Part-Whole Relationships and the Unity of Ecology

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Introduction: Part-Whole Relationships in Science

The forest is more than a collection of trees. (Odum 1953, p. 88)

One of the most exciting things about science is the access that it provides to phenomena remote from everyday experience. Through science we delve into the distant past, explore other cultures, peer across vast reaches of space, and assay the microscopic structure of the world. As our understanding extends in all these directions, philosophers and scientists often ask how the resulting branches of knowledge are related.

One common answer, dating at least as far back as the Greek natural philosopher Democritus (~460-370 BCE), is that the parts explain the wholes. That is, in modern terms, the properties of sub-atomic particles explain the properties of the atoms they constitute. The behavior of atoms explains the behavior of the molecules they make up. Molecules of protein, fat, and nucleic acid explain the cells they compose. And so on. This view of the explanatory relationships between different levels of organization – e.g., atoms, molecules, cells, organisms, societies, ecosystems, etc. – is a very common, and perhaps the most common, type of <u>reductionism</u>.

The main attraction of this position is that it offers a way to unify the knowledge accumulating in different scientific fields. However, most philosophers of science now consider the strongest version of reductionism – the idea that the parts <u>completely</u> explain the wholes – to have been debunked (e.g., by Fodor 1974 and Putnam 1975). And some (e.g., Kincaid 1990) have identified non-reductive routes to unity in science.

Nevertheless, a slightly milder version of reductionism has gone virtually unchallenged in both philosophy and science: the notion that while parts may not completely explain their wholes, effects of parts on wholes are still somehow much more important than effects of wholes on parts. I believe that this view not only distorts our understanding of the world, but also unjustly skews scientific attention – and funding – away from more "holistic" research. For example, health research has generally neglected environmental, as opposed to genetic, causes of cancer (Steingraber 1997). And "mainstream" economists have mostly ignored the global ecosystem that contains, and sustains, the human economy. Economists have instead focused almost exclusively on interactions between the people, and/or perhaps the institutions, <u>within</u> that economy (Daly and Farley 2004).

Perhaps the most successful attempt to explain a whole in terms of its parts is the explanation of certain properties of an "ideal" gas – e.g., the fact that it obeys both the ideal gas law and the second law of thermodynamics – in terms of the properties and interactions of the molecules composing the gas. However, to extrapolate from this case to any biological or social case – or perhaps even to most other physical or chemical cases – would be a massive blunder. The ideal gas law and the second law of thermodynamics apply only to isolated systems. In contrast, cells, organisms, populations, cultures, economies, ecosystems, etc. – in other words, virtually all biological and social systems – depend crucially on regular inputs of energy, matter, and/or information from their environments. In general, a biological or social system isolated from its environment would be impossible. If it were isolated, it would not be biological or social – it would be dead.

Since the existence of any biological or social system depends on interactions with its environment, it is reasonable to expect aspects of that environment to figure prominently in explanations of that system's behavior. As a working hypothesis, I propose that in general, the properties of an object's environment are just as important as the properties of its parts, when it comes to explaining properties of the whole object. Of course, depending on which properties are being explained, either the parts or the environment may end up being more important in specific cases.

Below, I shall defend this anti-reductionist thesis in the context of ecology. I will first rehearse four arguments against reductionism in that context. I will then address an implicit challenge to these arguments posed by a new research program "toward a metabolic theory of ecology" (Brown *et al*. 2004). Finally, I will examine a connection between these issues and ethical perspectives on levels of ecological organization.

Unity through (One-Way) Reduction vs. Two-Way Integration

[I]ntegration should… eventually lead to the disappearance of current rival 'schools of thought' and their replacement by a unified approach. (Pickett *et al*. 1994, p. 6)

Ecologists study many levels of organization in nature. Three of these – organisms, populations, and communities – form a hierarchy of parts and wholes. Each population is composed of organisms (of the same species). And each community is composed of populations (of different species).[1]

What are the explanatory relationships between these levels of organization? Schoener (1986) offered a strongly reductionistic answer to this question. Unlike many other writers, he was careful to specify what he meant by this: "[A]s Wimsatt (1980…) points out, advocacy of a reductionist approach coincides with emphasizing internal, rather than external, factors when simplification is necessary." Thus, for example, an ecologist wishing to explain the dynamics of a given population would "stress behavioral and physiological detail" – that is, properties of the organisms composing the population – "at the expense of, say, food-web detail" – i.e., properties of the community that contains the population.

Schoener's (1986) emphasis on internal rather than external factors privileges "upward" causation and explanation over "downward" causation and explanation. Upward causation is when the parts of an object affect the behavior of the whole object; downward causation is when the whole affects the parts (Campbell 1974). Upward and downward explanation, then, invoke upward and downward causes, respectively. In Schoener's example, the behavior and physiology of the individual organisms composing a given population exert upward causal influences on properties, e.g., the overall size, of the population as a whole. The food-web structure of the community in which the population is embedded, on the other hand, has downward effects on the population.

[1] Other levels include the ecosystem (a community plus the abiotic matter and energy with which it interacts), and the landscape (a connected group of communities or ecosystems).

Levins and Lewontin (1980) advocated a more balanced, "dialectical" treatment of upward and downward causation than Schoener's (1986) reductionism would allow (see also Lefkaditou and Stamou 2006). Studies launched in the 1990's, concerning the effects of species diversity on various other ecological variables, favor such a balanced view over a reductionistic one. Important downward effects of diversity – a property of entire communities – include various impacts on the stability of component populations (Mikkelson 2004, 2009),[2] and enhancement of the health and vigor of component organisms (Hector 2001, Tilman *et al*. 2001, Wills *et al*. 2006, Swaddle and Calos 2008). The latter effect bears an interesting analogy to recently discovered consequences of income inequality for human health. More equitable human societies, like more diverse ecological communities, tend to comprise healthier organisms (human beings in this case; Kawachi and Kennedy 2002).

The "dialectical" or "systemist" (Bunge 2000) approach thus paints a more fair and accurate picture of causal relationships between higher and lower levels of ecological organization. It also promises to unify ecology more effectively than reductionism. This is because it promotes the study of both upward and downward causal and explanatory links between levels, rather than upward connections only.

Besides the fact that reductionism precludes scientists from doing justice to downward ecological causes, three other considerations motivate its rejection in ecology. First, reductionism may have induced ecologists to commit the fallacy of composition (cf. the introduction to this section of the book). This, in turn, seems to have created

[2] Diversity also tends to enhance the productivity and stability of the entire community. These are same-level, rather than an upward or downward, effects since diversity, productivity, and community stability are all community-level properties.

unwarranted biases in certain mathematical models and experimental designs (Mikkelson 1997). Second, reductionistic models may incorporate unnecessary lower-level details that compromise verisimilitude and predictive success (Mikkelson 2001). Finally, such models fail to account for mechanisms involving higher levels of organization (Mikkelson 2007). In the next section of this paper, I shall consider a new research program that, at first glance, seems to challenge the anti-reductionist position recommended by these arguments.

A Test Case: Metabolic Theory

It has been pointed out by Boltzmann that the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy. (Lotka 1922, p. 147)

Ecology seems to be in the midst of a renaissance. Within the past several years, ecologists have achieved profound advances in knowledge about the effects of species diversity on many variables that collectively span several levels of organization (as touched upon above). They have engaged in fruitful dialogue about the relative importance of "niche-based" vs. "neutral" dynamics, and have teamed up with economists to address the daunting socio-ecological problems currently facing the planet (as noted in the introduction to this section of the book). And most recently, some scientists have embarked on a quest for a grand, unified "metabolic theory of ecology".

The rhetoric employed by these latter ecologists poses an implicit challenge to the anti-reductionism espoused above. Their rhetoric implies that major higher-level phenomena can be completely explained in terms of the lowest level in the ecological hierarchy: the individual organism. Here are a few remarks that I think give this impression:

> [O]ur results indicate that many macroecological features of communities may emerge from a few allometric principles operating at the level of the individual. (Enquist and Niklas 2001)
>
> Here we show that species diversity can be predicted from the biochemical kinetics of metabolism. (Allen *et al*. 2002)
>
> Eventually, metabolic theory may provide a conceptual foundation for much of ecology, just as genetic theory provides a foundation for much of evolutionary biology. (Brown *et al*. 2004)

A closer look at the impressive results attained by the metabolic theorists reveals that they do not, in fact, explain species diversity in terms of organismal traits alone. The metabolic theory predicts only certain features of the relationship between diversity and temperature, for example.[3] Metabolic theorists provide no reason to doubt that downward causation plays a role in shaping that relationship.[4] And their theory relies on crucial population- and community-level assumptions that neither it nor any other theory, reductionistic or otherwise, can (yet?) explain.

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[3] It predicts the slope, but not the intercept, of the linear relationship between mathematically transformed measures of diversity and temperature (Allen *et al*. 2002).

[4] As Marquet *et al*. (2005) put it, while "[t]he usual convention… has been to use body size as the independent variable… there is no way to prove this causal relationship logically, for body size and physiological, ecological and evolutionary traits do not evolve in isolation, but affect each other through complex interactions. In fact, plant ecologists have traditionally treated the size of individuals as if they were determined by population density (i.e., the 'thinning law') and the same is observed in the analysis of size-structured food webs…"

Kincaid (1990) points out that cell biology has not been, and probably will never be, reduced to, i.e., completely explained by, molecular biology. Among other things, the explanations offered by molecular biologists assume, rather than explain, certain pieces of information about higher-level structures like a cell's organelles. The explanations offered by metabolic ecology theorists do exactly the same thing with important pieces of information about populations and communities.

In particular, their explanation of why ectothermic[5] species diversity increases from the poles to the tropics depends crucially on two assumptions – one at the population level, and the other at the community level. The "energetic-equivalence rule" (EER) states that all populations, everywhere – no matter what species – metabolize approximately the same amount of energy per unit time and area (around 80 joules per second per square kilometer; Allen *et al*. 2002). This is surprising, since the amount of energy used per organism per unit time varies systematically with both body size and body temperature. Larger organisms, of course, metabolize more energy than do smaller ones. And "hotter" organisms process more energy than do "colder" ones. The EER entails that population density, the number of organisms in a given species per unit area, varies in such a way as to roughly counter-balance the effects of body size and temperature on energy use at the organismal level.

At least one critic of metabolic theory (Storch 2003) admits that there is good empirical evidence for the population-level EER. But as he points out, no one has yet offered a convincing theoretical explanation of it. The community-level assumption

[5] An ectotherm is an organism (such as a plant or "cold-blooded" animal, e.g., a lizard) whose body temperature is determined by the environment, rather than through homeostasis (as in "warm-blooded" birds and mammals).

employed in the metabolic theory is in the same boat. Allen *et al*. (2002) offer evidence, but no explanation, for the temperature-invariance of total community abundance. When attention is restricted to a given type of organisms, such as trees or amphibians, each multi-species community – whether tropical, temperate, or polar – contains approximately the same total number of organisms per unit area. Ecologists may one day arrive at explanations for both the population-level EER, and this community-level total-abundance "law". But if Kincaid's (1990) point about molecular biology holds more generally within science, those ecological explanations – like the metabolic theorists' current explanation of species diversity – will <u>not</u> be strictly in terms of organismal properties.

In conclusion, then, it seems reasonable to agree with Storch (2003), that what metabolic theory has achieved is a striking "quantitative description of several interrelated phenomena, rather than any comprehensive theory based on first principles". In particular, the theory has not explained species diversity in terms of first principles restricted to the organismal level. Whether the phenomena currently addressed by metabolic theorists end up supporting reductionism, or the "more balanced" view promoted above, will depend on how important upward vs. downward causes turn out to be for explaining those phenomena. And regardless of which type of cause ends up being most important in the case of relationships between temperature and species diversity, a full assessment of reductionism in ecology must weigh that case against others, such as the effects of species diversity on population stability, organismal health, etc.

A Connection to Environmental Ethics

[A] land ethic changes the role of *Homo sapiens* from conqueror of the land-community to plain member and citizen of it. It implies respect for his fellow-members, and also respect for the community as such. (Leopold 1949, p. 240)

Environmental ethicists, like ecological scientists, have given quite a bit of thought to relationships between different levels of ecological organization. And like scientists, ethicists fall within a range from strict reductionism, or "biocentrism", to mild holism, or "ecocentrism".[6] According to biocentrists and ecocentrists alike, we owe direct moral consideration to human and non-human organisms. But for biocentrists, any concern for higher-level entities is strictly indirect, incidental, or instrumental. Ecocentrists, on the other hand, ascribe intrinsic moral value to ecological communities, as well as to the organisms they comprise (cf. the epigraph by Leopold above; see also Callicott 2001).

I am not aware of any strict holists in either ecology or environmental philosophy. In other words, I do not know of any scientists who think organisms are completely explicable in terms of the populations and communities that contain them, with no reference, for example, to the organisms' anatomies, physiologies, or genotypes. And I have not encountered any strong ethical holists who believe that organisms are completely subordinate, from a moral point of view, to some higher-level ecological entity.

[6] For clarity of exposition, I am simplifying the range of alternatives here. For example, biocentrism, which recognizes the intrinsic value, or independent moral considerability, of all individual organisms, is not the only form of "reductionism" in environmental ethics. "Sentientism", which extends moral considerability only to animals, including humans, able to experience pleasure and pain, is another version (Varner 2001).

One could argue that even-handedness toward the organismal and community levels lands ecocentric ethics in a "Catch-22". The more that fostering the well being of organisms conflicts with promoting such traits as "the integrity, stability, and beauty of the biotic community" (Leopold 1949, p. 262), the less tenable is the idea that those conflicts can be resolved. This, in turn, increases the temptation to adopt a strictly reductionistic, or holistic, stance. But the more that doing right by individual organisms coincides with enhancing the community, the less practically important might seem the distinction between biocentrism and ecocentrism.

Some of the downward effects mentioned toward the beginning of this paper suggest that the second horn of this dilemma may threaten ecocentrism more than the first horn does. For example, consider species diversity (again). Leopold (1949) repeatedly underlined its importance for protecting the intrinsically valuable community traits listed in the previous paragraph. Recent research confirms the same-level link between diversity and community stability (see Footnote 2 above, and the introduction to this section of the book). But it also has revealed a downward positive impact of diversity on organismal health.

Boyd (1988) refers to harmony between different moral goods as "homeostatic unity". Although he does not explicitly apply this idea to goods at different levels of organization, positive effects of species diversity on community stability and organismal health suggest that the homeostatic unity concept does apply in this context. This gets ecocentrism around the first horn of the dilemma posed above.

But what about the second horn? If fully informed biocentrism and ecocentrism converge on similar recommendations, e.g., promoting species diversity, is there any reason to prefer one over the other? I think there is, but it has more to do with human psychology than with ecological ontology. Since ecocentrists profess direct moral concern for both organisms and communities, they are presumably more inclined than are biocentrists to take an interest in understanding both levels of organization. This interest, in turn, puts them in a better position to perceive both upward and downward connections between the two. Ironically, this may provide a biocentric motive for adopting ecocentrism (cf. Nelson 1996).

Conclusion: A "Mature" Science?

[E]cology has come to "conform closely to the paradigm of reductionistic… science", to the extent that it has been "perverted in the interests of making it acceptable to the scientific establishment and to the politicians and industrialists who sponsor it"… (Hay 2002, p. 137, quoting Goldsmith)

One group of environmental ethicists who have considered psychological aspects of their philosophical project is the "deep ecologists". For deep ecologists, the ability to connect emotionally and intellectually not only with other humans, but also with non-human organisms and higher-level ecological entities, is a sign of psychological maturity:

> The movement from an atomistic, egocentric sense of self toward an expansive, ecocentric or transpersonal sense of self is seen as representing a process of psychological maturing. (Eckersley 1992)

Modern science began in the 17th Century with a strongly "atomistic" bent. If individual human beings are capable of progressing to something more holistic, can science as well? The man who coined the term "ökologie" in the 19th Century seems to have intended "his" new science to do so, by balancing out the overly reductionistic approaches to organisms taken within other branches of biology:

> So far physiology… has, in the most one sided fashion, almost exclusively investigated… among the functions of relationship, merely those which are produced by the relations of single parts of the organism to each other and to the whole. On the other hand, physiology has largely neglected the relations of the organisms to the environment, the place each organism takes in the household of nature. (Haeckel, quoted in Cooper 2003, p. 5)

As we have seen, the rhetoric and practice of many ecologists conflicts with Haeckel's position, and instead harks back to the reductionistic worldview of the 17th Century. The first section of this paper reviews some potentially important drawbacks of that worldview. Will ecology evolve to the point where its practitioners more open-mindedly explore both upward and downward causation? And even if ecology does, is there any chance that science in general might also? I agree with the epigraph to this section of the paper, that significant political-economic barriers stand in the way of such a desirable evolution. But I am nonetheless hopeful that science will achieve it one day, and in the process help to reform the socio-economic forces that currently distort the scientific enterprise.

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References

Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545-1548.

Boyd, R. N. 1988. How to be a moral realist. In: Sayre-McCord, G., editor. Essays on Moral Realism. Cornell University Press. Ithaca, NY. Pp. 181-228.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771-1789.

Bunge, M. 2000. Systemism: The alternative to individualism and holism. Journal of Socioeconomics 29:147-157.

Callicott, J. B. 2001. The land ethic. In: Jamieson, D., editor. A Companion to Environmental Philosophy. Blackwell. Malden, MA. Pp. 204-217.

Campbell, D. T. 1974. "Downward causation" in hierarchically organised biological systems. In: Ayala, F. J. and T. Dobzhansky, editors. Studies in the Philosophy of Biology. University of California Press. Berkeley, CA. Pp. 179-186.

Cooper, G. J. 2003. The Science of the Struggle for Existence: On the Foundations of Ecology. Cambridge University. New York, NY.

Daly, H. E. and J. Farley. 2004. Ecological Economics: Principles and Applications. Island. Washington, DC.

Eckersley, R. 1992. Environmentalism and Political Theory: Toward an Ecocentric Approach. State University of New York. Albany, NY.

Enquist, B. J. and K. J. Niklas. 2001. Invariant scaling relations across tree-dominated communities. Nature 410:655-660.

Fodor, J. 1974. Special sciences (or, The disunity of science as a working hypothesis). Synthese 28:97-115.

Hay, P. 2002. Main Currents in Western Environmental Thought. Indian University. Bloomington, IN.

Hector, A. 2001. Biodiversity and the functioning of grassland ecosystems: Multi-site comparison. In: Kinzig, A. P., S. W. Pacala, and D. Tilman, editors. The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions. Princeton University Press. Princeton, NJ. Pp. 71-95.

Kawachi, I. and B. P. Kennedy. 2002. The Health of Nations: Why Inequality Is Harmful to Your Health. The New Press. New York, NY.

Kilpatrick, A. M. and A. R. Ives. 2003. Species interactions can explain Taylor's power law for ecological time series. Nature 422:65-68.

Kincaid, H. 1990. Molecular biology and the unity of science. Philosophy of Science 57:575-593.

Lefkaditou, A. and G. R. Stamou. 2006. Holism and reductionism in ecology: A trivial dichotomy and Levins' non-trivial account. History and Philosophy of the Life Sciences 28:313-336.

Leopold, A. 1949. A Sand County Almanac. Oxford University Press. New York, NY.

Levins, R. and R. Lewontin. 1980. Dialectics and reductionism in ecology. Synthese 43:47-78.

Lotka, A. J. 1922. Contribution to the energetics of evolution. Proceedings of the National Academy of Science 8:147-154.

Marquet, P. A., R. A. Quiñones, S. Abades, F. Labra, M. Tognelli, M. Arim, and M. Rivadeneira. 2005. Scaling and power-laws in ecological systems. The Journal of Experimental Biology 208:1749-1769.

Mikkelson, G. M. 1997. Methods and metaphors in community ecology: The problem of defining stability. Perspectives on Science 5:481-498.

Mikkelson, G. M. 2001. Complexity and verisimilitude: Realism for ecology. Biology and Philosophy 16:533-546.

Mikkelson, G. M. 2004. Biological diversity, ecological stability, and downward causation. In: Oksanen, M. and J. Pietarinen, editors. Philosophy and Biodiversity. Cambridge University. New York, NY. Pp. 119-129.

Mikkelson, G. M. 2007. Ecology. In: Hull, D. L. and M. Ruse, editors. Cambridge Companion to the Philosophy of Biology. Cambridge University Press. New York, NY. Pp. 372-387.

Mikkelson, G. M. 2009. Diversity-stability hypothesis. In: Callicott, J. B., R. Frodeman, V. Davion, B. G. Norton, C. Palmer, and P. B. Thompson, editors. Encyclopedia of Environmental Ethics and Philosophy. MacMillan. Farmington Hills, MI. Volume 1:255-256.

Nelson, M. P. 1996. Holists and fascists and paper tigers… Oh my! Ethics and the Environment 1:103-117.

Odum, E. P. 1953. Fundamentals of Ecology. W. B. Saunders. Philadelphia, PA.

Pickett, S. T. A., J. Kolasa, and C. G. Jones. 1994. Ecological Understanding. Academic Press. New York, NY.

Putnam, H. 1975. Philosophy and our mental life. In: Mind, Language, and Reality. Cambridge University Press. New York, NY. Pp. 291-303.

Schoener, T. W. 1986. Mechanistic approaches to ecology: A new reductionism? American Zoologist 26:81-106.

Steingraber, S. 1997. Living Downstream: An Ecologist Looks at Cancer and the Environment. Addison-Wesley. New York, NY.

Storch, D. 2003. Comment on "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule". Science 299:346.

Tilman, D., J. Knops, D. Wedin, and P. Reich. 2001. Experimental and observational studies of diversity, productivity, and stability. In: Kinzig, A. P., S. W. Pacala, and D. Tilman, editors. The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions. Princeton University Press. Princeton, NJ. Pp. 42-70.

Varner, G. 2001. Sentientism. In: Jamieson, D., editor. A Companion to Environmental Philosophy. Blackwell. Malden, MA.

Wills, C. *et al.*. 2006. Nonrandom processes maintain diversity in tropical forests. Science 311:527-531.

Wimsatt, W. C. 1980. Reductionistic research strategies and their biases in the units of selection controversy. In: Nickles, T., editor. Scientific Discovery Volume II: Case Studies. D. Reidel. Dortrecht, Netherlands. Pp. 213-259.

Swaddle, J. P. and S. E. Calos. 2008. Increased avian diversity is associated with lower incidence of human West Nile infection: Observation of the dilution effect. Public Library of Science ONE 3:e2488.