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Antoni HOFFMAN *

PUNCTUATED-EQUILIBRIA EVOLUTIONARY MODEL AND PALEOECOLOGY

Model naruszanej równowagi ewolucyjnej a paleoekologia

Abstract. — Evolutionary stasis of species may result not only from the genetic and developmental homeostatic mechanisms but also from the constraints of ecological structure on particular species. This hypothesis is necessarily followed by the prediction of speciation events occurring more or less randomly within simple communities, while somewhat clustered and generally limited to major ecological reorganizations within integrated communities. The hypothesis can, therefore, be tested in the fossil record.

In a recent paper, Gould & Eldredge (1977) reconsidered and reaffirmed their evolutionary model of punctuated equilibria (Eldredge & Gould 1972). The main argument can be briefly summarized as follows: Evolutionary stability of species occurs very commonly and over very long periods of geological time. New species arise almost instantaneously throughout the fossil record. The commonness of such events and relative scarcity of well-documented gradualistic cases suggest that the punctuational model is adequate to the main (but not the only) mode of species evolution.

As clearly stressed by Gould & Eldredge (1977), the crucial point in further evaluation of their model is to analyse the relative frequency of differential evolutionary tempos; that is to ask whether species stasis does, indeed, occur more commonly than phyletic gradualism. Thus far, very few counter-examples to the punctuational model have been convincingly described; Ozawa's (1975) study of a Permian foraminifer from East Asia is among the exceptions. In contrast, several paleontologists have supported the model by claiming that speciation period is very short relative to the subsequent duration of species (Johnson 1975, Robison 1975, Ager 1976, among others). The model makes also

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* 00-490 Warszawa, Wiejska 14 m. 8.

the basis for a more general theory of macroevolution advocated by Stanley (1975, 1976). However, when considering the model of punctuated equilibria, one has also to solve the problem of a causal explanation to both the stasis and speciation events.

In their original paper, Eldredge & Gould (1972; cf. also Eldredge & Tattersall 1975) referred in this context to the mechanisms resulting from both genetic and developmental homeostases, as advocated by Lerner (1954). Then, allopatric speciation appears as the main mode of evolution because the homeostasis can be overcome but in small isolated populations where the inertia of large numbers is considerably reduced. Nevertheless, nobody can deny that phyletic gradualism and sympatric speciation do also occur in the nature even though perhaps less commonly than their opposite. These very phenomena cannot be explained by any disturbance in genetic or developmental homeostases, as such a disturbance has been argued to be possible but in peripheral isolates.

In fact, one may claim that some other homeostatic mechanisms are also involved in maintaining long-term stability of species through evolutionary time. I propose that stasis may as well result from a centripetal selection for the maintenance of ecological role in a stable community structure; community structure is here meant as the whole of biological interactions among all community members, and of their autecological relations to the abiotic environment. This is not to imply that communities can be justifiably treated in holistic terms, i.e., regarded as superorganisms subject to some ecological and evolutionary processes. Communities are nothing more than mere associations of organism populations interrelated and co-occurring at a single locality. Nevertheless, community structures are often highly complex and integrated which results in their homeostatic properties irreducible to the properties of component populations. Some communities are also stable in ecological time and persistent in evolutionary time. Then, system approach appears appropriate to analyse community behavior.

Recently, Gecow (in press) demonstrated some general properties of cybernetic self-improving systems. He analysed aggregates of automata involved in a transformation of one set of signals into another set. The former set is to be considered as the environment of an aggregate; the latter one represents its normal function. When the environment (i.e., the input set of signals) changes significantly, the aggregate has to evolve if it is to endure and perform its previous function (i.e., to get the output set of signals just the same as previously).

The evolving aggregate changes its own structure in such a way as to transform the new set of environmental signals into the previous one. This can be most easily accomplished by adding new automata between the source of environmental signals and the old receptor automata. Then, the old structure of aggregate is able to persist in constant form under the cover of additional automata. This cover assures that the old receptors receive all the same set of environmental signals. In other words, in each long-term permanent aggregate performing a constant function, one may distinguish its unchanged original form and its cover consisting of additional automata added successively to the aggregate in response to perturbations in the set of environmental signals.

Each particular automaton is to be characterized not only by its transmitting function but also by its cone of influence on other automata making part of the aggregate. Cone of influence is here meant to designate size of the group of automata affected by a change in signal send by a given automaton. The smaller is the average cone of influence in an aggregate, the less its structure is integrated. Gecow (in press) demonstrated by means of a computer simulation that the less integrated is aggregate structure, the more easily can be developed an adequate cover because the weaker are the constraints of system structural homeostasis.

When translating the above cybernetic model into ecological terms, the structure characteristic of a community type can be regarded as its original form, while taxonomic composition of a particular community would represent the cover. In fact, in order to persist under changing environmental conditions, a community has to permit either speciation of the affected taxa, or immigration of replacement species. Both these processes can be treated in terms of cover development. Then, the above cybernetic discussion implies that structurally simple communities can more easily develop an adequate cover than integrated communities can. Community composed exclusively of mutually independent species is here regarded as an extremely simple one. In other words, the ecological constraints imposed by a community structural homeostasis on newly evolving species are much more rigid in integrated communities than in simple ones.

This conclusion provides a paleoecological test for the hypothesis proposed herein. In fact, the hypothesis that species stasis is partly induced by the constraints of ecological structure is necessarily followed by the prediction of speciation events occurring more or less randomly within simple communities, whereas somewhat clustered and generally limited to major ecological reorganizations within integrated communities. The term community reorganization is here meant to designate such a community reaction in evolutionary time which leads ultimately to system break-down and loss of its structural identity. A community type can be expected to undergo an ecological reorganization in response to some major changes in its abiotic or biotic environment which cannot be absorbed by the ecological structure. In system terms, reaction of this type is beyond the limits of system adaptation. Under the conditions of ecological reorganization, the constraints of community structure on evolutionary behavior of particular species are released. Such a release allows the community members to rapidly evolve. The considered prediction appears directly testable by paleoecologists. To test it, one has just to test for randomness time sequences of first appearances of species within communities differing in complexity.

By the way, be evolutionary stasis of species related not only to the genetic and developmental homeostases but also to the constraints of ecological structure, the occurrence of phyletic gradualism and sympatric speciation would be quite easily explained. One might even claim that speciation of this type is to be expected to occur rather commonly within very simple communities where the ecological framework is very weak or absent at all.

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STRESZCZENIE

Model naruszanej równowagi ewolucyjnej (Eldredge & Gould 1972, Gould & Eldredge 1977) postuluje powszechność raptownego przyspieszenia tempa ewolucji w momencie specjacji. Przez resztę czasu ewolucyjnego gatunki trwają w zasadzie niezmienne. Autorzy modelu utrzymują, że ta stabilność gatunków w czasie ewolucyjnym wynika z homeostazy morfogenetycznej osobników i homeostazy genetycznej populacji. Te mechanizmy homeostatyczne mogą być przełamane jedynie w niedużych izolowanych populacjach. Na poparcie modelu naruszanej równowagi ewolucyjnej przytacza się w literaturze paleontologicznej wiele przykładów.

Nie sposób jednak zaprzeczyć, że linie filogenetyczne ewoluują niekiedy w stałym tempie na przestrzeni czasu geologicznego, bez żadnych okresów równowagi naruszanej przez momenty specjacji. Dla tych zjawisk szukać trzeba innego wyjaśnienia niż zakłócenia homeostazy osobników i populacji, bo takie zakłócenia możliwe są tylko w małych izolowanych populacjach.

W rzeczy samej — stabilność gatunków w czasie ewolucyjnym może również zależeć od ograniczeń nakładanych na ewoluujące gatunki przez strukturę ekologiczną biocenoz, to znaczy przez dobór naturalny wywołany dążeniem do zachowania roli ekologicznej gatunku w biocenozie. Analiza systemów cybernetycznych prowadzi do wniosku, że ograniczenia takie są znacznie słabsze w systemach prostych niż w systemach złożonych i zintegrowanych.

Hipoteza o znaczeniu mechanizmów homeostatycznych biocenozy dla stabilności ewolucyjnej gatunków może zatem być bezpośrednio testowana przez paleoekologów. Jej konsekwencją jest bowiem teza, że w biocenozach zintegrowanych nowe gatunki zjawiają się całymi grupami i przede wszystkim w momentach zasadniczej reorganizacji ekologicznej, natomiast w biocenozach prostych — zupełnie przypadkowo.