WHAT HAPPENS AFTER EXTINCTION?

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ABSTRACT

The situation after an extinction is considered. An important post-extinction event is diversification and three main aspects concerning this must be taken into account: a) ecological aspects; b) natural selection, adaptation and morphogenesis, and c) macroevolutionary aspects. Adaptive radiations come usually after a mass extinction. The first point deals with ecology; morphological novelties and a suitable internal structure of ecosystems are as important as good physical environments for diversification. A second point considered is how natural selection works in the case of dealing with constrained or unconstrained developmental systems. The third point considers the action of non adaptive macroevolutionary processes at the beginning of diversification and later, strong natural selection if ecological niches are gradually filled. Chance as a macroevolutionary factor is also considered.

Keywords: Post-extinction events, Adaptive radiation, Ecology, Developmental constrictions, Macroevolution.

RESUMEN

En este trabajo se va a considerar lo que ocurre después de una extinción. En esa fase son importantes los acontecimientos de diversificación, y hay tres aspectos principales a tener en cuenta: a) ecológicos; b) de selección natural, adaptación y morfogénesis, y c) macroevolutivos. Las radiaciones adaptativas son frecuentes después de una extinción masiva. El primer punto trata de problemas ecológicos: las novedades morfológicas y una adecuada estructura interna de los ecosistemas son tan importantes para la diversificación como el conveniente ambiente físico. El segundo punto considera la forma de actuar de la selección natural cuando opera sobre sistemas en desarrollo sometidos, o no, a constricciones. El tercer punto considera la acción de procesos macroevolutivos no necesariamente adaptativos al comienzo de la diversificación (y divergencia), seguidos de fuerte acción de la selección natural si los nichos se van llenando gradualmente. También se ha considerado el azar como factor macroevolutivo.

Palabras clave: Acontecimientos post-extinción, Radiación adaptativa, Ecología, Constricciones en el desarrollo, Macroevolución.

INTRODUCTION

This paper aims to explore the situation subsequent to an extinction. The main process that may be produced after an extinction is diversification, and this is concerned with macroevolutionary events. Macroevolution is understood as evolution at the species level and its consequences (Goldschmidt, 1940; Vrba and Eldredge, 1984; De Renzi, 1986). Diversification may not only take place after extinctions but may also be produced in other ecological scenarios.

Valentine (1980) has proposed a game model for this process. This model considers the biosphere

like a great mosaic board composed of mosaic tiles or *tesserae*. Each tile is a relatively uniform set of environmental conditions. Extinction may be at random. Thus, several *tesserae* may become empty. These empty places may be occupied again by inhabitants of neighbouring tiles. This conception of the board is static. Nevertheless, we need a dynamic concept of the board game. Massive extinctions change the shape of tiles. Some *tesserae* arise and other *tesserae* disappear. This dynamic model permits its author to study the subsequent evolutionary phenomena after a massive extinction (Fig. 1). This model is proposed qualitatively. More recently (Valentine and Walker, 1987), a computer model for extinction in a taxonomic hierarchy has been designed, and makes possible its use in real cases. This computer model is the quantitative version of the mosaic model.
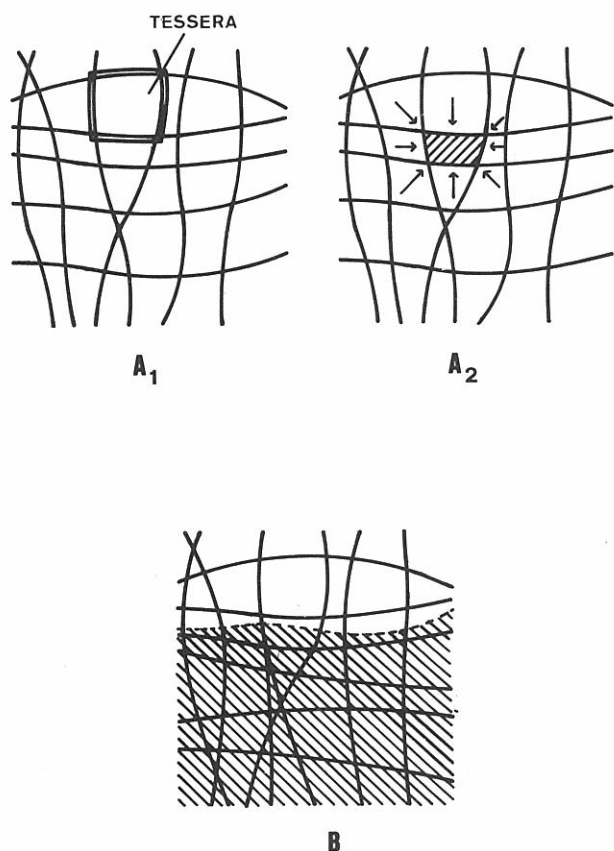
Figure 1. The board of the Valentine game model. A_1) General aspect and its parts. A_2) An extinction is produced in a *tessera* (shadowed tile), but general conditions are not changed (static board). This *tessera* may become filled again with migrants of adjacent *tesserae* (arrows). B) A massive extinction modifies the shape of many old *tesserae*; new *tesserae* arise and others disappear (shadowed zone). The limit (dashed line) does not necessarily coincide with old limits of tiles.

Many ecological niches become empty after an extinction. Thus, other groups of unspecialized organisms, unaffected by the extinction, can occupy the niches left. Many times the process is an adaptive radiation. The extinction rate must be taken into account. Valentine (1977) calls for an adaptive model of rapid diversification when there are many free niches. Changes in growth gradients and re-ordering of organ systems would be ruled by repatterning of regulatory genomes. However, several actual macroevolutionary hypotheses neglect the improvement of adaptation at the organism level and there may be non adaptive evolutionary trends (Vrba, 1983; Vrba and Eldredge, 1984). On the other hand, there is an alternative to the interpretation of classical adaptive radiation. Gould (1970) emphasizes that adaptive radiation is a group of competitive experiments to test the possibilities of a new construction (or evolutionary novelty). Then, the degree of success of each experiment is different. The survival of a little group of these experiments is the result of natural selection. This viewpoint will be taken, together with modern ideas on developmental biology, to study some features of evolutionary events after extinctions.

Thus, my paper deals with three main points: 1) the ecological situation after a mass extinction, 2) natural selection, adaptation and morphogenesis, and 3) macroevolutionary hypotheses.

ECOLOGICAL SITUATION AFTER A MASS EXTINCTION

This situation is characterized by many free ecological niches. This does not only happen after an extinction; there are other similar situations in the geological record, which are not subsequent to a mass extinction. A good example is the situation prior to the adaptive radiation of Metazoa at the beginning of the Cambrian. Good physical conditions for this process were already present before Cambrian times (an enrichment of the atmosphere in oxygen and an important biomass production by the autotrophic unicellular organisms must have helped the appearance and diversification of the heterotrophic multicellulars). I want to consider the Stanley (1976a) analysis of the question, because I deem it very useful for my purpose.

The Stanley's basic question is why animals appear so much later. According to him, the causes may be summarized in two main points:

1)   There must be an evolutionary novelty that makes possible the diversification (in this case sexuality, which starts multiple speciation events and thus, the evolution of multiple body plans).

2)   The state of ecosystems must be suitable to accept diversification (absence or presence of predators played a crucial role in the Cambrian metazoa radiation).

Both internal causes have the same importance in this context, but physical adverse conditions may remain and hamper diversification after a mass extinction. When suitable physical conditions are attained again, internal features may begin to work.

The sharp irruption of Metazoa is a remarkable fact (Stanley, 1976b). The successful and fast irruption of an unspecialized group of organisms occupying empty niches after an important extinction is also a common event. Such evolutionary events are known as adaptive radiations.
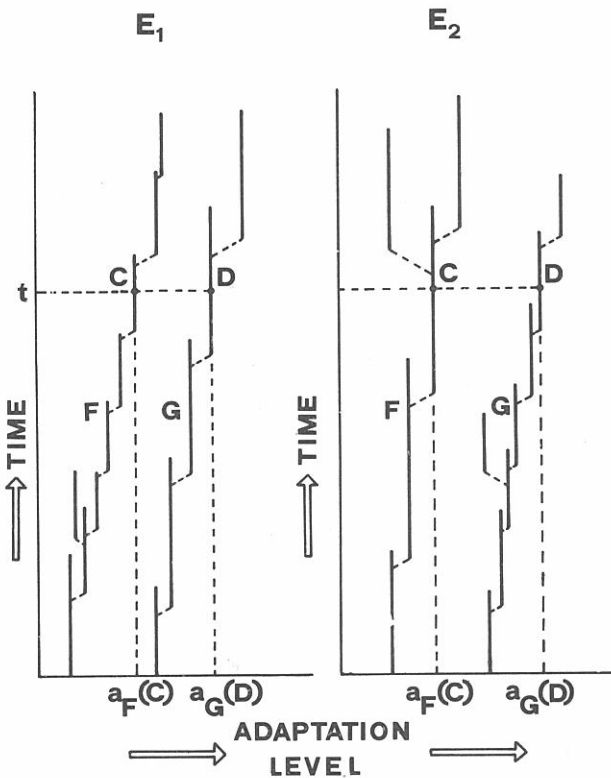
Figure 2. Two clades F and G following punctuated equilibria models and a more or less parallel evolution. E_1) It is inferred from the plot that $r_F > r_G$. If C invades the ecological niche of its contemporaneous D (or D invades the niche of C), C becomes extinct because $a_F(C) < a_G(D)$. E_2) This is the inverted situation, because $r_F < r_G$. However, C would be also removed because $a_F(C) < a_G(D)$. The results are identical whether F follows a punctuated equilibria model and G a gradualistic model with branching points (or without them), and so on.

Adaptive radiations require the punctuated equilibria model —or rectangular model— according to Stanley (1975). However, it is possible to imagine a more parsimonious situation of phyletic change different from the adaptive radiation. I want to make some predictions about these possibilities. Two clades F and G are suposed evolving more or less parallely (Fig. 2). Their branching rates are r_F and r_G, and their adaptive levels are a_F and a_G. At the time t, species C and D are contemporaneous and the coexistence of C and D may be favoured as the ecospace approaches the saturated condition. If r_F is larger than r_G and a_F is, generally, smaller than a_G, when C and D are together, C becomes extinct. If r_F is smaller than or equal to r_G and a_F is, in gene-

ral, larger than a_G, both situations also favour D. If $r_F = r_G$ and $a_F = a_G$, random factors may affect the survival of both C and D (Fig. 2). We can imagine a non parallel evolution referring to adaptation. In this case, if a_C is smaller than a_D, C will be removed when D invades its niche.

However, real cases generally consist of a single group occupying empty niches. The concurrence with members of his own group or another group may come later. The concurrence of species for an ecological niche may be interpreted as competition. Competition is usually prevented in "normal" ecological scenarios. When the input of a new species takes place in an ecosystem, natural selection promotes deviations from species with similar adaptations already present in the ecosystem.

NATURAL SELECTION, ADAPTATION AND MORPHOGENESIS

For our discussion, it is first necessary to make before some remarks on natural selection, morphogenesis and adaptation. How can natural selection work? There are two hypotheses. We may imagine developmental systems as unconstrained or constrained systems (Fig. 3).

A continuous spectrum of morphologies may be produced under the premises of the first hypothesis. Natural selection removes the unfit. The result would be a typical adaptive landscape (Sewall Wright in Raup, 1972; Frazzetta, 1975), with adaptive peaks and valleys. All the developmental ends would be possible and discontinuities of the morphospace would be due to natural selection.

There are only a few developmental ends under the premises of the second hypothesis (Alberch, 1982; Gould, 1982). Other intermediate ends are impossible from a developmental viewpoint and the morphospace would have empty developmental zones. Thus, natural selection cannot fashion indefinitely the adaptive characteristics of organisms and only may work in the developmentally possible zones. So, morphological convergences would be very frequent and competition takes place in many cases, when the diversification process has advanced enough and the ecospace becomes gradually saturated. However, convergence may also be possible in unconstrained developmental systems, because there is a small number of adaptive peaks. This may be the end situation of an adaptive radiation. Nevertheless, saturation may not be reached; thus, competition would not be necessary.

Adaptive radiations are exemplified as important post-extinction events. I want to take an old idea exposed by Gould (1970). According to him, in an adaptive radiation, an innovation is tested in competitive experiments and natural selection removes the unfit. This is a good idea, but actual concepts of developmental biology, such as that of developmental constraint, ask a reformulated expression.
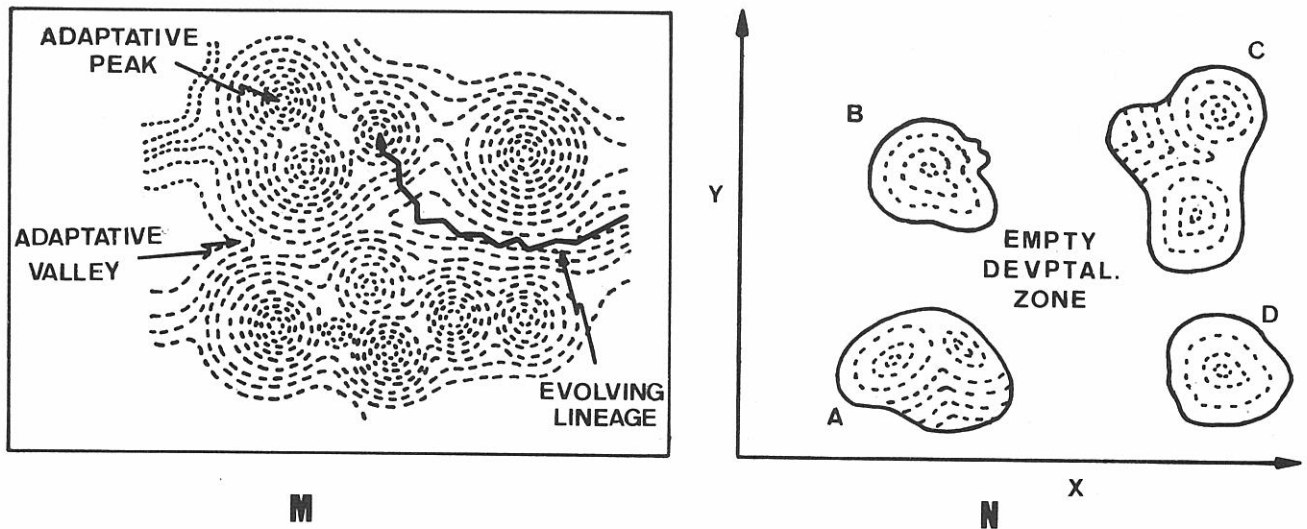
Figure 3. M) A classic Sewall Wright adaptive landscape with peaks and valleys. An evolving lineage may climb any peak and its choice is at random (from Raup, 1972). Evolution is represented by a continuous phenotypic pathway. N) The morphospace has only a few isolated possibilities (A, B, C, D) from a developmental viewpoint. Transitions; e.g. from B to C, have different probabilities. There may be classic adaptive landscapes in the interior of any of these isolated zones (from Alberch, 1982, modified).

Developmental pathways originate a certain number of constructions that use an evolutionary novelty, without intermediate forms. A subset of these constructions become unfit when competition is established.

Developmental systems would be stressed by changes in their genetic foundation, with the subsequent canalization ruptures and the emergence of new kinds of organisms. Random genetic drift would be the main stressing process in action in small populations occupying wide empty regions (e.g. mammals'postcretaceous diversification), but different selection pressures would also be possible in new conditions as causes of canalization ruptures. New constructions could be weakly adapted to their function in new niches (initial sloppiness in evolutionary novelties evolves easier than precise organic machinery; Frazetta, 1975), but the initial absence of competition would avoid the extinction. Later, natural selection would act and a gradual adaptation (phyletic change or punctuated equilibria models) would take place. Thus, the first steps would be intraspecific competition. New phenotypes having sharply emerged in a population could also avoid intraspecific competition in occupying non exploited subniches (Ludwig effect in Frazzetta, 1975). Interspecific competition comes later and the gradual process of filling niches may become logistic, if a saturated condition is reached (Sepkoski, 1978, 1979).

MACROEVOLUTIONARY FEATURES

The possibilities for non adaptive macroevolutionary processes are important at the beginning of such an ecological situation. There is physical space and many free ecological niches.

Two examples of hypotheses that give rise to non adaptive evolutionary trends are *species selection* (from Stanley, 1975, with an accurate criticism of Vrba, 1984; according to the latter, "species selection is that interaction between heritable, emergent character variation and the environment which causes differences in speciation and/or extinction rates among the variant species within a monophyletic group") and the *effect hypothesis* (Vrba, 1983, and Vrba and Eldredge, 1984; the effect hypothesis explains trends as the result of traits of the organisms or their genomes that determine *a fortiori* or fortuitously the probabilities of extinction and speciation, but does not as the result of adaptation at the organism level). Strong natural selection may operate later, when the niches are gradually filled, and interspecific competition is gradually established.

Rates of extinction may be slow or very fast (see Raup, 1987). In a low extinction rate, the replacing organisms may also appear at the same rate as the rate of the extinction, but this does not involve a phyletic gradual change in the replacing group. Both phyletic change or punctuated equilibria models with a low speciation rates may govern the replacement. The static mosaic model of Valentine is very suitable for a situation in which extinction is random and has a low rate.

A fast gradual extinction rate may be considered. The branching and extinction rates can be unequal. At the beginning, branching rate is larger than extinction rate. The situation is reversed at the end. This supposes a time-inhomogeneous model (Raup, 1985). Models like those of Sepkoski (1978, 1979) or Carr and Kitchell (1980) must be seen from this viewpoint. Carr and Kitchell remark that a positive

perturbation of diversity in a satured condition results in a rapid decrease of diversity and this has a delayed recovery with a slower rate from an undersaturated condition. Their example is the transition of the invertebrate fauna from the Permian to Triassic.

The morphologic potential for diversification is an evolutionary situation that must be attained, but this does not necessarily occur. Random factors in evolution have been emphasized as null hypotheses by Raup (1972, 1977), Schopf (1979) and other authors. The appearance of an evolutionary novelty preadapted to several conditions may be a random choice in the phylogeny (Raup, 1972). Thus, the replacement of extinct groups may not be immediate, in spite of its possible achievement. The appearance of an innovation or innovations may be a random event and they might not appear, even though ecological barriers do not take place. In terms of an adaptive landscape, the choice of an adaptive peak by an evolving lineage may be at random (Raup, 1972). On the other hand, if developmental constraints have to be considered, they may prevent the morphogenesis of the necessary structures to work more or less successfully in empty ecological niches. In this latter case, there would be a jump between two possible developmental ends, but these jumps are not all equiprobable from a developmental viewpoint (Alberch, 1982). See figure 3 again.

Finally, massive extinction could be a random event (Raup, 1981; Schopf, 1979), and there are no ecological barriers for the immediate occupation of a niche or niches. If this is the real situation, the static mosaic model of Valentine is again useful. For Hoffman (1986) there is no reason to reject stochastic models of diversification and to substitute them for deterministic models. Thus, patterns explained from a deterministic viewpoint (like the pattern of the three evolutionary faunas; Sepkoski, 1981) may be reproduced by stochastic simulations in some cases. Random models must be tested as null hypotheses, but as Raup (1977) —referring to stochastic models— says, "the success of the simulation (with a stochastic model) does not prove the model; it proves only that the simulation represents one way in which the... observed patterns could have developed. The logical next step is to use the model *to make other kinds of predictions that can be tested with real world data*. If these tests are successful, the model can be elevated to the status of a generalization or statistical law" (the underlined is mine).

The sentence *to make other kinds of predictions that can be tested with real world data* poses important problems when stochastic models fit well.

CONCLUSIONS

A remarkable post-extinction fact is diversification. This diversification usually takes the form of adaptive radiation. Adaptive radiations are competitive experiments. They require suitable physical conditions as well as an evolutionary innovation to be exploited in several ecosystems, but internal structures of these latter must accomplish certain conditions for evolving the morphological novelty.

Morphological novelties have developmental bases. We can consider unconstrained or constrained developmental systems. In the first case, there will be a continuous morphological spectrum and discontinuities are the result of natural selection. In the other case, discontinuities may be the result of the very nature of development plus the action of natural selection, which removes some results reached in the evolution. Thus, in this latter conception there may be "islands" with a classical adaptive landscape structure. Populations of the new diversifying group will have small size. Thus, canalization ruptures will take place and new phenotypes arise from them. At first, competition after extinction may be low (intraspecific competition), but later it may be intense (intra and interspecific competition).

Non adaptive macroevolutionary mechanisms (species selection, effect hypothesis) may operate during the former phases of post-extinction diversification. Strong natural selection may work later, if ecological niches are gradually filled. Chance may have an important role in this macroevolutionary context, but its effects must be carefully assessed.

Finally, gradual extinction does not require gradual phyletic change for a replacing group. Punctuated equilibria models with a low speciation rate are also suitable.

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