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SYSTEM-ANALYTIC CONCEPTUAL FRAMEWORK FOR COMMUNITY PALEOECOLOGY

Analiza systemów a paleosynekologia

Abstract. A conceptual framework derived from the general system theory is here applied to community paleoecology. Six distinct categories of community development through time are defined in terms of system regulation, adaptation, and loss of structural identity. Three of these (ecological stability, ecological resilience, and community replacement) deal with ecological time. Three others (community permanence, community evolution, and community reorganization) deal with evolutionary time. When considering evolutionary time, one deals however not as much with single communities as with community types which term is here meant as a group of communities resembling each other very closely in their taxonomic composition and ecological structure, and limited by the same environmental factors. Some actual examples of community development through evolutionary time are interpreted in the system-analytic terms.

INTRODUCTION

In a recent paper, Gould (1977) proposes that since the very inception of evolutionary paleontology three main questions organized paleontological research. One may claim that the same questions are also the most pervasive topics of modern community paleoecology. In the latter field, one deals however with another organizational level of organic life and hence, the questions are usually expressed in another theoretical language. Since the pioneer papers by Valentine (1968) and Bretsky (1969) appeared, community paleoecologists ask whether the history of ecological organization of the biosphere is unidirectional or steady-static; does it depend mostly upon environmental or biological factors; is it gradual or spasmodic? All these problems are to be approached through careful empirical studies.

The aim of this paper is to present a conceptual framework for such empirical community-paleoecological investigations. In fact, I feel that after the early vigor a dozen years ago, further developments in the field of community paleoecology have become slow. Despite conti-

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nuous efforts by Scott (1972, 1974, 1976, 1978) to provide standards for paleocommunity description (see also Hoffman 1978a, Hoffman & al. 1978), the data presented by different authors are usually incompatible. The investigations are commonly organized as purely descriptive works without any reference to the theoretical background; or at best, as mere illustrations of ecology-derived principles (there are obviously a few outstanding exceptions). The theories, concepts, and terms have become so vague and cloudy that they cannot even provide the paradigm needed by a normal science to develop. I believe that system methodology may prove useful at least in clarifying the ideas, providing precise terminology and more or less unequivocal criteria, and organizing the scope of a future community-paleoecological research.

In this paper, I assume that communities are open systems (sensu Bertalanffy 1968). In other words, I regard community structures as more or les integrated and homeostatic webs of biological interactions, imposing some constraints upon both ecological and evolutionary behavior of the constituent populations. This point is in hot dispute among ecologists. One may actually suppose that the above assumption is valid only for those communities separated clearly from other communities by sharp environmental gradients. In fact, the very concept of ecological and evolutionary equilibria derived from the theory of island biogeography (MacArtur & Wilson, 1967; Wilson, 1969) recalls the notion of open systems.

When communities are treated in terms of open systems, their behavior must be made clearly distinct from that of their constituent populations. This distinction does not imply that one may attribute a selection value to communities. Neither complexity, stability, nor even efficiency of communities is selected for in ecological time. In contrast, such "rewards" may hinder a community from persisting Holling, 1973). This is also the case in evolutionary time (Hoffman, 1978b). There is no ecological or evolutionary process operating directly upon communities. Communities appear actually as mere epiphenomena of species evolution (Hoffman, 1979a) but nevertheless, their ecological and evolutionary behavior may be irreducible analytically to species-level processes.

SYSTEM BEHAVIOR

Weinberg (1972) has recently developed a conceptual framework for analysis of system behavior in time.

Owing to the homeostatic properties of its structure, an open system performing its normal function maintains a steady state. System function reflects the system characteristics which is here meant as a set of rules determining the way the system responds to advan-

tageous events in its surroundings. As a first approximation, community characteristics can be described in terms of energy exchange with the immediate environment and energy flow through the trophic structure.

A system responds also to disadvantageous events. The reaction is called regulation if a disturbed system does not change its characteristics when tending to an equilibrium state. Then, the system returns to its original steady state.

Disadvantageous events may however disturb a system so severely that a regulative response appears insufficient to achieve an equilibrium. The reaction is called adaptation if a disturbed system does change its characteristics in order to endure.

Very severe disturbances require of a system very far-reaching adaptations. This may result in a loss of system identity. In fact, there are no unequivocal criteria to distinguish clearly between a post-adaptation system state and a new system.

COMMUNITY DEVELOPMENT THROUGH ECOLOGICAL TIME

A community disturbed by some environmental factors is degraded, that is some of its constituent populations appear unable to resist the stress and become exterminated. When the previous environmental conditions are re-established, a degraded community may return to its original equilibrium state. The community structure reflecting system characteristics remains then unchanged and hence, the community response can be treated in terms of system regulation. This ability of communities to return to their original equilibrium state after a temporary disturbance was termed by Holling (1973) ecological stability.

An environmental disturbance may also be so severe as to induce significant changes in the structure of a degraded community tending to an equilibrium state. The constituent populations and their interactions may remain the same as they were but the population sizes and hence, the pattern of energy flow through the ecosystem may become sharply different due to some unique historical events. In fact, natural communities do often display multiple equilibrium points (Sutherland, 1974; Horn, 1976). One may then claim that the community characteristics has changed. Nevertheless, the identity of ecological system is maintained perfectly and hence, the community response is to be treated in terms of system adaptation. This ability of communities to absorb change and disturbance and still maintain the same web of biological interactions was termed by Holling (1973) ecological resilience.

In response to very severe and long-lasting environmental disturbances, a community may receive ecologically new species. This results finally in a loss of the community identity. Such process of a funda-

mental change in community composition due to a change in environmental conditions may be termed community replacement (cf. Hoffman & Narkiewicz, 1977). According to R. G. Johnson (1972), this process includes two distinct phases intergrading one into the other; namely, ecological degradation of the original community and introduction and subsequent development of the new community.

There is a real continuum of ecological events between the extremes of a community resilient response and community replacement. The boundary may be traced but arbitrarily. More or less precise identity of community taxonomic composition is here proposed for the criterion of ecological resilience.

COMMUNITY DEVELOPMENT THROUGH EVOLUTIONARY TIME

Scaling may have its usual effects on community development and therefore, ecological time must be made clearly distinct from evolutionary time. Evolutionary time is compatible with specific longevities. Actually, changes occurring in ecological time imperceptably intergrade into changes occurring in evolutionary time. However, the processes can be distinguished at least conceptually.

When considering evolutionary time, one deals notasmuch with single communities as with community types, since communities themselves disapear as soon as their particular biotopes vanish or undergo major changes; recall the Quaternary history of Indo-Pacific coral reef ecosystems (Chappell, 1974; Taylor, 1978). The term community type is here meant as a group of communities resembling each other very closely in their taxonomic composition and ecological structure, and limited by the same environmental factors. The taxonomic composition may vary among particular communities but the replacement species are very close ecologically to each other. Dispersal of the larvae and migration of the adult individuals permit a continuous exchange of species between communities assigned to a single community type. Moreover, such communities may also share a set of homeostatic mechanisms developed through co-evolution among the species. Thus, community type can be regarded as a biological unit, eventhough hidden in a background of the ecological organization of the biosphere. Metaphorically speaking, the relationship between communities and community types appears analogous to that between local populations and species. In fact, community type can be regarded as a pool of species or a range of taxonomic variation within the constant framework of an ecological structure. The concept of community type may resemble Thorson's (1957) parallel communities but I believe the former one to be much less vague. Actually, much precise ecological work is

needed in order to permit the ultimate assignment of some communities or paleocommunities to a single community type.

Let us consider a community type. Under significantly changing environmental conditions, it has to respond if it is to endure because at least some constituent taxa are affected by the stress. The affected taxa may adapt perfectly to the new environment, eventhough perhaps under the form of descendant species. Then, the community type persists through evolutionary time owing to subsequent co-adaptation (if needed) of other community members. The ecological structure reflecting system characteristics remains constant provided that communities of different geological ages display a taxonomic identity at the generic level, which may be regarded as a criterion for system regulation. I propose to restrict the use of the term community permanence to this particular category of community-type development.

Taxa unable to evolve into descendants adapted to the new environmental conditions may be replaced by some other taxa unadapted to the original biotope. Despite this introduction of new community members, the web of biological interactions may remain more or less constant due to the ecological equivalence of particular replacement taxa. Communities of different geological ages appear then homeomorphic in their ecological structure despite their considerable taxonomic variation. Nevertheless, the patterns of energy flow and hence, the system characteristics appear usually quite different, which shows that one deals here with system adaptation. I propose to restrict the use of the term community evolution to this particular category of community-type response in evolutionary time. In fact, this definition seems to be less vague than used thus far in community paleoecology (cf. Valentine, 1968; Bretsky, 1969; Boucot, 1975, Watkins & Boucot, 1975). It is advantageous because the criterion of structural homeomorphy among communities can be treated at least semi-quantitatively (Hoffman & al. 1978).

Ecological structure of a community type may also undergo major changes due to the lack of ecological equivalence between particular replacement taxa. Then, the ecological system does not only change its characteristics but also loses its structural identity. The system identity can be treated merely in functional terms in such a case. The function of a community type within the whole biosphere is here meant as the position of the involved communities in a specified set of physical environments. One might suppose that structural identity is a necessary prerequisite to the functional identity of a system. In fact, were the biosphere constant throughout evolutionary time, a specified set of environmental conditions would strictly determine the structure of respective community type. And yet the biosphere does change. Therefore, constancy of community-type function may or may not be re-

lated to the constancy of ecological structure. I propose to use the term community reorganization for such a response of community types in evolutionary time which leads to the system break-down and loss of its structural identity.

There is a real continuum of evolutionary-ecological events between the extremes of community evolution and community reorganization. One may claim that when a considerable proportion of ecologically new taxa (representative of previously absent families) appear within a community type, the process is to be assigned to the latter category.

Reorganized structure of a community type may also become quite similar to the ascendant one. Such a community congruence appears extremely close to the effects of community evolution as defined in the present paper. Nevertheless, one can hardly expect that communities largely different in taxonomic composition will exhibit identical webs of biological interactions and identical patterns of energy flow; unless the very concept of community structural identity is reduced to mere resemblance of organism-biotope relationships.

ADEQUACY OF THE CONCEPTUAL FRAMEWORK

Adequacy of this conceptual framework to the actual development of communities through ecological time can be finally tested only by neoecologists. As a paleoecologist, I can merely assume its appropriateness to very precise research on short-term stratigraphic sequences like those studied by Walker & Alberstadt (1975), Hoffman (1977, 1979b), or M. E. Johnson (1977).

When dealing with evolutionary time, adequacy of the system model and terminology to the actual development of community types can be tested solely in the fossil record. Then, all the limitations and biases inherent in each paleoecological interpretation must be always kept firmly in mind (cf. Stanton, 1976; Stanton & Dodd, 1976; Fürsich, 1978; Hoffman, 1979a, b). Thus far, very few examples have been described precisely enough to permit their unequivocal assignment to the above-defined categories of community-type development through evolutionary time.

Community permanence may apper somewhat abstract or even unrealistic. Nevertheless, some fairly clear examples have already been documented. Benthic communities dominated by turritellid gastropods are well known to occur in almost all tropical to cool Recent seas. Owing to their gregarious habit and high competitive potential for space at and just below the sediment-water interface, these largely sessile gastropods usually make the infaunal habitat inaccessible for

most other macrobenthic invertebrates. Predatory naticid gastropods are however an exception. Thus, the ecological structure characteristic of this community type appears very simple. Turritellid-dominated, high-density, low-diversity paleocommunities have been commonly recorded at least since the Paleocene (e. g. Hecker & al. 1963; Menesini, 1976; Hoffman, 1977). The long-lasting history of this community type may provide an example of community permanence.

Development of corbulid-dominated, high-density, low-diversity community type persistent under the same form and in the same environment at least since the Paleocene to Miocene (e.g. Hecker & al. 1963; Boekschoten, 1963; Báldi, 1973; Hoffman 1977) may also be attributed to community permanence.

Both these community types possess some Cretaceous counterparts (Scott, 1974; Sohl, 1977). However, in both the cases the Cretaceous communities appear to have been more species-diverse and less densely packed than their Cenozoic descendants. This difference may be attributed to community evolution consisting in introduction of the naticid predators to these ancient community types and their effect upon the taxa showing a lower reproductive potential than the turritellids and corbulids.

Development of tropical seagrass-associated community type at least since the Miocene through Recent probably represents another example of community evolution. In fact, the ecological structure of some Miocene paleocommunities has recently been demonstrated to resemble very closely the present-day seagrass-associated macrobenthic communities (Hoffman 1977). Nevertheless, some taxa rare or even absent from those Miocene paleocommunities occur rather commonly in their Recent counterparts (e. g. tellinid, pinnid, and epibyssate arcid bivalves); while some formerly common taxa have become very rare or absent from the modern seagrass beds (e. g. nuculoid bivalves and scaphopods). Such an assignment of the development of the tropical seagrass-associated community type is however a mere supposition for the moment since the interpretation is based upon fairly vague qualitative criteria. Much work on both ancient and modern communities of this type is needed before the use of more rigorous criteria will be allowed.

The Middle Paleozoic development of carbonate intertidal and shallow-subtidal communities leading ultimately to the structural congruence of paleocommunities widely separated in evolutionary time (Walker & Laporte, 1970) provides a clear example of community reorganization.

CONCLUSIONS

One may conclude that the system-analytic terminological framework (Table 1) appears applicable to natural communities and community types. It is advantageous because its theoretical background is very clear, the terms are precisely defined, and semi-quantitative criteria can be easily applied (cf. the methodology of paleocommunity description in Hoffman & al. 1978). Then, the above-outlined framework may substantially facilitate conceptualization of the major field of change in ecological organization of the biosphere through time.

Up to date, there is no sufficient empirical evidence to recognize whether the ecological organization of the biosphere evolves at a slow but noticeable rate, or whether most community types undergo but major breaks-down and reorganizations. Possibly, both these processes are equally common. As a matter of fact, even the very mechanisms of community development through evolutionary time, involving supposedly co-evolution among several taxa, remain unclear. One may only claim that they are to be analysed within long-lasting habitats where the misleading effects of species immigration and local extermination can be easily recognized; otherwise, community replacement might be misinterpreted as community evolution or reorganization.

As to the factors controlling community-type development through evolutionary time, one may only state that there is no single major feature of community types responsible for their ability to develop or persist. In fact, this ability appears related to both the virtual eurytopy of constituent species and the simplicity of ecological structure (Hoffman, 1978b). Simplicity of a community structure (and its opposite, complexity) is here meant as a measure of interdependence among the community members. A community composed exclusively of mutually independent populations is to be regarded as an extremely simple one. When an ecological structure is very simple and virtual eurytopy of the species very large, community permanence can be expected. When an ecological structure is very complex and virtual eurytopy of the species very small, even a slight change in environmental conditions may result in community reorganization. Between these two extremes, there is a continuum of evolutionary-ecological events reflected in more or less dramatic changes in community composition and structure.

To study the frequency distribution of particular categories of community-type development through evolutionary time and its dependence upon various environmental as well as biological factors is the means of recognizing the mode of ecological evolution of the biosphere.

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STRESZCZENIE

Przedmiotem pracy jest próba stworzenia systemu pojęciowego odpowiedniego do rozważań nad rozwojem biocenoz zarówno w czasie ekologicznym, jak i ewolucyjnym. Podstawowym założeniem całej pracy jest, że biocenozy można traktować jako systemy otwarte, że — innymi słowy — struktura biocenozy to mniej lub bardziej zintegrowana i homeostatyczna sieć interakcji biologicznych narzucająca ograniczenia rozwojowi poszczególnych populacji. Założenie to nie pociąga jednak za sobą przypisania biocenozom jakiejś wartości selekcyjnej. Nie ma żadnego procesu ekologicznego czy ewolucyjnego działającego bezpośrednio na biocenozy, a same biocenozy to nic innego jak przejaw ewolucji gatunków. Ich rozwoju w czasie ekologicznym i ewolucyjnym może się jednak nie dać sprowadzić analitycznie do samych tylko własności gatunków.

Zdolność biocenoz do powrotu do swego pierwotnego stanu równowagi po chwilowym wahnięciu warunków ekologicznych określa się jako stabilność ekologiczną. Odpowiada ona regulacji systemu. Gdy struktura ekologiczna wytrąconej ze stanu równowagi biocenozy osiąga nowy stan równowagi, zachowując jednak wszystkie populacje składowe, mówić można o adaptacji sytemu. Tę zdolność biocenoz określa się jako elastyczność ekologiczną. Gdy natomiast wskutek zmiany warunków ekologicznych zmienia się skład biocenozy, a zatem traci ona swoją tożsamość, mówić można o następstwie biocenoz. W kategoriach analizy systemów nie sposób przeprowadzić jednoznaczną granicę pomiędzy adaptacją systemu a kompletną jego przebudową. Granicę między elastyczną reakcją biocenozy a następstwem biocenoz można więc przeprowadzić tylko arbitralnie. Adekwatność tych trzech podstawowych kategorii ekologicznych do rozwoju biocenoz w czasie ekologicznym sprawdzić można jedynie na materiale współczesnym.

Kiedy mowa o czasie ewolucyjnym, rozważać trzeba nie tyle pojedyncze biocenozy, ale ich typy. Typ biocenoz rozumie się tutaj jako grupę biocenoz bardzo do siebie zbliżonych pod względem składu taksonomicznego i struktury ekologicznej i zamieszkujących takie same środowiska. Gdy takie same środowiska zamieszkane były w dwóch momentach czasu ewolucyjnego przez biocenozy identyczne pod względem składu taksonomicznego (na poziomie rodzaju), mówić można o przetrwaniu biocenozy. Odpowiada to regulacji systemu. Gdy takie biocenozy różnią się poważnie składem taksonomicznym, ale są homeomorficzne strukturalnie, mówić można o ewolucji biocenozy, co odpowiada adaptacji systemu. Kiedy jednak utracona zostanie nawet tożsamość strukturalna i jedyną wspólną cechą rozważanych biocenoz będzie ten sam charakter ich środowiska fizycznego, mamy do czynienia ze świadectwem reorganizacji ekologicznej. I znów — granicę między ewolu-

cją biocenozy a reorganizacją ekologiczną przeprowadzić można jedynie arbitralnie.

Żeby sprawdzić adekwatność tych kategorii do rozwoju typów biocenoz w czasie ewolucyjnym, zastosowano je do kilku przykładów znanych z literatury. Okazuje się, że w dziejach biosfery rzeczywiście napotkać można zarówno przetrwanie i ewolucję biocenoz, jak reorganizację ekologiczną. Zaproponowany tu system pojęciowy nadać się więc może do rozstrzygnięcia kwestii, w jaki sposób zmienia się organizacja ekologiczna biosfery. Jak dotychczas bowiem za mało udało się zebrać porównywalnych danych paleosynekologicznych, by można było na to pytanie odpowiedzieć.