Abstract -- The relevance of the hierarchy concept in biology has been questioned, but it is nevertheless a useful way to organize our perception of nature. The hierarchical ordering of nature is both structural and dynamic, with the vertical separation of levels dependent on behavioral frequencies and the horizonal separation the result of the degree of interaction between systems. Within this hierarchy of natural systems, one can perceive both upward and downward causation. This perception provides a philosophical midground between holism and reductionism. At the ecological levels of organization, ecosystems are comprised of interacting organisms. Communities and populations are not natural systems and can best be recognized as subunits of ecosystems. Advances in ecosystem ecology must proceed from an understanding of ecosystem level behaviors and laws.

Chapter **5**

HIERARCHICAL ORGANIZATION OF ECOSYSTEMS

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1. INTRODUCTION

In a recent commentary, Guttman (1976) stated that the levels of organization concept of biological organization "if stated in any but the sloppiest and most general terms ... is a useless and misleading concept." This conviction contrasts with the observations of other scientists. Weiss (1969) stated, "... the principle of hierarchic order in living nature reveals itself as a demonstrable descriptive fact." Von Bertalanffy (1968) observed, "Such hierarchical structure ... is characteristic of reality as a whole and of fundamental importance especially in biology, psychology, and sociology."

The usefulness of the levels or hierarchy concept in biology is in

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pedagogical organization of biological knowledge and identification of interests and training of biologists. A hierarchical perspective also provides a mechanism for interaction among scientists with interests at different hierarchical levels. The vagueness of biological hierarchies stems in part from imprecise terminology and careless analogies (Bossort *et al.*, 1977). But the essence of hierarchical organization is a vagueness and loss of detail in proceeding from one level to a higher level. As recognized by Poincaré (1905), understanding and explanation in science involves generalization and simplification, hence the emergence of hierarchical levels in our object of study. Whether Nature is truly organized hierarchically is moot. Man's perception of nature is hierarchical.

Hierarchy theory with its coupled debate of reductionism versus holism has been covered in several recent books (Koestler and Smythies, 1969; Whyte *et al.*, 1969; Pattee, 1973; Ayala and Dobzhansky, 1974). In application to biological organization, these books have concentrated on the levels from organism down. Using ideas developed in these four books and elsewhere, I have focused this chapter on ecological levels of organization; organism, population, community, and ecosystem.

2. DEFINITION OF HIERARCHY

A hierarchy is formed by a partial ordering of a set (Simon, 1973). That is, a hierarchical organization of a set, U, with subsets $A, B, C, \ldots$, is formed by ordering the subsets by a relation, R, which specifies that the elements of A are higher than the elements of B which are higher than the elements of C.... The relation R is a binary relation in U such that:

(1) b higher than c and c higher than b, where b and c are elements of U, implies $b = c$ (R is antisymmetric); and

(2) b higher than c and c higher than d, where b, c, and d are elements of U, implies b higher than d (R is transitive) (Bunge, 1969).

There are many relations which satisfy these criteria. In the strictest use of the term hierarchy, R would be a ranking or dominance relationship. As an example, an army (U) is composed of personnel (the elements of U) which are ranked (R) into a hierarchy: generals ... lieutenants ... sergeants ... privates. R thus divides the set into levels.

Simon (1973) used a Chinese box to exemplify a hierarchy. The boxes, large and small, are the elements of U. R implies containment: A box is higher than another box if it contains that box.

In each of the previous hierarchy examples, the elements of U were independent except through their relation defined by R, and all the elements of U were similar, all soldiers or all boxes. In many interesting examples of hierarchies, this is not so. In a structural hierarchy each element of U is composed of other elements of U. A book is a good example. A book is made up of chapters, pages, paragraphs, sentences, words, and letters. Each chapter, page, etc., may be considered an element of U, the set of all things which are part of the book. R may be interpreted as "consists of." A book (level 1) consists of chapters (level 2), chapters consist of pages, and so forth. R is antisymmetric—a sentence does not consist of paragraphs, and transitive—a book consists of letters.

Two important properties of structural hierarchies must be noted. First, the entire structure, the book, exists completely at all levels. The levels represent only different perspectives on the book. Consider the different ways in which a reader, publisher, printer, copy editor, and typesetter view a book. Each sees the book at a different level, yet each ultimately sees the entire book.

Second, Guttman (1976) would have that elements at each level consist entirely and exclusively of elements of the next lower level. This may be true for some structural hierarchies, but for generality it is unnecessary. Taken out of the abstract, a page of a book consists not only of words, or sentences, or paragraphs, but also of the paper on which they are printed. More restrictive hierarchies also exist, for example, the hierarchy of taxonomic categories. A class consists of orders; not some orders, some families, and a few other nondescript groups. Even if a class has only a single species, there are still appropriate family and order names into which the species is categorized.

Proceeding up this hierarchy of hierarchy examples (R might be defined as "is more complex than"), the elements of U need not be physical objects. As in systems theory (e.g., as described by Caswell *et al.*, 1972), an abstract object may be defined by its dynamic behaviors. A set of such abstract objects may then form a hierarchy by a relation defined on the behaviors. History exemplifies such a dynamic hierarchy in which R is based on behavioral frequencies. If we are interested in a very brief period of history, we might concentrate on day-to-day occurrences. However, in a comparison of political administrations, such day-to-day happenings would be glossed over in monthly or yearly generalities. At higher levels even these behaviors would be lost, such as in comparison of the Greek and Roman Empires. At a level far above this is the perspective of H. G. Wells' "The Outline of History." Each perspective represents a viable historical endeavor; however, the hostility with which "The Outline of History" was received by some historical specialists (Toynbee, 1935, in Iberall, 1972) is analogous to similar hostility in the natural sciences (Iberall, 1972).

3. THE HIERARCHICAL ORGANIZATION OF NATURE

Odum (1959) visualized the biological spectrum as protoplasm, cells, tissues, organs, organ systems, organisms, populations, communities, ecosystems, and biosphere.[1] This spectrum can be extended down into the nonbiological realm: macromolecules, molecules, atoms, subatomic particles, and upward to astronomical proportions. This hierarchy is an ordering of the set of all natural (i.e., not man-created) systems. The ordering relation is both "consists of" and "behaves at a lower frequency than." This hierarchy, known as levels of organization or levels of integration hierarchy, is both a structural and dynamic hierarchy. Each element, that is, each natural system, consists of systems of the next lower level and is characterized by behaviors occurring more slowly than behaviors at the next lower level. Behaviors of atoms and subatomic particles occur in fractions of milliseconds. Organismic behaviors occur over hours, days, and years. Ecosystem behaviors occur over much longer time periods, hundreds of years, possibly even hundreds of millions of years.

The levels of organization hierarchy was recognized by Aristotle: "Nature proceeds little by little from things lifeless to animal life in such a way that it is impossible to determine the exact line of demarcation, nor on which side thereof an intermediate from should lie" ("Historia Animalium," Book VIII, Chapter 1). However, only relatively recently has there been any formal treatment of structural and functional aspects of the levels of organization hierarchy.

3.1. Structure of the Levels of Organization Hierarchy

Simon (1962, 1973) described the structure of this hierarchy as having both a vertical separation that isolates each level from levels above and below, and a horizontal separation that segregates the components of any level into groups, thus defining the level above. Vertical separation is based on behavioral frequencies. If we focus on a single level of this hierarchy, higher level behavior occurs so slowly that it is perceived as constant. Lower level behavior occurs so rapidly that all we observe is a sampled statistical behavior. Unfortunately, we cannot observe this hierarchy from outside. We human organisms are ourselves part of the levels of organization hierarchy. We exist at the organismal level, and in our attempts to perceive various levels, we cannot extricate ourselves from our level. Unaided, we see only a narrow band of frequencies, from seconds up to a human lifespan, and a narrow band of structures. To look either up or

[1] As discussed below, there is disagreement over these levels.

down we must use tools. Examples of tools which allow us to look downward in space/time are microscopes, which give a finer spatial resolution, and chromatography which allows us to separate compounds based on molecular velocities. Looking upward from the organismic level requires other kinds of tools, for example, H. T. Odum's "macroscope" (1971). For spatial phenomena we have aerial photographs and LANDSAT imagery. Earth pictures taken from the moon present a striking new perspective of the biosphere. For examining higher level dynamic behaviors, we have historical records, sediment analysis, and fossil records.

The horizontal structure of the levels of organization hierarchy depends on the isolation of the systems making up any level and upon their segregation into groups which form the systems of the next higher level. A system is a set of interacting objects (in this case the objects are lower level systems). Since all but abstract systems are open systems, interacting with "outside" objects, a specific system exists only by definition. One way of isolating one system from another is by the degree of interaction. As Simon (1973) describes the situation, "Everything in the world is connected with everything else..., but some things are more connected than others." Thus at the atomic level, all atoms interact, at least indirectly, but the atoms that make up specific molecules interact more strongly with each other than they do with atoms of other molecules. The integrity of a system exists by its high degree of internal interaction. Each system is connected with other systems by the weaker connections between component objects. These systems exhibit a "loose horizontal coupling" (Simon, 1973). But the loose or weak connections are the object interactions that identify the next higher level of the hierarchy. This reveals a third ordering relation for the levels of organization hierarchy, bond strength. Nuclear particles are held together by pion fields with energies of the order of 140 MeV. Atomic bonds are much weaker. Covalent bonds between molecules involve energies of only on the order of 5 eV (Simon, 1973).

3.2. Function of the Levels of Organization Hierarchy

It is essential to recognize that from whatever level we view nature, we see exactly the same system. The observed behaviors are manifestations of behaviors at other levels. Various philosophies of science have related different level behaviors in different ways. From a strict holistic philosophy, a behavior at one level cannot be explained in terms of lower level behaviors. The higher level behavior results from a synergism. It is something more than the sum of the lower level parts.

Antithetical to this philosophy is reductionism. From a reductionistic viewpoint, higher level behavior is nothing more than a definable combination of lower level behaviors. The dichotomy of these philosophies developed during the nineteenth century and has extended into the twentieth century. For certain emergent behaviors, life and consciousness, the dichotomy may never be resolved, as neither holism nor reductionism is provable (Platt, 1969a). However, in general, a midground between mystic holism and Laplacian reductionism has been described (Novikoff, 1945; Muller, 1958; Koestler, 1967, 1969; Weiss, 1969). At each level, there are behaviors and laws relative to these behaviors which are specific to that level and not defined for other levels. These behaviors cannot be predicted from the laws of lower levels, but they are entirely consistent with lower level laws.

The best example of this relationship was presented by Rosen (1969). A gas can be considered at two separate levels, macroscopically as a continuous fluid and microscopically as a large number of individual particles. At the macroscopic level, the gas laws are applicable. The relevant behaviors are temperature, pressure, and volume. At the microscopic level, Newton's laws of motion apply. The behaviors are position and velocity. Can the transition from Newton's laws to gas behavior be made? Without invoking Heisenberg's Uncertainty Principle, it is easy to see that simply because of the number of particles involved, the transition is impossible. There is, however, a connection between levels, statistical mechanics. Gas behavior can be related to an average particle behavior.

There is also downward causation (Cambell, 1974) in the levels of organization hierarchy. Higher level organizations place constraints or boundary conditions (Polayni, 1968) on lower level behaviors. An infinite variety of nuclear particle arrangements are possible, yet in only a hundred or so do the interacting forces produce a stable nucleus. The atoms can be abstractly arranged in an infinity of molecules, but only a relative few actually exist. Only a very few molecular associations manifest attributes that we call life (Muller, 1958). The organization at each level provides a stability to the lower level systems and in so doing constrains the possibilities of lower level behavior. This is not really a downward causation but a selection of persistent organizations. Since multilevel systems cannot form instantly (Gerard, 1969), the lower level of organization must have existed before the higher level. The higher level organization then evolved to include those lower level systems which through their interaction obtained the greatest stability (Levins, 1973).

Within the levels of organization, there are both upward and downward behavioral constraints. The systems at each level conform to lower level laws and through natural selection the behaviors have been constrained by higher level organization. Koestler (1967) proposed the term "holon" for these "Janus-faced" systems. He intended this term to supplant thinking in terms of parts and wholes, by a multilevel, stratified approach to natural science (Koestler, 1969). In the following section, the proposed ecological levels of the levels of organization hierarchy are examined as holons (see also Patten and Finn, Chapter 8, this volume).

4. HIERARCHICAL LEVELS OF ECOLOGICAL INTEREST

The ecological levels of the levels of organization hierarchy are often given as organisms, populations, communities, and ecosystems. For each of these levels to exist according to Simon's (1962, 1973) hierarchy concept, each system at each level must have greater interaction among its subsystems than interaction with other systems. That is, each system is defined by strong internal interaction and weak external interaction. Certainly there are more and stronger interactions within an organism than between organisms. Similarly, at the ecosystem level there are more interactions within an ecosystem, for example, a lake or a forest, than between ecosystems, such as interactions across the land–water interface. However, this system identification may not hold for populations and communities. Phytophagous insects of a forest canopy insect community do not interact more strongly with each other than with the forest tree community. Organisms of a phytoplankton community do not interact more among themselves than with the abiotic and zooplankton components of an aquatic ecosystem. Or, using community in the broader sense as all the organisms of a defined area, interactions among the organisms of a forest community are no stronger than their interactions with the nonliving parts of the forest. A community is not a subsystem but a conceptual part of an ecosystem (Schultz, 1967). In the third edition of his ecology textbook, E. P. Odum (1971) revised the ecological levels to organism systems, population systems, and community systems, that is, ecosystems. The ecosystem concept is based on recognition of strong interactions between living organisms and their abiotic environment. Artificial separation of the living components from an ecosystem is seldom useful, and in practice, seldom considered.

Identification of populations as subsystems of an ecosystem is also questionable. Do the organisms comprising a population interact more strongly intraspecifically or interspecifically? That is, are interactions among members of a population stronger than interspecific competition and trophic relations? Aristotle recognized that the life of animals may be divided into two acts—procreation and feeding ("Historia animalium," Book VIII, Chapter I). Recognition of one or the other of these two activities as stronger represents a schism among ecologists. Evolution depends on procreation; ecological function depends on trophic interactions. We might in fact think of two intertwined hierarchies with the ecological hierarchy in a sense cutting across the genetic hierarchy (Wright, 1959). Although much has been written to bridge the schism between evolution and ecology, or perhaps evolutionary ecology and functional ecology, the division still remains with many unanswered questions (Hutchinson, 1965; Smith, 1975).

From a functional standpoint, ecosystems are comprised of interacting organisms. Rowe (1961), from a different viewpoint, recognized that populations and communities are not part of the levels of organization hierarchy. He suggested that components at each level must have physical boundaries. For example, individual organisms and specific ecosystems can be identified by existent or defined boundaries. This is not true of populations or communities. One cannot place or define a physical boundary around a population or community and have only that community or population within the boundary. The isolate is certain to also contain some of the abiota of the ecosystem. In practice, Rowe's physical boundaries often coincide with minimum interaction surfaces. Wilson (1969) pointed out that natural boundaries may be recognized by either minimum interaction or some form of closure, either topological or temporal. The most useful boundaries for scientific study are those which coincide with boundaries for other properties (Platt, 1969b). For example, a watershed divide is not only a physical boundary but also a minimum interaction surface—water on one side of the divide does not interact with water on the other side.

Are there, then, any levels between organism and ecosystem? Trophic levels (Lindeman, 1942), functional groups (Cummins, 1974; Botkin, 1975), and guilds (Root, 1973, 1975) fail to fill this void for the same reasons that populations and communities do. The major interactions are between groups rather than within. Rowe (1961) found no intermediate levels, only larger and smaller ecosystems. The only satisfactory subdivision of an ecosystem is into smaller physical subunits which exhibit a high level of internal interaction. A forest might be divided into canopy, forest floor, and soil subsystems; a lake might be divided into littoral, pelagic, and benthic subsystems. Within these systems the interacting subsystems must be recognized as organisms.

5. APPLICATION OF HIERARCHY THEORY TO ECOSYSTEMS

MacFadyen (1975) suggested that the most obvious problems in ecology arise because ecology is concerned with at least two levels of organization. This should be turned into a strength rather than a weakness. All natural investigations should proceed at at least two levels (Feibleman, 1954; Bartholomew, 1964; Schultz, 1967). Behavior at any level is explained in terms of the level below, and its significance is found in the level above. Ecosystem behavior can be explained in terms of organism behavior. The significance of organism behavior can then be found in ecosystem behavior. But, as elaborated above, ecosystem behavior cannot be predicted from the laws of organism behavior. This is a philosophical mistake made in many ecosystem models. We cannot expect ecosystem behavior to emerge from a set of organismic equations. Fortunately the mistake is not made in practice. No one has attempted to model an ecosystem by writing a differential equation for every organism in an ecosystem. Populations, trophic levels, and functional groups or guilds are used as concepts for lumping organisms with similar traits, that is, for defining average organism behavior. Overton (1975; White and Overton, 1974) has been more specific in applying hierarchical structure to his modeling "paradigm." Behavior at a mechanistic level is translated into behavior at a higher level by a "ghost" module in the model structure.

Advances in ecosystem ecology must proceed first from an understanding of ecosystem level behaviors and laws. Next comes specification of organism-level dynamics and finally identification of the statistical formalism connecting the two. In biology, and especially ecology, this order, from higher level behavior to lower level behavior, and then the connection between the two, has been reversed (Rosen, 1969). Poincaré (1905) suggested that physical chemistry at that time was hampered by a general grasp of third and fourth decimal places. Perhaps the same is now true in ecology. We know so much about organism behavior that we have difficulty finding the larger regularities. We must search for overriding simplicity in the large-scale complexity (Odum, 1977). The start of this search is the definition of ecosystem behaviors, as we have few such concepts (Overton, 1975). Schultz (1967) listed six ecosystem properties: productivity, stability, cyclicity, diversity, trophic structure, and entropy. Odum (1977) called for measurement of ecosystem level properties in impact evaluation, but gave only two examples, P/R ratios and diversity. However, in an earlier paper (Odum, 1969) he listed 24 ecosystem attributes which deserve consideration. In our examination of these properties, our search for other properties, and our expressions of rules governing these properties (hypotheses), we should look for simplicity, not a rigorous or exact simplicity, but an approximate simplicity (Poincaré, 1905).

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