CHAPTER 13

Mechanistic Approaches to Ecology: A New Reductionism?

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Community ecology is chronically among the most tumultuous and at the same time alluring of ecology's subdisciplines. Presently there is as much controversy over method as over fact (see symposia volumes by Price et al. 1984; Strong et al. 1984a). During the past decade or so, a rather distinct methodology in community ecology, called the mechanistic approach, has been slowly coming into prominence. This approach can be most simply defined as the use of individual-ecological concepts—those of behavioral ecology, physiological ecology, and ecomorphology—as the basis for constructing a theoretical framework with which to interpret the phenomena of community ecology. The approach contrasts with the "descriptive" one, in which community phenomena are represented by models with no lower-level derivations, but which have one or both of descriptive prowess and mathematical convenience. Of course, any given work may contain both mechanistic and descriptive elements. Hence in principle there exists a continuum of mixtures, although the distribution of actual studies may be bimodal. Somewhat informally, I will use "mechanistic" to refer to studies primarily employing the mechanistic approach. . . .

Reducibility of Community Ecology

Formal Conditions for the Reduction of One Area of Science to Another

While most philosophers (review in Wimsatt 1980a) now advocate a broader concept of reductionism than did Nagel (1961) in his classic work, Nagel's formalism, because of its precision and primacy, is an attractive place for our discussion to begin. In general, "a reduction is effected when the experimental laws of the secondary science (and if it has an adequate theory, its theory as well) are shown to be the logical consequences of the theoretical assumptions . . . of the primary science" (Nagel 1961: 352). By experimental

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law, Nagel means generalizations about the phenomena of the science in question, whether they be absolute or statistical. An example of an absolute experimental law is "lead melts at 327°C." Nagel distinguishes "theoretical laws" or "theories" from experimental laws (32) as statements "whose basic terms are not associated with definite experimental procedures for applying them . . . so that a theory cannot be put to direct experimental test" (85). An example of a theoretical law would be a statement dealing with the atomic theory of matter. Nagel admits the distinction is in some ways not hard and fast, and given the statistical and often weakly verified nature of "laws" in ecology, it is even looser here than it is in physics and chemistry.

A problem with reduction can be that the laws of science to be reduced may contain terms not found in the reducing science. Under such circumstances, reduction can be said to be effected formally when the following two conditions are met (Nagel 1961: 353–94). The first is *connectability,* in which terms not in the to-be-reduced science must be related to terms in the reducing science. These relationships can take three forms: (1) logical connections between established meanings; (2) conventions, or definitions; and (3) facts, i.e., relations established empirically. The second condition is derivability, in which all laws of the to-be-reduced science, including those with terms not in the reducing science, must be derivable from the theoretical principles of the reducing science, using where necessary the connectability relationships.

Various difficulties with Nagel's criteria have been summarized by Wimsatt (1980a; see also Hull 1976b). On the one hand, the use of approximations makes a literal execution of Nagel's conditions problematical (in what sense are they logical deductions?) and jeopardizes most conceivable realizations in actual science. On the other hand, if such difficulties can be overcome, the in-principle satisfying of Nagel's conditions may generally be possible, even though the in-practice realization may be too complex to be useful to science and may merely satisfy a philosophical desire for ontological simplification. Because scientists seem often to show reductionist behavior, broadly construed, Wimsatt (1976b, 1980a) argues that rather than emphasizing Nagel's idealization, we should adopt a broader characterization which corresponds more closely to the actual practice of science. Toward this end, Wimsatt (1976a, 1976b) proposes "explanatory" reduction, in which one has "an explanatory relation between a lower-level theory or domain of phenomena and a domain . . . of upper-level phenomena" (Wimsatt 1976b: 220). Further, one "attempts to identify or explain the upper-level whole and its properties with or in terms of a configuration of lower-level parts and their known monadic or relational properties" (ibid.: 208). A consequence of Wimsatt's modification is that practical aspects of reductionism, e.g., "research strategies," are emphasized over formal aspects; if the lower-level characterization becomes too intricate or cumbersome, it is no longer explanatory.

My tactic in this section is to evaluate how closely Nagel's conditions might be met by a mechanistic approach to community ecology. I will try to show that, while of course community ecology has not been reduced *in toto,* some prototype reduction exists for certain of its aspects that appear explicitly to satisfy Nagel's conditions in most major ways. In so doing, I will be trying out the notion that to the degree Nagel's conditions are met by extant mechanistic approaches without excessive postulation of links and deductions not now existing, and without excessive complexity, the reduction is usefully explanatory. The existence and success of such prototype reductions, I will argue, makes a much broader reduction at least plausible.

Levels of Ecology

To attempt application of Nagel's conditions, we must first decide what the various subdisciplines of ecology are; each of these will then be considered a separate "science" in the above terminology. Moreover, as reduction proceeds from "higher" to "lower" sciences in some sense (Medewar 1974), we need to arrange the subdisciplines, inasmuch as possible, into a hierarchy of levels. Hierarchies are perhaps best defined with respect to objects, such as organisms or populations, which are in fact the "parts" composing the various levels. I am going to assume in what follows that these "parts" are the objects of *principal* focus with respect to a particular subdiscipline, rather than being any kind of object that is mentioned in the phenomenology or theory of the subdiscipline. Hence, *term* is obviously a more inclusive label than *part.*

Beckner (1974) has stated the formal conditions for a perfect hierarchy as follows:

a. every part P_i is assigned to exactly one level L_i;

b. every part P_i (except those of the highest level) is a part of exactly one part at each level above L_i; and

c. every part P_i (except those of the lowest level) is exhaustively composed of parts at each level below L_i.

I will now attempt to show that while a perfect hierarchy exists for a subset of ecological subdisciplines, not all such subdisciplines are members of a perfect hierarchy. This is despite the fact that one of the latter subdisciplines is often considered to deal with the highest level of ecology.

The three disciplines of ecology that, when narrowly enough constructed, do form a perfect hierarchy, are *individual ecology* (the parts are individuals); *population ecology* (the parts are single populations, defined as those individuals in some place belonging to a single species); and *community ecology* (the parts are collections of populations occurring in some place). Individual ecology is itself decomposable into physiological, behavioral, and functional-morphological ecology; all such disciplines focus on the individual but have somewhat different objectives and theoretical structures. Population ecology deals with single-species populations one at a time. Phenomena of interest include kinds of items in the diet, behavioral and physiological thermoregulation, territory size, and mating strategies. The phenomena of interest in population ecology are aggregate properties of the individuals composing the population; examples are age structure, sex ratios, growth rates, and reproductive schedules. Community ecology deals with a group of populations in some place. Here the aggregate properties of interest concern the various species populations: abundance distributions, species diversity, species-turnover rates, and so on. These three kinds of ecology satisfy all of conditions (a)–(c), at least ideally. That condition (a) is satisfied follows from the definition of the subdisciplines. That (c) is satisfied follows from the definitions of populations and communities. Condition (b) is satisfied if communities comprise mutually exclusive populations. Because communities are in practice rather arbitrarily and dissynchronously defined, this need not be the case, but one might imagine that a study by a consortium of researchers would designate communities in this fashion, and if the world's communities were ever catalogued, that they would consist of nonoverlapping populations.

A fourth subdiscipline of ecology, often considered the highest level, is ecosystem ecology. The parts are ecosystems; an ecosystem is defined as a community or communities plus the physical environment (Whittaker 1975). Once the physical environment is brought into the picture as a part, condition (c), that each level is exhaustively composed of parts from lower levels, is clearly violated. One might try to argue that physiological ecology also has "parts," e.g., environmental input such as solar radiation, that are purely physical; if so, however, then individual ecology would violate condition (b) and the perfect hierarchy would be destroyed from below. For reasons expressed in the following paragraphs, I prefer not to think of physiological ecology this way, and I would argue that ecosystem ecology is skewed aside from the hierarchy from individuals to communities.

For the sake of completeness, a final subdiscipline of ecology is often recognized—evolutionary ecology. It can be defined as that portion of the larger science of evolutionary biology which is relevant to ecology. (One might simply recognize evolutionary biology as the "science" in question, but I am trying to relate terms used here to those commonly found in the literature.) I see evolutionary ecology as arranged almost entirely laterally with respect to ecology's other subdisciplines, and certainly not in any perfect hierarchy. It is not so clear what the "parts" of evolutionary ecology are. If they are alleles and/or genotypes, and if evolutionary ecology were the lowest level, then condition (c) is violated. If its "parts" also include individuals and populations, then condition (a) is violated, and either or both of conditions (b) and (c) are also violated. Less formally, some ecologists are interested in evolutionary phenomena at various levels: the individual, the population, and the community (e.g., Lewontin 1970; Wilson 1980). All this may mean that evolutionary ecology is better considered a "perspective" (in Wimsatt's (1976b: 254) sense; for more on identifying boundaries of sciences, see Darden and Maull (1977)).

As mentioned, the rationale for proposing a hierarchy is that typically reduction is attempted from higher-level sciences to lower-level sciences. However, the fact that one science stands higher than another in a perfect hierarchy is neither a necessary nor sufficient condition for reduction of the higher to the lower science. Levels are defined with respect to parts; reduction is defined with respect to theories. Hence reduction may or may not be possible, given a perfect hierarchy (Beckner 1974). It is also false to argue that if sciences are not in a perfect hierarchy, one cannot be reduced to another. One might be misled by making the argument that parts in the higher-level science may not be exhaustively composed of parts in the lower-level science; therefore connectability is violated. But connectability refers to terms, not parts; the former is a more inclusive category than the latter, so that even if there are "parts of parts" in a higher-level science not occurring as parts in the lower-level science, they may still occur as terms at the lower level, or at least be relatable to terms at the lower level.

A related complication is that the theoretical structure of a particular ecological subdiscipline may include as "terms" those predominantly used at higher levels, or even include the "parts" of higher levels. For example, in models of the costs and benefits of territorial defense, a major conceptual issue in individual ecology, the term "rate of intrusion" is necessary. In turn, this term is strongly related to "number of individuals in a population," a term of major explanatory focus in population ecology. But the fact that there exists another subdiscipline of ecology devoted to explaining such properties as population number need not destroy the integrity of lower-level subdisciplines using those terms. In individual ecology, population number might simply be considered an input parameter in the same sense as radiant energy or some other physical quantity whose etiology is unnecessary for some kind of explanation in that subdiscipline. On the other hand, there might exist some "metatheory" spanning several disciplines such that, for example, understanding population phenomena may contribute to predictive power at the individual level. . . . More generally, the subdisciplines that we showed stand in a perfect hierarchy on the basis of their parts may not have entirely discrete bodies of theory. Moreover, if in some sense theories can be said to be hierarchical, a perfect hierarchy defined with respect to parts may not imply the equivalent sort of hierarchy with respect to theories or descriptions (Wimsatt 1974). . . . In short, our analysis of levels has left entirely open the question of the reducibility of ecology's subdisciplines. We now attack that issue directly.

Formal Reducibility of Community Ecology

This section considers the possible reductive relationships between community ecology, population ecology, and individual ecology. I will first attempt to show that the population-dynamical approach to modeling community-ecological phenomena makes a reduction of community to population ecology plausible. I will then attempt to show how much if not all of the theoretical model-structure of population ecology might be reduced to individual ecology.

Community phenomena such as numbers of species and their abundance distributions can in principle be understood by analyzing a set of differential (or difference, or hybrid) equations, each having the abundance of a component species as the dependent variable. For each such equation, independent variables may include population abundances of other species on the same trophic level and/or on different trophic levels and physical quantities such as the supply of some nutrient. The equations represent changes in abundances through time, as these are affected by the independent variables and parameters through births, deaths, immigrations, and emigrations. Such equations in fact compose a large part of the theoretical machinery of the subdiscipline population ecology. Certain phenomena of interest there, e.g., population growth, are directly representable by such equations; others, such as age structure, are representable by a more extensive set of equations whose output can be combined to give changes in total number of individuals in a population.

So commonplace is the use of such equations in community ecology that it is easy to miss that this usage in fact may automatically constitute a reduction of that subdiscipline to population ecology. To be convinced that this interpretation makes sense, it is helpful to imagine theoretical approaches in community ecology that do not involve population-dynamical equations. A number of prominent ones exist, including the early MacArthur (1960) broken-stick models for species abundances and the MacArthur-Wilson (1967) theory of island biogeography. The fact that the first has been declared obsolete by its founder (MacArthur 1966) and the second by Williamson (1983) may indicate a general trend of declining popularity of such models. Although many, myself included, are far from ready to write off the second as yet, replacement of MacArthur-Wilson dynamics (where the dependent variable is number of species) with population-dynamical models is certainly conceivable. All this illustrates that the reduction of community to population ecology is far from complete although it is plausible that it will eventually become entirely or nearly so.

A second difficulty for the just-proposed course of reduction is that a theory having to do with evolution in communities (e.g., character displacement) may not be representable using models whose variables are of the kind listed above.

Because the same problem arises for the reduction of population ecology, I discuss the two together below.

A much stronger kind of reduction of community ecology to population ecology would occur were there to exist no experimental laws or valid theoretical laws that in any major way entail interaction between species populations. Something like this view has been favored by ecologists from Gleason (1926) to Simberloff (1983; see Simberloff 1980 [reproduced in this volume] for the weakest of disclaimers). The latter writes, for example, "We are asking if species' individual responses to the physical environment suffice to explain their distributions" (Simberloff 1983). If it can be shown that neither vertical (e.g., predation) nor horizontal (e.g., competition) connections in the food web are very important, then the ecology of single-species populations is sufficient to explain the phenomena of focus in community ecology—species diversity, relative abundances of species, species turnover, and so on. (Notice that almost certainly predation and competition will be shown either both important or both unimportant, as they march in logical lock-step. That is, significant resource competition at one level implies significant predation at the level of the resources and vice versa (Hairston et al. 1960).) In a very literal sense the community then becomes a whole which is entirely the sum of its parts, and the limits that one places on the set of species composing the community become totally arbitrary. This does not mean that community-level phenomena would necessarily disappear from ecological consideration. But it does mean that the theoretical explanation for such phenomena would at best involve large-number concepts such as the central limit theorem—e.g., the log-normal distribution of species abundances results from many independent effects acting multiplicatively on independent populations (May 1975).

A lot of the controversy in present-day community ecology can thus be viewed [as being] about the strong reducibility of community to population ecology, i.e., whether or not species populations are additive or conjunctive. If Simberloff and colleagues can show that species interactions are minor, then community ecology will cease to exist as an interesting theoretical discipline. As is well known among ecologists, many persons, myself included, strongly oppose the view that anything like this has been shown or even that recent research results are headed in that direction (e.g., Schoener 1982; Connell 1983; Quinn and Dunham 1983; Roughgarden 1983; Schoener 1983a; Paine 1984). The only reason the issue is not yet settled is that so little research has been done, relative to the number of existing systems, to make a statistically valid generalization. . . .

In summary of this section, I have argued that a nonevolutionary community ecology is in principle reducible to a nonevolutionary individual ecology via a reduction through population ecology, and that an evolutionary community (and population) ecology is probably in principle reducible to either a nonevolutionary individual ecology plus evolutionary ecology or to an evolutionary individual ecology by itself. Furthermore, I have argued that for certain aspects of the upper-level theory, the reduction is practical and/or has already taken place. Notice that there is nothing but complexity barring the way from systems of equations with many variables being reduced in the same way as [a] logistic equation. . . . For example, we could have many species in a food web rather than a few, and we could be interested in modeling indirect effects (those passing through intermediate species) rather than direct ones—the reduction could in principle still go forward. Moreover, the behavioral complexity focused upon by the non-population-dynamical mechanistic approach could in principle be incorporated into population-dynamical equations. Finally, when there is one equation per species, the sometimes unsatisfactory assumption that all individuals are equal could be taken care of by replacing it with a set of equations for each species, distinguishing (as is often done) age classes, or size classes, or sexes. The resulting complexity, while not being a formal impediment, could of course be a major practical impediment, so that the reduction would contribute little to understanding. We shall return to this possibility. . . .

The Mechanistic Approach as a Research Strategy

Wimsatt (1980a) has written that "the in principle claim of the reductionist is seldom in dispute," and that in the fields he is familiar with, "the issue between scientists who are reductionists and holists is not over the in principle possibility of an analysis in lower-level terms but on the complexity and scope of the properties and analyses required." Whether this is true or false for community ecology (I doubt community ecologists have thought much about it until recently), Wimsatt is certainly correct that, given that reduction is in principle possible, its execution may not be worth the trouble in terms of insights gained or research facilitated. Toward evaluating this possibility, I now discuss the pros and cons of the mechanistic approach to community ecology as (to use Wimsatt's phrase) a "research strategy."

Many advantages of the mechanistic approach have been mentioned above and discussed. . . . For myself, its chief advantage is that it allows a theoretical understanding of how variation in individual-ecological properties—those of behavioral and physiological ecology—affect population and community structure. As Wimsatt (1976a) points out, this would not be so vital were there few exceptions to laws at the macrolevel, or were exceptions homogeneous when translated into microlevel terms. In fact, variation at the community (and population) level is extensive, so much so that rather than exceptions

to a few "laws," it appears that community ecology is a genuinely pluralistic field, with many different "laws," each restricted to a rather narrow domain (Schoener 1985).

There are at least three major consequences of the advantage just discussed. First[,] qualitative predictions about how behavioral and physiological properties affect community and population dynamics and equilibrium become possible. For example, does an energy-maximizing predator stabilize or destabilize a predator-prey relationship? What behavioral traits would result in a population with a leptokurtic utilization distribution? How does metabolic rate affect population growth rate and stability of species interactions?

Second, from an array of possible submodels available for a community (or ecosystem) model, the mechanistic approach suggests which to select. The most appropriate model would not be an issue were all models with roughly similar qualitative properties to behave the same way. But it is becoming obvious that in some major cases, and perhaps in many, they do not. Two relevant examples from community ecology stand out. In the first, Gilpin and Justice (1972) showed that, depending upon whether the zero-isocline of a competition model were linear (Lotka 1956; Volterra 1926) or concave, two *qualitatively* opposite predictions would be made about the outcome of competition in an actual system, two species of *Drosophila.* In fact, the isoclines were in reality concave, and the Lotka-Volterra model gave the incorrect prediction. At a more general level, Turelli (1981) showed that which of three qualitatively similar population-growth functions were used in a stochastic model determined the degree *and direction* of the effect of environmental variation on community stability: one gave a positive effect, one a negative effect, and one no effect! Ecosystem ecologists are also becoming aware of the problem. After citing some examples, Watt (1975: 140), in a spate of disillusionment with ecosystem modeling, wrote:

> What is the meaning of the phrase "a general function which describes this curve is . . . ?" Does it mean that the function was plucked out of thin air as being reasonable, or that it was tested against various sorts of ecological data to ensure that it described reality reasonably well, or that it was the product of some type of deductive process which will be outlined at some later time so as to be completely intelligible? Particularly where the function is new in ecological writings, and the explanation for its origin is not given, the critic is basically trapped in a guessing game with the author.

My suspicion, as also voiced above, is that the first of Watt's alternatives is almost always true, and unfortunately, it appears that this may be no longer good enough. The above examples make me less than optimistic, contra Levins

(1966; see also Wimsatt 1980b), about the robustness of community-ecological models, even regarding small details, much less at the scale he is talking about.

If choice of model or submodel makes a difference, how is one to choose? The answer may well lie with the mechanistic approach: select an appropriate mechanistically derived model, rather than one that is arbitrary or at best purely descriptive. And as a coda, do not hesitate to change models or submodels when the situation changes.

The third consequence is perhaps the most ambitious in its claims, but some outstanding examples of its success exist. It is that the mechanistic approach allows *quantitative* predictions to be made about community structure from behavioral and physiological considerations which can be tested with independently gathered macrolevel data. Four studies illustrating this advantage . . . are briefly reiterated here. First, Belovsky (1984, 1986) fitted by nonlinear regression population data describing competition between moose and hare. The "best-fit" population parameters were then translated into behavioral parameters, via a mechanistic model, and those estimates were compared with independently derived estimates of the behavioral parameters obtained from behavioral-ecological (feeding-strategy) considerations. The two were found to be very close, greatly increasing our confidence in the theory.

Second, Tilman (1976, 1977, 1986) used Michaelis-Menten growth considerations to predict quantitatively the values of nutrient ratios that determine different kinds of competitive outcomes. These predictions were verified with experiments. Third, Abrams (1981) checked his estimates of a competition "coefficient" obtained from a model of shell dynamics with observations of marked shells in the field. Again, the two were very close. Fourth, Spiller (1986) evaluated a mechanistic competition-coefficient formula with field observations, then performed field experiments to measure the coefficient directly. Again, agreement was very good. All four of these studies are extremely powerful, in that they allow two independent assessments of a community-ecological theory. When the two are in agreement, our confidence in the theory is greatly increased.

One might wonder from the rosy picture I have just painted why ecologists have not all boarded the mechanistic bandwagon. I think the basic caution of the dissenters is that this approach may portend an extraordinary degree of complexity when many-species interactions are considered. The complexity could arise in two kinds of places in the theory. First, any particular model, if it is to incorporate enough behavioral or physiological variation, may have to be so complex as to be analytically opaque. Already, a tradeoff in this area is detectable within the mechanists themselves. Those who delete population dynamics from their approach can incorporate more behavioral variation than those who do not. . . . Second, even if individual models are manageable, too

many models, each with a very narrow application, may render the entire theory so massive and arcane that community ecology will become an impossibly esoteric field, unteachable to undergraduates and run mainly by experts in information retrieval. Worse, a theory too composed of special cases may be untestable, at least without intergalactic travel, as the earth may not contain sufficient communities to provide adequate statistical power.

Some ecologists are probably willing to give up a lot of precision and linkage to lower levels if these things can be avoided. Moreover, as Wimsatt (1980a) points out, advocacy of a reductionist approach coincides with emphasizing internal, rather than external, factors when simplification is necessary. Thus mechanistic people will stress behavioral and physiological detail at the expense of, say, food-web detail. Two-species systems rather than many-species systems, and direct rather than indirect effects, will be emphasized. This is already to some extent happening (see contrasts in Diamond and Case 1985, for example).

As pointed out above, it is not that in principle the mechanistic approach is unable to handle phenomena involving numerous population or community-level variables, e.g., numerous species. It is just that in practice, this may be too overwhelming. The hope that computer technology can make any "in principle" actual is dashed by reading Boyd (1972) and Wimsatt (1980a). For example (Wimsatt 1980a), there are approximately 10^{130} possible chess games of one hundred moves, larger by about forty-one orders of magnitude than the number of elementary particles in the universe and by about eight orders of magnitude of the number of physical events between such particles since the "big bang." So there have not been enough actual states to represent the chess game even if the universe since its inception were a computer! Those who have ever contemplated a very microreductionist approach to community ecology, e.g., following the fate of *each* individual (rather than representative individuals) in a set of interactions potentially very much more complicated than chess should be sobered by these calculations. That which is in principle possible may in fact not be physically possible. The mechanistic people, of course, are not advocating such an approach, and their hope is that reduction (in the way I have described it) may actually sometimes lead to meaningful simplification, not greater complexity.

Even for the same degree of complexity (as measured, say, by the number of free parameters in a model), the descriptive approach may be more suitable than the mechanistic one *if description is an end in itself.* That is, it is conceivable that the most descriptive model for a particular case is nonmechanistic, or more likely, that the single model describing a set of cases better than any other is nonmechanistic. Because, as stressed above, ecological phenomena *in toto* rarely fit any single model well, the latter is in my opinion not so likely; an example is found in my own work on habitat shift (Schoener 1974b). This is also why the role of upper-level generalizations in "winnowing out" inappropriate lower-level representations (as suggested by Wimsatt 1976b, footnote 11) is not likely to be conspicuous for population and community ecology even if it were looked for carefully.

A related advantage for nonmechanistic models, especially linear ones, is their typically intimate association with statistical estimation. Again, however, estimation is possible with nonlinear models; it is just more cumbersome. Moreover, if the assumptions of the estimation (e.g., linearity) are far from true, reliability of the estimation is compromised, and a more complicated estimation procedure (or no procedure) may be preferable.

Finally, of course, reduction has to stop somewhere along its downward path. While I have argued that it may often be practical to reduce community and population ecology to individual ecology, would it be sensible to go farther? That is, should we use physiological laws such as the metabolic-rate-to-body-weight function in their simple descriptive form, or should we use a probably more complicated mechanistic version were one available? And if the answer is yes, should we continue through biochemistry, physical chemistry, and physics? If this *reductio ad absurdum* (or *ad nauseum*!) were possible in principle, it would be strangulating in practice. Scientists will place bounds on a train of reductions that are in principle possible when the sequence becomes too long to have explanatory power (Wimsatt 1976b).

Despite occasional bursts of ambitious pronouncement, we are not going to know for a very long time how the balance of advantages and disadvantages will finally fall. But it is amusing, not very risky, and perhaps even a bit inspirational to speculate, which I now do.

A Mechanistic Ecologist's Utopia

What if the mechanistic program realized its wildest aspirations? What would ecology be like then? Here I imagine the characteristics of a mechanistic community ecologist's utopia. I distinguish six such characteristics.

First, the macroparameters of community ecology will be deemphasized. Less use will be found for concepts like "niche overlap," "niche breadth," and indeed even "niche." "Niche overlap," for example, might be represented by an array of more specific concepts, such as Abrams's (1980) competition ratio, Schoener's (1974a) competition coefficient, and so on.

Second, theoretical models will have proliferated, and each will have a rather specific domain. A pluralistic theory will have replaced an attempted universal one. Pluralism will involve specificity at both the organismic and environmental levels, i.e., with respect to the biological traits of the type of organism being

considered (e.g., generation time) and the environmental traits of the community's location (e.g., degree of spatial fragmentation). Elsewhere (Schoener 1985), I have suggested a first list of such traits.

Third, arbitrary models whose sole virtue is mathematical convenience will no longer be acceptable. In order to be used, a model will have to be mechanistically justifiable. It may be that manipulation of such models will require a great deal of mathematical skill with approximations and so on, and perhaps a lot of computer time as well.

Fourth, in both observational and experimental approaches, a greater emphasis will be placed on discovering the mechanism of an interaction or process, not just its existence and strength. The ingenuity required to get at such mechanisms will probably be much greater than that to design the removal or introduction experiments that most of us do today.

Fifth, individual-ecological terms, e.g., those from behavioral and physiological ecology, will commonly appear in designations of kinds of ecological communities. Thus we might have ectothermic communities, semelparous communities, or long-generationed communities.

Sixth, population and community-level hypotheses will be framed in much more precise and obviously testable terms than is presently the case. Perhaps Beckner's (1974) application strategy involving event reduction (see above) will be realized: the "revision of higher-level theory in a manner that facilitates event reduction; that is, the introduction of higher-level descriptions with an eye toward the lower-level explanation of events under those descriptions." The use of quantities and units from behavioral and physiological ecology may bring testability of population- and community-ecological models on a par with that currently possible for, say, feeding-strategy models (e.g., Krebs et al. 1983).

Notice that nothing in this scenario suggests *replacement* of community ecology by individual ecology as a science, despite the prospect of reduction. The phenomena of community ecology will still be of interest[,] although as stressed above, there will be a good deal more unity between the subdisciplines than presently exists. (In this regard, I am supporting Wimsatt's (1976b: 222) view of "interlevel" reduction.)

Of course, as already noted, actualization of the mechanistic program could well falter on complexity and unwieldiness. Exactly what will happen remains to be seen, but we may ask in closing about the effect this and other philosophical analyses might have on the development of community ecology. Will a philosophically self-aware science pursue a different path than one that is philosophically ignorant? Philosophers are sometimes surprisingly self-effacing on this question (e.g., Beckner 1974), and in fact [it] is probably unanswerable; we are participants in an experiment without a control.

CHAPTER 14

The Emergence of Ecology as a New Integrative Discipline

Eugene P. Odum

It is self-evident that science should not only be reductionist in the sense of seeking to understand phenomena by detailed study of smaller and smaller components, but also synthetic and holistic in the sense of seeking to understand large components as functional wholes. A human being, for example, is not only a hierarchical system composed of organs, cells, enzyme systems, and genes as subsystems, but is also a component of supraindividual hierarchical systems such as populations, cultural systems, and ecosystems. Science and technology during the past half century have been so preoccupied with reductionism that supraindividual systems have suffered benign neglect. We are abysmally ignorant of the ecosystems of which we are dependent parts. As a result, today we have only half a science of man. It is perhaps this situation, as much as any other, that contributes to the current public dissatisfaction with the scientist who has become so specialized that he is unable to respond to the larger-scale problems that now require attention. There is a rich literature on hierarchical theory and philosophy which deserves to be read by today's specialists (Koestler and Smythies 1969; Whyte et al. 1969; Pattee 1973). As expressed by Novikoff (1945), there is both continuity and discontinuity in the evolution of the universe. Development may be viewed as continuous because it is never-ending, but also discontinuous because it passes through a series of different levels of organization.

An important consequence of hierarchical organization is that as components, or subsets, are combined to produce larger functional wholes, new properties emerge that were not present or not evident at the next level below. Feibleman (1954) has theorized that at least one new property emerges with each new integrative level of organization. Whatever the emergent rate, we can conclude that results at any one level aid the study of the next level in a set but never completely explain the phenomena occurring at that higher level, which itself must be studied to complete the picture. The old folk wisdom about "the forest being more than just a collection of trees" is indeed the first working principle for ecology. For example, intensive research at the cell level has established a firm basis for the future cure and prevention of cancer at the organism level, and perhaps for genetic engineering at the population level, should we ever choose to experiment in this direction. However, cell-level science will contribute very little to the well-being or survival of human civilization if our understanding of supraindividual levels of organization is so inadequate that we can find no solutions to population overgrowth, social disorder, pollution, and other forms of societal and environmental cancer. This is not to say that we abandon reductionist science, since a great deal of good for mankind has resulted from this approach, and some of our current short-range problems can perhaps be solved by this approach alone. Rather, the time has come to give equal time, and equal research and development funding, to the higher levels of biological organization in the hierarchical sequence. It is . . . the properties of the large-scale, integrated systems that hold solutions to most of the long-range problems of society. Again, Novikoff (1945) expressed it well when he wrote, "Equally essential for the purposes of scientific analysis are both the isolation of parts of a whole and their integration into the structure of the whole. . . . The consideration of one to the exclusion of the other acts to retard the development of biological and sociological sciences."

From *Science* 195 (1977): 1289–93. Notes omitted. Odum's unconventional use of *hierarchal* has been replaced with the more common *hierarchical*.

The New Ecology

The rise of what I have previously called the "new ecology" (E. P. Odum 1964) is—in part, at least—a response to the need for greater attention to holism in science and technology. Since the word *ecology* is derived from the Greek root *oikos* meaning "house," it is an appropriate designation for the study of the biosphere in which we live. However, until quite recently, ecology as an academic subject had a much more limited scope than the name indicated. When I first came to the University of Georgia as a young instructor in 1940, my suggestion that a course in ecology be included in a core curriculum for majors received an exceedingly cold reception. My colleagues of those days confused ecology with natural history and voiced the opinion that no new ideas or principles were likely to be revealed in an ecology course that had not already been covered in courses in taxonomy, evolution, physiology, and other subjects considered to be more basic. As a partial result of this rebuff I decided to write a textbook that would emphasize unique principles that emerge at the supraindividual levels of organization. The first edition of *Fundamentals of Ecology* (E. P. Odum and H. T. Odum 1953; see also 1959, 1971), written in collaboration with my brother, Howard T. Odum[,] was revolutionary in two respects: (i) principles were presented in a whole-to-part progression with consideration of the ecosystem level as the first rather than the last chapter, and (ii) energy was selected as the common denominator for integrating biotic and physical components into functional wholes. As the book passed through two more editions and was translated into other languages, these approaches and viewpoints became generally accepted, not only by professionals, but by the public at large. As the environment-awareness movement began to emerge in 1968, some professional ecologists actually resented the public's use of "their" word, but we welcomed it as a long overdue recognition of holistic concepts. Although *ecology* is frequently misused as a synonym for *environment,* popularization of the subject is having the beneficial effect of focusing attention on man as a part of, rather than apart from, his natural surroundings.

A joint research study on a coral reef by my brother and me in 1954 (H. T. Odum and E. P. Odum 1955) can perhaps serve as an illustration of how ecosystem-level study can reveal emergent properties which tend to be missed in piecemeal study. At Eniwetok Atoll we measured the metabolism of the intact reef by monitoring oxygen changes in the water flow. We also did a detailed trophic analysis as a means of charting major energy flows, and were able to construct an energy budget for the whole system. It became evident from the latter that corals and associated algae were much more closely linked metabolically than had previously been supposed, and that the inflow of nutrients and animal food from surrounding ocean waters was inadequate to support the reef if corals and other major components were functioning as independent populations. We theorized that the observed high rate of primary production for the reef as a whole was an emergent property resulting from symbiotic linkages that maintain efficient energy exchange and nutrient recycling between plant and animal components. Our work created considerable controversy and stimulated a number of investigations. Teams of researchers with expertise in chemistry, microbiology, invertebrate zoology, and other fields descended onto the reefs, but remained loosely united in their interest in testing directly or indirectly basic hypotheses about the reef as an ecosystem. Some theories were verified, others refuted, with the result that today there is a rather good understanding of coral-algal relationships and mineral cycling mechanisms in reef systems (Johannes et al. 1972). We like to think that setting up radical but testable hypotheses at the beginning had much to do with this progress. Scientists work together best when motivated by some common idea, even if—or perhaps, especially if—that idea is controversial.

Do these coral reef discoveries have any significance for urban industrial man? Perhaps they do. The Pacific coral reef, as a kind of oasis in a desert, can stand as an object lesson for man who must now learn that mutualism between autotrophic and heterotrophic components, and between producers and consumers in the societal realm, coupled with efficient recycling of materials and

use of energy, are the keys to maintaining prosperity in a world of limited resources.

Since the study of ecosystems is best carried out by teams of investigators who are united in their objective of seeking to discover the emergent properties of the whole but have different skills and secondary interests, I realized early that it would be necessary to establish some kind of organization to promote such teamwork. At the University of Georgia we established the Institute of Ecology for this purpose and, with the help of outside financial support, we carry out long-term studies. The Sapelo Research Foundation has provided continuous support that enabled us to mount an unhurried study of the Georgia salt marsh estuaries. A long-term contract with the Atomic Energy Commission (now the Energy Research and Development Administration) has provided a similar opportunity for population and ecosystem-level study of terrestrial and freshwater environments on a large area set aside for atomic research along the Savannah River, an area recently designated as the nation's first national environmental research park.

The complex of Georgia salt marshes and estuarine channels belongs to a general class of ecosystems which we have designated fluctuating water-level ecosystems. They are pulse-stabilized by tidal flows which act as energy subsidies that enhance productivity as much as ten times over that which would be achieved without this natural use of tidal power. Because we could document the work potential and, therefore, the value of these estuaries, our findings have been widely used as a basis for formulating laws and other measures to protect the U.S. coastal zone from insidious alterations (Gosselink et al. 1974). This work, along with parallel investigations of other natural landscapes, has led to the recognition of an important class of ecological systems which from the holistic viewpoint may be termed subsidized, solar-powered ecosystems. Human agriculture belongs to this class. We have much to learn from natural systems of this sort since most of our agroecosystems lack stability and tend to behave in a boom-and-bust manner, perhaps because we do not yet understand the network of feedback energy flows necessary to maintain continuous high productivity.

While much of the work at the Savannah River area has of necessity involved piecemeal studies on the effect and environmental fate of radionuclide and thermal discharges from atomic reactors, we did at the onset select ecosystem development as our central or unifying focus. The locale provided an unusual opportunity to observe and experiment with the process of natural ecological succession, and to study the impact of artificial reforestation as well, because hundreds of fields were taken out of cultivation when the atomic energy facilities were constructed in 1952. We theorized that new systems properties emerge in the course of ecological development, and that it is these properties that largely account for the species and growth form changes that occur

(E. P. Odum 1969). The idea that there is a holistic strategy for ecosystem development remains controversial. An alternate theory that species aggregations do not interact as a whole, and that ecological succession can be adequately explained on the basis of competitive exclusion and other species-level processes, has also been vigorously promoted (Drury and Nisbet 1973; Horn 1974). Again, controversy is welcome since disagreement on the "big ideas" is certain not only to generate useful knowledge, but to promote the art and science of both the experimental and analytical approaches.

The somewhat disappointing performance of the U.S. effort [in] the International Biological Program (IBP) can, in hindsight perhaps, be attributed to the fact that unifying theories or concepts were not set up for testing on the onset. Hundreds of investigators with widely different training and expertise were funded and were expected to work together as a team without a clearly defined common denominator (Mitchell et al. 1976). The biome program as a major part of the U.S. effort under the IBP was conceived in a holistic vein, and the idea of studying the totality of major solar-powered natural ecosystems such as grasslands, forests, deserts, tundras, and so forth was a uniquely American concept. But in practice there was a shortfall of integration. For example, in the grassland studies, which received the first and largest funding, there was never any "grassland theory" for the reductionists to rally around. A prodigious effort by a handful of systems ecologists did manage to link some of the fragmented data into something approaching an ecosystem-level model, but even the most sophisticated mathematical models cannot compensate for inadequate planning, uncoordinated data gathering, or, most of all, the lack of [a] central theme.

The new ecology, then, is not an interdiscipline, but a new integrative discipline that deals with the supraindividual levels of organization, an arena that is little touched by other disciplines as currently bounded—that is, by disciplines with boundaries established and strongly reinforced by professional societies and departments or curriculums in universities. Among academic subjects, ecology stands out as being one of the few dedicated to holism. But I do not mean to imply that ecology is emerging by default; other disciplines, including perhaps even economics, as I will note later, are striving to climb upward on the hierarchical ladder.

The Link with Social Sciences

From another context, the new ecology links the natural and the social sciences (E. P. Odum 1975). In the bottom of the Great Depression of the 1930s sociologists began to shift from the dictum that the proper study of man is man (alone) to the idea that the proper study is man in environment. For example, my father, the late Howard W. Odum, directed a major effort within

the Institute for Research in Social Sciences at the University of North Carolina toward development of the concept of regionalism, which he viewed as an approach to the study of society based on the recognition of distinct differences in both cultural and natural attributes of different areas, which, nevertheless, are interdependent (Odum 1936; Odum and Moore 1938). Regional study of social science was widely misinterpreted in those days as being merely an inventory device designed to upgrade "backward" regions so they would contribute to, rather than detract from, the total economy of the nation. Rather, Howard W. Odum envisioned the real goal as the integration of regions, and he hoped that the concept would provide an antidote to divisive sectionalism, which was then spawning bitter economic and political warfare between sections of the nation. To a remarkable extent the philosophy of regionalism did help smooth social and economic transitions in the Southeast, but as a major theory of sociology the concept stalled because there was no appropriate linkage with natural science (applied ecology had not yet emerged to this level of thinking) and because statistical methods of the day were totally inadequate to cope with the mountains of data collected by social science researchers. Now, advances in systems science and electronic data processing promise to alleviate the data processing problem, and we have the new ecology as an improved link with the rest of science.

At the national level, I believe, the current effort to mount a program of research and management for the coastal zone may be the first major test of whether we are yet ready to combine the best of reductionist and synthesis science as a basis for rational decisions. Experience in mounting team research at the ecosystem level suggests that one or more major theories or paradigms that can be tested (and refuted, if possible) must provide a focus if the coastal zone effort—which of necessity must involve local, state, regional, and federal groups—is to be a truly scientific enterprise and not just another series of expensive and frustrating inventories. The tidal subsidy theory and the concept of regionalism stand as two unifying focuses for productive team research in this area.

Since the kind of sectional conflicts which for so long hampered our national development are now appearing on a truly frightening scale in the confrontations between so-called "advanced" and "backward" nations, even a partial success at coastal zone management could have a favorable global impact by demonstrating that action based on holistic values and properties is a viable alternative to development on the basis of competitive exclusion alone.

Technological and Environmental Impact Assessments

The need to raise thinking and action to the ecosystem level is especially evident as the practices of technology assessment and environmental impact analysis assume increasingly important roles in decision-making, especially with regard to public works and energy and industrial development. As a member of the advisory committee of the Office of Technology Assessment (OTA) established by Congress, I can vouch for the fact that there is a serious dichotomy of thinking between those who urge that OTA restrict its work to piecemeal assessment of new technology on the grounds that greater precision can be achieved in this manner, and those who argue for broadening the studies to include environmental, social, and economic aspects on the grounds that a holistic level of assessment is more realistic (Shapely 1973; Decker 1975). The point is that the questions and answers can be quite different depending on the level of assessment. For example, a thoroughly competent study restricted to the technical performance of a fission nuclear reactor could well show that this method of power generation is reasonably safe. Since technologists have stressed safety as *the* limiting factor and the public has logically followed in making safety *the* issue, then a favorable technology assessment of the safety problem would become a powerful signal for government and industry to launch a massive development of this form of atomic energy. Yet a total assessment that includes economic and environmental components (and covers the whole chain of events from mining to waste disposal) might show that as a first-generation attempt to utilize atomic power the light-water fission reactor is badly flawed technology, and thus not yet ready to play a major role in power production, especially where alternatives are available.

In the pages of *Science* the writing of environmental impact statements, as required by the National Environmental Policy Act, has been denounced as a "boondoggle" (Schindler 1976) and defended as a necessary step in the right direction (Peterson 1976). In my opinion, most impact statements, as now almost mass produced, are inadequate because they focus on the wrong level—often, for example, on the species or factor level when the questions and decisions clearly involve the ecosystem level. In other words the practice of environmental impact assessment is not so much bad or inadequate applied science as it is wrong-level applied science, a viewpoint that has not been emphasized in published discussion on the subject. For example, most would agree that important chemical factors such as oxygen concentration and basic biological characteristics such as species composition should be included in a baseline assessment of a body of water. However, a table of dissolved oxygen measurements and a long list of species present, as often included in current impact statements, provide little useful information for assessing the impact of a projected perturbation such as a thermal discharge from a power plant. With little, if any, additional effort in terms of time and money, one can increase the useful information content manyfold by assessing more functional and integrative properties that relate to oxygen and species. By measuring dissolved

oxygen over diurnal cycles, the balance between the two major metabolic processes, photosynthesis and respiration, can be determined; systems-level information of this sort is usable in judging the potential impact of a procedure that might change the temperature of the water, alter the input of organic matter, and so forth. Likewise, arranging species data into a diversity profile reveals how numbers and kinds interact and gives a clue as to the developmental status of the community, thus providing a far better basis for impact assessment than would a mere list of species. Accordingly, environmental impact assessment, as well as technology assessment in general, should move from mere component analysis, wherein factors and organisms are treated as if they were independent entities, to more holistic approaches wherein interactive, integrative, and emergent properties are also included. The "new ecology," of course, must provide the basic theory for this necessary evolution in practice. In the meantime, there is much to be said for a procedure that combines a few carefully selected systems-level properties that monitor the performance of the whole, with selected "red flag" components such as a game species or a toxic substance that, in themselves, have direct importance to the general public (E. P. Odum and Cooley 1977).

Economics and Ecology

The ultimate in a holistic approach to preparing environmental impact statements must involve integration of economic and environmental values. In the real world monetary values are always going to weigh heavily in any decision regarding man's use of his environment. Regrettably, environmental and economic assessments usually are made by different teams or individuals. Not only do these teams rarely communicate with one another, but each also tends to restrict evaluation to its own preconceived narrow world of the natural or man-made environment, respectively, ignoring the fact that it is the interaction between these systems that is of paramount importance. Environmental and economic assessors should work together, or at least the results of study by different groups of specialists should be integrated. There are ways to scale economic and ecologic values which at first might seem incapable of comparison. For example, where alternate choices are involved one can set up a numerical scaling system in which the maximum quantitative value for each component is set at one (or one hundred), and all other values scaled accordingly. These scaled values can then be weighted according to a Delphi or other technique based on consensus of knowledgeable assessors (E. P. Odum et al. 1976). Another approach involves using energy as a common denominator for man and nature (Gosselink et al. 1974; H. T. Odum and E. P. Odum 1976).

If subjects were organized according to the literal derivation of their names, then ecology and economics would be companion disciplines since the words are derived from the same Greek root, with ecology translating as "the study of the house" and economics as "the management of the house." The disciplines remain poles apart on college campuses as well as in the minds of the general public as long as each restricts itself to only a part of the house, nature's and man's part, respectively. As ecologists have begun to take an interest in the man-made environment a few economists, notably Kenneth Boulding, Nicholas Georgescu-Roegan, William Nordhouse, James Tobin, and Herman Daley, have begun talking about an emerging "new economics" that is more attuned to natural laws and that includes a more equitable valuation of the natural environment (see especially Georgescu-Roegen 1971).

A closer liaison between ecology and economics makes good sense because in so many cases actions which benefit the general environment also benefit the general economy in the long term. It is in the short term, especially the two- to four-year electoral cycle of political action, where the most recalcitrant conflicts occur. Take, for example, strip-mining for coal or other earthbound resources. In the short-term view government should encourage and subsidize rapid exploitation of the resource and place few, if any, restrictions on strip-mining on the theory that the national economy would quickly benefit from a substitution of domestic coal for imported oil. In the long-term view just the opposite would be indicated, namely, that careful, well-planned mining, including mandatory land rehabilitation, is in the best interest of both the economy and the environment. Land valuable for food production, recreation, and life support would be preserved or restored. The steady, moderate production of coal would ensure that energy conservation would be pursued while air pollution and other threats to health would be less likely to get out of hand. New industry and towns would have a long life in contrast to local booms and busts that generally accompany unrestricted mining. Water, which is required in huge quantities to use or process coal, would be less likely to be squandered. Otherwise, dry-country cities such as Los Angeles and Phoenix might have to use all the newfound energy to obtain water, with a probability of net economic loss. As the ecologist might say, it is the secondary impacts that will get you if you do not consider the whole. Best of all, the long-range scenario would ensure that the nation has coal long after the easily obtainable Mideast oil is gone, thus making us less dependent and more secure in terms of national defense.

Politics and Ecology

Finally, there is yet another divided world, the scientific and the politico-legal spheres of action, where holistic thinking might help. In a recent editorial in *Science* Gerald Edelman expresses pessimism that these two disciplines will ever intersect, and states that we are left with "two extreme ideological positions—scientism and anti-scientism" (Edelman 1976). As long as students and practitioners of both disciplines insist on fragmenting their subjects, rigidly adhering to their own way of thinking and calling each other derogatory names, adversary interaction will continue to predominate. I am much more optimistic about the integration of these spheres because I have found that a meeting of minds in study panels and public commissions begins with the general acceptance of the idea that large-scale problems and issues might have common denominators that could be assessed along with the more narrowly defined scientific, political, or legal aspects. If hierarchical theory is indeed applicable, then the way to deal with large-scale complexity is to search for overriding simplicity. Sometimes, it appears, this turns out to be old-fashioned common sense. As noted, the dichotomy inherent in short and long time spans imposes a major stumbling block in acting on common sense judgment.

In summary, going beyond reductionism to holism is now mandated if science and society are to mesh for mutual benefit. To achieve a truly holistic or ecosystematic approach, not only ecology, but other disciplines in the natural, social, and political sciences as well must emerge to new hitherto unrecognized and unresearched levels of thinking and action.