
Holism and Reductionism in Evolutionary Ecology

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of system under consideration, then it gradually becomes incorporated into the body of theory/law.

The development of theory in ecology differs from that in the physical sciences only in proportion to the complexity of the systems involved. The structure of ecological systems is complex enough (in terms of state variables and pathways of interaction) that substantial simplifying assumptions are often required even before the majority of observational/experimental data gathering is begun. This simplification is accomplished, just as it is in the physical sciences, by constructing mechanistic models. The structure of ecological models comprises the biotic and abiotic variables of state plus the pathways of matter/energy and information transfer. The system behavior of interest, or in some cases the observations/experiments themselves, will determine the original spatial and temporal scales. Later sampling or observational scales will depend on the particular causal explanation(s) invoked as hypotheses and the scales within which their deducible conclusions apply. Thus in the example given above, the agricultural runoff explanation of lake eutrophication requires a much different model and set of observations or experiments than would the species-interaction explanation.

Once sufficient data are available from which to infer an appropriate mechanistic explanation for the interaction, the model can be used exactly like any other explanatory hypothesis, i.e. it can be used to deduce conclusions. In the case of simulation models, this usage is to predict system behavior under "normal" conditions and again under conditions produced by any one or a variety of changes in the parameter values in the model. The big advantage of a computer simulation model is that it is an exceptionally fast deductive tool with impeccable logic. The disadvantage of most models is that they incorporate so many individual mechanistic explanatory hypotheses that it may be difficult to show that any given conclusion depends on the truth of all of them, in other words, falsification may be difficult.

Thus the trick in the development of ecological theory is to be able to restrict the range of inference to the members of a class of system restrictive enough so that the simplest possible set of explanations will suffice to produce testable conclusions. This implies some severe, but nonetheless realistic and measurable constraints on the range of application of the given mechanism(s). The explanation may invoke larger scales than observed initially (holism) or may require the investigation of subsets of the system observed (reductionism). The choice is not between a better or a worse method, but rather a choice of the scale that best fits the particular phenomena under consideration. In the following papers my colleagues present some detailed insights into the factors governing this choice between holistic and reductionistic explanation in specific subdisciplines of ecology.

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Holism and reductionism in evolutionary ecology

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One reason that the terms holism and reductionism are difficult to define is that they do not refer to single concepts. Rather, they are umbrella terms, covering a number of different concepts that really should be separated from each other. A lot of mischief can be created by these umbrella words, especially when the speaker has one concept in mind and the listener has another.

This note therefore has two purposes: the first is toidentify several different senses of holism and reductionism, and the second is to defend a fairly strong form of holism in ecological and evolutionary thought.

Mechanistic holism

Let us begin with a quote from a paper about the evolution of body size (Roff 1981:418): "Most examinations of body size center on a single factor. However, because body size is directly or indirectly linked to many, if not most, life history characters a more holistic approach is advocated".

To Roff, it is reductionistic to explain body size with a single factor and holistic to explain it with a number of factors that interact with each other. Obviously, if body size is influenced by a number of factors (as it probably is), then there is no alternative to a holistic approach. In this fashion the term holistic is often used merely to say that more variables must be considered to understand the object of study.

Two observations can be made about this use of the word holistic. First, many people would think it is inappropriate, and merely sets up reductionism as a straw man. Reductionists don't deny that nature is complex or that the things we study are influenced by several variables. At the molecular level nature is notoriously complex, yet molecular biology is regarded even by holists as a triumph of reductionism. Reductionism is usually described as a *way of thinking* that begins by breaking complex entities into simpler parts, studies the parts separately, and then "puts them back together" to understand the whole. The phrase "puts them back together" can only mean studying the interactions among the parts. Despite the frequent holistic statement that "the whole is more than the sum of its parts", reductionists do not expect interactions among parts to be additive (Wiegert 1988), as even the most casual glance at molecular biology or any other discipline will affirm. In the case of the body size study quoted above, Roff examined the effect of body size on fecundity, development time, and survivorship, at first separately and then as these parameters interact in the Euler equation. His way of thinking about the subject is firmly reductionistic.

Second, whatever you call it, Roff's multi-factor approach to the evolution of body size is an improvement over the previous single-factor models. More generally, ecology and evolution abound with single-factor explanations that turn out to be inadequate and yield to multi-factor explanations. Now, perhaps this is just the reductionistic program fulfilling itself – first studying the parts, then putting the parts together, and so on. There is a very important class of people who disagree with this assessment, however; the people who advance the single-factor models. They usually claim that their single factor alone suffices to explain the behavior of the whole, and resist the idea that their factor might becontext dependent or interact with numerous equally important factors. Today we might wisely say that community ecology is a pluralistic discipline, but there was a time when many people truly believed that competition could explain it all, and resisted efforts to integrate this one factor with numerous others.

To summarize, a common use of the word holistic is philosophically mundane, but nevertheless signals an important event, namely the appreciation of complexity. Wimsatt (1980) has argued this point very well:

> The metaphysical position that the reductionist defends holds that a reductionistic analysis of upper-level phenomena must exist in terms of lower level entities... The holist, as antireductionist, is taken normally as denying this metaphysical claim, and thus to be holding the equally metaphysical (and to most people, radically implausible) claim that no analysis of whatever complexity in lowerlevel terms could be adequate. But, despite appearances, the in principle claim of the reductionist is seldom in dispute. In the cases I know in population biology, in neurophysiology, and in the history of genetics, 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. The more holistically inclined scientists usually argue that higher-order relational properties of the lower-level entities are required, and the reductionists argue that a given simple, lower-level model... is adequate. To the extent that this is true, the portrayal of the dispute between reductionist and holist as over the in principle claim (a portrayal favored by most philosophers and many scientists) is seriously in error and turns a usually serious, comprehensible and important empirical dispute into a usually one-sided and poorly motivated metaphysical one.
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> The net effect of these considerations is that the holist can get the significance and autonomy of upper-level entities, laws and phenomena which he desires while accepting a kind of in principle (but "complex") reductionism. The significance of what follows... are to be interpreted as espousing this kind of holism. (Wimsatt 1980:145–147).

I think there is no question that this kind of holism, purged of its metaphysical claims, has a solid place in any discipline, including ecology and evolution.

Descriptive holism

A second use of the word holistic is illustrated by the following passage from Rigler (1975:201):

> ... we have a tendency to speak of [reductionism] as if it is the only route to true understanding. By contrast, holistic limnology is said to use the "black box" approach, and the connotation of this term is that we will not know why the holistic approach works, if it ever does. In other words, holism may give us predictive ability, but it will not give us understanding.

For Rigler, holism involves inspecting a complex system for patterns, which once discovered can be described in quantitative terms. The patterns are merely correlations, however, and say nothing about the causal rela tionships among the parts. That is why they are predictive without giving true understanding. Searching for the causal relationships that generate the correlations is by definition a reductionistic enterprise. Schoener's (1986) paper on "a new reductionism" in community ecology employs very similar meanings. When defined in this way, holism is primarily a practical rather than a conceptual tool. Nevertheless, it is important to be practical and Rigler is eloquent in his account of why he abandoned reductionism in favor of a more holistic approach:

> Perhaps one should not normally be too concerned about efficiency in science. Barzun (1964) was not maligning science when he referred to it as "the glorious entertainment", and if experiments entertain us, that is usually adequate justification for them. But now, when science is state-supported, and when ecological predictions are desperately needed to provide the basis for management and environmental decisions, one should be more concerned with the practical value than with the entertainment value. At least, that is how I felt when I hesitated to talk to you about the entertaining intricacies of the P cycle in lakes, and also when, a few years ago, I decided to give up this game and look more purposefully, for useful pattern in the behavior of lakes (p. 205).

So far I have described two concepts of holism, which perhaps could be called mechanistic and descriptive, and both have important messages attached to them. One is the message of complexity, and the other is the message of practicality. The two concepts differ in many ways, and already we can see the mischief that is created by lumping them under a single term. Roff and Wimsatt expect reductionistic approaches to be supplanted by holistic approaches, while Rigler and Schoener expect the reverse. Roff and Wimsatt regard holism as a tool for "true understanding", while Rigler and Schoener do not.

Metaphysical holism

Both mechanistic and descriptive holism are philosophically bland, and succeed only by abandoning metaphysical claims such as this one:

> Now organismic biologists do not deny that physico-chemical explanations are possible for the activities of parts on the "lower" levels of a hierarchy. Nor do they deny that the physico-chemical properties of the parts on lower levels "condition" or "limit" in various ways the occurrence of modes of action of higher levels of organization. They do deny, on the other hand, that the processes found at higher levels of a hierarchy are "caused" by, or are fully explicable in terms of, lower-level properties (Nagel 1961, p. 415).

This is the kind of flagrantly holistic statement that reductionists love to hate. Nevertheless, there is at least one strong sense in which it is true, and which constitutes yet a third legitimate concept of holism. Imagine studying the evolutionary effect of predation on snails, seeds, and beetles. Suppose you show that for all three groups, species exposed to heavy predation have harder and thicker exteriors than species not exposed to predation. Now ask the question "why are the exteriors hard and thick for some species and soft and thin for others"? The proper answer to this question is "the presence and absence of predation, coupled with a long history of natural selection". The question cannot be answered by examining the physicochemical materials that make up the exteriors. The materials *permit* the species to have their properties, but they do not *cause* them to. After all, the same patterns apply to snails, seeds and beetles, whose exteriors are composed of completely different materials. Not only are the material parts insufficient to explain the properties of the whole, but the whole can be explained without any knowledge of the material parts, beyond the fact of "permissiveness" – heritable variation.

The process by which natural selection causes higher levels to impose order on lower levels of a hierarchy was labelled "downward causation" by Campbell (1974). Its correspondence with metaphysical holism is remarkable, but it is even more remarkable that no one before Campbell explicitly made the connection. Here we have a major method of reasoning, sometimes known as the adaptationist program, that comprehends complex systems without examining their physicochemical parts, and yet which no one – least of all practitioners of the method – calls holistic!

Even so, the connection between natural selection and metaphysical holism is very deep, as the following example will show. Imagine two experiments, both of which begin by growing plants in a large number of pots. The goal of both experiments is to increase a property of the plant, for example yield. In the first experiment, seeds are taken from the largest plants and grown in a new set of pots. This obviously is a standard artificial selection experiment, which has been performed countless times. In the second experiment, the *soil* is taken from the pots that produced the largest plants, and used to innoculate a new set of pots with sterilized soil, in which a new generation of plants are grown.

It is important to emphasize the similarity between these two experiments. Plant size is influenced both by genes on the inside and the soil community on the outside of the plant. Understanding the genetic determinants of plant size reductionistically (sensu Rigler) will take many lifetimes. Fortunately, we need not wait for this "true understanding". If the plants vary in their genetic composition in a way that is causally related to yield, then by picking seeds from the largest plants we are selecting a sample of genes that is biased towards producing large plants. The prediction is purely empirical (and holistic sensu Rigler) but effective nonetheless.

In just the same way, it will take many lifetimes to understand the numerous effects that soil bacteria, fungus, nematodes and micro-arthropods have on plant growth. We can still create a large number of soil communities, however, that vary in their species composition and also the genetic composition of the component species. By picking soil from beneath the largest plants, we might select a sample of soil communities that is biased towards producing large plants. Iterating this procedure many times, it might be possible to produce a soil community that is functionally integrated to increase plant yield.

Whole industries are devoted to artificially selecting desirable properties in single species, but to my knowledge the artificial selection of communities has never been attempted, even though the experiment is straightforward and the economic benefits potentially great. There is some evidence, however, that natural selection occasionally operates on the community level to create assemblages of species that are functionally organized to perform certain tasks. To make the idea of community-level selection intuitive, it might help to describe two examples. Many species of kangaroo rats (Heteromyidae, *Dipodomys*) store vast quantities of seeds in underground caches (Smith and Reichman 1984), which are ideal environments for fungal growth. How do fungi colonize there caches? Spores could exist on the seeds prior to harvest, or they could come from the soil surrounding the caches. In addition, the rodents themselves seem to be important innoculators of the seeds. Wicklow and Rebar isolated approximately 30 species of fungi from the check pouches of the banner-tailed kangaroo rat (*D. spectabilis*; unpublished study cited in Reichman et al. 1985).

Assume the rodents are the primary source of fungal innoculation in their handling of the seeds. We might then have a situation remarkably similar to the soil selection experiment described above. The rodents create a large number of caches, each of which develops a fungal community. Some of these communities develop in a way that is palatable for the rodent, and others in a way that is toxic. If the rodents avoid toxic caches, then the fungal communities that cause toxicity will fail to be transmitted to future caches. Conversely if the rodents selectively handle seeds from the most palatable caches, fungi that confer palatability will be selectively dispersed to future caches. After many iterations of this procedure – the experiment has been in progress for over ten million years (Voorhies 1975) – we might expect a fungal community whose species interact in a way that preserves and even enhances the nutritional quality of seeds, excludes other species that render them toxic, and so on. Unfortunately, while Reichman and his colleagues have done much to understand the rodent-seed-fungus system, their research has not been directed towards demonstrating community level selection by the rodent on the fungi, which only remains a plausible scenario.

Stronger evidence for community-level selection is provided by phoretic associatons (Wilson 1980, 1983, 1985, Wilson and Knollenberg 1987). Phoresy refers to the use of one animal for transport by another. This form of dispersal is especially common in mites and other wingless creatures that specialize on patchy ephemeral resources such as dung, carrion, and rotting wood. These creatures are adapted to insects that themselves are specialized on the same resource. When the insects colonize a fresh resource patch, they carry with them an entire multi-species community of phoretic associates, which disembarks to pursue a free living existence. The density and diversity of phoretic communities can reach spectacular proportions. To choose an example from my own research, at a single study site over 14 species of mites from four families are associated with the carrion beetle genus *Nicrophorus* (Silphidae). Over 95 % of the beetles carry mites, at average densities that can exceed 500 mites/beetle (depending on the beetle species and time of year). With few exceptions the mites are found exclusively on carrion and arrive exclusively on the bodies of carrion beetles. Comparable examples could be listed for dung beetles, bark beetles, and other insects that specialize on patchy ephemeral resources. The phoretic associates include not only mites but pseudoscorpions, nematodes, fungi and microbes.

It is easy to imagine how community-level selection might operate on phoretic associations. Imagine a large number of resource patches, each of which develops into a community composed of the insects, their phoretic associations, plus other species that arrive independently. The community of phoretic associates varies from patch to patch in species composition and in the genetic composition of the component species. Some of these variant communities have the effect of killing the insect. These will be "selected against", as surely as the experimenter who discards the soil from beneath the smallest plants. Others have the effect of promoting insect survival and reproduction, and these will be differentially transported to future patches. After many iterations of this procedure – this experiment also has been in progress for millions of years and for thousands of phoretic associations – we might expect phoretic communities to have the property of not exploiting the insect carriers and perhaps even protecting them. This prediction has been confirmed for at least two phoretic communities; the carrion beetle association studied by myself and the bark beetle association studied by John Moser and his colleagues (Wilson 1980:119–124, Kinn 1980, Bridges and Moser 1983).

The extent to which community-level selection operates in nature, and the feasibility of artificial community-level selection in the laboratory, are matters to be decided empirically. Even now, however, two important conclusions can be drawn. First, functional interpretations of biological communities are as old as ecology itself. Clements (1916), Emerson (1960), and Odum (1969) all portrayed communities as "superorganisms" whose parts function to maintain the integrity of the whole. These theories are widely regarded as holistic by proponents and critics alike. They also are widely regarded as false. In my opinion they are not false, butrather vastly overextended. Communities molded by community-level selection really do have the functional organization that the above mentioned authors envisioned for all communities. It can be quite proper to say "species X functions to protect species Y", or "species Z functions to increase the efficiency of nutrient cycling". In a literal sense, these species exist because they perform their functions – other less functional species were among the communities that were selected against. The great failing of the grand holistic theories is to apply such thinking to all communities, ecosystems, "living systems", "hierarchial systems" and so on. Functional organization is not an emergent property that appears at every level of a hierarchy. Many communities are just a hodge-podge of species interactions. Functional organization at a given level can only be produced by natural selection operating at that level.

Second, when confronted with a biological community, the first instinct of a community ecologist is to break it into parts – species and their interactions, trophic levels and their interactions, and so on. If the community is molded by natural selection, however, this approach is as misguided as studying hardness and softness in snail shells by looking only at the materials that make up the shell. The properties of such communities are caused by community-level selection, and only permitted by the component species. Bark beetle and carrion beetle phoretic associations have no species in common, but they share the properties of commensalism and mutualism towards the insect carrier. More generally, the adaptationist program, that is so indispensable for our understanding of single organisms, can also be usefully applied to certain multi-species communities.

These two points together demonstrate that even the metaphysical concept of holism can be justified, although not as generally as most metaphysical holists would like.

To summarise, the word holism is used in at least three different ways – mechanistic, descriptive, and metaphysical. Each concept of holism has a profound message for ecologists and evolutionists – the message of complexity, the message of practicality, and the message of integrated wholes that impose order on their parts. It is unfortunate that such different concepts must share the same word, and that the entire word has been spoiled for many people by the misuse of metaphysical holism. I have no solution to offer, but can only urge people to heed the three messages of holism, and to be explicit when using the word themselves.

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