

Chapter 19

Ecosystems

KENT A. PEACOCK

The *ecosystem* is the central unifying concept in many versions of the science of ecology, but the meaning of the term remains controversial, and a few authors (e.g., Sagoff, 2003) question whether it marks any clear or non-arbitrary distinction at all. The following definitions will do as a fairly uncontroversial starting point: The terms “ecology” and “economics” themselves come from the Greek root *oikos*, meaning “household.” *Ecology* is the branch of biology that deals with the ways in which living organisms organize themselves into dynamic structures that facilitate the exchange of energy, materials, and information between themselves and the larger physical and biological environments in which such structures are situated; while *ecosystems* themselves are, loosely speaking, the structures in question.

This chapter will begin with observations on the meaning and scope of ecology itself. It will then outline the ways in which ecosystems can be understood from a number of perspectives: the ecosystem as the *descriptive unit* of the working field biologist; the *history* of the concept of the ecosystem; the ecosystem as a *dissipative structure*; the ecosystem as *symbiotic association*; the ecosystem in evolutionary theory; and skeptical views according to which the ecosystem is little more than a *descriptive convenience*. The applications of these conceptions to environmental ethics and the problems of ecosystem health and sustainability will then be reviewed. Ecosystems are not merely of theoretical interest, for understanding them may make a critical difference to how successful we humans are in responding to the ecological crisis precipitated by the unprecedented impact we are currently having on the environment. In the end, the practical perspective must serve as our touchstone; the observations of field ecologists, working agronomists, foresters, soil scientists, and conservationists should temper our flights of theoretical fancy.

1. The Scope of Ecology

K. de Laplante (2004) argues that in recent years there have been two major ways to think about ecology itself, a narrowly orthodox approach and what de Laplante calls the “expansive” approach. The orthodox approach holds that ecology should concern itself largely or entirely with nonhuman communities of species, and that the value of

ecology is primarily the prediction of the population dynamics of organisms. The expansive approach is more in the spirit of E. Haeckel's original (1869) definition of ecology as "the investigation of the total relations of the animal both to its inorganic and to its organic environment; including above all, its friendly and inimical relations with those plants and animals with which it comes directly or indirectly into contact – in a word, ecology is the study of those complex interrelations referred to by Darwin as the conditions of the struggle for existence" (Haeckel, 1869/1879, quoted in de Laplante, 2004, p.264). Both views accept the fact that even very subtle features of human culture (broadly understood to include our art, science, economy, religion, architecture, technology, and philosophies) could have ecological significance on a planetary scale (Peacock, 1999b); a stock market fluctuation, a change in communications technology, or the promulgation of a novel philosophical doctrine could trigger chains of cause and effect leading to dramatic disruptions of the nonhuman ecosystem. (A fashion trend in Europe in the period 1900–10 led to the extinction of the New Zealand huia bird; Day, 1989.) Because human activities, for better or worse, are so deeply entangled in the present functioning of the planetary system (E. Odum, 1971, p.36, has referred to "man the geological agent"), the notion of an ecological theory that could do even as much as predict animal population distributions and numbers, without taking into account the myriad ways in which human activity impacts nonhuman nature, seems naïve. The essential distinction between the orthodox view and the expansive view is that the latter is concerned not merely with population dynamics, but with all properties of organisms and communities of organisms insofar as they can be understood as consequences or features of their interactions with their physical and biotic environments. In particular, the expansive view understands virtually all aspects of human thought and activity as ecological in nature or implication, and opens the door to a rethinking and redirection of the whole human enterprise on ecological grounds. It is virtually impossible to make sense of most of the notions of the ecosystem that we shall review here without implicitly taking the expansive view of ecology.

It is understandable that many working ecologists have chosen to narrow their focus to matters about which one has a hope of making testable predictions, for a theory that says (as ecology is often taken to say) that "everything connects" and that wholes resist analysis into the interactions of parts risks falling into vacuity. However, it is just a brute fact that the living world is profoundly complex and abounding with interdependencies that resist tractable mathematical description. These barriers to scientific analysis are only compounded by the challenge of scale (some ecosystems span continents or the whole planet itself), the inseparability of the human observer from many biotic systems under study, and the fact that the operations of ecosystems must often be inferred from indirect observations. Thus the challenge for ecologists of all stripes is to arrive at accounts of ecological entities and processes that allow for the complexity, openness, and nonlinearity of ecological systems, but which are at the same time scientifically meaningful.

A number of authors have noted the relative lack of predictive power, especially quantitative predictive power, of ecosystems theory as compared with other branches of science such as chemistry or physics. Predicting the behavior of ecosystems suffers from many of the same difficulties as weather forecasting – nonlinearity, sensitive dependence on initial conditions, complexity, and our lack of full understanding of the

dynamics. We cannot accurately model climate without modeling the earth system as a whole, but as with weather and climate forecasting, it is reasonable to hope (as Schneider and Sagan 2005 argue) that the ever-increasing power of computer modeling will allow more effective predictions, both qualitatively (will the icecaps melt?) and quantitatively (when will they melt?). As a quantitative science, ecology is in its infancy, but it has already yielded many qualitative insights that could make a material difference to the probability of the survival of the human species.

2. General Description of Ecosystems

Ecology began as branch of science driven by observations of communities of plants and animals and their interactions with their physical surroundings. In this loose sense even Aristotle was an ecologist. The pre-theoretical aspect of ecology as an observational practice must always remain the essential reference point for ecological theorizing (Odum, 1971). Relatively self-contained entities such as ponds are well studied and their properties suggested that groups of organisms in an approximately bounded physical setting tend to interact in such a way as to define a coherent entity. (See, e.g., Golley, 1993.)

We will first review some generally accepted terminology.

Populations are commonly defined as interbreeding groups of organisms of the same species. A *community* is a group of interacting populations, and it is usually identified relative to a geographical area. However, what counts toward defining communities, ecosystems, and symbiotic associations is causal connectivity, not merely physical proximity; a pod of great whales and their prey may be spread over thousands of square kilometers of ocean, and yet remain connected by underwater sound signals. E. Odum (1964, p.15) emphasized that “coordination at ecological levels involves communication across non-living space.”

A *biome* is a grouping of communities in a specific climate region, and characterized usually by plant type; various desert or forest environments (such as the montane cloud forest) are typical biomes. The term *biosphere* has been used in more than one sense. Conventionally it is taken to mean the regions on or in the Earth where life is found, between the lowest ocean depths to the lower atmosphere. The term *biosphere* as introduced by V. I. Vernadsky (1926/1988) is a broader conception: it is, he said, the “surface that separates the planet from the cosmic medium” (1926/1988, p.43), a layer that extends down as far as the lithosphere.

An *ecosystem* or *environment* can be defined loosely as the combination of a community of organisms and the abiotic physical surrounding with which the organisms interact. This leaves open the question of how we identify those features of the abiotic world that constitute the environment for the community in question. This is difficult not only because of the complexity of the causal interactions, both direct and indirect, of life with its surroundings, but because many of the materials in an environment with which organisms interact were once living or are byproducts of life; for instance, carbonate minerals are mostly residues of long-ago marine organisms. The environment proper of a community could include the entire planet, and in this inclusive sense there is, strictly speaking, only one ecosystem.

One non-arbitrary way we can distinguish ecosystems from their surroundings is by the presence or absence of feedback. The CO₂ in the atmosphere both affects and is affected by the biota, but the ultraviolet (UV) flux at the top of the atmosphere can safely be viewed as an external influence because there is no reason to think that the solar output of UV is in any way affected by life on earth. Within the earth system proper, however, it is very difficult to find anything from the top of the stratosphere down to several kilometers into the crust that has not been to some degree affected causally by life.

Ecosystems are open in the sense that they both actively and passively exchange energy, materials, and information with their surroundings in a myriad of ways. (A passive process is driven by gradients such as temperature, pressure, or concentration, while active exchange is driven by expenditure of free energy by the organisms of the system and which can therefore run counter to gradients.) Ecosystems also exhibit periodicities and quasi-periodicities. Long before the term “ecosystem” was coined, biologists noted the phenomenon of *succession*, in which communities develop and apparently reach maturity in a *climax* community which may be approximately stable unless perturbed by outside forces. (Many ecologists today question the existence of climax communities, not only because the notion smacks of teleology, but because it may simply not be the case that ecosystems, particularly vigorous ecosystems, always or even often attain a long-running dynamic equilibrium; Sarkar, 2005a.) There are ecosystems within ecosystems, but many of the characteristic features of ecosystems are, as argued by Odum (1964, 1971), scale-invariant – another factor that makes the concept useful.

Ecosystems are powered by the *autotrophs*, which are photosynthetic or chemosynthetic organisms which derive energy from inorganic sources such as the sun, geothermal sources, or various inorganic chemical reactions. In their relations to the earth system, they are the producers, since they trap the free energy used by all other organisms. The consumers are the *heterotrophs* (including humans), who require organic sources of energy to survive. As will be discussed later in more detail, the sharp distinction between producers and consumers is misleading; it is also tempting to think of the heterotrophs as parasitic upon the autotrophs, but this, too, can be a mistake.

3. History of the Term “Ecosystem”

The term *ecology* predates the term *ecosystem*. As noted above, the discipline of ecology was founded, at least in name, by Haeckel in 1869, though biologists had been practicing ecology for very much longer than that. For some decades following Haeckel, ecologists groped for terms that would capture the sense of the holistic entities, the “quasi-organisms” (Tansley, 1935) that they were studying in nature. The term “biocoenosis” (ecological community) was introduced by K. Möbius in 1877; in 1939 limnologist A. Thienemann used the term *biotope* for the physical environs with which the biocoenosis interacts, and referred to the sum of the biocoenosis and biotope as the *holocoen*, roughly synonymous with our present ecosystem. The term “biogeocoenosis” (synonymous with ecosystem or holocoen) was suggested by the Russian ecologist

V. N. Sukachev in the 1940s. Although more precise than *ecosystem*, this term understandably did not catch on.

The term *ecosystem* was first used in print by botanist A. G. Tansley (1935; Golley, 1993). Tansley defined the ecosystem as

the whole *system* (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense. It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. (1935, p.299)

Tansley's ecosystem includes not only the community or communities of organisms, but the physical surroundings – the atmosphere, water, soil, rock – with which they interact. For instance, a body of topsoil considered as an ecosystem includes not only the plants, microorganisms, and numerous other life-forms that inhabit the soil, but also (among other things) the minerals of the soil crumbs, the soil water, and the air which interpenetrates the soil and with which the soil organisms interact.

Viewed this way, the boundaries of ecosystems may seem arbitrary (for instance, soil air is continuous with the entire atmosphere of the Earth); so it must be asked whether it is possible to delineate smaller ecosystems within the biosphere in a non-arbitrary way. Tansley (1935) argued that the distinguishing feature of an ecosystem was that it is a type of *physical* system having an identity defined by a "relative dynamic equilibrium." Although the task remained to explain precisely what this phrase means, Tansley's view implies that subsystems can be picked out from their backgrounds by the presence of cycles of energy, materials, food, or information, in the same sense in which a live electrical circuit could be distinguished from a tangled mass of wiring and components.

There are no truly stable structures in nature, but some structures can be approximately stable (or at least fluctuate around a mean) over thousands or even millions of years, some only over short times. [SEE COMPLEXITY, DIVERSITY, AND STABILITY]. Tansley thought it obvious that natural selection favors ecosystems which tend to be stable. He conceived of ecosystems as founded on plant life, but they could also involve animal and human activity as integral parts. Tansley argued that the "prime task of the ecology of the future" was to investigate the ways in which the components of the ecosystem "interact to bring about approximation to dynamic equilibrium" (1935, p.305). On Tansley's view, communities and biomes are descriptive units, while ecosystems are defined by their underlying dynamics, which may not always be immediately apparent.

In a paper that was to have a strong influence on ecology in the coming decades, R. L. Lindeman (1942, p.400) defined the ecosystem as "the system composed of physical-chemical-biological processes active within a space-time unit of any magnitude, i.e., the biotic community *plus* its abiotic environment." Lindeman's definition is less inclusive than Tansley's, since the latter implicitly points not only to processes within a region of study, but any processes which contribute to dynamic stability. As well, the term "space-time unit," although unclear, suggests physical contiguity, but the type of dynamic coherence indicated by Tansley could be produced by causal interactions acting at quite long range. Lindeman mainly considered the trophic dynamics

of ecosystems, which has to do with how energy – primarily in the form of food – is cycled within the ecosystem. This is an important way of accounting for the dynamic stability indicated by Tansley, but is also a narrower conception, since Tansley's definition would in principle allow for any sort of causal interactions (such as amplification and information exchange) that tended to stability. Still, Lindeman and Tansley's conceptions have in common the key notion that the ecosystem is defined in terms of dynamic cycling.

Lindeman's view was adapted by H. T. Odum (1983) and E. P. Odum (1964, 1971) and became the central concept in so-called *systems ecology* or New Ecology (Worster, 1977), the dominant trend in ecology from the 1950s until at least the 1980s. The New Ecology describes the dynamic stability of Tansley as a *homeostasis* in much the same sense in which this term is used in physiology: a quasi-stable state maintained by organisms actively balancing their responses to positive and negative feedbacks. In the systems approach the ecosystem is defined as a *circuit of energy* but it can also be defined in terms of the types of materials in circulation; L. Margulis, for instance, has defined an ecosystem as "the smallest unit that recycles the biologically important elements" (1998, p.105).

It is difficult to define the term "stability" in a non-tendentious way, but it can be loosely defined as resistance to external perturbations and forcing. More precisely, it can be defined as the maintenance, in the face of perturbations, of biophysical parameters within a range suitable for the survival of the life-forms in the system. An important characteristic of homeostatic systems is that they tend to *return* to equilibrium when subjected to perturbations within a certain range of tolerance.

Recent elaborations of the ecosystem concept include ecosystems as complex adaptive systems (Levin 1998) and as self-organizing critical systems (Jørgenson, Mejer, & Neilsen, 1998). What all such conceptions have in common is some notion of a quasi-steady state maintained by cycling of energy, materials, or information.

E. P. Odum was especially influential in defining and promoting the ecosystem as the central unifying concept in ecology. He argued (see, e.g., 1964) that it is necessary to distinguish between physical structure and dynamic function; while cells are structurally very different from forests, there are, on the systems ecology view, key similarities in the way diverse ecosystems at all sizes scales circulate energy, materials, and information. Odum insisted that a purely reductionist approach to biology would lose sight of the emergent structures and properties that appear only at the level of complex systems. By an "emergent property" one means a property that can be meaningfully applied to a complex system as a whole but not the parts of the system. For instance, the sense in which a person may be "healthy" is quite different from the sense in which a cell in that person's body may be said to be healthy. In physical terms emergence takes the form of *synergism*, in which properties of subsystems combine to produce a system-wide effect which is not a linear function of the properties of the parts. (See, e.g., Fath & Patten, 1998.)

Most treatments of the ecosystem in systems ecology focus on the direct interchange and circulation of free energy and nutrients between organisms and their non-living surroundings. However, there are other ways that the dynamic equilibrium cited by Tansley and Odum can be maintained: the circulation of information can be decisive since organisms respond to informational feedbacks from the environment with which

they interact; also (and this turns out to be crucial in the discussion of sustainability) organisms can contribute to the energetic synergism of an ecosystem indirectly as well as directly. External energy flows can be steered into the ecosystem by a variety of manipulations; for instance, humans can plant trees and thus promote the input of far more photosynthetic energy than they consume.

In recent years the systems-theory conception of the ecosystem has come under criticism (e.g., Sagoff, 2003) but because it was so influential it must serve as a reference point for ecology for some time to come.

4. Ecosystems as Symbiotic Units

Symbiosis is often taken to be a topic in community ecology, not ecosystems ecology. However, E. Odum (e.g., 1971) frequently stressed the importance of his interpretation of the ecosystem as a kind of *symbiotic* association. This aspect of Odum's view of ecosystems has received relatively little attention, but it is crucial in understanding the possible application of ecosystems theory to sustainability. On this interpretation, a community becomes an ecosystem precisely when it becomes symbiotic.

The term *symbiosis* was introduced by A. de Bary (Paracer & Ahmadjian, 2000). It is often used loosely to suggest cooperation, but as de Bary apparently intended it, and as it is usually used in the professional literature today, it is a more general concept. To say that organisms are symbiotic is to say that in some manner they include each other in their life cycles, but this does not necessarily entail a mutually beneficial interaction; for instance, the malaria parasite is in a symbiotic relationship with its hosts. Some interactions which appear to be parasitic are mutualistic when looked at on a larger scale; predator-prey relationships are typical examples. A wide variety of causal interactions, direct and indirect, can play a role in maintaining a symbiotic state. Fath and Patten (1998) argue for "mutualism as an implicit consequence of indirect interactions and ecosystem organization," and show how indirect interactions contribute to network synergism in ecosystems.

There is a range of symbiosis from pathogenic parasitism to symbiogenesis; this can be defined in terms of increasing degree of cooperation and also in terms of increasing energetic synergism. Pathogenicity occurs when a mutant or emergent parasite overwhelms the defenses of its host and both host and parasite perish; unpleasant medical examples such as metastatic cancer come to mind, but the sort of overpopulation crisis identified by Malthus is also an example of pathogenic parasitism in which the host is the whole biophysical environment exploited by the overpopulating species. There are various degrees of parasitism in which the parasite is partially tolerated by the host. A commensal (such as the human forehead mite *Demodex*) is a parasite which generally cannot survive without the specialized environment provided by its host, but which (usually) neither benefits nor harms its host. Mutualists are organisms which benefit each other in the precise sense that each somehow increases or maintains the other's reproductive success. Mutualistic relations can be facultative (optional) or obligate. In animals such as humans with a complex neurology, mutualistic relations, if they occur, tend to be learned rather than instinctual or biochemically mediated. (In humans, therefore, the maintenance of mutualism is partially a function of culture, broadly

understood.) Highly obligate mutualisms sometimes lead to *symbiogenesis*, the creation of a new type of organism. In symbiogenesis, branches of the tree of life occasionally converge, contrary to the classical Darwinian picture where they always keep splitting. L. Margulis (1998) suggests that the formation of symbiotic associations could be a source of evolutionary novelty comparable in importance to mutation, but this view is highly controversial.

Margulis has played a leading role in demonstrating the importance of symbiogenesis in cellular evolution (Margulis, 1998). There is, by now, a large body of evidence supporting serial endosymbiosis, the view that eukaryotic cells are highly obligate mutualistic associations of bacteria.

Margulis and E. Odum (1971) highlighted the importance of the “symbiotic transition” in which an opportunistic parasite can move along the symbiotic scale from parasite, through commensal, to obligate mutualist. Such a transition from parasite to mutualist played an essential role in the evolution of eukaryotic cells, in which parasitic bacteria apparently became organelles of the cells they had originally preyed upon. Symbionts will coevolve even if they do not necessarily become mutualists, because a host will evolve to defend itself from a parasite, while the parasite may evolve to cope with the host’s defenses.

There is evidence from cell biology that a transition from parasitism to mutualism will be favored in environments that are closed in a way that leads to resource restriction (Margulis and Sagan, 1995), and this is consistent with Kropotkin’s observation (1902/1989) that mutualism is favored over competition in harsher environments. However, the conditions under which mutualism and symbiogenesis are adaptively favored remain unclear, and this remains an important unsolved problem that has much significance for ecology.

5. Ecosystems as Dissipative Structures

The earliest conceptions of the ecosystem defined it in terms of dynamically maintained homeostasis, energy circuits, and feedback loops. Recently, a number of authors have extended this approach by controversially suggesting that the problem of explaining ecosystem stability is the same as the problem of explaining how life itself is thermodynamically possible (Schneider & Sagan, 2005; for a skeptical response, see Farmer, 2005). Schrödinger (1944) noted that any living system apparently violates the Second Law of Thermodynamics within its boundaries, for it maintains a highly ordered or low entropy internal state by the expenditure of energy released through its metabolism. The key to the puzzle, Schrödinger realized, is that living systems shed entropy by actively expelling waste heat. Living organisms and ecosystems belong to the class of *dissipative structures*, far-from-equilibrium, highly ordered states that can only exist where there is a generous externally-applied flow of free energy from a source such as the sun. This suggests a notion of the ecosystem as a dissipative structure – an “eddy,” as it were, in the relentless flow of energy down entropic gradients. Paradoxically, an ecosystem’s stability is a function of how efficiently it can degrade free energy. Presumably the ecosystem maintains its highly ordered internal cycling of energy because that is the most efficient way for it to produce waste heat.

The dissipative-structure view of ecosystems can be combined with the symbiotic view. An ecosystem proper can be understood as a mutualistic association of organisms, whose mutualistic symbiosis is defined by their thermodynamic relationships (Peacock, 1999). On this view, mutualism involves sharing free energy and thereby implies dynamic coupling between members of a mutualism; the system acts, as it were, as a quasi-rigid body under selective pressure. By combining the non-equilibrium thermodynamic view with the symbiotic understanding of ecosystems, we arrive at the view of ecosystems as quasi-stable dissipative structures, characterized by a circulation of energy, information, and/or materials, in such a way as to confer selective advantage on the association as a whole.

The dissipative-state theory of ecosystems suffers from two related problems. First, it has not so far been shown to have much quantitative predictive power. Second, non-equilibrium statistical mechanics still lacks its Boltzmann, someone who could provide a clear explanation of the principles of the theory in purely statistical terms. In equilibrium thermodynamics it is easily seen that higher-entropy states are more probable. (For instance, air pressure in a closed room is uniform simply because there are enormously more ways for the air molecules to be distributed approximately evenly than unevenly.) But in what sense are there more microstates associated with the vortical motion of a tornado than with turbulent motion? Why would cyclic motions be entropically favored simply because they move material through the system faster? Until such questions can be answered in a rigorous and clear way, the application of dissipative-systems theory to ecosystem dynamics remains an intuitively plausible but still essentially analogical and qualitative hypothesis.

5.1. *The Gaia hypothesis*

Possibly the most speculative or visionary conception of the ecosystem is the Gaia hypothesis. This is the proposal that it is scientifically meaningful to regard the entire planetary biosphere as a single, self-regulating ecosystem. In its modern form this hypothesis was devised by J. Lovelock, D. Hitchcock, and L. Margulis (Lovelock & Margulis, 1974; Lovelock, 1988; Lovelock, 2003). The Gaia hypothesis was suggested by the observation that many components of the earth's atmosphere are so far from chemical equilibrium that their relative abundance could only be explained by the mediation of life. The atmosphere, Lovelock argues, is a "contrivance" (in the sense that a coral reef or an ant-hill is a contrivance) which maintains temperature, atmospheric composition, and other variables suitable for life by means of an elaborate network of feedbacks. Lovelock's Daisyworld model (1988) demonstrates, apparently, that a sufficiently diverse system of biota could generate its own set-points, so long as the planet remained within a fairly wide range of solar input.

Lovelock has tended to explain Gaia as a biologically mediated control system, but Gaia can also be understood either from a thermodynamic point of view (as a dissipative structure) or the symbiotic point of view (as a planetary-scale mutualism). Opinions differ strongly on whether the Gaia hypothesis is scientifically well founded or arrant speculation. One of its virtues is that it provides a plausible explanation for the maintenance over billions of years of the far-from-equilibrium conditions in the earth favorable to life. However, the Gaia hypothesis has so far been short on predictive power. It

is also difficult to square with evolutionary theory; T. M. Lenton (1998) offers a detailed attempt to work out how self-regulation on a planetary scale could be brought about by natural selection.

6. Ecosystems and Evolutionary Biology

The idea that organisms are subject to selective pressure by their biophysical environments is one of the central tenets of Darwinism. What ecology, and ecosystem theory in particular, adds to this is a special emphasis on the fact that organisms can affect their environments as much as the environments affect their organisms. What one might call the “post office” theory of the ecological niche holds that the survival problem for a species consists in adapting itself to a preexistent slot in a much larger backdrop ecosystem. (No one literally believes this any more, but it is a useful approximation when the back-reaction of the organism on its environment is not very important.) The central fact of ecology, however, is that the lines of influence between organism and ecosystem run both ways: organisms adapt to their ecosystems, but they also adapt their ecosystems to themselves, sometimes in ways that are favorable to their future survival, sometimes not. The way in which organisms alter their ecosystems then poses additional survival challenges or opportunities for themselves and other species, and this must be taken into account in any complete picture of the evolution of life.

The existence of self-supportive and cooperative biological systems, which ecosystems are presumed to be on many accounts of ecosystems theory, is a challenge for evolutionary biology. In the late nineteenth century the Russian emigré ecologist P. Kropotkin (1902/1989) criticized the view of T. H. Huxley that “the animal world is on about the same level as a gladiator’s show.” (Huxley, 1888/1989, p. 330). Kropotkin pointed out that cooperation occurs at many levels in nature, and argued that fitness can just as easily amount to the ability to cooperate as well as to compete, depending upon the demands of the ecological context.

The Kropotkin/Huxley controversy is being replayed today. If it is correct to speak of the persistence of ecosystems as a form of adaptive success (as Tansley and many other ecosystem theorists believed) then that fact might be difficult to understand from the narrow adaptationist/selfish gene point of view, which tends to be skeptical of natural selection acting beyond the level of the individual organism. [SEE THE UNITS AND LEVELS OF SELECTION]. Could ecosystem stability (which could be read as the tendency of an ecosystem to *survive* over time) be a sign of “group selection”? (Group selection in this context would mean the tendency for organisms to be favored by natural selection partially on the basis of their ability to contribute symbiotically to ecosystem functioning.) The prevalent view in evolutionary theory today is that there is group selection but it is not a dominant factor in evolution. (Sober & Wilson, 1998.) However, this view would have to be revised if ecosystem theorists (in alliance with evolutionary biologists) can succeed in showing that the evolution of many organisms cannot be understood unless their traits were selected for, in important part, on the basis of their ability to contribute to the relative stability and persistence of the ecosystems which support their existence. This remains an open and controversial question. [SEE COOPERATION].

7. Skeptical Critiques of Ecosystem Theory

Ecosystem theory has been criticized from a number of philosophical and scientific directions. American plant ecologist H. Gleason (1882–1975) was an early skeptic about the prevailing theories of F. Clements and others according to which biotic communities were “superorganisms” with definable internal parts, a coherent structure, and law-like behavior (Keller & Golley, 2000). Gleason proposed his “individualistic hypothesis” according to which the plant association was merely a descriptive convenience, and the character of every biotic community in nature was unique and dependent upon statistical variations and the vagaries of individual organisms within it.

M. Sagoff (2003) offers an up-to-date critique of ecosystem theory that is much in the spirit of Gleason. Sagoff points out that there are two complementary trends in many branches of science. Physics usually takes what Sagoff calls a top-down approach in which one attempts to understand the complexities of nature in terms of simple mathematical laws of wide applicability, and from which predictions are derived deductively. Biology perforce tends to use a bottom-up approach which sees nature as irreducibly complex; predictions are made statistically, and every general rule is expected to have exceptions. Sagoff argues that ecosystem ecology is in effect an attempt to turn ecology into a branch of physics, and charges that much of ecosystems theory is circular, vacuous, and incapable of generating testable predictions. While the New Ecologists define ecology as nothing other than the study of ecosystems, Sagoff, in effect, proposes that there is such a thing as ecology without the ecosystem. K. deLaplante and J. Odenbaugh (in press) offer a response to Sagoff’s critique. Whether or not Sagoff is entirely correct, this debate should usefully spur ecosystems theorists to a renewed effort to demonstrate the relevance of their model-building to the real world of ponds and people.

For a skeptical view of the notion that nature can be viewed both as a biophysical machine and as a superorganism, see Botkin (1990).

Another approach that is critical of the dominant systems paradigm is non-equilibrium ecology, which charges the New Ecology as exaggerating the degree of stability of ecosystems. These authors insist that real ecosystems such as grasslands (as opposed to idealized mathematical models) are rarely close to equilibrium and cannot be managed effectively were they expected to be such. (Walker & Wilson, 2001; Rohde, 2005.) E. Odum responded that fluctuations within localized systems or even periods of time as long as the glacial epochs should not distract us from the fact that the earth system as a whole has maintained sufficient stability over hundreds of millions of years to permit the continuance of life.

The notion of the ecosystem could also be subjected to the same sort of skeptical critiques that have been directed toward the reality of other scientific entities. The causal workings of ecosystems must often be inferred by indirect evidence; even the descriptive ecosystems of the working field ecologist are to a large extent inferential and theory-laden. However, ecosystems do not seem to have caught the attention of instrumentalists or antirealists within the philosophy of science.

There are also post-modernist and constructivist critiques of ecology (e.g., Evernden, 1992). Keller and Golley (2000, p.13) argue that “scientific ecology . . . is at odds with social constructivism,” and defend the view of an “extrasubjective, transcultural

meaning in nature which humans can [however imperfectly] discern." If Sagoff is right, however, then ecosystem theory leaves itself open to constructivist criticism by not doing a good enough job of making its concepts operationally meaningful and testable.

8. Ecosystem Integrity and Health

Bodily health in the medical sense can be given a sharp definition as a state of homeostasis (actively maintained equilibrium) that fulfills certain quantitative norms. There is a substantial literature exploring parallels between bodily health and the health or integrity of ecosystems (Costanza, Norton, & Haskell, 1992).

The concept of ecosystem health plays an important role in some conceptions of environmental ethics. Aldo Leopold's influential *Land Ethic* (1966) elevates the "biotic community" (conceived of as a symbiotic "energy circuit") to an object of ethical regard, and proclaims that a "thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." This is one extreme along a continuum of views about ethical obligations to the environment. One could well have regard for the well-being of the environment that supports human life without subscribing to the theory of the ecosystem as energy circuit. Also, the idea that ecosystems can be treated as objects of ethical regard could not be in itself a *sufficient* basis for environmental ethics (as Leopold's concise wording seems to suggest); whales do not merit protection *merely* because they are parts of an oceanic ecosystem. A further problem is that Leopold freely mixes normative concepts such as "beauty" with descriptive concepts such as "stability." However, Leopold's ideas draw attention to the important notion of ethics as having a crucial role in any human-land symbiosis. For more on the aesthetics and ethics of ecology, see Peacock (1999b) and Schmidtz and Willott (2002). For an up-to-date discussion of the very difficult problems of elucidating the meanings of ecological stability and biodiversity, and the relations between them, see Sarkar (2005a). [SEE COMPLEXITY, DIVERSITY, AND STABILITY].

If anything like E. Odum's conception of ecosystems is correct, the general principles for maintaining ecosystem health would include the preservation (and perhaps judicious repair) of existing pathways of energy and materials. It could be quite important for conservation biology to be able to identify ecosystems in terms of the circuits of energy, information, and materials that define them, and one would want to avoid misguided attempts to "improve" an ecosystem that result in severing those circuits. Certainly both advocates and critics of ecosystems theory would agree that sensitivity and caution are essential in any attempt to apply ecology to real situations where human well-being is at stake.

9. Sustainability from an Ecosystems Point of View

One of the most important applications of ecosystems theory is to help define a possible basis for the sustainability of the global ecology that supports the human species and its complex global civilization. In 1987, the World Commission on Environment and

Development (WCED) published the influential Brundtland Report. This document argued that two interrelated factors constitute the world's current ecological/economic crisis: poverty and the threat to humanity caused by breakdown of "ecosystem services" caused by human over-exploitation of the earth system. It is development (exploitation of the found ecology for human purposes) that presumably is necessary to eradicate poverty, and yet it is precisely exploitive development that undermines the capacity of the earth system to sustain humans indefinitely.

As a solution to the twin imperatives – to advance human prosperity and to respect ecological limitations – the Brundtland Report advocated *sustainable development*, which it defined as "development that meets the needs of the present without compromising the ability of future generations to meet their own needs" (WCED, 1987). Many observers (e.g., Livingston, 1994) have argued that this notion is incoherent. *Prima facie*, the phrase sounds oxymoronic, since the very notion of development seems to imply exploitation of a natural resource for human ends in such a way as to permanently use it up.

The weakness of the Brundtland Report is that it did not define "development" precisely. The Report itself implicitly assumed that development must amount to tapping into the resources and free energy of nonhuman ecosystems: "Development tends to simplify ecosystems and to reduce their diversity of species" (WCED, 1987, p.46).

The question is therefore whether sustainability can amount to anything other than rationing. According to several influential authors, we are in a lifeboat with a finite initial supply of resources which cannot be replenished by any conceivable human action (Georgescu-Roegen, 1977; Daly, 1985; Rees, 1987. For a more nuanced version of the lifeboat picture, see Meadows, Meadows, & Randers, 1992). This neo-Malthusian view is often stated in terms of thermodynamics. H. Daly, for instance, states, "Low entropy is the ultimate resource which can only be used up and for which there is no substitute" (1985, p.90), and according to W. Rees, "The thermodynamic interpretation of the economic process therefore suggests a new definition of sustainable development . . . [as] development that minimizes resource use and the increase in global entropy" (1990, p.19). These authors adduce in support of their lifeboat view of sustainability that version of the Second Law of Thermodynamics which states that entropy can never be decreased in a closed, isolated system. This is not the form of the Second Law that is relevant to ecology, however; the earth system is not thermally isolated, since it is bathed by more solar and geothermal energy than it can possibly use. The lifeboat view of sustainability thus seems to be founded on an elementary misunderstanding of the physics of ecosystems; it is the ecology of the thermos flask. In fact, it is not negentropy (negative entropy, a measure of order), but the capacity of the autotrophic components of the earth system to generate negentropy, which is the "ultimate resource." It is not immediately obvious that humans cannot contribute positively to this in many ways.

There is a sound notion behind the Brundtland definition of sustainable development, despite its unfortunate formulation. The aim is to avoid the *ecological bind*: the tendency of an organism to undermine its own future by the very means that give it a survival advantage in the first place. From the viewpoint of ecosystem theory, it therefore seems natural to define sustainability in this sense in terms of symbiotic concepts, since the biotic relationships that do have the tendency to self-perpetuate are precisely

those that are mutualistic, or part of larger symbiotic cycles that are mutualistic. Transitions from parasitical to mutualistic symbioses are frequently noted (Odum, 1971), especially when resources are restricted (Margulis & Sagan, 1995), although this phenomenon requires further scientific study. The achievement of sustainability for human culture would amount to a symbiotic transformation from parasite to facultative mutualist.

This notion of human mutualism is not merely a metaphor; rather, it has the concrete sense that the means by which we garner the resources we need would be also the means by which we sustain the environment. G. A. Whatmough (1996, pp.418–19), citing the horticulturally intensified ecologies of rural England and Japan, observes that “the increase in the density and luxuriance of the whole spectrum of local flora and fauna [was] an entailed consequence of the techniques by which those populations then produced their necessary supplies . . . It can only be by some such means that our species can possibly transform our present parasitic dependence on the found ecology to some kind of symbiotic alternative.”

There are two components to sustainability: the conservation and preservation of existing ecosystem function, and (more controversially) the enhancement and intensification of the ecosystem. Although the concept of ecosystem intensification was mooted by A. J. Lotka in 1922, it has received very little discussion. Lotka argued that “suitably constituted organisms [may] enlarge the total energy flux through the system. Whenever such organisms arise, natural selection will operate to preserve and increase them” (1922, p.147). On Lotka’s view, an ecosystem may be thought of as a sort of battery that can be charged up by its autotrophs.

At first glance it might seem that humans are inherently incapable of such a mutualism, since we are obligate heterotrophs. However, from a thermodynamic point of view the distinction between autotrophs and heterotrophs is not as sharp as is usually supposed. Consider how an algae cell shunts solar energy into the ecosystem it supports. It has within its body an elegant biochemical mechanism which captures solar energy and uses it to reduce CO₂ and H₂O to carbohydrates and free oxygen. The algae uses a small proportion of the captured energy to support its own metabolism, and the rest is ultimately made available to other organisms in the ecosystem. In effect, the algae acts like a *valve*, diverting part of the external flow of energy into the system and thereby increasing the total circulation of usable energy and materials in the system. What is definitive of this function is the valving capacity. Valves expend far less energy than they can divert or modulate, and there is in general no theoretical limit to an amplification factor.

It is incidental that the mechanism by which the algae diverts energy into the ecosystem is inside its own cellular envelope. A heterotroph (not itself photosynthetic) can do the same thing by manipulations carried on outside its body. Heterotrophic life vastly multiplies the number and kinds of niches within which autotrophic life can operate. Humans can contribute to this process as well: we can, for instance, do things such as plant trees or regenerate topsoil, and if these things are properly done they can divert far more solar energy into the planetary ecosystem than they require for their execution.

Eugene Odum has expressed the problem of sustainability from the ecosystems point of view:

Obviously it is time for man to evolve to the mutualism stage in his relations with nature . . . if understanding of ecological systems and moral responsibility among mankind can keep pace with man's power to effect changes, the present-day concept of "unlimited exploitation of resources" will give way to "unlimited ingenuity in perpetuating a cyclic abundance of resources." (1971, p.36)

On this view, sustainable development – or more precisely the development of sustainability – amounts to the rearrangement of human affairs so that by means of the techniques we use to survive on this planet, we “pump up” the earth system instead of drawing it down.

Philosophers have an important role to play in helping to define the vision of moral responsibility that could help make this symbiotic transition possible (Norton, 2005). A sense of responsibility usually begins with an awareness of what is required for self-preservation (though it need not end there). As Odum indicates, any such sense of responsibility must be coupled with a sound scientific understanding; the *scientifically informed* sense of ecological moral responsibility called for by Odum is therefore, for humans, nothing other than an indispensable survival tool.

If, on the other hand, scientific and philosophical critiques of ecosystems theory show that Odum's vision is *not* tenable, then humanity needs to know it, and soon, for the study of ecology possesses a particular urgency not shared by most other branches of theoretical science.

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