

DIALECTICS AND REDUCTIONISM IN ECOLOGY

The philosophical debates which have accompanied the development of science have often been expressed in terms of dichotomous choices between opposing viewpoints about the structure of nature, the explanation of natural processes, and the appropriate methods for research:

Are the different levels of organization such as atom, molecule, cell, organism, species, and community only the epiphenomena of underlying physical principles or are the levels separated by real discontinuities? Are the objects within a level fundamentally similar despite apparent differences or is each one unique despite seeming similarities? Is the natural world more or less at equilibrium or in constant change? Can things be explained by present circumstances or is the present simply a reflection of the past? Is the world causal or random? Do things happen to a system mostly because of its own internal dynamic or is causation external? Is it legitimate to postulate hypothetical entities as part of scientific explanation or should science stick to observables? Do generalizations reveal deeper levels of reality or destroy the richness of nature? Are abstractions meaningful or obfuscatory?

As long as the alternatives are accepted as mutually exclusive, the conflict remains one between mechanistic reductionism championing materialism, and idealism representing holistic and sometimes dialectical concerns.

It is also possible to opt for compromise in the form of a liberal pluralism in which the questions become quantitative: how different and how similar are objects? What is the relative importance of chance and necessity? Of internal and external causes (e.g., heredity and environment)? Such an approach reduces the philosophical issues to a partitioning of variance and must remain agnostic about strategy.

When we attempt to chose sides retrospectively, we find that it is

not possible to be consistent: we side with the biologists who opposed theological idealism in insisting upon the continuity between our species and other animals or between living and nonliving matter. But we emphasize the discontinuity between human society and animal groups in opposition to various 'biology is destiny' schools.

As long as we accept the terms of the debate between reductionism and idealism, we must adopt an uncomfortably *ad hoc* inconsistency as we see now one side, now the other advancing or holding back science. Simberloff's essay (1980) seems to us to embody the false debate by being based on three fundamental common confusions. These are: the confusion between reductionism and materialism, the confusion between idealism and abstraction, and the confusion between statistical and stochastic. As a result of these confusions, Simberloff, in his attempt to escape from the obscurantist holism of Clements' 'superorganism,' falls into the pit of obscurantist stochasticity and indeterminism. For if one commits oneself to a totally reductionist program, claiming that *in fact* collections of objects in nature do not have properties aside from the properties of these objects themselves, then failures of explanation must be attributed ultimately to an inherent indeterminism in the behavior of the objects themselves. The reductionist program thus simply changes the locus of mystification from mysterious properties of wholes to mysterious properties of parts.

We will discuss these three confusions, and some subsidiary ones, in order to outline our disagreements with Simberloff, but also to develop implicitly a Marxist approach to the questions that have been raised. Dialectic materialism enters the natural sciences as the simultaneous negation of both mechanistic materialism and dialectical idealism, as a rejection of the terms of the debate. Its central theses are that nature is contradictory, that there is unity and interpenetration of the seemingly mutually exclusive, and that therefore the main issue for science is the study of that unity and contradiction rather than their separation either to reject one or to assign relative importance.

REDUCTIONISM AND MATERIALISM

The confusion between reductionism and materialism has plagued biology since Descartes' invention of the organism as a machine. Despite the repeated demonstrations in philosophy of the errors of vulgar reductionism, practicing biologists continue to see the ultimate objective of the study of living organisms to be a description of phenomena entirely in terms of individual properties of isolated objects. A recent avatar is Wilson's (1978) claim that a scientific materialist explanation of human society and culture must be in terms of human genetic evolution and the Darwinian fitness of individuals.

In ecology, reductionism takes the form of regarding each species as a separate element existing in an environment that consists of the physical world and of other species. The interaction of the species and its environment is unidirectional: the species experiences, reacts to, and evolves in response to its environment. The reciprocal phenomenon, the reaction and evolution of the environment in response to the species, is put aside. While it is obvious that predator and prey play both the roles of 'organism' and 'environment,' it is often forgotten that the seedling is the 'environment' of the soil in that the soil undergoes lasting evolutionary changes of great magnitude as a direct consequence of the activity of the plants growing in it, and in turn feeds back on the conditions of existence of the organisms. But if two species are evolving in mutual response to each other or if plant and soil are mutually changing the conditions of each other's existence, then the ensemble of species or of species and physical environment, is an object with dynamical laws that can only be expressed in a space of appropriate dimensionality. The change of any one element can be followed as a projection on a single dimension of the changes of the n-tuple, but this projection may show paradoxical features including apparent lack of causality, while the entire ensemble changes in a perfectly regular manner. For example, a prey and predator will approach an equilibrium of numbers by a spiral path in the two dimensional space whose axes are the abundances of the two species. This path is completely unambiguous in

the sense that given the location of a point in two dimensional space at one instant of time, a unique vector of change can be established predicting its position at the next instant. Each of the two component species, however, is oscillating in abundance so that given only the abundance of the predator, say, its impossible to know whether it will increase or decrease during the next interval. The description of change of the n-dimensional object may then itself be collapsed onto some new dimension, for example, distance from the equilibrium point, which again may behave in a simple monotonic and predictable way. The rule of behavior of the new object is not an obscurantist holism but a rule of the evolution of a composite entity that is appropriate to that level of description and not to others. In the specific case just given, neither the prey nor the predator abundances converge monotonically to their final equilibria, and the monotone behavior of the pair object is not predictable from the separate equations of each species. Moreover, the separate behavior of each species is not itself predictable from the form of their separate equations of motion, since neither of these equations is intrinsically oscillatory and the damped oscillation of the two species is a consequence of their dynamic coupling.

The Clementsian superorganism paradigm is indeed idealist. Its community is the expression of some general organizing principle, some balance or harmony of nature. The behavior of the parts is wholly subordinated to this abstract principle, which causes the community to develop toward the maximization of efficiency, productivity, stability, or some other civic virtue. Therefore, a major priority would be to find out what does a community maximize.

Having correctly identified the Clementsian superorganism as idealist, Simberloff then lumps with it all form of 'systems modelling.' But the large-scale computer models of systems ecology do not fit under the heading of 'holism' at all. Rather they are forms of large-scale reductionism: the objects of study are the naively given 'parts' – abundances or biomasses of populations. No new objects of study arise at the community level. The research is usually conducted on a single system, a lake, forest, or prairie, and the results are

measurements and projections for the same lake, forest, or prairie without attempting to find properties of lakes, forests, or prairies in general. It requires vast amounts of data for its simulations, and much of the scientific effort goes into problems of estimation. We agree with Simberloff that this approach has been generously supported and singularly unproductive.

Idealism and reductionism in ecology share a common fault: they see 'true causes' as arising at one level only with other levels having only epistemological but not ontological validity. Clementsian idealism saw the community as the only causal reality with the behaviors of individual species populations as the direct consequence of the mysterious organizing forces of the community. One might *describe* the community for some purpose by a list of species abundances, but that description was of epiphenomena only. Reductionism, on the other hand, sees the individual species, or ultimately the individuals (or cells, or molecules, for there is no clear stopping place in the reductionist program), as the only 'real' objects while higher levels are again descriptions of convenience without causal reality. A proper materialism, however, accepts neither of these doctrinaire positions but looks for the actual material relationship among entities at all levels. The number of barn owls and the number of house mice separately are important causal factors for the abundance of their respective competitors and are material realities relevant to those other species, but the particular combination of abundances of owls and mice is a new object which is a material cause of the volume of owl pellets and therefore of the abundance of habitat for certain bacteria.

THE COMMUNITY AS A DIALECTICAL WHOLE

Unlike the idealist holism which sees the whole as the embodiment of some ideal organizing principle, dialectical materialism views the whole as a contingent structure in reciprocal interaction with its own parts and with the greater whole of which it is a part. Whole and part do not completely determine each other.

The community in ecological theory is an intermediate entity, between the local species population and biogeographic region, the locus of species interactions.

The region can be visualized as a patchwork of environments and a continuum of environmental gradients over which populations are distributed. A local community is linked to the region by the dynamics of local extinction and colonization. Local extinction depends on local conditions affecting the populations in question. Colonization depends on the number of propagules (seeds, eggs, young animals) the local population sends out, which depends on the population size achieved locally. It also depends on the behavior of these propagules, their ability to cross the gaps between suitable habitats, their tolerance of conditions along the way, and their capacity to establish themselves (anchor on the the new substrate, grow under the shade of established trees, defend an incipient ant nest). These properties are biological characteristics of the individual species which are not directly responsible for abundance and survival in the local community. Finally, colonization depends on the pattern of the environmental mosaic – the distance between patches and whether the patches are large or small, the structure of the gradients (whether different kinds of favorable conditions are positively or negatively associated). These biogeographic properties are not implicit in the dynamics of the local set of species.

The whole ensemble of species of a region depends on the origin of the biota, the extinction of species in the whole region, and the processes of speciation.

Therefore, the biogeographic level gives us a dynamic of extinction, colonization, and speciation in which the parameters of migration and extinction are givens, partly dependent on local dynamics but not contained therein.

Below the community are the component species populations. They enter the community at a rate which depends on their abundance in other communities, in the region as a whole. But once in the locality their abundance, persistence, variability and sensitivity to environmental variability depends on their interactions with other species and on the parameters of their ecology – birth rate, food and microhabitat

preferences, mobility, vulnerability to predators, physiological tolerances which come from their own genetic makeup. The genetic makeup in turn is a consequence of the processes of selection, mutation, drift, and gene exchange with other populations of the same species, which form the domain of population genetics and reflect past evolutionary history. The other members of the community affect the direction of natural selection within the community and therefore influence these parameters, but they are not deducible from the general rules of community ecology.

Thus the claim that the ecological community is a meaningful whole rests on its having distinct dynamics—the local demographic interactions of species against a background of biogeographic and population genetic parameters.

From this point of view the question which Simberloff considers to be of great importance—whether communities exist as discrete entities or are abstracted from a continuum of variation—loses its significance. Population genetics has also had to deal with the question of whether to treat a species as a single interbreeding population with non-random mating, a series of discrete “demes” with exchange of migrants, or a one, two, or three dimensional continuum with a diffusion process, gene flow and local selection producing patterns of isolation by distance. The solution is usually one of convenience: if the rate of migration between habitats is very low, we use the laws of local population genetics and correct for migration. As the movement of genes increases, we have the models of patchy environments, multiple niches, etc., with random mating then corrected by some inbreeding coefficient.

Similarly, if a patch of habitat is large enough so that interactions are mostly within the patch and the probability of members of different species encountering each other closely enough for mutual influence is proportional to their abundances, we can treat the ensemble as a community with correction for migration. If the patches of habitat are small compared to the range of interaction and propagation then a within-patch model will not work, and it is better to conceive of the community as itself a mosaic of habitats.

On small islands, the terrestrial community is bounded from the

aquatic one in a sharp way which allows the models of island biogeography to ignore the distinction between island and community and treat each island as a community. On continental areas or large islands, the internal structure of the terrestrial habitat is more important but boundaries among communities less clear. Nevertheless, the island biogeography approach to distributions of organisms has been a fruitful one and usually picks out as "islands" pieces of habitat that may be regarded as communities.

Simberloff makes three assertions about these distributions: (a) organisms tend to have continuous distributions without abrupt boundaries; (b) different species' boundaries do not usually coincide, preventing the identification of discrete communities; and (c) when (a) and (b) are violated, there is usually some discontinuity in the physical environment.

The question of the boundaries of communities is really secondary to the issues of interaction among species. There is nothing inherent in the community concept which excludes physically determined boundaries. However, the insistence on a one-to-one correspondence between physical and biotic distributions makes it more difficult:

(a) To recognize the very rich patchiness of nature, especially for smaller organisms.

(b) To allow for threshold effects. For instance, a continuous environmental gradient can change the relative frequency of a plant species, precluding the maintenance of its own herbivores and building an alternative insect community.

(c) To examine the structure of environment. While in some ways plants ameliorate severe environmental conditions and smooth over differences, they also create new kinds of environmental heterogeneity. The patchiness of the ant species mosaic described by Leston (1973) and also observed elsewhere reflects the amplification of small environmental differences into more pronounced patchiness.

(d) To cope with alternative communities. As a limiting case, the species which is established first in a site may exclude colonists of other species. This takes place because competition is occurring between established, mature adults of one species and the propagule of the other. This life cycle difference may often outweigh differences

in physiological responses to environment. Then physiological differences may affect the frequency with which a patch of a given type is occupied by one species or the other, and a reductionist view would lose the competitive excursions once it found the environmental correlation.

This situation obtains in the interaction of the neotropical fire ant *Solenopsis geminata* and the introduced cosmopolitan *Pheidole megacephala*. Both are omnivorous, aggressive, and form large colonies. *Pheidole* is less tolerant of heat than *Solenopsis* but is more able to nest and forage in trees. They are almost completely mutually exclusive on small islands where the established mature colonies prevent successful colonization by the other. But on large islands, where patches of mature colonies come in contact, the outcome depends more on their ecological differences. Each species is also associated with other ants, making the alternative patches more than a single species substitution.

Other differences – the polymorphism of *Solenopsis* vs. the clearcut dimorphism of *Pheidole*, the polygynous *Pheidole* colonies vs. the single-queen fire ant colony – are external to the present context, and represent effectively random intrusions into the system.

Thus the notion of multiple alternative steady states of communities is a natural consequence of the recognition of biological complexity, not the *ad hoc* patching of a dying paradigm as Simberloff claims.

Our view, a dialectical materialist approach, assigns the following properties to the community:

1. The community is a contingent whole in reciprocal interaction with the lower and higher level wholes, and not completely determined by them.
2. There are properties at the community level which are definable for that level and which are interesting objects of study regardless of how they are eventually explained. Among such properties are diversity, equability, biomass, primary production, invasibility, and the patterning of food webs. What makes these objects interesting is first that they appear as striking (tropical as against temperate diversity, the invasion of oceanic islands by cosmopolitan species, the rapid

overgrowing of abandoned fields) and demand explanation; secondly that they seem to show some kind of regularity geographically; or finally that they have been invoked to account for some of the previously given properties and are then seen to have their own curious features (e.g., Joel Cohen's claim that food webs often correspond to interval graphs). This is the weak form of the community paradigm since it makes no claims as to the locus of explanation.

3. The properties of communities and the properties of the constituent populations are linked by many-to-one and one-to-many transformations.

Many-to-one-ness means that there are many possible configurations of populations which preserve the same qualitative properties at the level of the whole. This allows communities to be seen as similar despite species substitutions, and allows wholes to persist over time although the individual parts are constantly changing. Not all many-to-one relations are obvious: the discovery of those community measures which are many-to-one functions of the component species is one of the major tasks of community ecology. Lane (1975) found that some of these measures for zooplankton communities persist over time, differ systematically among lakes, and change with eutrophication.

A second consequence of many-to-one relations is that it is not possible to go backward from the one to derive the many. Thus laws at a community level expressed as some persistent properties act as only weak constraints on the parts. From the perspective of the community, there are many degrees of freedom for the species populations and these have the aspect of randomness with respect to community levels.

The one-to-many relation of parts to wholes reflects the fact that not all properties of the parts are specified by rules at the level of these parts. For instance, the habitat may specify that all the species must be able to tolerate or avoid extreme heat. Whether this is accomplished by physiological tolerance, behavioral versatility in finding and staying in the cool spots, or dormancy during the hot season is not deducible from the fact of heat but depends on the past evolution of the species, yet will be of great importance in determin-

ing species interactions. And the mobility of the animal is not directly related to the habitat but will affect its geography.

Therefore, one-to-many-ness is seen as an indeterminacy or randomness of the higher level with respect to the lower.

Together, the many-to-one and one-to-many couplings between levels determine both the emergence of persistent features characterizing communities and also guarantee that different examples of the same kind of community will be different. Looked at over time, they allow us to see the unity of equilibrium (persistence) and change, determination and randomness, similarity with difference.

Things are similar: this makes science possible. Things are different: this makes science necessary. At various times in the history of science the important advances have been made either by abstracting away differences to reveal similarity or by emphasizing the richness of variation within a seeming uniformity. But either choice by itself is ultimately misleading. The general does not completely contain the particular as cases; the empiricist refusal to group, generalize, and abstract reduces science to collecting if not specimens then examples. We argue for a strategy which sees the unity of the general and the particular through the explanation of patterns of variation which are themselves higher order generalities that in turn reveal patterns of variation.

4. The interchange of law and constraint.

Scientific explanation within a given level or context is often the application of some law within constraints of some initial or boundary conditions. These constraints are external to the domain of the law and of no intrinsic interest. Thus a physics problem might be posed as "given a string 15 centimeters long, at what frequencies will it vibrate?" Nobody asks why the string is 15 centimeters long. The interesting phenomenon is the relation among the frequencies. Similarly, from the point of view of biophysics, the particular configurations of molecules and membranes in a cell are the boundary conditions within which the laws of thermodynamics happen to be operating: biophysics is the study of the operation of physical laws in some rather unusual conditions presented by living things. But from the viewpoint of cell biology, the configurations of molecules

and membranes are precisely the objects of interest. The questions concern their formation, maintenance, function, and significance. The laws of thermodynamics and conservation are now the constraints within which cell metabolism and development take place.

This interchange of law and constraint also characterizes the population-community relation.

From the perspective of the population genetics of each single species in the community, 'environment' consists of the physical conditions and those other species which impinge on it directly. The other members of the community are relevant only insofar as they affect the immediately impinging variable, but their influence is indirect and does not enter the equations of natural selection. The directly impinging variables act as determinants of 'fitness.' In general we expect that those genotypes which survive or reproduce more than other genotypes will increase in frequency, thus changing the parameters of the life table and ecology of the population.

But from the perspective of the community, the genetically determined parameters of reproduction, survival, feeding rates, habitat preferences, and species interactions are givens, the constraints within which the dynamics of population change operate. These dynamics depend very sensitively on the structure of the community. They lead to conclusions of the following kinds: the more strongly the feeding preferences of species overlap, the less uniform will be their relative abundances, and the greater the fluctuations over time; nutrient enrichment in lakes will be picked up mostly as increase in the inedible species of algae; environmental variation entering a community at the bottom of the food web generates positive correlations among species on adjacent levels, but variation entering from above generates negative correlations; populations which are preyed upon by a specialist will be buffered against changes arising elsewhere in the system and will respond through their age distribution more than through total numbers. Note that these results take the structures as given, without inquiring as to the origins of specialists, inedible species, or perturbations from above and below.

The looseness of the coupling of population genetic and community

phenomena prevents the complete absorption of the one into the other and requires instead the shifting between perspectives. It therefore precludes both the mechanistic reductionism and idealist holism.

5. The species of a community interact. This may be direct as in the predator/prey relation, symbiosis or aggression, or it may be indirect through the alteration of their common environment; immediately through impact on each others' abundance, age distribution, and physiological state or over evolutionary time by determining the conditions of natural selection acting on each one.

This claim would seem to be obvious enough not to require stating. However, Simberloff cites with approval the view that "the spatial distribution of plants ... (is) ... a consequence of the individual, relatively uncoordinated responses of individual species to gradients in the physical environment ..."

If that were true, we would expect to find (a) a species is most abundant where the physical environment is closest to its physiologically optimum conditions; (b) if all species but one are removed from a physical gradient, that one would increase but its relative abundance would remain unchanged; (c) species should succeed each other in time or space in the same direction as their physical tolerances.

These expectations have not been tested systematically, but cases are known where it is not true. For example Dayton (1975) studied the distribution of the alga *Hedophyllum sessile*. The optimum physiological conditions for maximum growth occur where there is greatest exposure to wave action, but in fact it is found only sporadically as a fugitive in such places and is dominant in areas of moderate exposure. Grassle and Grassle (1974) discussed the recolonization by polychaete worms of a bottom area depopulated by oil spill. In terms of physiological tolerances *Nereis succinea* should have come in before *Capitella capitata*, but the reverse was true.

There are many cases of species such as the brine shrimp reaching its greatest abundance where it can escape predators despite increased physiological stress, or of plants which are normally restric-

ted to certain soil types becoming ubiquitous on islands in the conditions of reduced competition, or the species composition of a pasture depending on the grazing pattern.

Finally, we note that the asymmetry of the predator/prey relation makes it impossible for both species to be most abundant where their interaction is most favorable: if the predator is most abundant where its food supply is most favorable, then the food supply (prey) species is most common where it suffers greatest predation. Or if the prey is at its highest levels where the predator is absent, then the predator is most common where the food supply is not optimal.

However, even where the abundance of a population correlates well with physical conditions, this is not evidence that species are distributed independently of each other. Here we come to one of the major harmful consequences of the individualistic approach to species distribution and abundance: it counterposes the biotic and abiotic factors of a species' ecology, and treats physical factors as statistical 'main effects' with relative weights.

In contrast, the community view is not that other species are more important than physical factors but rather that there is a mutual interpenetration of the physical and biotic aspects, that the ecological significance of physical conditions depends on relations with other species, that the strong interactions among the components of a community make the components of variance approach misleading, and gives spurious support to the original bias.

Consider as an example the distribution of the harvester ants of the genus *Pogonomyrmex* in western North America. Their eastern boundary falls between the 18" and 24" rainfall lines, identifying them as ants of arid and semi-arid regions. Yet these conditions are quite severe for the ants: the temperature at the surface of the soil often gets into the 50's celsius, and the ants, which normally cease foraging in the upper 40's, have only a few hours a day available for gathering seeds. Experimental shading or watering of their nest area extends their activity period and food intake. However, it also permits increased activity by the aggressive fire ants (*Solenopsis* species) and competitors. The habitat requirement is first of all that there be a

sufficient time span available for foraging when it is too hot for the other ants but still tolerable to *Pogonomyrmex*.

Aridity affects the ant distribution in several ways: dry air shows a very steep vertical temperature gradient in the sun, permitting the acceptable temperature range to occur; in arid habitats vegetation is sparser so that more surface is exposed; a greater proportion of plants of arid regions have dormant seeds which can be stored more easily, while dry air reduces spoilage in storage; the predators of the ants – spiders, lizards, wasps – and the competitors – birds, rodents, other ants – also have their own climatic relations that are equally complex. The net result of these interactions is indeed a boundary correlated with rainfall, but to assert that therefore the distribution of the harvest ant is determined by physical conditions is to eliminate the richness of ecology in favor of a statistical correlation.

Simberloff does not insist on physical determination exclusively. He will allow the importance of two or three other species. But here again the same issues arise: first, a strong correlation with another species is not sufficient grounds for assigning it causal predominance; second, if it is indeed the major cause of a species' abundance this must itself be explained by its position in the community.

6. The way in which a change in some physical parameter or genetic characteristic of a population affects the populations in community depends both on their individual properties and the way the community is structured.

This is perhaps the critical claim of community ecology. It is not the assertion that all components are equally important or that what happens is the result of some superorganismic imperatives.

It is a necessary consequence of species interactions, relatively independent of how those interactions are described. Despite Simberloff's misunderstanding of it, it certainly does not depend on the assumptions of the logistic model. If species do interact, then community structure determines the consequences of the interaction; and if the outcome were to turn out to be deducible only from the unit interactions themselves, this would not constitute a refutation of the role of community structure but rather would reveal a remarkable

behavior of that structure which would have to be accounted for.

One way of representing community structure is by a graph in which the vertices are variables in the system, the lines connecting them interactions identified only by sign: \longrightarrow for positive effect and $\longrightarrow\bigcirc$ for negative effect. The mathematical procedures are given in Levins (1975). The technical problems associated with identifying the appropriate graph are not relevant to its use here: the demonstration that community structure determines what happens in communities, that these qualitative results do not depend on the fine details of population level interactions but only on a few many-to-one qualitative properties.

This particular approach deals with systems in a moving equilibrium. More recent work shows that many but not all the results can be extended to more general situations, and that even where the particular results are different the relevant result – that the response depends on community structure – still holds.

Experimental verification of some of the predictions of this analysis was provided in the recent experiments of Briand and McCauley (1978).

In the graphs of Figure 1, we show some hypothetical communities of a few species. The corresponding table shows the direction of change in each variable when some parameter change enters the system in such a way as to increase the variable shown in the first column.

Figure 1a is a simple nutrient/consumer system. Any increase in the input of nutrient to the system is completely taken up by the consumer, but a change in conditions affecting the survival of A affects A and N in opposite directions, generating a negative correlation between them.

In Figure 1b, A is density-dependent in some way other than by consumption of N. Now changes in N are absorbed both by N and A in the same direction. The correlation between N and A depend on the relative magnitudes of variation entering from above and from below.

In Figure 1c, A is consumed by H. Now A no longer responds to changes in N, which are passed on to H. (Although the population

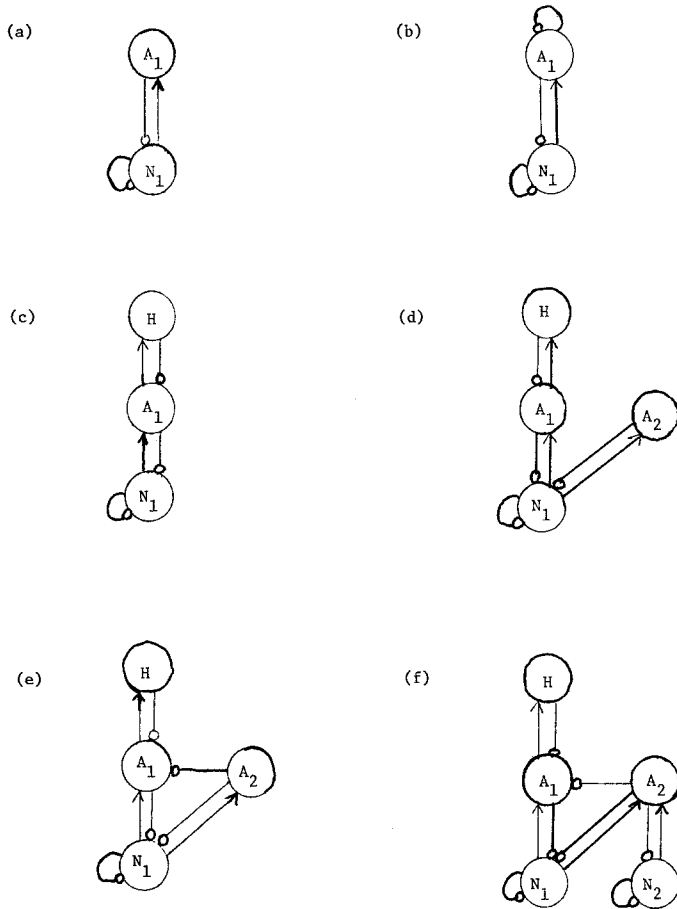


Fig. 1. Graph representation of community structure.

level of A is unaffected, its turn-over rate and age distribution are altered.) Once again we observe that change from above generates positive correlation.

Figure 1d introduces a second, inedible consumer. A_2 picks up all the effect of changing the input of N , leaving A_1 and H relatively insensitive.

In Figure 1e, the second consumer, A_2 , also inhibits the growth of A_1 (perhaps by secreting a toxin, as in the case of blue-green algae).

The effect of this change in graph structure is seen only in the impacts on H of variation entering the system via N_1 or H.

Finally, Figure 1f introduces a second nutrient consumed only by A_2 . This alters the responses of N_1 to parameters entering the system at N_1 or H and introduces ambiguities into the responses of H.

An examination of the graph models of Figure 1 and the consequences of parameter change derived from them in Table I show the following:

(a) The response of a species to the direct impact of the external environment depends on the way that species fits into the community. Species A_1 responds differently to direct inputs or changes in N_1 in

TABLE I The direction of response of community variables to parameter changes entering the system at different nodes. The responses are those of a slowly moving equilibrium after transient effects are damped.

Model	Change entering through	effect on:				
		N_1	N_2	A_1	A_2	H
a	N_1	0		+		
	A_1	-		+		
b	N_1	+		+		
	A	-		+		
c	N_1	+		0		+
	A	0		0		+
	H	+		-		+
d	N_1	0		0	+	0
	A_1	0		0	0	+
	A_2	-		0	+	-
	H	0		-	+	0
e	N_1	0		0	+	-
	A_1	0		0	0	+
	A_2	-		0	+	-
	H	0		-	+	-
f	N_1	+	-	0	+	?
	N_2	-	+	0	+	-
	A_1	0	0	0	0	+
	A_2	-	-	0	+	-
	H	+	-	-	+	?

Figure 1a and 1b from its response in all other graphs, and H responds in opposite ways to the same physical impact in 1c and 1e.

(b) Some species respond to changes arising almost anywhere in the system (A_2 , H) while A_1 is insensitive to most inputs, responding only to the changes arising in H wherever H is present. This might be misinterpreted as insensitivity to the environment or resource changes, or be taken as evidence of lack of competition with A_2 , but is really due to H playing the role of a sink that absorbs impacts reaching A_1 from elsewhere.

(c) Some species (A_2 , H) affect most other variables in the community, whereas changes entering through A_1 are observed only in changes in H. Thus the graph analysis supports the observation that one or two species may dominate the community, but gives a completely different explanation.

(d) A change in the structure of a community may be detectable not at the point of change but elsewhere. The difference between models (d) and (e) is only in the A_2 —○ A_1 link, but the effects are seen only in the response of H to changes entering at H or N_1 .

(e) In table 1f we see that changes in parameters produce correlated responses in the variables of the system, and that the same pair of variables may have positive or negative correlations depending on where the variation enters the system (see the relation of A_2 to N_1 and N_2 , of N_1 with N_2 , and H with N_2).

(f) Parameter changes may be the result of natural selection. In general, the response to selection is to increase a parameter having a positive input to a variable. But this positive input may have positive, zero, or negative effects on the population size: population genetics alone does not determine the demographic response to selection. But since population size does affect the numbers of migrants sent out to colonize new sites, there is a discontinuity between population genetic and biogeographic processes that can be bridged only by specifying community structure.

(g) The notion of a species being of critical importance or dominant has at least three different meanings: H may be the major cause of death of A_1 or only minor; N_2 may be the main food for A_2 or only a supplement. That in itself does not determine whether A_1 responds to

changes in H , A_2 to changes in N_2 . Nor does it answer the question of whether a species is critical to the structure in the sense that for example the addition of N_2 in model 1f changes the response of N_1 to its own parameters and to A_2 .

(h) The graph analysis opens up new possibilities for research strategy: in 1f it indicates where measurements are needed; consequences of parameter change which are concordant across models are robust results insensitive to details of the models; where different models give different results we are directed to the critical observation for deciding among them.

This dialectical approach to the ecological community allows for a greater richness than the reductionist view. It permits us to work with the relative autonomy and reciprocal interaction of systems on different levels, shows the inseparability of physical environment and biotic factors, and the origins of correlations among variables, makes use of and interprets both the many-to-one relations that allow for generalization and the one-to-many that impose randomness and variation.

Where particular techniques are unsatisfactory, the remedy is likely to be not a retreat from complexity to reductionist strategies but a further enrichment of the theory of complex systems.

ABSTRACTION AND IDEALISM

It is Simberloff's view that abstractions are a form of idealism and that the materialism in science necessarily overthrows abstraction and replaces them with sort of 'real' entities which are then each unique, because of the immense complexity of interacting forces on each and because of the underlying stochasticity of nature. However, he cannot really mean that all abstractions are to be eliminated or else nothing would remain but chronicles of events. If any causal explanations are to be given, except in the trivial sense that an historically antecedent state will be said to be the cause of later ones, then some degree of abstraction is indispensable. There is no predictability or manipulation of the world possible except that events can be grouped into classes, and this grouping in turn means that unique

properties of events are ignored and the events are abstracted. Thus, we can hardly have a serious discussion of a science without abstraction. What makes materialist science is that the process of abstraction is explicit and recognized as historically contingent within the science. Abstraction becomes destructive when the abstract becomes reified and when the historical process of abstraction has been forgotten so that the abstract descriptions are taken for descriptions of the actual objects.

The level of abstraction appropriate in a given science at a given time is an historical question. No ball rolling on an inclined plane behaves as an ideal Newtonian body, but that in no way diminishes the degree of understanding and control of the physical world that we have acquired from Newtonian physics. Newton was perfectly conscious of the process of abstraction and idealization that he had undertaken, and he says in the *De Motu Corporum*:

Every body perseveres in its state of rest, or of uniform motion in a right line, unless it is compelled to change that state by forces impressed thereon.

Yet Newton points out immediately that even “the great bodies of the planets and comets” have such perturbing forces impressed upon them and that no body perseveres indefinitely in its motion.

On the other hand, the properties of falling bodies that have been abstracted away are replaced when necessary; Newton himself, in later sections of the *Principia*, considered friction and other such forces. Landing a space capsule on the moon requires the physics of Newtonian ideal bodies moving in vacuums for only part of its operation. For other parts, an understanding of friction, hydrodynamics, and aerodynamics in real fluid media must be involved. Finally, there are correction rockets, computers and human minds to cope with the idiosyncracies of actual events. No space capsule could land on the moon without Newtonian abstractions nor solely with them. The problem for science is to understand the proper domain of explanation of each abstraction rather than becoming its prisoner.

The argument given by Lewontin (1974) that Darwin and Mendel represented a materialist revolution in biology was not based on the assertion that they overthrew *abstractions* but that they overthrew

Platonic ideals. Darwin's and Mendel's works are filled with abstractions (species, hereditary factors, natural selection, varieties, etc.). The error of idealism is the belief that the ideals are unchanging and unchangeable essences that enter into actual relationships with each other in the real world. Ideals are abstractions that have been transformed by fetishism and reification into realities with an independent ontological status. Moreover, idealism sees the relationships entered into by the ordinary objects of observation as direct causal consequences, albeit disturbed by other forces, of the actual relations between the essences. Marx, in discussing the fetishism of commodities in Chapter I of *Capital*, draws a parallel with "the mist-enveloped regions of the religious world. In that world the productions of the human brain appear as independent beings endowed with life, and entering into relations both with one another and the human race." In a similar way idealistic, pre-Darwinian, biology saw the actual organisms and their ontogenetic histories as causal consequences of real relations among ideal, essential types, as opposed to the materialistic view that sees the actual physical relations as occurring between actual physical objects with any 'types' as mental constructs, as *abstractions* from actuality. The precise difficulty of pre-Darwinian evolutionary theory was that it could not reconcile the actual histories of living organisms, especially their secular change, with the idea that these histories were the causal consequences of relationships among unchanging essences. The equivalent in Newtonian physics would have been to suppose (as Newton never did) that if a body departed from perfectly rectilinear, unaccelerated motion, there nevertheless remained an entity, the 'ideal body,' that continued in its ideal path and to which the actual body was tied in some causal way. What appears to be the patent absurdity of this view of moving bodies should make clear to us the contradictory position in which pre-Darwinian evolutionists found themselves.

In ecology the isolated community is an abstraction in that no real collection of species exists which interacts solely with its own members and which receives no propagules from outside. But the total isolation of a group of species from all interactions with other species

is not a requirement of the usefulness of the community as an analytical tool. Some of Simberloff's confusion on this point arises from a failure to appreciate that general principles of interaction are not the same as quantitative expressions of these interactions. It is undoubtedly true that every body in the universe creates a gravitational field that, in theory, interacts with every other one. Yet when we get up in the morning, our muscles and nerves do not have to compensate for the motion of every body in the universe, or even of every other person in the same house with us. The intensity of gravitational interaction is so weak that, except for extraordinarily massive objects like planets or extraordinarily close objects like nucleons, it is irrelevant, and we can treat our own persons as gravitationally independent of each other. In like manner, all species in the biosphere interact, but the actual matrix of interaction coefficients is essentially decomposable into a large number of submatrices separated by zeroes. The problem for the ecologist is not to replace these zeroes by the infinitesimally small actual numbers, but to find the boundaries of the submatrices and to try to understand the rather large interaction coefficients that exist within them. Thus, it is not an argument against the population or the community as entities, that boundaries are not absolute between them, any more than that the existence of some intersexes destroys the usefulness in biology of distinguishing males and females.

To put the matter succinctly, what distinguishes abstractions from ideals is that abstractions are epistemological consequences of the attempt to order and predict real phenomena, while ideals are regarded as ontologically prior to their manifestation in objects.

STOCHASTICITY AND STATISTICS

Simberloff correctly observes that a major trend in ecology and evolutionary biology has been the replacement of deterministic models by stochastic ones. He draws from that observation two conclusions, however, with which we disagree. First, he concludes that stochastic models are in essential contradiction to predictive models, and that stochasticity is the negation of cause-and-effect.

Thus, he writes "The neo-Darwin syntheses sounded the death-knell for Newtonian cause-and-effect determinism in biology." As a general statement about *biology*, this certainly is not and cannot be true. As an historical fact, the entire development of molecular biology shows the continuing power of simple deterministic models of the 'bête-machine' nor is there the slightest reason to introduce stochasticity into models of, say, how an increase in adrenalin secretion will affect the concentration of sugar in the blood. Indeed, stochasticity may be an obfuscation rather than a clarification in such cases. The neurosecretory system is a complex network of non-linear dynamic relations that are incompletely understood. If two individuals (or the same individual at different times) are given identical treatments of a hormone, there may be qualitatively different and even opposite consequences. That is because in such a non-linear system, the consequences of a perturbation in one variable are strongly dependent on the levels of the other constituents. The lack of repeatability of response could be passed off as the consequence of 'stochasticity' or the inherent failure of 'Newtonian cause-and-effect,' but to do so would be to prevent progress in understanding and control of the system. The example of Park's experiments in ecology, cited by Simberloff as a triumph of stochastic modelling, is right to the point. Mixed populations of *Tribolium confusum* and *T. castaneum* sometimes resulted in replacement of one species, sometimes of the other. Conditions of food, moisture, etc were made as nearly identical as possible and the initial population mixtures were also controlled. A stochastic model of this competitive experiment was constructed by Neyman, Park and Scott (1956) which was consistent with the variable outcome of the experiments. But in constructing such a stochastic model, which seems untestable, an alternative that would lead directly to experiment and measurement has been rejected. This alternative is that there are two stable states of dynamic systems, one at pure *Tribolium castaneum*, one at pure *T. confusum*, and that the domains of attraction of these stable states are demarked by a separatrix along an axis that has not been controlled in the initial population mix, so that the experiments begin sometimes on one side of this separatrix, sometimes on the other. Park did not examine, for example, the effect of small

perturbations in the initial age distribution within species, or in the initial *actual* fecundities of the samples of beetles in each vial.

It may indeed be true that notions of cause-and-effect are inapplicable at the level of the spontaneous disintegration of a radioactive nucleus, but there is no reason to make uncertainty an ontological property of all phenomena. It is a curious inversion of the idea of materialistic explanation to suggest that "the next great breakthrough may come when we have the courage to junk cause-and-effect entirely, and strike off at some other angle." Astrology, perhaps, or E.S.P.?

The question of whether non-predictability of outcome is to be subsumed under a general stochasticity, or whether previously uncontrolled variables are to be controlled in an attempt to produce predictable outcomes, is an *ad hoc* issue to be decided in each case.

If we wish to understand the changes in gene frequency in a population, it may be quite sufficient to invoke the 'chance' nature of Mendelian segregation and the Poisson distribution of the number of offspring from families in a finite population of size N . That is because such a stochastic explanation is a sufficient alternative to a theory of perfect adaptation by natural selection. It is an explanation at the same level of phenomena as the adaptive story. On the other hand, if we are interested in the consequences of human demographic change, the probability distribution of family sizes is not a sufficient level of analysis, and we must look into the differentiation of family size by region, class, etc. The demand that all phenomena must be explicable by deterministic cause and effect *at an arbitrary level of explanation* is clearly doomed to failure, as for example the attempt to explain all evolutionary change as the result of determinative natural selection. But the assertion that cause-and-effect at a lower level cannot replace the stochasticity at higher levels, if it becomes useful to do so, is obfuscatory.

Moreover, the shift from stochastic to deterministic statements about the world can occur in changing from one level of explanation to another in either direction. Not only can the apparently random be explained as a result of deterministic forces in higher dimensionality

with more specification, but a *reduction* in dimensionality by averaging also converts stochasticity into determination. The stochasticity of molecular movements in a gas lies at the basis of the completely deterministic gas laws that relate temperature, pressure and volume. Even if the disintegration of a radioactive nucleus is an 'uncaused' event and thus perfectly stochastic, clocks accurate to millionths of a second are built precisely on the basis of the randomness of those disintegrations. Thus stochastic processes may be the basis of deterministic process and deterministic the basis of stochastic. They do not exclude each other.

Stochastic and deterministic processes interact also at the same level of organization of phenomena, and this interaction is of especial importance in population biology and evolution. The notion of determinism may carry with it the false implication that only single end state is possible for processes if all of the parameters of the dynamic system are fixed. But this is not true. Because of the non-linear dynamics of evolutionary processes, there exist multiple possible outcomes for a process even with fixed parameters. In mathematical terms, the vector field has multiple points of attraction, each surrounded by a domain of attraction. Which end point the process actually achieves depends upon in which domain of attraction the system begins, its initial condition. Thus, the same force of natural selection may cause a population to evolve in different directions dependent upon the initial genetic composition. If, in addition to the deterministic force of natural selection, there are random variations in genetic composition from generation to generation because of finite population size and random migration, a population in one domain of attraction, may be pushed into another domain and thus may achieve a final state different from that predicted on the basis of its previous trajectory. Indeed, a good deal of evolution by natural selection is only made possible by stochastic events, because these events allow a population that has been restricted to a domain of attraction in the genotypic space to evolve into other compositions. The synthetic theory of evolution developed by Wright (1931) is based upon this 'exploration' of the field of possible evolutionary outcomes by the interaction of stochastic and deterministic forces, both operating at the level of

genotypic composition. Again we see that the apparent contradiction between stochastic and deterministic is resolved in their interaction.

Second, Simberloff's discussion of stochasticity also turns on its head the relationship of material explanation and statistical explanation. He writes that "Statistics is inherently materialistic and anti-typological since it takes 'noise' as its object of study." Nothing could be further from the truth. Some of the greatest problems of scientific explanation come from concepts and practices that lie at the heart of modern statistics which, in many ways, is the embodiment of idealism, at least as practiced by natural and social scientists.

In the first place, statistics does not take 'noise' as its object of study, but on the contrary consists largely of techniques for reducing, discounting or separating 'noise' so that 'real' effects can be seen. The theory of hypothesis testing and most of the theory of estimation had as their primary purpose the detection of true difference between objects or the assignment of intervals in which parameters of universes are thought to lie, *in spite of* variation between individuals. While statements about differences or parameters must of necessity be phrased in terms of probabilities, that is not regarded as a virtue by statistical theory, but as a limitation. The reason for searching for *efficient estimators* and *uniformly most powerful tests* is precisely in order to minimize the effect of variation between individuals on the desired inferences about ideal universes. The distinction between first and second moments is absolutely fundamental to statistical theory¹ and the purpose of statistical procedures is to distinguish that fraction of the difference between first moments which is ontologically the same as the second moment, from that fraction which arises from different causes, the 'real' differences between the populations. Most of the theory of experimental design such as randomization, orthogonal plots and stratification are a substitute for complete knowledge and control of all relevant variables. The purpose is not to study the 'error' variance, but to tame it and minimize it and finally to remove, if possible, the veil of obscurity that it interposes between the observer and those ideal universes whose parameters are the object of study.

The branches of statistics that seem at first glance to be concerned most directly with variance as an object of study, the analysis of variance and multivariate correlation and regression theory, are as practiced by natural and social scientists, if not by sophisticated statisticians, the most mystified by idealism. The analysis of variance is a tautological partitioning of total variance among observations into main effects and interactions of various orders. Yet, as every professional statistician knows, the partitioning does not separate causes except where there is no interaction. (See Lewontin, 1974, for a discussion of this point in the context of population genetics.) Yet natural and social scientists persist in reifying the main effect and interaction variance that are calculated, converting them into measures of separate causes and static interactions of causes. Moreover, they act as if 'main effects' were really 'main' causes in the every day English meaning of the word and that interactions are really of a second order of importance. Interaction in this view is what is left over after main effects are accounted for. This attitude toward main effects and interactions is a form of the *ceteris paribus* assumption that plays such a central role in all Cartesian science, but that has become an unconscious part of the ideology of the analysis of variance.

The most egregious examples of reification are in the use of multiple correlation and regression and various forms of factor and principal components analysis by social scientists. Economists, sociologists, and especially psychologists believe that correlations between transformed orthogonal variables are a revelation of the 'real' structure of the world.

Biologists are apparently unaware that in the construction of the correlation analysis itself they impose a model on the world. Their assumption is that in performing a correlation analysis they are approaching the data in a theory-free manner and that data will 'speak to them' through the analysis. If, however, we examine the actual relationship between dynamic systems and correlations, it becomes clear that correlation can create relationships that do not exist. For example, the simplest prey-predator relations predict that as prey increase there will be a consequent increase in predators, so the correlation between prey and predator should be positive, but as predators increase, all other

things being equal, prey should decrease so there will be a negative correlation in abundance. The spiral nature of the dynamics in the two dimensional prey-predator space shows us immediately that prey and predator abundances may be either positively or negatively correlated depending upon the particular part of the spiral the populations are in historically. If an atheoretic correlation analysis is carried out, a correlation will be observed and, in the absence of any *a priori* theory, the correlation will lead to a theoretical story that reflects the particular sign that the correlation has in that set of data. Thus, correlations may be the consequence of causal processes, but they cannot be used reliably to infer those processes.

Because the methodology of correlation is intrinsically without theoretical content about the real world (that is thought to be its greatest virtue) any statements about the real world must come from the content imported into the analysis. So, if we wish to understand the causes of some variable, say species abundance, by using a correlational approach, it becomes necessary to decide which aspects of the world are to be measured to correlate with species abundance. Having chosen the independent variates, the correlations that are calculated come to be interpreted as real causal connections. So if temperature turns out to be highly correlated with abundance, it will be asserted that temperature itself is an important causal factor; as if the data themselves rather than the observer had chosen this variable. Of course every investigator will repeat endlessly that correlation should not be confused with causation and that, in the example given, temperature may be only a proxy for some other variable or variables with which it is in turn correlated. But such a disclaimer is disingenuous. No one would bother to carry out a correlation analysis if they took seriously the *caveat* that correlations are not causations. After all, what is the use of the analysis unless it is to be used for inferences about causation?

Unfortunately, it is nearly always the case that in a collection of multivariate data in which the set of independent variables accounts for a reasonable proportion of the variance, a rather large proportion of that variance will be associated with a small proportion of the variables. This loading of the variance onto a small set of variables is a purely numerical consequence of assembling a heterogeneous group of independent

variates in a multiple regression analysis. A consequence of this loading is that one or two variates will always appear to be the 'main' dependent variable. Yet, if the analysis is repeated with a different set of variables, some other may now appear as the 'main' causes. In this way the practice of multivariate analysis is self-reinforcing since it appears from the analysis that a few real 'main' causes have been discovered and so faith in the methodology is built.

When extrinsic variables are not introduced specifically as explanatory factors, a complex set of data may be examined internally for pattern or structure whose discovery is thought to be a revelation of real world, while, in fact it is only a tautological relationship among a set of numbers. The most famous example is the *g-factor* that is created in the factor-analytic treatment of I.Q. tests and which is widely believed by psychologists to be a real thing, general intelligence. Statistical methodology in the hands of natural and social scientists thus becomes the most powerful form of reinforcing praxis of which idealism is the theory.²

CONCLUSIONS

Biology above the level of the individual organism – population ecology and genetics, community ecology, biogeography and evolution – requires the study of intrinsically complex systems. But the dominant philosophies of western science have proven to be inadequate for the study of complexity:

(1) The reductionist myth of simplicity leads its advocates to isolate parts as completely as possible and study these parts. It underestimates the importance of interactions in theory, and its recommendations for practice (in agricultural programs or conservation and environmental protection) are typically thwarted by the power of indirect and unanticipated causes rather than by error in the detailed description of their own objects of study.

(2) Reductionism ignores properties of complex wholes; the effects of these properties are therefore seen only as noise; this randomness is elevated into an ontological principle which leads to the blocking of

investigation and the reification of statistics, so that data reduction and statistical prediction often pass for explanation.

(3) The faith in the atomistic nature of the world makes the allocation of relative weights to separate causes the main object of science, and makes it more difficult to study the nature of interconnectedness.

Where simple behaviors emerge out of complex interactions, it takes that simplicity to deny the complexity; where the behavior is bewilderingly complex it reifies its own confusion into a denial of regularity.

Both the internal theoretical needs of ecology and the social demands that it inform our planned interactions with nature require an ecology that makes the understanding of complexity the central problem: it must cope with interdependence and relative autonomy, with similarity and difference, with the general and the particular, with chance and necessity, with equilibrium and change, with continuity and discontinuity, with contradictory processes. It must become increasingly self-conscious of its own philosophy, and that philosophy will be effective to the extent that it becomes not only materialist, but dialectical.

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NOTES

¹ We owe this realization to a remark by William Kruskal.

² Thus, we subscribe completely to the point of view expressed by Isadore Nabi in his essay 'On the Tendencies of Motion.' Dr. Simberloff is off the mark, however, in his attribution of its authorship.

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