層級-生態複雜性的觀點

Hierarchy –Perspectives for Ecological Complexity

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Some scientific and technological endeavors have been singularly fruitful. Physics and electronics are spectacular in this regard. Even protein chemists begin to develop a clear view of their material. Then there are the poor cousins, the disciplines which have recruited no less dedication and intelli- gence but which seem still to be primitive, whose secrets still are well kept. Ecology is one such discipline. That ecology is young is not reason enough, for the turn of the century saw much better descriptions of prairies (Pound and Clements 1901) than proteins. It must be something else.

Weinberg (1975) introduces his ideas on general systems theory by distin- guishing between small-number simple systems and large-number simple systems. The former group is treated appropriately by differential equations (e.g. planets), and in the latter case statistical approaches to the entities replace exact values with averages (e.g. gas laws). May's (1976a) recent discussion of simple difference equations provides an insightful bridge be- tween the small- and large-number cases. Nevertheless, as the inter- relationships between parts (entities or averages) increase in complexity, both calculus and statistics quickly reach the limits of their analytical power.

There is a third class of systems that neither approach satisfies, even when the interrelationships between the parts are simple. These are what Wein- berg (1975) calls the middle-number systems. These are cases where there are too few parts to average their behavior reliably and too many parts to manage each separately with its own equation. An example could be metal sheets when they approach monomolecular thinness; they cease to behave like ordinary macrostructure metals where the atoms are so numerous in every direction that a description in terms of the average atom is quite sufficient for most purposes. In monomolecular metal sheets the atoms are few enough so as to be self-assertive and noticeably unique in their behavior while remaining, at the same time, too numerous to be modeled one at a time with any economy or understanding. Middle-number systems need a differ- ent approach, that of general systems theory. General systems ideas also apply to large- and small number systems, but more importantly they provide in aggregate one of the few working models we have for middle-number systems.

As the complexity of the relationship between the parts increases, these middle-number systems become quite unmanageable analytically, and even standard general systems methods fail. Examples of middle-number systems with intractably complex relationships between parts are the exact day-to- day behavior of a human being, the thought process, the exact behavior of a whole cell, or the behavior of an ecological community. The poor-cousin subjects, those whose achievements are rather limited, are often faced with complex middle-number systems in the daily exercise of the discipline. Ecology is in just this position. Some schools of ecology artificially isolate simple ecological entities and use classical Newtonian mathematics to describe and explain their behavior.

Ground here is hard won, and the necessary simplifying assumptions might weaken faith in the general relevance to empirical field or laboratory studies of that which is found. Robert May would call this theoretical ecology; E. C. Pielou calls it mathematical ecology. Other schools seek to use a statistical approach to organize extensive field collections. Arguments as to the power and relevance of this and that taxonomic procedure are fierce. The heat of the arguments might lead one to expect great achievements on the part of the prevailing view; but such ex-petitions are not fulfilled. A statistical treatment of a system whose parts are importantly heterogeneous gives fuzzy results not worthless but certainly more vague than would be fully satisfactory. Perhaps it is this in- conclusiveness that allows such fervor. With little definite to go on, conviction is the only thing left. Then there is the school which recently flowered in the International Biological Program. The approach here is one of reductionism, but on a large scale: it worked for the atom bomb so why not for the exorcises? The best of this approach has great utility in its predictive power, particularly where industry and ecosystem interact. Unfortunately, ecosystems are middle-number systems (more so than nuclear fission) and so the massive reductionism simulations seem to have offered all the insightful summary that they easily can. Nontrivial exact workings of the large explicit models cannot be coupled to the structures being modeled with much confidence. In response to this problem, smaller simulation models which ask very specific nontrivial questions are being constructed. For example, Bartell (1978) models predation to investigate only its influence on phosphorus cycling. Alternatively, models with rather general carefully chosen constraints and heavy reliance upon stochastic processes are found to be generating rich and realistic be- havior (e.g. Shugart and West 1977). This indicates that ecosystems are put together with more slack than is implied by the greater determinism of the prior generation of models. All this leaves us with an unyielding mass of complex middle-number systems. The present lines of attack appear to have encroached on these systems about as far as they can. The different assaults are running into strategic problems more than tactical setbacks (figure 1). The theoretical approach is hampered by its simplifying assumptions, the statistical approach is less and less justified in its use of averages, and the simulation approach is limited financially and technologically by its need for more data to set unreasonably exact initial and boundary conditions and by its exponential requirement for computational power. It is the aim of this book to attempt to parachute-drop as deep as possible into middle-number system territory. One worries that this is another Anzio, or worse still, Amhem, but otherwise we appear to face an impasse. What is new here is a formal acceptance of complexity in its own right. It is more than something encountered in the systems at hand complexity is some-thing that needs more than an ad hoc treatment. We see most important complexity as related to the interaction of different Mac Arthurian population biology

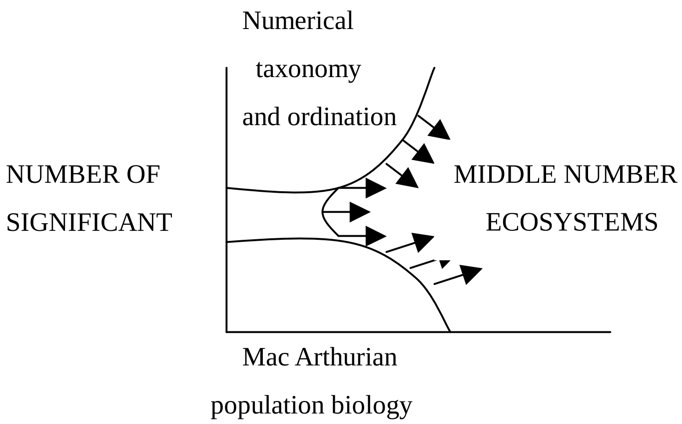

Fig. I Weinberg's graph of the number of parts and complexity of interaction modified to identify the systems upon which major schools of ecology work.

levels of organization; in order to give complexity proper account in our scientific models, those models are almost required to be hierarchical. We suggest that there is something about either our facility for observation or that which generates our observations which gives patterns that generally remain opaque unless we model using hierarchies. By hierarchy is under- stood a system of behavioral interconnections wherein the higher levels constrain and control the lower levels to various degrees depending on the time constants of the behavior. Upon that dependence we expand later. Since bulkier structures in biology generally behave more slowly, not only do slow entities constrain fast, but also large entities usually constrain small. Sometimes the lower levels of the hierarchy are nested inside and in aggregate make up the higher levels (cells and tissues), but sometimes this is not the case (ecological consumers and resources). In the nested and non-nested cases, complexity comes from the no linearity and asymmetry of an entity affecting while also being affected by its environment. The environment is the higher level, and it responds more slowly than entities it constrains. For all hierarchies there is complexity associated with the relationship between the rate-independence of constraint itself and the rate-dependence of the dynamical interaction of the constrained entities (parts in a nested structure). In the non-nested case there is further complexity in spontaneous behavior coming from undefined extra degrees of freedom at both the higher and the lower levels. Complexity need have little to do with the number of variables. The strategy in this book is to develop a philosophical construct and a suite of methods for dealing with such hierarchical structure both nested and otherwise. A body of literature already exists, some of it formal and general, some of it solving problems encountered in particular investigations. We attempt to pull that literature together into a manageable package which can be used to develop further theory that we then apply to ecology. Much of what we say has been said before but in fragments and separate places. We see our main contribution as a juxtaposition of a series of individual discoveries belonging to others. There is also something of our own. We begin with a formal statement of the problem for a historical perspective in the first chapter. In the next three chapters we attempt to lay a foundation and develop a vocabulary so that complex middle-number systems can be formally investigated. Since the discussion must be general, specific tangible examples are first kept to a minimum. It was felt that too many examples at the beginning would be redundant later and would intrude between the parts of a cohesive first statement. Everyday examples follow in abundance once a base platform is laid. The theoretical frame is presented as tersely as we could manage in chapters 2-4. Further abstractions in need of a unifying theme arise from the first part.

The ideas here are a restatement of some of the tenets of general systems theory but in the context of scale and hierarchy. One reasonable way to organize these ramifications of the first part is in a progression where in systems gradually increase in complexity. To this end the second part uses the evolution from a biotic to fully living systems as the vehicle for discussion. Chapter 5 considers the meaning of evolution in terms of complex systems. The role of anticipation and symbolic or linguistic structures in the functioning of complexity is emphasized at this point. Chapter 6 discusses the nature of boundaries in such systems. A distinction is made between functional boundaries such as the separation of enzyme systems from other organic reactions by reaction rate, and structural boundaries such as cell membranes. Structural boundaries are considered a special case of functional boundaries.

Having reached living cells, we continue by emphasizing the important role of self-replication in complex organic forms. Chapter 7 looks at the processes of self-replication with their attendant memory and symbolic components, while chapter 8 identifies resilience in the face of perturbation; reproduction has important consequences pertaining to that resilience in hierarchical complexes. By this point in the book, familiar examples, even ecological examples, are used regularly.

With many of the implications of complex reproducing systems presented, the book is free to address ecology using a language developed to deal with middle-number complexity. In the third part we develop the thesis of this book and address only ecological questions. We find that stability in ecological systems, a matter of primary concern in the literature, has an important relationship to the degree of connectedness. Hierarchies allow very economical descriptions of system connectedness in that stems of a hierarchy have their junction points clearly defined without any reference to un- necessary detail about the particular behavioral messages that travel through a given connection. Diversity has an indirect relationship to connectedness, and this we define. We make our attempt to unravel the diversity/stability discussion using hierarchies as a new tool in this context.

In the third (and last) part of the book we also criticize mathematical modeling in ecology and report ways that coupling of portions of models in a hierarchical way can be achieved. We see the dichotomy of behavior and structure as artificial and arbitrary; it precludes evolution of the constants of structure. Perhaps surprisingly this even applies to most extant models forgone flow and selection. We emphasize that hierarchical structure can look quite different de-pending on the time and space constants used by the observer in the collecting data. The need for formality in the selection of those observational parameters is clear. Casual choice of parameters, despite meticulous use of parameters, leads to models which are unnecessarily restricted to the set of scales that reflect only commonplace experience. We attempt to unify ecology by introducing scale with some formality into the various ecological sub disciplines.

We see this book as something of a sister to Margalefs (1968) Perspectives in Ecological Theory. Like his ideas, ours have an origin in the study of aquatic ecosystems and in the tension and unity that come about when aquatic and terrestrial systems are compared. Although we do not emphasize information theory per se, we share his interest in a signal-and-message approach to ecology. The flowing of water seems to engender thoughts on information flow. We are also pleased to share with him the University of Chicago Press.

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