is much disagreement on this point. In fact, all paleontological and statistical attempts to clearly distinguish between mass extinctions and the so-called background or normal extinction have thus far failed (Hoffman, 1986a).

For more than a century, paleontologists have pondered on the causes of mass extinction. Dozens of hypotheses were proposed to explain mass extinctions. They range from such mundane scenarios as gradual changes in climate (most likely, a cooling trend) or in the sea-level to such extraterrestrial causes as the radiation from explosion of a nearby supernova or the effects of Earth's collision with a bolide.

Recently, Alvarez *et al.* (1980, 1984a, b) proposed that the Maastrichtian extinction had been caused by impact of a large meteorite and its immediate aftermath. Their proposal sharply differs from similar suggestions made earlier, because it stems from a considerable body of empirical evidence independent of the evidence for extinction itself. In a large number of widely distant places, the sediments that were deposited precisely at the time of the extinction of marine plankton are strongly enriched in iridium and other elements that are likely to have come from an extraterrestrial source. They also contain considerable amounts of microtektites, that is, minute glassy spherules that are likely to represent remains of a meteorite passing through the atmosphere and hitting the Earth. Grains of quartz changed under the shock of extremely high pressures, as at the site of a nuclear explosion, are found in sediments of approximately that age (Bohor *et al.*, 1984). From this evidence, Alvarez *et al.* postulate an extraterrestrial impact at the end of the Maastrichtian Stage, which caused all the effects envisaged by the nuclear-winter scenario and thus led to mass extinction.

This hypothesis is not uncontested. McLean (1985a, b, c) and Officer and Drake (1985; Officer *et al.*, 1986) argue that all the evidence can also be explained by a series of enormous volcanic explosions spread over thousands or even hundreds of thousands of years. They also point out that no crater has been found which could be regarded as the site of the postulated extraterrestrial impact, whereas, on the other hand, vast amounts of volcanic rocks of that age occur in India, thus suggesting a possible site of the volcanic explosions.

The issue is far from settled. The major problems that must be resolved in order to corroborate one or the other (or perhaps still another) hypothesis primarily refer to the poor quality of the fossil record. Paleontologists are not at all certain that the extinction of marine plankton, the ultimate demise of terrestrial dinosaurs, and the extinction of many larger marine invertebrates all happened simultaneously; the incompleteness of the record at the Cretaceous/Tertiary boundary leaves a considerable room for debate (Dingus, 1984). There is also no good data to determine whether dinosaurs and such marine invertebrates as ammonites and many other mollusks became extinct virtually instantaneously, or rather gradually, over several millions of years (Clemens *et al.*, 1981; Alvarez *et al.*, 1984b; Hoffman, 1984; Padian and Clemens, 1985). Perhaps the most troubling question, however, is this: How could a catastrophe of the apocalyptic dimensions envisaged by the hypotheses of extraterrestrial impact and immense volcanic explosions leave so many groups of organisms essentially unaffected? Both these mechanisms directly lead not only to the nuclear-winter scenario but also to the prediction of a tremendous contamination of sea-water with toxic elements. Yet the majority of marine groups, even those living in very shallow water, survived.

The real dilemma, however, which now confronts paleontologists interested in mass extinctions, involves the other periods of this kind. Can we extrapolate from what we know, or suspect, about the Maastrichtian extinction to the other mass extinctions?

The traditional paleontological answer was, no. According to this view, each mass extinction could be caused by its own unique combination of factors and, therefore, should be judged on its own. In fact, microtektite fields and an enrichment in iridium are associated also with the Late Eocene, which sometimes was regarded as a mass extinction (but see Corliss *et al.,* 1984; Snyder *et al.,* 1984), but no compelling evidence for a physical catastrophe of this sort has been found in association with the other mass extinctions.

Raup and Sepkoski (1984, 1986), however, developed a powerful argument for validity of such extrapolation from the causal mechanism of the Maastrichtian extinction to the other mass extinctions. They calculated the intensity of extinction of marine animal families in each geological stage over the last 250 million years. They defined extinction events as stages during which extinction intensity had been higher than in the preceding and the succeeding stages. There are 12 such extinction events in the time interval they considered. Raup and Sepkoski then analyzed the empirical distribution of these extinction events in time and concluded that it is best explained as a periodic phenomenon one extinction event approximately every 26 million years.

Such a periodicity suggests a causal unity of extinction events. The apparently catastrophic circumstances associated with the end of the Maastrichtian Stage might, therefore, be extrapolated also over the other extinction events during the last 250 million years: the Late Permian, Late Triassic, Late Eocene, and a host of other, minor extinctions. There is no simple earthly mechanism that could be invoked as an explanation. Naturally, then, astronomers were called upon to provide a mechanism that would account for periodic extraterrestrial impacts like the one envisaged by Alvarez *et al.* (1980) for the end of the Maastrichtian.

Not surprisingly, several different mechanisms were proposed, each of them predicting a shower of comets falling periodically on the Earth. Perhaps the most attractive hypothesis was presented by Davis *et al.* (1984; Hut, (1984), who suggested that the Sun has a distant and unseen companion star which periodically passes through the Oort Cloud, perturbs the orbits of the comets, and sends several of them toward the inner Solar System; some comets hit the Earth and cause mass extinctions. Lest the public got scared by this scenario of repeated apocalypses, Davis *et al.* reassured the readers that the postulated companon star —or Nemesis, as they poetically called it— «will present no danger to the Earth until approximately AD 15,000,000», because we are now right in the middle of the cycle.

There has been a hot debate among astronomers about the causation of the periodicity of catastrophic mass extinctions. The Nemesis star, the hypothetical planet X, and the oscillations of the Solar System about the plane of our galaxy were most commonly invoked as the culprits (Clube and Napier, 1984; Rampino and Stothers, 1984a, b; Schwartz and James, 1984; Whitmire and Jackson, 1984; Whitmire and Matese, 1985). Less attention was paid, however, to the paleontological evidence for periodicity itself. Hallam (1984) cautioned that the dating of the geological stages employed by Raup and Sepkoski (1984) is too crude to allow for such a detailed analysis. The margin of uncertainty in radiometric dating of particular stage boundaries often reaches ±10 or even ±15 million years in the Mesozoic Era. Kitchell and Peña (1984) demonstrated that randomness cannot be easily dismissed as a description of the empirical distribution of extinction events. Stochastic processes can produce pseudoperiodic patterns that offer a remarkable fit to the actual paleontological data. These arguments, however, have been largely overlooked or glossed over by the advocates of an astronomic mechanism of mass extinctions.

I pointed out another possible source of bias in the analysis of paleontological data on time distribution of extinction events (Hoffman 1985a, b). The definition of extinction event given by Raup and Sepkoski (1984) assumes that whenever extinction intensity goes up relative to the preceding stage and then goes down, this is considered an extinction event. For example, in the series $\underline{U}DD\underline{U}DU\underline{U}DDDUU\underline{U}DDU\underline{U}D$, where U stands for extinction intensity going up and D for extinction intensity going down, the underlined letters mark extinction events. Assuming that the probability of going up and down at each step is 50%, there is a 25% probability that a particular step will represent an extinction event. In other words, if such extinction events are distributed among geological stages at random, one should expect that, on the average, one stage in four will be an extinction event. The time scale employed by Raup and Sepkoski (1984) assumes, in the absence of better dating, that the majority of geological stages are approximately equal in duration—6.2 million years on the average in the considered time interval. Under the hypothesis of randomness, then, extinction events defined according to Raup and Sepkoski, may be expected to occur every 4 x 6.2 = 24.8 million years on the average. This figure does not significantly deviate from the 26-million-year periodicity postulated by Raup and Sepkoski. Hence, I suggested that the apparent periodicity of extinction events may well be an accidental byproduct of the definition and the time scale employed by Raup and Sepkoski (1984).

It might be argued that although the average distance in time between the extinction events conforms to the spacing predicted by the hypothesis of randomness, the empirical pattern is nevertheless more regular, more periodic than such random walks (Gould, 1985; Gilinsky, 1986; Sepkoski and Raup, 1986). However, when the number of geological stages which separate the extinction events is considered as a yardstick, almost 8% of the ten thousand random walks (40 steps long, as the empirical series of data on extinction intensity) generated by Kitchell and Estabrook (1986) are more regular than the empirical series of extinction events. The standard limit for unlikely phenomena is 5%, or even only 1% if more strict requirements are accepted. This means, then, that it is not at all unlikely that a random walk will appear even more periodic than the actual data on extinction intensity over the last 250 million years (Hoffman, 1986b).

This result strongly undermines the hypothesis of periodic extinctions and, consequently, also the astronomic theories proposed to explain such periodicity. If randomness may provide a satisfactory description of the temporal pattern of mass extinctions, and their biological patterns are different (McKinney, 1985; Jablonski, 1986), there also is no reason to suspect that they all share a common causality. They may well be due each to a different set of factors, although their causal unity cannot be ruled out either.

DIVERSIFICATION

The problem of supposedly periodic extinctions exemplifies a much broader question concerning the history of the biosphere. Extinctions are accompanied and, on the average, outweighed by originations of new taxa. If they were not, we would not be around to discuss the whole issue. The number of taxa coexisting at any time reflects the balance of extinctions and originations and gives the simplest measure of taxonomic diversity of the biosphere. Paleontologists have for decades attempted to explain the pattern of change in taxonomic diversity throughout the Phanerozoic. The dilemma is the same as in the case of mass extinctions: Can the pattern of diversification be explained by a single causation, or does it rather represent a joint result of a large set of different causal factors?

Sepkoski (1979, 1981, 1982; Sepkoski and Hulver, 1985) compiled a compendium of the records of the first and last appearances in geological strata for all known families of marine animals. On this basis, he was able to reconstruct the pattern of change in family number (or diversity) through time. He then proposed a model devised to explain the pattern. Sepkoski (1979; see also Sepkoski, 1978) assumed that the origination rate of families should decrease with increasing number of families present in the biosphere, whereas the extinction rate should increase. This assumption stems directly from the ecological theory of island biogeography. It is based on the idea that, on the one hand, the greater the diversity of taxa around, the smaller is the likelihood that a new taxon will be able to establish itself successfully in the competition; on the other hand, the greater the current taxonomic diversity, the smaller is the average population size and, hence, the larger is the likelihood of extinction by some accidental causes. This assumption of the converse relationship of the rates of family origination and extinction with family diversity leads to the logistic pattern: diversity at first increases exponentially but it later levels off and tends asymptotically to an equilibrium point.

Sepkoski (1981) also demonstrated that all marine animals can be subdivided into three huge groupings, or «evolutionary faunas», each of them characterized by a common history of diversification. If these evolutionary faunas are characterized each by a unique interrelationship between origination, extinction, and diversity; and if they are regarded as entities interacting with one another, Sepkoski's model is capable of reproducing the empirical pattern of family diversity of marine animals throughout the Phanerozoic. The fit of this model to the actual data is considerably improved when extrinsic perturbations of the system are allowed, such as mass extinctions (Sepkoski, 1984). On this basis, then, a single biological causation in conjunction with a single astronomic mechanism are proposed as the explanation for the history of diversification of the biosphere.

Again, however, the hypothesis of randomness cannot be easily dismissed. The pattern of family diversity is a composite, secondary pattern. It is the net result of speciation and species extinction. I proposed a model assuming only that the rates of speciation and species extinction vary at random and independently of each other, although the rate of speciation is on the average somewhat higher (Hoffman, 1986a; see also Hoffman and Ghiold, 1985). This model cannot be rejected as an adequate description of the available paleontological data (Hoffman, 1986a; Hoffman and Fenster, 1986). There is no significant correlation between extinction, origination, and diversity on the global scale. The rates of origination, and extinction behave as two independent random walks, as expected under the model I proposed. Stochastic simulations also reproduce the pattern of three evolutionary faunas.

CONCLUSIONS

The changes in taxonomic diversity of marine animals in the Phanerozoic can be represented by a logistic model as well as by a random one. The distribution of extinction events in time can be represented by a periodic model and by a random one. These two sets of paleontologic data can be explained either by a single causal mechanism each, or by reference to a multitude of causally independent forces.

This conclusion does not necessarily imply that random models provide the correct explanations for the paleontological observations but only that there is no reason to reject them. Some methodological criteria must be applied to decide which kind of explanation should be accepted—at least provisionally, until better evidence is found. Scientists employ a wide variety of criteria in such situations. They consider the plausibility of rival hypotheses, their theoretical simplicity and elegance, their proneness to refutation and corroboration by further research, their promise for opening new fields of inquiry, and so on. It is often a matter of taste, however, which one of the competing hypotheses should be chosen on the basis of such criteria. Certainly, each of these criteria has been repeatedly violated in the history of science—to the benefit of scientific progress.

Perhaps the oldest methodological device applicable to this problem is Occam's Razor, that is, the principle formulated by the fourteenth-century nominalist philosopher William Occam who demanded that *entia non sunt multiplicando praeter necessitatem* (beings be not multiplied beyond necessity). Occam developed his principle in response to Plato's realism, which prevailed at that time and postulated that each particular object is an exemplification of a general idea having a real existence in another world. Occam's Razor states that although such general ideas may indeed exist, we have no way of knowing this; their existence is not conceptually necessary and, hence, should not be accepted. As a methodological tool, therefore, Occam's Razor is a conservative principle which advocates the economy of intellectual means employed to explain the world.

Occam's Razor may also be applied to scientific theories. No complex, hierarchical theories should be accepted unless it is demonstrated that their simpler rivals actually fail to account for some phenomena. I have called this methodological rule the principle of pragmatic reductionism—reductionism, because it tends to reduce the number of levels of scientific explanation, and pragmatic, because it is not a metaphysical statement about the nature of the world but only a rule of thumb to deal with such scientific dilemmas as the one that is now facing paleontologists (Hoffman, 1983).

The logistic model of taxonomic diversification at the family level is an example of macroevolutionary theory. It effectively implies that the history of the biosphere is determined by a process that operates at the family level of taxonomic hierarchy. It thus demands that the neodarwinian or synthetic theory of evolution be expanded into a hierarchical theory which would envisage not only such microevolutionary processes as natural selection or genetic drift (within species and populations) but also some macroevolutionary processes (at higher levels).

Acceptance of the random model, in turn, may lead to two different conclusions. Either it is taken to imply that the quality of paleontological data is so poor that the statistical noise overwhelms any underlying pattern and hinders us from discovering the single causation of the history of the biosphere; or it may be considered to mean that the average rates of speciation and species extinction in each geological stage are determined by so many independent factors, both biological and physical, that their changes from one stage to another are unpredictable and do not constitute any orderly pattern. In either case, however, evolution occurs entirely within species and populations. It is only the vast array of biological makeups of individual species and the bewildering diversity of their ecological context that cause their evolutionary behaviors to vary and, hence, to result in randomness at the intersection of a myriad of largely independent processes of speciation and species extinction.

Randomnes of the overall pattern of changes in the global taxonomic diversity is entirely consistent with the neodarwinian theory. That the random model may account for this empirical pattern, demonstrates that there is no need for macroevolutionary theory of diversification. Under the principle of pragmatic reductionism, therefore, the random model of diversification should be preferred over its macroevolutionary alternative.

The implications of this conclusion may go far beyond the particular dilemma of choosing between two rival models aiming at explanation of some paleontological observations. For if the logistic model of taxonomic diversification were accepted, the history of the biosphere would appear as an orderly pattern produced by some macroevolutionary laws. If, on the other hand, the random model is more appropriate, this would mean that the history of the biosphere is an aggregation of a huge number of independent events and causal processes. In such a case, paleontologists would have to abandon their quest for general patterns reflecting the existence of general laws. They would have to reaffirm the nature of paleontology as a historical science.

An analogy to human history may be instructive. Historians have for centuries sought general patterns in the history of societies and cultures. From the eighteenth-century philosopher Giambattista Vico to Georg Hegel, Karl Marx, Oswald Spengler, and Arnold Toynbee, historians envisaged various patterns—from unidirectional progress to dialectic spiral to strict cyclicity. All these attempts, however, have failed. There is no general pattern and no single process in history which would enable us to predict or postdict historical events. The timing of major social restructuring in my native Poland after World War II is almost perfectly periodic (1944, 1956, 1968-1970, 1980-1981), but it does not indicate to any serious historian any causal process which would periodically stimulate social upheavals. A variety of independent causal chains have happened to produce this pattern, and there is no reason to suppose that the periodicity will continue. Historians do not ask questions about the laws that could have resulted in such patterns but they focus instead upon individual events.

If randomness is indeed a satisfactory description of the general historical patterns reconstructed by paleontology, paleontologists may also have to focus on particular events and chains of events—for example, the Maastrichtian and Late Permian mass extinctions—rather than continue the search for general laws of the history of the biosphere.

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