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Ecological systems and the concept of biological organization

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ABSTRACT An axiomatic system is proposed to improve identification, description, and analysis of complex ecological systems. Such systems are assumed to be organized and have structure. Organization is the complex of interactions and properties of structure that make the perpetuation of structure possible. An entity of structure is assumed to be composed of other entities. The term entity is adopted as a "primitive term." The concept of minimum interactive structure is imposed as an epistemological constraint on the structural infinity of real systems. Other terms are defined as either relations between entities of structure, derived properties resulting from combining such entities into entities of higher order, or conditions necessary for this assembly. Organization is a composite term and consists of complementarity, coordination, integration, and hierarchy. Evaluation of overall organization of an ecological entity appears theoretically possible through parametrization and quantification of these components of organization.

Although ecology studies various entities, there is no general theory that might aid in the study of organization and principles by which ecological entities might be maintained (1). Here, we present a system of concepts for identifying ecological entities, analyzing their basic properties, and determining relations between entities. We propose a set of definitions that are necessary to build a precise conceptual framework. Addressing the problem of ecological units requires a theory of self-maintaining units, or a theory of organization.

Our system differs from the current thrust in hierarchy theory. Our method uses axioms and our approach gives priority to ontology of ecological entities over epistemological concerns. Hierarchy theory identifies adequate scales for studying operationally defined ecological units. Such operationally defined units may be underlaid by hierarchically organized structures. The axiomatic approach may help to study this underlying structure. Thus, rather than searching for adequate scales to study operational ecological units driven by specific questions (2-5), we focus on the broader problem of organization of ecological systems.

The objectives of this paper are to define organization, determine its component phenomena, and ultimately permit ecologists to abandon imprecise and unusable notions of "emergence." This exercise offers a basis for a general theory of organization of ecological systems and provides prerequisites for operational measurements of the components of organization. Such a theory will require much more development than a single paper can present. The system of notions will help identify ecological entities throughout all scales of organization; clarify distinctions between structure, function, and process; and indicate new research directions.

We assume that basic ecological units are organized. Researchers may use other units, which may not be organized (sensu stricto), as a matter of convenience or to address specific questions. As a result of the distinction between organized units versus those of convenience, organization becomes a central concept in ecology. None of the available definitions of organization (6-20) is sufficient to support a rigorous research program addressing the problem of entities. Indeed, there is no ecologically relevant account that considers organization as a composite property the component phenomena of which are subject to analysis and measurement.

Construction of an axiomatic system will necessarily go through various stages (21). The current state of theorizing about organization is intuitive-preaxiomatic. This paper attempts to advance the theory to the intuitive-axiomatic stage, which consists of an open set of proper statements accepted as true and statements derived from them. The rational sequence leading to these axioms can be summarized as follows: (i) There are ecological entities. (ii) These entities cannot exist without organization. (iii) Organization is a composite property. (iv) Some of the components of organization are always present and can be defined and identified.

An earlier attempt to formalize general properties of biological systems (22) has considered the notions of coordination and integration that we also use in this article. The fundamental difference is the linkage among the notions of organization, entity, and the function of organization, which is the persistence of the entity. This linkage does not play a major role in Mesarovic's considerations, which are largely concerned with human organizations where the function is understood in social terms. By contrast, Beer's viable system model (23) emphasizes the importance of persistence (viability) to analysis of organization and unit boundaries. We think that such a linkage is particularly suitable for a broader range of ecological systems.

ELEMENTS OF THE SYSTEM

In this section we define the terms used later. Terms range from "primitive definitions," through axioms, theorems, and derived definitions to other components of theory involving boundary conditions and terminological conventions (21).

Primitive Terms. Some terms needed to construct a conceptual system cannot be defined *within* this system; such terms are called primitive (1). "Entity" is such a primitive term. Its meaning is intuitively understood, but it will be clarified within this conceptual system.

Axiom 1. Each ecological entity has structure consisting of other entities. Entities have content and, so far, no empty objects have been shown to exist in the physical world. Thus, objects exist through and are observable because of their content. The content is nothing but other, component (lower-level) objects (elements). This originally philosophical view explains our concern with the content of objects and leads to the definition of structure. *Structure of an entity is an internal complex of' other entities and their static connections to each other.* This definition precludes identifying structures outside the context of entity.

Axiom 2. Every structure results from the properties and interactions of lower-level entities within a higher-level entity. Properties and interactions that allow units to combine and that result in the persistence of the structure constitute organization of the higher-level entity. Organization is, thus, considered a phenomenon internal to the entity. The structure of this entity is both a source and carrier of organization.

Axiom 3. The structure of an entity changes. Thus far all physical objects are known or presumed to change (second law of thermodynamics, except at 0 K). At certain time scales, some elements of structure are relatively permanent in relation to the entity itself, whereas others are transient. Such differences can be perceived as a rate dependent hierarchy (cf. ref. 5). We consider change as the loss, addition, or replacement of a component of the first- or lower-order structure. On the basis of *Axioms 2* and 3 a refined definition of organization is possible: *Organization is the mode of 'dynamic perpetuation of structure.* Organization includes the interactions and connections among structural elements that allow the static structure to persist.

DERIVED STATEMENTS

THEOREM 1. Structure is hierarchical. This theorem is a direct and simple consequence of the definition of structure in *Axiom 1.* If each entity contains other entities that, by definition, contain still other entities, then a hierarchy of entities emerges. This permits a definition of hierarchy of structure: *Hierarchy is a condition of being composed of subunits.* The first-order structure of an entity is the first hierarchical decomposition of that entity. The components of the first-order structure contain all other structural elements of an entity. Therefore recognition of an entity is based on identifying the first-order structure because this structure is necessary and sufficient for the entity to be complete.

THEOREM 2. Lower-level entities change with higher frequencies than higher-level entities. This statement is obtained from *Theorem I* and *Axiom* 3. Structure has been so far defined as involving presence or absence of lower-level entities. Higher-order structure requires the presence of entities of lower order. Change, therefore, requires deletion, addition, or replacement of lower-order entities. If a higher-order entity changes, it is only because its lower-order(s) components have been changed. In a given time interval, deletion of lower-order entities must, therefore, precede deletion of higher-order entities. This must be true of any level – i.e., between any hierarchical couple represented by an entity and its first order structure. As a result, a sequence of increasing frequencies of change from the uppermost to the lowest level of organization will be seen. *Theorem 2* echoes an empirical generalization (24, 25). We consider this the first empirical hurdle for the axiomatic system, and confidence in the system is increased by this test. As a consequence of *Theorem 2,* the first-order structure is considered persistent relative to the lower-level structure of a given entity.

Minimum Interactive Structure. The axioms and their extensions so far introduced clarify ideas about entities and structure. These axioms allow a scale-independent and case independent view of entities. The entities are allowed to have a hierarchical structure open downward and to aggregate upwards without apparent limits. Because the structure of entities is hierarchical *(Theorem 1),* we can examine the relationship between any entity and its elements as representative of all such relationships. Although the axioms are intended to reflect established facts about the world, they may not provide instructions on how to analyze ecological entities. A more operational and restrictive set of terms is needed.

Practical considerations justify the introduction of more restrictive and operational terms. Such terms may allow the following: (i) analysis of relations between entities of various levels, (ii) description of units, (iii) evaluation of structural change, and (iv) derivation of other useful definitions.

Suppose that we need to know whether, as a result of internal dynamics or a disturbance, an ecological entity has changed. To find out, we need to compare its structure at two different moments. As no entity has exactly the same structure at two moments, a conclusion that the entity has changed would be a trivial one. To discriminate significant versus trivial changes, we introduce the concept of *minimum interactive structure* (MIS). Recognizing MIS requires that at one level we see the structure as an entity, while on the next lower level we see the first-order structure of this unit – i.e., a complex of subunits (26). At an even lower level, the structure of subunits appears. The first-order structure is the minimum structure that must remain unchanged if the system is to be considered unchanged *(Theorem 2).* As the structure of an entity changes at some level(s) *(Axiom 3),* changes must occur somewhere at levels lower than that of the first-order structure. Many configurations of the lower-order structure(s) have no bearing on the conclusion as to whether the entity has changed at the level of its first-order structure. Hence, the remainder of the entity's structure, that is its second- and lower-level structures, are configurational structures (27).

We can now answer the original question of determining whether an entity has changed or not. If it has changed, then its MIS has changed; if it has not, then changes must have occurred in its configurational structure. Isomorphism of MIS of an entity between successive times is thus a sufficient criterion of its identity.

Function. Having defined MIS, other properties of organization can be introduced. Formation of MIS through organization leads to emergence of a new, higher-level entity *(Axiom 2).* From *Axioms 2* and *3* and *Theorem 2,* a relation between an entity, its structure, and time can be derived. The entity's existence through time is obtained by interactions of its structural elements alone. Such interactions can be considered to be functions from the perspective of MIS. We define function *as that part of interactions of a component of' MIS that contributes to persistence of the higher-level entity.* Function defined in this way may occasionally be the same as traditionally recognized functions but, in general, it will have to be determined through an analysis of MIS. For example, reproduction may be a function of individuals relative to a population, and the traditional meaning of function coincides with our definition. In contrast, respiration, often considered as an ecosystem function, is not a function because it does not have a one-to-one correspondence (except, perhaps, in a closed system) with any interaction arising between hypothetical elements of minimum structure of an ecosystem. Before any process, or relation, is identified as a function, the entity and its MIS must be assessed (27).

Axiom 4. <u>*Components of minimum interactive structure are complementary*</u>. This axiom is a logical extension of *Axioms I* and *2.* It brings attention to a condition that components of MIS must fulfill to form a higher-level entity. It is also introduced because the notion of complementarity may ultimately be used in empirical studies of organization. Like MIS, complementarity can be ascertained only when a higher-level entity is specified. *Complementarity is the capacity of entities to remain components of the minimum interactive structure of an entity by acting as functional supplements to one another, or being functionally dependent upon each other.* Defining complementarity by using MIS implies a state of completion achieved by entities because MIS constitutes the whole of the higher-level entity E_0 (Fig. 1). Establishing that a complementary relation exists may determine whether a higher-level unit has been properly identified. What is occupied or performed by one of two complementary parts is precluded for the other at the same moment. If the complementarity of an entity were considered to have a value of 1, then values of all complementary units of MIS should sum to 1.

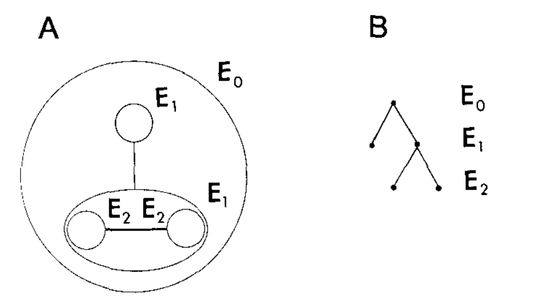

Fig. 1. Schematic of a hierarchical system and the symbolism used throughout the text. (A) Nested-set diagram of E0, a high-level entity and the interactions (straight lines) yielding its structure. El is the first level of component entities, and E2 is the second level of components into which E0 can be decomposed (circles and ellipses). (B) Schematic of the hierarchical nesting of the entities shown in A.

Two other properties of organization, *coordination* and *information*, can be viewed as mechanisms of achieving and maintaining complementarity.

THEOREM 3. For *entities that persist, changes of structure are constrained in such a way that minimum interactive structure is preserved.* For entities that persist, (i) *Axiom 3* says that structure does change, (ii) *Axiom 2* requires that structure forms a higher-level entity, despite the changes it necessarily undergoes on lower levels, (iii) *Axiom 4* makes existence of the higher-level entity possible through complementarity of the elements of MIS. The changes of structure must then be compatible with the preservation of complementarity. It follows that some limits on the nature and magnitude of changes must exist and that these limits are determined by complementarity. Apart from the constraints imposed by complementarity, MIS requires functions that define the allowable change. These two constraints, by complementarity and by function, permit a coordinated change only. The significance of the notion of function is exposed here because not all interactions among MIS contribute to coordination. **Coordination** *is an action of one element of minimum interactive structure in response to behavior of another (others) such that they remain complementary.*

A coordinated response of one unit to the action of another unit of MIS is impossible without **communication**. Communication is here treated as an impulse or a series of physical impulses emanated by one such unit and received by another. Some of these impulses are filtered by the receiving unit, and some of those filtered will actually incite a response (6). Only a specific *form of communication resulting in coordination is defined as information.*

Integration. Intuitively, some entities are deemed to be more integrated than others. Those units that we consider more integrated appear to us as more distinct and, perhaps, discrete, than other, less integrated entities of the same type. We examine the possibility of defining integration based on the properties and relations of MIS.

Elements of MIS (i) are complementary, (ii) communicate and exchange information, and (iii) behave in a coordinated way. Although all these properties occur simultaneously, some are prerequisites for the others. There is no higher-level entity without complementarity. Also, complementarity is necessary for communication to acquire functional meaning – i.e., for the transmission of information. Coordination is constrained by the magnitude of information transfer. The extent to which MIS will appear as a distinct entity will ultimately depend on coordination. Thus, we have identified an important link between coordination and integration.

There are several ways to assess integration. If two otherwise identical minimum structures differ in coordination, we would conclude that the less coordinated entity is less integrated. Alternatively, if two otherwise identical minimum structures are equally well coordinated, but the replacement of components of one is faster than the other, we would also conclude that the entity changing faster is less integrated. Substitutability of components is thus another useful criterion for evaluating integration. As integration depends on both the degree of coordination and the degree of substitutability (or change in general) of the minimum structure, *integration is defined as an aggregate index of both coordination and rate of configurational change within the minimum interactive structure.*

The meaning of integration as a composite (as opposed to mere summing up) property of an entity can only be further analyzed by examining the place of that entity within the minimum structure of some higher-level entity. From the perspective of a higher-level entity, it may be that the integration of the focal entity affects the function of the higher-level entity. This perspective differs in emphasis from the analytical approach to the minimum structure of a focal level used up to this point in our argument. The shifted perspective does not necessarily decompose the minimum structure of the focal entity and analyze its complementarity, communication, information, and coordination. Rather it uses the composite index of integration to assess the role of the focal entity in some higher-level function.

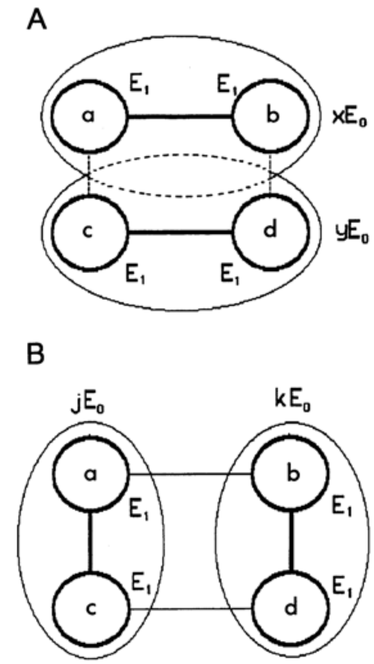

Fig. 2. Relationship between the bond strength and emergence of higher-level entities. The bonds of the lower-level entities must always be stronger (compare A and B). j,k; x, y – entities of the higher level E_0 ; a-d, entities of the lower level E_1.

THEOREM 4. *An entity is always less integrated than its component entities.*

To prove this theorem we propose its opposite: entities of one minimum structure (aE_1 and bE_1; Fig. 2) are bonded more strongly to entities of another minimum structure (cE_1 and dE_1) than with each other (Fig. 2B), which would be more integrated than the original entities (xE_0 and yE_0). Consequently, they could not be components of the original minimum structures as initially assumed because $xE_0 \neq jE0$, $yE_0 \neq kE_0$, etc., which leads to a contradiction.

The link between the appearance of hierarchy and the gradation in bond strengths has been identified much earlier empirically (28).

DISCUSSION

Discreteness of Entities. The distinction between discrete objects and a *continuous ecological universe* may be false and useless. This distinction is a matter of the cognitive resolution at which observation and description is conducted. Neither our definitions nor graphical representation of structure are intended to imply that the entities of structure are necessarily discrete. The entities might equally well be represented as fuzzy, intergrading circles or sharply bounded ones, but all the relations within them would remain the same. The emphasis is on the interactions rather than on the boundedness or concreteness of entities. The difficulty is thus operational only.

In our system, discreteness of entities is a function of their ability to maintain themselves. The more their persistence depends on a higher-level entity, the less discrete they are. For example, if frequencies of alleles in a local Great Lakes trout population depend on 90% internal reproduction, then the population is highly discrete. But if the same pattern of frequencies depends on 10% internal reproduction and 90% on the gene flow from adjacent populations, then this population is much less discrete, whereas the whole group of populations may still be distinct (Fig. 2).

Based on the concepts of MIS and function, it should be possible ultimately to measure parameters of organization (complementarity, coordination, and information) and thus determine the degree of discreteness of entities. This operation is, however, an application of this framework, not an *a priori* assumption. It can be achieved by placing arbitrary boundaries around a presumed minimum structure. Measuring the parameters of minimum structure and comparing them for differently bounded systems will expose the one that conforms most closely to the actual minimum structure.

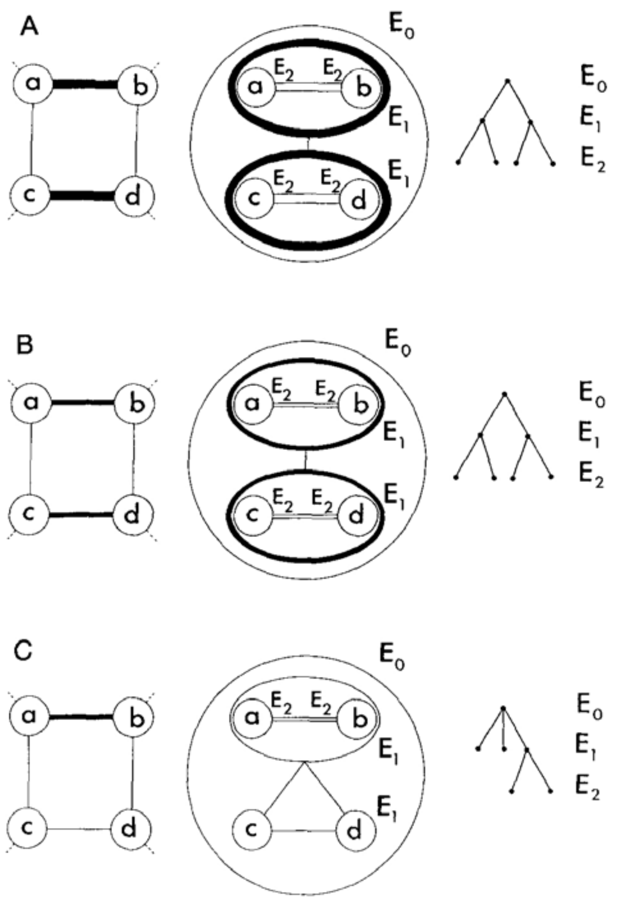

Fig. 3. Relationship between the bond strength and discretness of entities in three hypothetical cases (*A-C*). The column at left shows the entities and their interactions. The middle column showes the discretenss of the higher level entities, indicated by the thickness of boundaries about the lower level entities. The corresponding hierarchical representatios of structure are shown at right.

The question of whether levels of organization are discrete leads to a different conclusion than that of discreteness of entities. Levels are necessarily discrete within a hierarchy of one entity, as long as a cascade of minimum structures is identified. The trout subpopulations mentioned above are at a next-lower level in relation to the whole trout population of the Great Lakes no matter how discrete the subpopulations are. The conceptualization of levels should not be confused with the problem of discreteness of entities

Relation to Scales. Observational scales may roughly correspond to organization such that the E_0 is equivalent to the coarsest level of resolution, and E_n is equivalent to the finest scale of resolution (5). However, this correspondence between the levels of organization and observational scales may be far from close because levels of organization are different from scales of measurement. For example, if aE_1, bE_1, cE_1 and their interaction constitute the minimum structure of E_0 and, thus, represent one organizational scale, these entities may actually be diverse physical and biological entities. For example, the minimum structure of a termite colony might consist of a queen, a caste of workers, and a caste of soldiers. Thus an individual (the queen) would be a component of MIS equivalent to castes consisting of many individual termites. Also, the different elements of the MIS of the termite colony may require several observational scales for adequate description. Although the behavior of the queen might be adequately assessed by a researcher equipped with a camera focused on a small spatial scale of the brood chamber, an analogous description of the worker caste would have to involve a much broader spatial scale, demographic censuses, and possibly a longer time scale. Thus, study of ecological objects and phenomena at different scales, as recently postulated (2, 5, 15), does not logically entail a direct, unequivocal description of ecological organization. However, recognition that different phenomena and entities appear at different observational scales can be considered as an auxiliary method to operationalize this prospective theory of organization.

Dynamics Versus Structure. Our system of axioms allows the description of structure that is rate-independent in the sense of ref. 2. Assessing dynamics requires taking both the observers' scale and rate-dependence into account (2, 29). Whether the axiomatic system is a suitable framework for such dynamic analysis as well remains an open question until a precise definition of dynamics is provided. Provisionally, we can distinguish a change of state from the change of structure by saying that the change of state is a change of structure of the components of minimum structure – i.e., configurational structure.

Concluding Remarks. The conceptual system we have proposed is tentative and is intended to stimulate the development of a more complete theory of organization for ecological entities. This conceptual system applies only to systems that are already organized. It does not address fragments or proto-entities. Development or evolution of systems must ultimately be incorporated in a complete theory of organization as well. To apply this conceptual system, a hierarchical model of the entities of interest must be constructed. Otherwise no progress into analyses of minimum structure is possible. The parameters we have proposed are intended for the analysis of entities into component parts and relations. Initial recognition of the focal entity, from which the model starts, will likely employ the rate-based approach of Allen and colleagues (5, 26). This approach precedes a more integrative approach that views entities "from above", without detailed reference to internal structure. The hierarchical models of systems may be cast to capture classes of phenomena or may be based on a particular entity.

The preliminary nature of the conceptual system we propose requires much work and suggests questions for the future. We hope that a mature theory of ecological organization will provide the general concepts and terminology to compare organization across systems. Application of the system will require operationalizing the concepts and constructing measures of complementarity, communication, information, and coordination.

Finally, the concept of organization suggests that the fundamental problem to be addressed by ecology concerns the nature of organization of ecological systems. Are the common objects and relationships studied by ecologists organized, in the strict sense, or not? To what degree are ecological systems organized internally versus constrained by higher-level entities or external events? That such questions are, indeed, fundamental is suggested by the persistence of debates about autogenesis versus allogenesis, density-dependence versus density-independence, equilibrium versus nonequilibrium structure of competitive systems, etc. These problems may persist, at least in part, because ecology has had no clear, unambiguous, general conceptual system to apply to the problem of organization. Our attempt to establish an axiomatic system is a contribution toward this goal.

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