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ON THE IMPORTANCE OF HIGHER-LEVEL MODELS IN ECOLOGY

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ABSTRACT

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Theoretical models in ecology are often criticized for not measuring up to impossible standards. Because real populations and ecosystems are not simple mechanical clockworks, no degree of refinement on mechanistic models can extend their prediction capability to the point where they will satisfy all rigid tests of falsifiability. Mechanisms, or efficient causes, constitute but one aspect of causality in ecosystems. Other agents, such as positive cybernetic loops appear to act as autonomous formal or final causes in effecting ecosystem structure. A more widespread knowledge about the range of causality in ecosystem development should foster greater tolerance for the limits of mechanistic models and at the same time should enhance appreciation of the indispensable role models play in understanding how communities evolve.

INTRODUCTION

It will come as a surprise to anyone familiar with my past work (e.g., Platt et al., 1981; Ulanowicz, 1986a) to see me undertake a defense of the use of mathematical models in ecology. Virtually my entire career has been devoted to declaring the short-comings of whole ecosystem simulations and to promoting alternative methods for quantifying ecosystem behavior. Why, then, try to preserve that against which one has railed for so long?

There are several reasons for rising to defend theoretical models, as will unfold in the course of this paper. My primary motivation should be stated at the very outset. Although I question the sufficiency of ecological modeling, I do not question its necessity. My previous criticism of ecological modeling has always been from the perspective of a phenomenologist – more particularly as a phenomenologist who perceives that events occur at a hierarchical level above that of a single population. I believe that the causes of these higher-level phenomena are to some degree autonomous of what happens at the lower levels. From this point of view, most (though certainly

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not all) of ecological modeling appears to me to be reductionistic in nature. The normal 'mechanistic' approach used in modeling can be summarized as: "Faithfully describe each component process of an ecosystem with an adequate (sometimes stochastic) mathematical expression, and then incorporate these constitutive functions into some bookkeeping scheme (usually a set of ordinary differential or difference equations) to produce the resulting clockwork that mimics the behavior of the system." The implicit assumption made by many modelers is that this analytical approach is both necessary and sufficient to describe ecosystem behavior. It is usually taken for granted that any inadequacy in the correspondence between model prediction and reality reflects the approximate nature of the constitutive formulations rather than any insufficiency in the approach itself. I disagree for reasons to be discussed presently.

Others, however, criticize ecological modeling from a standpoint diametric from my position as a holist. They perceive fundamental problems with the assumption that a population can be treated as a unit. Some say that the idea of a trophic level is an egregious misconception (Cousins, 1985). Others feel there is no evidence for cybernetic behavior at the ecosystem level and, at the extreme, adopt the nominalist stance and question whether the ecosystem is a real or useful concept (Engelberg and Boyarsky, 1979). The failure of ecosystems modeling to deliver what overzealous proponents had earlier claimed they would do has created in the community of ecologists a disappointment that the reductionistic nominalists have been quick to exploit.

Now, it is not easy for me to argue in support of system-level autonomy and inveigh against unbridled nominalism without at the same time recognizing the necessity for some intermediate constructs. Ecosystem simulation is such an intermediate; and I come, therefore, to defend ecological modeling as a legitimate and *necessary* aspect of ecosystems research. What I hope to achieve in the remainder of this paper is to sketch out where I *believe* theoretical ecosystem models belong in our agenda for understanding ecosystems. I stress the word 'believe' because I wish to acknowledge that at the periphery of everyone's philosophy of science are to be found assumptions that perforce remain metaphysical. Anyone who believes his/her outlook to be immune to this condition would do well to read what Goedel (1962) has to say about self-consistent logic.

CAUSALITY IN PHYSICS

I agree with Simberloff (1981) that ecosystem modelers are inclined towards an unnecessary envy of physics as the epitome of precise mathematical formulation. I agree, not out of any disdain for mathematics, but because the image so many ecologists have of physics seems more suitable to the late 18th century than to the late 20th. It was during the Enlightenment that the view of the world as a precise clockwork was ascendant. LaPlace's (1814) "divining angel" knew the precise location and momentum of every particle in the universe and could apply Newtonian mechanics to this knowledge to calculate the entire future of the world. Similarly, if we knew the ecosystem population levels and could precisely formulate the interpopulation interactions, what would keep us from predicting how the community would behave well into the future?

Physicists today assure us that the world is much more complicated than a precise clockwork. Problems with LaPlace's angel appeared initially in the 1820's with Sadi Carnot's (1824) quantification of that which is irreversible in the macroscopic world. But an entirely reversible Newtonian mechanics cannot give rise to irreversible phenomena. Early in this century our capability to know position and momentum with arbitrary precision was shown by the development of relativistic and quantum mechanics to be impossible. As late as 25 years ago, applied physicists and mathematicians were discovering that our ability to predict events in some systems described by sets of ordinary non-linear differential equations (the form of most theoretical population and exosystems models) was severely compromised (Lorenz, 1963; May, 1975; Ulanowicz, 1979).

The modern physicist is fully aware that the actual phenomena studied under the rubric of quantum mechanics bear almost no resemblance to those studied earlier in classical mechanics. Yet the suffix 'mechanics' is retained, partly because of a superficial formal connection to the older discipline, but probably also out of deference to a widely-held mechanistic view of the universe. Some see this proclivity to retain the mechanistic vision as the chief impediment to bridging the gap between physics and biology. Modern physics is ostensibly non-Newtonian, but many practicioners maintain the restricted Newtonian view that causality can be only material or efficient in nature (Rosen, 1985). However, causality in the living world is clearly much more complicated than it appears in the classical Newtonian format (Salthe, 1985).

With all due apologies to those who decry the influence of Hellenistic thought in modern ecology, I would like to note that Aristotle maintained no simplistic view of causality. He taught that an event could simultaneously have four types of causes: (1) the material, (2) the efficient, (3) the formal, and (4) the final. In the building of a house, these are represented by (1) the bricks, mortar, wood, etc., (2) the construction workers, (3) the architectural plan, and (4) the need for shelter of those for whom the house is being built, respectively. Despite a brief flirtation with final cause as suggested by Hamilton's (Goldstein, 1950) variational description of mechanics, the consensus has precipitated that only the first two types of cause are necessary to describe nature. By their ostensible dispensability the latter two have acquired an air of the methaphysical.

CAUSALITY IN ECOSYSTEMS

I maintain that it is possible to treat both formal and final causality in nature in a quantitative fashion that is not unduly metaphysical. Furthermore, I would hazard to speculate that efforts to address living systems without recourse to other than efficient causalities inevitably lead to propositions that bear less relation to reality than the ones those proposing them sought to avoid. For example, an overly literal reliance on the reductionistic aspects of neo-Darwinism has caused some to attribute the higher-level functions of selfishness (Dawkins, 1976) or directive agency to genes, or to invoke extra-terrestrial seeding of the first germ plasms.

It is helpful to invoke some recent insights from the burgeoning school of hierarchy theory as it pertains to ecology to see how formal and final cause might arise in nature (Allen and Starr, 1982; O'Neill et al., 1986; Salthe, 1985). It seems that we humans are constrained both physically and mentally from apprehending nature synoptically. We are forced to confine our attention to a finite range of size and duration, which in hierarchy theory is called the focal level. The focal level was once limited by the senses and the rate of neural activity, but with technology we are now capable of mentally constructing higher or lower levels. The most familiar series of levels is the nested hierarchy of molecule–cell–organ–organism–population–ecosystem–biosphere.

According to the strict reductionist's view of the world, causality can flow only up the hierarchy in mechanical fashion, i.e., events at higher levels are the mechanistic results of those below. Entities at higher levels are either dismissed as epiphenomenal or else as arising purely by chance from the chaos below. The positivist's view of the world matches this reductionistic image hand-and-glove. The competing hypotheses to explain a phenomenon usually point to alternative causes – sometimes at the focal level, but usually below it.

It is not necessary that one be inclined toward the religious or transcendental to feel that strict reductionism is an overly-simplistic view of how things happen. For example, the existence of larger-scale entities often constrains passively what can happen at smaller scales. These larger objects serve as boundary conditions on the dynamics at the microscale, or, as Weiss (1958) put it, order at the higher level is superposed upon radical heterogeneity at the lower level. Influence may propagate down the hierarchy, but when it does, it is not readily amenable to definition in positivist fashion.

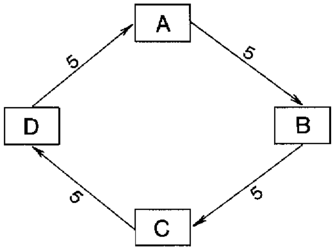

Fig. 1. An ideal, four-element autonomous loop of material causality.

Hence, causality may appear by accident at the focal level or higher. But accident is not an agency in the ontological sense. Does an active agent exist at these levels? I have argued at length elsewhere (Ulanowicz, 1986a, 1988) that positive feedback is an example of an active agent that exists at higher levels and that is capable of ordering affairs at smaller scales. Briefly, the argument is predicated on the identification of six attributes of autocatalytic feedback that contribute to its capacity to give order to dynamic systems. Autocatalysis can be: (1) autonomous, (2) emergent, (3) growth-enhancing, (4) selective, (5) competitive, and (6) formal in nature.

An ideal autocatalytic loop is illustrated in Fig. 1 wherein each of the four components catalyzes the next one in turn. Here the material flows (causes), each five units in magnitude, have been illustrated; but in general the arrows could represent any form of influence. This ideal loop is wholly autonomous in that it requires no sustenance from outside the system. Of course, real, dissipative systems by definition can never be wholly autonomous. Instead, they look more like the one in Fig. 2, which is replete with exogenous transfers. But the existence of the supporting transfers does not make the real system entirely non-autonomous. To see how an element of autonomy persists in the system of Fig. 2, one could readily decompose that network

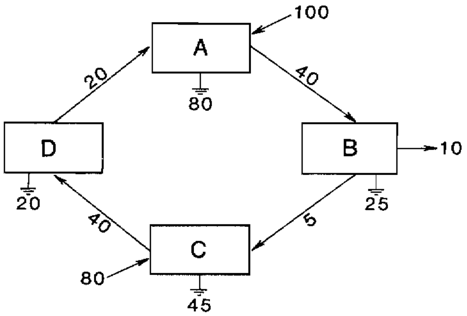

Fig. 2. A hypothetical, but plausible feedback loop like the one in Fig. 1, but including transfers with the external world.

into two abstract component systems. One would be a once-through, non-autonomous chain of material causality, and the other would be identical to the perfectly autonomous loop in Fig. 1.

To see how autocatalytic feedback might appear as an emergent property, it is useful to suppose that one begins by looking at only components A, B and their adjacent flows as they appear in Fig. 1. This particular subsystem viewed in isolation acts like a strictly non-autonomous chain of causality. If, however, one expands the domain of interest to include C and D, the system suddenly appears autonomous.

That the configuration in Fig. 2 is growth-enhancing is practically a tautology. Any increase in the activity of any one element will be propagated positively to all other elements (including itself).

Perhaps the most important property of a positive feedback configuration with respect to its impact on ecological modeling is its capacity to exert selective pressure upon its components (H.T. Odum, 1977). If any element in an autocatalytic loop changes in an arbitrary (possibly stochastic) way that enhances its catalytic effect upon the next member, that gain will be propagated around the loop and the alteration will be reinforced. Conversely, a negative change in the behavior of any element will be self-dampening. The characteristic being altered could be quite general. It might be an element of the relationship between two adjacent elements, i.e., the constitutive relationships (as mathematically described in conventional modeling) may themselves be the objects of selection by the agency of autocatalytic feedback.

Strongly coupled with selection is competition. In Fig. 3 an immigrating or mutant species E interacts with A and C in parallel to B. It happens to be more efficient than B in responding to A and catalyzing C, so that eventually all flow is routed through E, which displaces (out-competes) B in the network. For a brief while there is competition, not only between B and E, but also between the two feedback loops as differentiated by the separate but parallel paths through B and E.

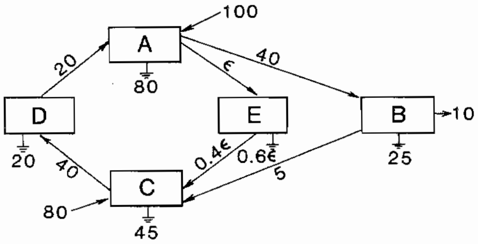

Fig. 3. The appearance of a new element, E, into the loop of Fig. 2.

By induction one might also conceive of the elements A, C and D subsequently being replaced by other competitors, but the *formal* configuration of objects (the loop) is seen to persist at this level of observation beyond the presence of its original constituents. Furthermore, the agency behind (or cause of) the system's growth and selection exists in the *form* of the relationship between the constituents. In some ways autocatalytic feedback is a more attractive example of formal cause than is a passive set of blueprints.

Autocatalytic feedback is one particular example of a semi-autonomous agent acting at the level at which we choose to focus our analysis. It is interesting to ask whether in general the perceived nature of agents might be determined more by where in the hierarchy of observation they are operating than by how they act. The answer is not yet clear and should provide grist for the philosophers, suffice it here to say that there does seem to be a correlation between the Aristotelean type of causality and the relationship of the causal agency to our scale of observation (Salthe, personal communication, 1987). For example, from one hierarchical level a feedback loop might appear as an efficient cause, whereas if it were seen from within one of its components its agency would look final in nature.

It is well and good to philosophize about causality in ecosystems, but if we cannot somehow specify and quantify the effects of cybernetic feedback on communities, we might as well be talking about angels on a pinhead. We now understand positive feedback to be one agent capable of affecting both the extensive and intensive nature of systems. It serves extensively in a ratchet-like way to increase the aggregate level of activity of a system. At the same time it acts intensively to winnow out less efficient pathways in a flow network, making the developing system appear progressively more articulated, or specific in its connections. I have shown elsewhere (Ulanowicz, 1980, 1986a) that both of these factors (as they appear in ecosystems flow networks) can be quantified by a single variable called the 'network ascendency'. For any arbitrary, quantified network, such as a food web, there exists a single value of the ascendency that measures the combined properties of network activity and network articulation irrespective of any underlying mechanisms that help maintain the system. (Like all many-to-one operations, the reverse is not true. Any single value of the ascendency may belong to a virtual infinity of network configurations.)

The chief practical advantage of the ascendency is that it can be used to chart the response of an ecosystem to positive feedback acting as a formal cause. Normal development (succession) is indicated by an increase in both factors of the ascendency. A perturbed system will evince a decrease in the configurational factor (Ulanowicz and Mann, 1981). In a eutrophic system the ascendency will rise because the overall increase in the system activity (the extensive factor) has a larger effect than the decrease in the configurational factor (Ulanowicz, 1986b).

Finally, we can simulate the increase of network ascendency as a problem in optimization with ascendency as the objective function (Cheung, 1985). Under a minimal set of constraints, a systematic search is conducted for that reconfiguration of the existing network with the highest ascendency. During the course of the search, as the system progresses from its starting form toward its optimal state, the individual components change as if driven by an external force, i.e., a final cause. So the potential exists for modeling ecosystems in a holistic fashion. There is a major problem, however, in that the many-to-one correspondence of network configurations to values of ascendency makes it unlikely that the pathway of states traversed by the mathematical optimization of the network will correspond closely to the actual evolutionary trajectory.

WHITHER ECOSYSTEM MODELING?

This long prologue has not been without its point. To repeat: Evolution is not a clockwork. However, most whole ecosystem models are clockwork in nature. Therefore, most whole ecosystem models are doomed to fail in the long run.

Of all the weaknesses of theoretical modeling in ecology, the lack of prediction capability is probably foremost (Peters, 1980). This fault was ascribed by earlier systems analysts to a lack of resolution. If only we knew the parameters better, if only data for parsing the system were more complete, if only we could specify the boundary conditions more precisely, if only, etc. The optimism endured that one day better computing machinery and more comprehensive data would fix everything. Then came the discovery of deterministic chaos, and the outlook for achieving accurate prediction was clouded. Now, if one subscribes to the hierarchical view of causality just espoused, the prospects for achieving prediction are grimmer still. In good Heraclitean fashion, the constituent mechanisms of which models are built are themselves transistory. Living systems evolve.

It appears that many of the expectations modelers held for full-systems models simply will *never* be realized. Knowing the reasons behind these limitations gives some stoic consolation. If one is caught in a dark maze, it is better to light a candle than to repeatedly walk into the walls. Those to whom prediction is the sine que non of science (Peters, 1980) will continue to dismiss theoretical models, but they seem concerned with only the darkness and not the maze.

Having stated the heavy constraints on prediction at the ecosystem level, I should hasten to add that the situation is not altogether hopeless. After all, mechanism is an essential feature of reality, and ecosystems are no exception. We simply need to adopt a more realistic attitude and confine the application of our mechanistic models to those situations where mechanisms dominate the causal scene. I am able to identify at least three situations where such might be the case: Firstly, if one confines the system of interest to a single population or a single process, and possesses sufficient data on those elements of the world communicating with the system, the chances for accurately predicting system response are markedly improved (Paloheimo and Dickie, 1966; Parsons et al., 1967; Jassby and Platt, 1976; Platt et al., 1981). It is only when one includes in the model many species interacting via multiple processes that predictability rapidly begins to suffer. Secondly, even at a high degree of complexity, there remains some hope for prediction into the immediate future. Mechanisms may appear transient over successional time, but remain relatively fixed in the short term. Should the ensemble of mechanisms behave in chaotic fashion, there is a finite temporal range within which a degree of prediction is still possible (Lorenz, 1969). Thirdly, there are systems that are so strongly dominated by physical influences that the degree of biological autonomy possible remains insignificant (e.g., the upper mixed layer of the ocean surface). The problem of forecasting in those communities devolves into one of predicting the physical driving forces (which, unfortunately, is often just as problematical!).

It is well and good that models may still be applicable in particular instances, but what are we to do about the larger picture? As C.A.S. Hall (personal communication, 1987) said to me, "The problem is not necessarily with modeling itself, but with how we've approached it." I suggest that we have spent too much time approaching modeling in backwards fashion. We have been eager to postulate mechanisms and reluctant to heed what the data are saying to us. We need to try harder to listen to what the data are saying, i.e., we need far more experimentation with phenomenological models. Phenomenological models are the attempts to encapsulate data into neat, concise formulae (Ulanowicz et al., 1978).

Many are bound to retort that this seems like a purile exercise, indeed! Why build what sounds like quantitative tautologies, when the positivist dictum bids us seek out only falsifiable hypotheses? However, I reply by pointing out that correct hypotheses can be formulated only in terms of an adequate 'vocabulary' of concepts. Creating that vocabulary is seeking after better quantitative tautologies, i.e., creating more cogent phenomenological models – The necessary first step. The notions of force and mass did not appear full-blown in Newton's mind as a falsifiable hypothesis. There was a considerable induction period that could be characterized as massaging data on 'fluctions of momeneta'. Ecology is now in such a stage of induction, where many are experimenting with new lexical elements. Jørgensen (and

Mejer, 1981) talks about exergy, Hannon (1984) about species discount rates, Cohen (1978) about intervality, and I about ascendency.

A new vocabulary for ecology is being created, and I am convinced through my personal experience (Ulanowicz, 1986a) that once the terminology exists, the grammar to connect the new concepts will quickly ensue. For all we know, prediction itself might follow, albeit of a different type than we had earlier sougtht (e.g., in the absence of major perturbations, the ascendency of a system will increase).

Even if such system level prediction turns out not to be all that we had hoped for, there is always valuable utility in postdiction. For example, Suter (1981) criticizes present ecosystem theory on the practical grounds that it does not supply managers (specifically those enforcing the National Environmental Protection Act) with useful principles and methods. While Suter is concerned (as most managers are) with the fate of individual populations, some issues of environmental legislation are directed towards determining whether human activity is stressing the system as a whole, e.g., whether a community remains 'healthy', or whether a particular impact can be classified as eutrophic. These 'macro-ecological' attributes are now within the realm of quantification (Ulanowicz and Mann, 1981; Ulanowicz, 1986b), and the results should eventually prove useful in court.

CONCLUSIONS

I would like to conclude by noting that mechanisms are most certainly a part of reality. They might not be the whole fabric of nature that many perceive them to be, but as Elsasser (1969) so eloquently overstates the case, "To conceive of life as a creative process without paying attention to the mechanisms involved in each case, is just plain nonsense". Like all other aspects of the living world, mechanisms need to be addressed in quantitative fashion. It is imperative that we recognize and reserve a proper place for theoretical and simulation models in ecology if the discipline is to continue to thrive.

At the same time we need to devote significant effort towards discovering the phenomenological 'laws' of whole-ecosystem dynamics. In the process we shall be creating a new ecological vocabulary that in time will lead to a new generation (and a new level) of hypotheses and models. It is even possible that the new theories that ensue will fulfill Eugene Odum's (1977) hope that ecology become the new integrative discipline.

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