

A theory of origination and extinction

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ABSTRACT: The several recently discovered large-scale patterns of origination and extinction probabilities prove to fit together into a coherent explanatory framework which emphasizes biotic interactions. There is evidence that most environmental pressure is biotic rather than physical.

Higher taxa occupy adaptive zones in the resource space. The initial occupancy of an adaptive zone produces a bloom-period of high origination and low extinction. The resulting crunch suddenly increases the extinction rate, which remains stochastically more or less constant thereafter because of the interaction of pressure from an exponentially declining origination rate with the greater resistance to extinction of the survivors. The opportunity for successful adaptive innovation, and so origination, is similar for all taxa combined as for them considered separately, but high-extinction groups are vulnerable and usually decline, so the overall extinction rate does too. Either immense catastrophes or new opportunities can reset the turnover clock to an earlier time. Diversity of specific taxa is usually expected to decline after a maximum.

As with the intermediate-disturbance hypothesis in ecology, equilibria on a higher level can result from interaction of nonequilibrium processes at a lower level. Natural selection above the individual level need not involve group-specific properties. Free energy, and its control and zero-sum partitioning, may ultimately control the course of evolution. Lyell proposed a somewhat similar view even before Darwin.

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Origination and extinction are the causal components of change in global taxonomic diversity. Their study has a long history. The first estimate (or guess) of normal extinction rate seems to have been that of Charles Lyell in 1832, at 1 species per year. This is remarkably close to my own unpublished estimate from data accumulated in the century and a half since then. Lyell even had, more or less explicitly, an equilibrium model of species turnover: Species were created (perhaps at random and at a constant rate, but he was not explicit about this aspect), but they had unequal fitnesses. By a quite Darwinian struggle for existence (published in 1832!), in which he invoked de Candolle's observations on plant competition and other early ecological results, the less fit species were driven to extinction. This was explicitly a selective process, not a random one, and it was Lyell's explanation for the change in biotas over geological time. He is often misrepresented as believing that there was no biological change over geological time, but this was for him true only for the major ecological and, by inference, taxonomic components of the biota. Indeed, Lyell was the originator of our subdivision of the Cenozoic, based on just such temporal differences in biotas as were expected from his theory. (This is real species selection, selection among species, and so are competitive exclusion, and less extreme changes in density caused by competition, at local or regional levels. What is usually called species selection is really lineage selection, whenever species per se are not the units with differential fitness.) Darwin received this volume of the Principles when in South America on the Beagle voyage, and he read it thoroughly. As I have noted

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elsewhere (Van Valen, 1977), Lyell's theory of community and biotic evolution by natural selection among species undoubtedly made Darwin receptive to Malthus's ecological theory (yes, Malthus discussed more than people) as a keystone for Darwin's own proposal of lower-level evolution by individual selection.

Lyell proposed an equilibrium between (?random) creation and selective extinction, an equilibrium which, as Darwin later saw, led to greater biotic evolutionary change than Lyell had realized. I present here a causal theory, also equilibrial on a basic level, to account for the empirical results of four recent papers (Van Valen, 1984a, 1985 a,b; Van Valen and Maiorana, 1985). It proves to have a wider domain as well. In different ways, the theory is in the spirit of Simpson (1953), Mac Arthur and Wilson (1967), and the Red Queen (Van Valen, 1973a) and, indeed, in the spirit of Lyell.

PATTERN

The main results to be explained are as follows. In the marine realm, for families (which have the best data), the probability of a lineage either giving rise to a new family, or becoming extinct, declined exponentially at an overall constant rate through the whole Paleozoic. The rates of origination and extinction were nearly equal on the average but declined in close concert more than an order of magnitude, with fluctuations about the trend being real but minor in comparison to the first-order effect. The great extinction in the late Permian completely reset this pattern. Both extinction rates and origination rates suddenly increased greatly, and another joint exponential decrease followed. For extinction this second decline probably continues today, but for origination there seems to have been another, smaller, resetting (for pelagic as well as benthic taxa) at the beginning of the Late Cretaceous, with a third decline, again exponential to first order, proceeding thereafter.

For individual higher taxa, like the Foraminifera, Bryozoa, or Osteichthyes, origination rates for families follow the pattern for the combined data. Extinction rates, however, do not. In fact there is, on the average, no detectable trend at all in extinction rates within such single groups. Some variation exists among groups in their overall trends for extinction, but the average is not detectably different from 0. Mass extinctions, and other intervals of unusually high or low rates, occur as superpositions on this long-term background constancy. The average trend is a stationary process with a characteristic interval of about 50 million years. This interval represents the more or less extreme time for return to the dynamically regulated state, at the family level, from perturbations of short or longer duration.

These patterns are not restricted to marine families. In the Cenozoic, mammalian families also experience stationarity in extinction, with a shorter characteristic interval, and an exponential decline in origination rate that is also faster (and extends farther) than that for marine families. Data for taxa below family are not yet adequate for most groups, but here too there does seem to be at least an approximation to stationarity of extinction rates, with characteristic intervals of perhaps 20 million years for marine genera and 5 to 10 million years for marine species. The maximum rates of origination for species of protists are at least as high as that for mammals, so the usual rate for mammals, much faster than that for protists, must be real (and probably ecologically caused) rather than a methodological artifact.

THEORY

How may we explain these patterns? That the following theory does so (unless I am mistaken) is not evidence that some other theory may not explain them at least equally well. However, I have not found another theory that is consistent with other results as well as with these.

Extinction and origination rates have remarkably similar patterns in some ways

but differ in others. The closeness of the two combined distributions to each other in both slope and position, until the late Cretaceous, implies that the two processes are closely interrelated. Origination can cause extinction and extinction can leave room for successful origination; the data do not distinguish between these effects, although the second of course causes the rebounds in origination rate which occur after major extinctions.

The approximate balance between origination and extinction, despite large and concomitant variation in each, implies that there has been an approximate equilibrium, regulated as such, and other evidence indicates ecological rather than intrinsic causes.

Extinction rates are fairly constant within higher taxa, over long and reasonable normal intervals, so the exponential declines come largely from changes in relative numbers of families within higher taxa, including some extinctions of higher taxa. Origination rates, however, change at least as rapidly within most single taxa as they do overall. These patterns apply to Cenozoic mammals as well as to the marine realm. Extinction is actively caused by the (biotic and physical) environment, while origination is permitted by environmental relaxation as well as actively pushed intrinsically by adaptive innovations.

The average effective harshness of the environment, which can be called effective environmental pressure, is measured by the extinction rate. Thus what I call "effective environmental pressure" incorporates the degree of resistance as well as the external stresses themselves. It is about constant over geological time, the various perturbations not causing average within-group extinction to deviate from stationarity, except at the extinctions we use to mark the ends of the Paleozoic and Mesozoic Eras. Smaller perturbations are not, at the family level, distinguishable from stationarity even though they can be recognized at the family level because they tend to be consistent among groups.

Origination rates measure the ease of adaptive change at a particular level. Species have niches (or geographic distributions) that are different in ways which permit them to coexist. Higher taxa are not random agglomerations of species, but rather have their own characteristic morphologies and adaptive zones as well as unique histories. We usually recognize taxa by their morphologies, but these morphologies and less visible characters (and, less often than for species, geographic separation) are what permit the higher taxa themselves to coexist and so determine, from the organisms's point of view, the nature of its adaptive zone. Adaptive zones are the niches of higher taxa. They exist independent of any occupants; there are empty adaptive zones and others where two or more higher taxa are in long-term competition. They need not have sharp boundaries, and indeed their boundaries in the resource space (Van Valen, 1971) may depend on their occupants. (The adaptive zone, as part of the resource space, exists whether or not it is filled, but the partitioning of the resource space, and so the nature of adaptive zones, may be arbitrary or changeable: cf. Van Valen, 1973b). For examples of adaptive zones see Simpson (1953); also, e.g., Van Valen (1971) for mammals, Anderson (1982) for beetles, and Porter (1976) for corals. The occupancy of a common adaptive zone is what causes species of one taxon to be more or less resistant, overall, to extinction at a particular time than are otherwise similar species of another taxon, and to have their other ecological correlations. Higher taxa may nevertheless overlap each other's adaptive zones, just as species can overlap each other's niches, without serious effect as long as each is adaptively superior overall in its own adaptive zone. Too much overlap causes progressive extinction (Van Valen and Sloan, 1966).

A taxon is demarcated from its ancestral taxon adaptively as well as morphologically. It may occupy a different adaptive zone, partition the ancestral zone, or merely be much better in the game of natural selection. Our recognition of taxa depends on characters correlated with, if not directly responsible for, the adaptive change, and it is undoubtedly sometimes wrong from the organism's perspective. (That it can be wrong shows that the theory is at least not vacuous here.) The change need not be abrupt but tends, strongly, to be larger the higher

the rank of the new taxon. The relevant aspect is not our perhaps superficial evaluation but what is important to the organism in its own struggle for coexistence. Genera of flies may be recognized (by human taxonomists) by positioning or number of bristles and yet have different foods. A higher taxon is an adaptively unified part of a phylogeny; it is an ecologically and phyletically natural unit which plays its own role in the processes of evolution (in the ways a species does and more besides).

Thus, indeed, the probability of origination of new taxa measures the ease at which adaptive change, at the level considered, can occur.

In the initial exploitation of an adaptive zone, the unused resources let a hundred flowers bloom, or a thousand mammals play. There is, in all analyzed cases, an initial period of low extinction (ostensibly none at all) and very high origination. (Archibald [1983] has questioned this conclusion for the bloom-phase of mammals immediately around the Cretaceous-Paleogene boundary, but he confounds pseudoextinctions [Van Valen, 1973a] with real extinctions.) The existence of such bloom-periods indicates that most extinctions are caused, at some level, by species interactions; these interactions are not yet strong. The evidence for predominance of biotic pressures comes from the fact that the probability of extinction, as well as the absolute number of extinctions, is very low in each bloom-phase. Physical stresses should not be unusually low then.

Soon comes the crunch: exponential increase is breathtakingly rapid (see Bartlett, 1980, for an extraordinary and well-reasoned application to human population). The adaptive zone is finite, and the taxa inhabiting it soon compete strongly; the expansion has also provided a new resource for predators and parasites. This crunch produces a suddenly high extinction rate. The existing taxa have not yet been much selected among, so there is still a large opportunity for new species or other taxa to evolve successfully. This can happen by expansion of the adaptive zone (or invasion of an adjacent one), by replacement of pre-existing taxa (diffusely or one-on-one), or by subdivision of the adaptive subzones of pre-existing taxa.

It becomes progressively more difficult for most taxa to find a new way to exploit the less resistant parts of the environment around them. The biotic part of this environment is itself evolving for its own benefit. This produces a decline in the probability of origination. The decline is exponential because the adaptive zone eventually becomes saturated with well-adapted species or other taxa; during the decline the proportion occupied by poorly-adapted species decreases at a decreasing rate, as a "randomly" produced new species will soon be more likely than not to find itself in an already well-occupied part of the adaptive zone. It becomes progressively harder for a new species or other subtaxon to find a new adaptive subzone or to be appreciably better than an existing inhabitant. Figure 1 diagrams this process in several stages.

Widespread taxa have low origination rates (Boucot, 1975), but Boucot's explanation from population size is implausible (Gould, 1976). Perhaps more narrowly adapted taxa (empirically correlated with smaller geographic range) find it easier to occupy another small subzone (cf. Eldredge, 1979; Jackson, 1974). There is indeed some evidence (Vermeij, 1978) that species with greater biotic interactions speciate more rapidly than do either stress-tolerant or opportunistic species.

Within an adaptive zone the environmental pressure does not decrease. In fact it presumably increases in real magnitude, but there is coevolution of competitors, predator-prey systems, and other specific and more diffuse interacting groups so that the effect of the increase on an average surviving species remains the same. (If the effective as well as real pressure were to increase, then more of the now susceptible species would be replaced by more highly resistant ones until the average resistance increases enough to resist the average pressure, perhaps but not necessarily with a lower total number of species. Otherwise the whole group would go extinct, but that is the next story.) Originations do continue to occur indefinitely, although at a declining rate, and because of this and because of the

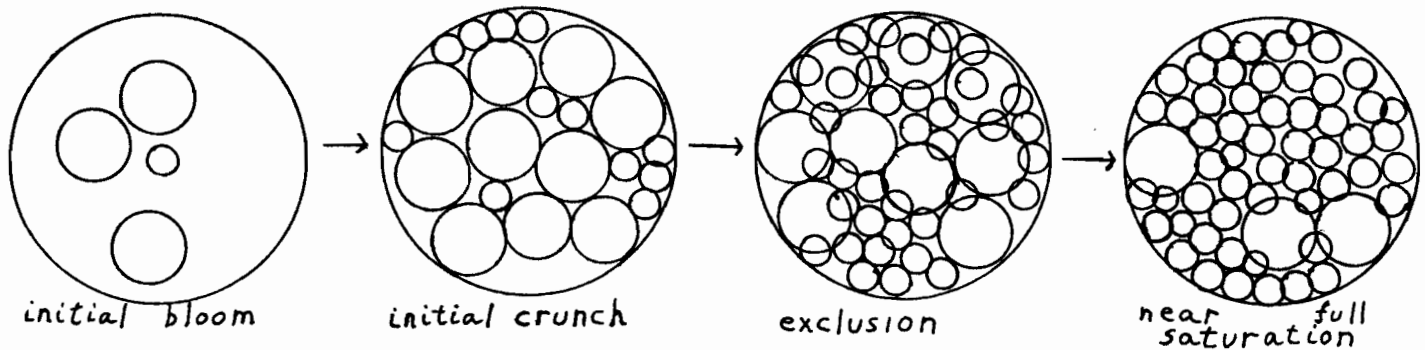


Figure 1. Simplified diagram of evolution in one adaptive zone (large circle). There are two kinds of species, the larger included circles being the poorer average competitors.

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increasingly effective competitors, pressure on existing species continues also. The physical environment produces stresses which fluctuate over different time-scales but which do not seem to have a long-continued increase or decrease for most organisms. They often do seem to cause extinctions, at least locally, and resistance to them seems to evolve rather rarely, at least in the marine realm. Why there is so little evolutionary response to physical stresses, if this is really the case, is obscure; perhaps successful response to potentially lethal stresses often interferes with adaptation to more common environmental pressures. And what proportion of those background extinctions which seem to be caused by the physical environment actually result from competitors better adapted to the changed habitat, is unknown. Overall, in each respect, the effective environment deteriorates at a stochastically constant rate.

For a set of interacting (or adjacent) adaptive zones, the occupants of each behaving about as described above, the overall opportunity for successful adaptive innovation, and so the probability of origination, does not change much. For if the inhabitants of one zone invade another, there is more opportunity for them, for a while, but equivalently less for the group whose zone they have invaded. Thus the overall origination rate declines exponentially just as does that within an adaptive zone.

Simberloff (1981) showed that successful human introductions of species to new geographic areas usually do not result in any obvious extinction of indigenes. This of course does not mean that there was unused energy now being used. It does not even mean that there is usually a vacant niche, partly because unsuccessful introductions may be prevented by the indigenes (as Simberloff noted) and partly because a new species may displace only part of the population of one or more indigenes. That there sometimes are empty niches seems to be shown by the comparisons of Lawton (1982) of herbivores on bracken in different regions, although the most relevant parameter may not be the number of herbivore species but their joint effect on the bracken. A more recent attempt (Walker and Valentine, 1984) uses as a measure of empty niches the ratio of the speciation rate at equilibrium to the maximal speciation rate. Yet a new species may drive another to extinction without there ever having been a vacant niche, in an extreme but not necessarily uncommon case.

Extinction behaves differently here. Groups with high extinction rates within their adaptive zones should be on the average susceptible to invasion from outside, because the part of the adaptive zone vacated by the extinction of one species or other subtaxon may not be soon occupied in its entirety by a more resistant species. And, by definition, the taxa of such a groups are unusually susceptible to extinction themselves. High-extinction-rate groups then usually decline, perhaps to complete extinction, and are partly or entirely replaced by an expansion of existing low-extinction-rate groups. Newly evolving groups have the same situation.

Therefore overall extinction rate declines. It declines exponentially because the most susceptible higher taxa decline first and most rapidly, with an eventual asymptotic approach to the within-zone rate of low-rate taxa.

To explain resetttings of this large-scale community evolution, there are at least two sorts of possibilities. Both seem to have happened. In the first case there is a catastrophe of sufficient magnitude to demolish the pre-existing structure of adaptive zones. The Permian-Triassic extinction did this; more than half the world's families completely vanished. Such a catastrophe resets the entire megaevolutionary clock back to near the beginning; with relatively open adaptive zones, the biotic but not the physical environment is greatly changed by the early Triassic. Both overall origination and extinction rates are then high and again decline exponentially. The Cretaceous-Paleogene extinction, the only other one detectably beyond the contemporary background level, was not large enough in the sea to have such an effect, although on land it permitted the evolutionary explosion of placental mammals. (This explosion started just before dinosaur extinction and may have been causally involved in it: Van Valen and Sloan, 1977, and Van Valen, 1984b).

In the second case of resetting there is no catastrophe, but rather one or more major adaptive innovations of ecologically critical sorts. The invasion of the land was a real expansion, with completely new adaptive zones. (Data are inadequate to document the results on rates, however.) Probably this is what happened at the beginning of the Late Cretaceous, or just earlier, although adaptive details are more obscure here. The "benthic revolutions" of greater mud-churning (Thayer, 1979, 1983) and more effective predation (Vermeij, 1977) more or less coincided with the great expansion of the teleost fishes in the water above them. Perhaps these events were somehow causally related beyond the obvious and inadequate respect that some teleosts eat some of the benthos. Perhaps, alternatively, these events are not causally related to the change in origination; the "benthic revolution" had been occurring for tens of millions of years already. But here again there were new adaptive zones, with others expanded or contracted or subdivided to a much greater extent (as probable for the teleosts, which also expanded into other zones and new ones) than was possible before. In cases like these overall origination rates can increase suddenly and then go into a normal exponential decline. Extinction rates, however, are more ambiguous, because the total available resources do not increase (cf. Gould, 1975; Van Valen, 1976). The innovations merely make part of the resource space relatively exploitable by the innovators. One would probably expect an increase in overall extinction rate too. Indeed, the results on overall extinctions themselves (Van Valen, 1984a) are ambiguous; although consistent with a single post-Paleozoic exponential decay, they are also consistent with two phases separated by a break exactly where it occurs more clearly for the overall origination rate.

This general picture fits well with the results of Bambach (1983), who found that the average number of species per ecological guild of benthos remained unchanged from the Paleozoic to the Neogene, whereas the number of guilds was larger in the Neogene. (He had no data for the Mesozoic or Paleogene.)

Figure 2 diagrams evolution within an adaptive zone in another way. Effective environmental pressure is stochastically constant over the long term, while the opportunity for escape or novelty declines exponentially. Initially diversity rises, as origination rates are very high and extinction rates are at their normal level. Where the lines cross diversity is at its maximum, and it declines thereafter. With suitable scaling changes this model produces the approximately normal distributions of diversity over time which Thomson (1976, 1977) found for relatively homogeneous groups of fishes, amphibians, and reptiles. Presumably in reality most of the diversity decline is caused by other groups, however. It also models, in at least this case correctly because both underlying rate functions are known (Van Valen, 1973a) the change in diversity of mammalian families in the Cenozoic. There are fewer families of mammals now (and even before the megafaunal extinction a few thousand years ago) than there were in the Miocene. A new

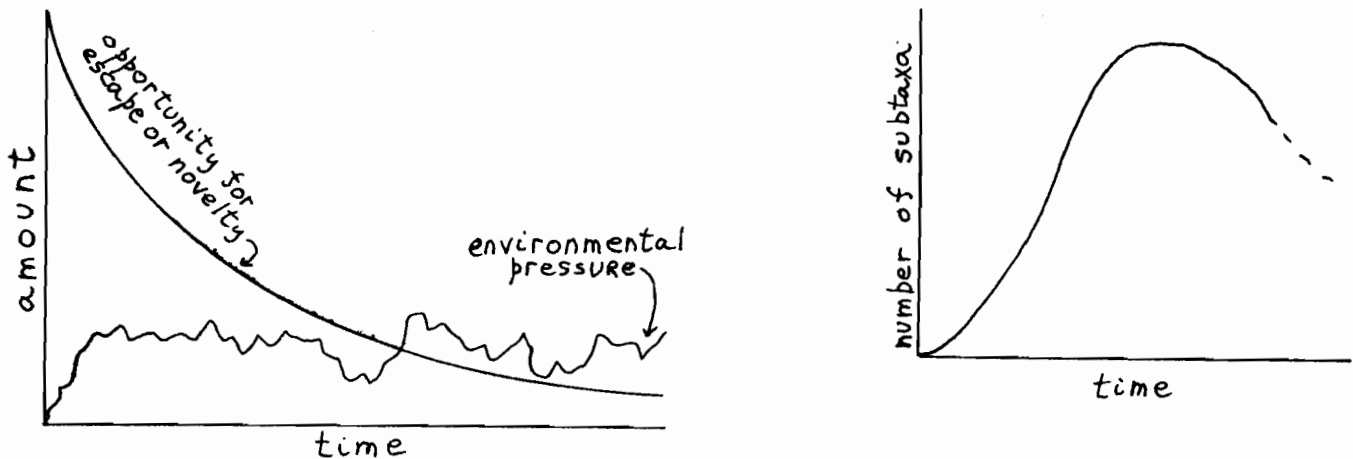


Figure 2. Diagram to show how ratios of the relevant classes of environmental parameters within one adaptive zone change with time and lead to a prediction of a pattern of diversity change.

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distribution starts, as with Thomson's fishes, when a lineage on one group is able to break out into a new adaptive zone or evolve a much better way of exploiting its old zone. Diversity appears here merely as an epiphenomenon, but in reality it probably affects extinction positively and origination negatively.

In this way we see that new adaptive zones, with their consequent patterns of origination, extinction, and diversity, can occur at different levels. The entire recycling of adaptive zones for genera may appear as merely background stochasticity for adaptive zones of families, and so on. Yet, rarely, events even at the species level can have repercussions much higher in the taxonomic and adaptive hierarchy, when they lead to a successful invasion of a new adaptive zone.

What is nonequilibrium at one level can become equilibrium at a higher level. This is equally true in ecology. Probably a major contributor to the maintenance of species diversity are the results of what is known as the intermediate-disturbance hypothesis. With too little disturbance, good local competitors take over; with too much disturbance, only pioneers can survive. With just the right amount, as our culture tells us is proper (from the Golden Mean to the Three Bears), all can continue to exist. Connell (1978) and others view this mechanism as nonequilibrium. So it is, for a particular patch of ground or a small reef. But on a broader scale, in both space and time, it is equilibrium. Disturbances become predictable in occurrence, if not in precise time or place, at this level. And it is on this level where the phenomena maintaining the diversity occur. Fugitive species are poor competitors at the local level but good ones at the regional level; there are several kinds of balance, in different ecological contexts, between competitors each having an advantage at a different level. As with really different levels of selection (and, indeed, species competition is a form of natural selection), competitive equilibria can exist which would collapse at a single level.

An ecological analogy can perhaps make it clear why natural selection above the individual level need not involve properties characteristic only of these higher levels. The regulation of population density is the central topic, if there is any such, of population ecology. Yet it operates entirely by death and reproductive inhibition of individuals. It is a population phenomenon based on properties of individuals. The individuals are not independent of each other, of course, but are indeed part of an ecological population, which interacts with populations of other species, and so on. Similarly, individuals in a species, or species in an adaptive zone, or whatever, are not independent of each other. Their interaction resembles that of individuals in a local population and permits the emergence of ensemble properties which act evolutionarily as such even though some such properties are causally reducible, from one perspective, to properties at a lower level.

Life runs, in evolution as in ecology and physiology, by the use of free

energy. Perhaps there has been some increase in available free energy in the sea since the early Cretaceous; the modern groups of phytoplankton, as well as the planktonic foraminiferans that eat them, have mostly evolved since then (Tappan, 1980). Possibly this even is related to the late Cretaceous change in origination rates, although the latter seems to happen too suddenly. Moreover, blue-green algae and other tiny unfossilizable cells are now known to be important photosynthesizers in the marine plankton, and their role may well have been reduced when the others evolved. Because most of the phosphorus and nitrogen in the photic zone is in organisms, and the availability of these elements (especially phosphorus) largely determines marine primary production, any important increase in primary production would presumably have to accompany a greater supply of these elements. I do not know of evidence for a sustained increase in them since the Early Cretaceous (Ronov and Korzina, 1960, indeed find an ostensible decrease in sedimentation of phosphorus in that interval) and cannot imagine a realistic mechanism for it to occur. There is no long-term change in the average reduced-carbon content of sediments (Ronov, 1959; Ronov and Korzina, 1960), although there are fluctuations and perhaps cycles. The free energy represented by this carbon therefore is itself about constant over long enough intervals, and it in any event represents much less than 1 percent of net primary production. Other evidence (Schopf, 1980) also supports an absence of major changes in productivity.

It therefore seems that at least most of the greatly increased diversity of the past 100 Myr has come about by a finer partitioning of the available free energy. Just how this change in partitioning occurred remains obscure, but its reality can hardly be doubted.

That the available free energy limits the joint abundance of animals and other heterotrophs is shown by the negligible amount of reduced carbon buried below the reach of mud-churners. That effectively all the free energy is used shows the importance of generalized competition. Perhaps the amount of available free energy has not changed since well before the Late Cretaceous. If so, the Red Queen's Hypothesis applies exactly: what one gains, the rest lose jointly. Any reasonable rate of increase in this free energy would not be enough to match that of taxonomic diversity, so the hypothesis holds at least approximately. Stenseth and Maynard Smith (1984) have criticized the zero-sum principle because they discovered another model which also produces constant evolutionary rates (It is less clear that their model would give constant extinction rates: in their model addition of a new species is equivalent, with respect to its effect on a species already present, to the loss of another pre-existing species.) But of course this says nothing about the validity of the principle itself, which has independent evidence.

Adaptive zones themselves need not be constant in the amount of free energy they control. The evolution of more efficient planktivores increases the amount in their adaptive zone, at least if the plankton themselves are not adversely affected overall, and decreases the amount available to adaptive zones of the benthos. More effective predators decrease the amount available to scavengers and other decomposers. And so on. Moreover, new adaptive zones arise even in addition to the occupation of previously empty ones, as the zone for gut parasites did when guts originated. With an ultimate currency of free energy, predation itself is merely one kind of competition, and the occupants of adaptive zones which are adjacent in the resource space can themselves compete, although on a longer time-scale than that within their own zone. We see here an underlying basis for the dynamic equilibrium theory of origination and extinction.

Darwin (1859), and many others since, have proposed that real fitness has increased over geologic time as a result of natural selection removing the generally less fit. An average Cenozoic starfish would be expected to outcompete an average Paleozoic one. Indeed, this is an expected result of Lyell's theory, although he did not notice it. (It would have upset his world view in the same way that Darwin eventually did.) The average constancy of extinction rate within taxa does not refute this view, just as the average overall decline does not support it (because, among other considerations, there are two declines rather than just one.) The

decline in origination would seem to imply a decrease, rather than an increase, in fitness at the family level, for reproduction is a major component of fitness. But in a zero-sum situation, even approximately, the failure of reproduction by one means that another retains its fitness, so that overall there is no net change in fitness in this respect. Stresses from the physical environment can be important, especially in times of major extinctions, but they seem to provide mostly low-level turbulence at other times.

The average constancy does support the view, which I proposed with respect to bloom-phases, that most environmental pressure is biotic rather than physical. If it were mostly physical, then there should indeed be a major decrease in extinction probability even within adaptive zones, as the generally inferior succumb, even without much successful adaptation within species. Only the biotic part of the environment evolves in concert with the organism itself.

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LITERATURE CITED

- Anderson, R.S. 1982. Resource partitioning in the carrion-beetle (Coleoptera: Silphidae) fauna of southern Ontario: ecological and evolutionary considerations. *Canadian Journal of Zoology* 60: 1314-1325.
- Archibald, J.D. 1983. Structure of the K-T mammal radiation in North America: speculations on turnover rates and trophic structure. *Acta Palaeontologica Polonica* 28: 7-17.
- Bambach, R.K. 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. In: *Biotic Interactions in Recent and Fossil Benthic Communities* (M.J.S. Tevesy and P.L. McCall, eds.), pp. 719-746. New York: Plenum Press.
- Bartlett, A.A. 1980. Forgotten fundamentals of the energy crisis. *Journal of Geological Education* 28: 4-35.
- Boucot, A.J. *Evolution and Extinction-Rate Controls*. Amsterdam: Elsevier Scientific. 427 pp.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Darwin, C. 1859. *On the Origin of Species*. London: Murray. 502pp.
- Eldridge, N. 1979. Alternative approaches to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History* 13: 7-19.
- Gould, S.J. 1975. Diversity through time. *Natural History* 84(8): 24-32.
- _____. 1976. (Review of Boucot, 1975). *Sedimentary Geology* 16: 158-160.
- Jackson, J.B.C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. *American Naturalist* 108: 541-560.
- Lawton, J.H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology* 51: 573-595.
- Lyell, C. 1832. *Principles of Geology*. Edition 1, Volume 2. London: Murray. 330 pp.
- Mac Arthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton: Princeton Univ. Press. 203 pp.
- Porter, J.W. 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. *American Naturalist* 110: 731-742.
- Ronov, A.B. 1959. On the post-Precambrian geochemical history of the atmosphere and hydrosphere. *Geochemistry* (1959): 493-506.
- _____. and G.A. Korzina. 1960. Phosphorus in sedimentary rocks. *Geochemistry*

- (1960): 805-829.
- Schopf, T.J.M. 1980. *Paleoceanography*. Cambridge, Massachusetts: Harvard Univ. Press. 341 pp.
- Simberloff, D. 1981. Community effects of introduced species. In: *Biotic Crises in Ecological and Evolutionary Time* (M. Nitecki, ed.), pp. 53-81. Chicago: Univ. Chicago Press.
- Simpson, G.G. 1953. *The Major Features of Evolution*. New York: Columbia Univ. Press. 434 pp.
- Stenseth, N.C., and J. Maynard Smith. 1984. Coevolution in ecosystems: Red Queen evolution or stasis. *Evolution* 38: 870-880.
- Tappan, H. 1980. *The Paleobiology of Plant Protists*. San Francisco: Freeman. 1028 pp.
- Thayer, C.W. 1979. Biological bulldozers and the evolution of marine benthic communities. *Science* 203: 458-461.
- _____. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. In: *Biotic Interactions in Recent and Fossil Benthic Communities* (M.J.S. Tevesz and P.L. McCall, eds.), pp. 479-625. New York: Plenum Press.
- Thomson, K.S. 1976. Explanation of large-scale extinctions of lower vertebrates. *Nature* 261: 578-580.
- _____. 1977. The pattern of diversification among fishes. In: *Patterns of Evolution, as Illustrated in the Fossil Record* (A. Hallam, ed.), pp. 377-404. Amsterdam: Elsevier Scientific.
- Van Valen, L.M. 1971. Adaptive zones and the orders of mammals. *Evolution* 25: 420-428.
- _____. 1973a. A new evolutionary law. *Evolutionary Theory* 1: 1-30.
- _____. 1973b. Are categories comparable in different phyla? *Taxon* 22: 333-373.
- _____. 1976. Energy and evolution. *Evolutionary Theory* 1: 179-229.
- _____. 1977. The Red Queen. *American Naturalist* 111: 809-810.
- _____. 1984a. A resetting of Phanerozoic community evolution. *Nature* 307: 50-52.
- _____. 1984b. Catastrophes, expectations, and the evidence. *Paleobiology* 10: 121-137.
- _____. 1985a. How constant is extinction? *Evolutionary Theory* 7: 93-106.
- _____. 1985b. Why and how do mammals evolve unusually rapidly? *Evolutionary Theory* 7: 127-132.
- _____. and V.C. Maiorana. 1985. Patterns of origination. *Evolutionary Theory* 7: 107-125.
- _____. and R.E. Sloan. 1966. The extinction of the multituberculates. *Systematic Zoology* 15: 261-278.
- _____. and _____. 1977. Ecology and the extinction of the dinosaurs. *Evolutionary Theory* 2: 37-64.
- Vermeij, G.J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3: 245-258.
- _____. 1978. *Biogeography and Adaptation*. Cambridge, Massachusetts: Harvard Univ. Press. 332 pp.
- Walker, T.D., and J.W. Valentine. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *American Naturalist* 124: 887-899.