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Ecology, thermodynamics and H.T. Odum's conjectures

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Abstract. The central rôle of energy in all life processes has led to the development of numerous hypotheses, conjectures and theories on the relationships between thermodynamics and ecological processes. In this paper we examine the theoretical and empirical support for these developments, and in particular for the widely published set of thermodynamic conjectures developed by H.T. Odum, in which the maximum power principle is put forward as a generic feature of evolution in ecosystems. Although they are widely used, we argue that many of the ecological studies that have adopted the ideas encapsulated in Odum's work have done so without being aware of some of the fundamental problems underlying this approach. We discuss alternative ways in which a general available-work concept could be constructed for use as a numeraire in an energy-centered ecological theory or paradigm. In so doing, we examine what is meant by material accessibility and energy stocks and flows with respect to traditional food web and food chain theories, and relate these to results from the evolutionary dynamics of ecosystems. We conclude that the various forms and uses of energy bound up in essential ecosystem processes present a formidable obstacle to obtaining an operational definition of a general, aggregated available-work concept, a prerequisite for the systems approach of Odum and others. We also show that the prototypical derivations of the maximum power principle, and its interpretation, are contradicted on many scales both by empirical data and models, thereby invalidating the maximum power principle as a general principle of ecological evolution. The conclusions point to the fundamental problem of trying to describe ecosystems in a framework which has a one-dimensional currency.

Key words: Critique – Systems ecology – Energy numeraire – Exergy

A key concept among those developed within thermodynamics is that of energy in its various forms. One reason is that energy is pervasive and perpetual. Whatever happens in the world may be described either as a transfer of energy from one place to another, or the transformation of energy between different forms. In particular, all biological processes involve at least one form of energy, and usually several (Table 1). At the outset, then, it must be made clear that in this paper we deal with thermodynamic concepts in a literal, physical sense, and

Table 1. Characteristics of energy in ecosystems; based upon Miller 1981

Types of energy flows found in ecosystems:

- Solar radiation (diffuse and direct)
- Photosynthesis
- Ingestion (mainly chemical energy)
- Assimilation of chemical energy in food
- Chemical transformations in organisms
- Egestion (chemical energy)
- Energy released by decomposition
- Energy stored in sediments or (?) peat
- Longwave radiation from the atmosphere
- Longwave radiation from the organisms in the ecosystem
- Longwave radiation from the abiotic environment excluding the atmosphere
- Sensible heat given off to or received from the atmosphere
- Sensible heat given off to or received from the hydrosphere
- Heat flow into and from the ground
- Heat of condensation
- Heat of melting and evaporation
- Wind

Variations in insolation:

- Diurnal cycle: from zero before sunrise to a peak and then back to zero
- Change in direction of the beam component during the day
- Flux density, direct/diffuse ratio, spectral distributions due to clouds; type and amount of clouds vary with weather conditions
- Seasonality of flux density and spectral compositions
- Seasonal change in azimuth angle
- Site-specific depletion enhancement, e.g. due to aerosols

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not with the common metaphorical use of terms such as entropy and energy.

Energy is a convenient concept. The continuous flow of primordial energy from the sun to the earth is a basic resource for life on earth, and at the physiological and biochemical level, energy inputs, mostly in chemical form, are also regarded as essential resources. Energy is thus a sufficient quantity for describing many essential phenomena, such as primary productivity and growth (Calow 1977). Even a detailed physical or chemical description of a complex process, such as the digestion of food, can be more simply pictured as the transformation of the chemical energy within the food into chemical, thermal and mechanical energy. Indeed most biochemical processes cannot be described without using the concept of energy. But whilst energy flow can be construed as an appropriate variable in the analysis of resource utilization, most ecosystem analyses use energy in an undifferentiated form.

In a survey of the members of the British Ecological Society (Cherret 1989), energy flow ranked third in importance among concepts in ecology (after the ecosystem and succession). This is hardly surprising given the dominant rôle that ecologists such as Hutchinson and his students Lindeman and H.T. Odum have played in ecological circles. In fact, in 1964, Odum's brother, Eugene P. Odum, nominated energetics as the new ecology, and ever since the publication of their collaborative book in 1953 (Odum 1953), H.T. Odum has repeatedly argued for the idea that energy is a central object of study in ecosystem analysis. In the approach adopted in the book *Systems ecology* H.T. Odum (1983) attempts to use a thermodynamics-based lingua franca to explain ecosystem behaviour, and as support for his arguments, puts forward numerous conjectures and makes several claims that new, fundamental or universal, principles of ecosystem development have been discovered. Of course other thermodynamic concepts have also been discussed (Gallucci 1973), including entropy (Brooks and Wiley 1988) and information theory (see, for example, Ulanowicz 1986), as well as the consequences of thermodynamics for the conceptual structure of evolutionary theory (Wicken 1985), biological growth and organization (Morowitz 1968; Zotin 1985) and the origin of ecosystems (Johnson 1981). Nonetheless, many of the current formulations of ecological energetics are closely related to the general ideas in Odum's systems ecology.

One of the key points we address in this paper is the rôle of energy in ecosystem evolution. Howard Odum takes it as central, and has argued for the maximum power principle as a community-wide optimization principle; from this Odum asserts that there is a fitness function, expressed in terms of energy, for natural group selection. In support of this claim, Odum refers to the work of Alfred Lotka (1922a) who stated:

> "The first effect of natural selection thus operating upon competing species will be to give relative preponderence (in number or mass) to those most efficient in guiding available energy in the manner indicated. Primarily the *path* of the energy flux through the system will be affected.
>
> But the species possessing superior energy-capturing and directing devices may accomplish something more than merely to divert to its own advantage energy for which others are competing with it. If sources are presented, capable of supplying available energy in excess of that actually being tapped by the entire system of living organisms, then an opportunity is furnished for suitably constituted organisms to enlarge the total energy flux through the system. Whenever such organisms arise, natural selection will operate to preserve and increase them. The result, in this case, is not a mere diversion of the energy flux through the system of organic nature along a new path, but an increase of the total flux through that system. ... This may be expressed by saying that *natural selection* tends to make the energy flux through the system a maximum, so far as compatible with the constraints to which the system is subject".

But Lotka also went on to say that: "It is not lawful to infer immediately that *evolution* tends thus to make this energy flux a maximum. ... It remains to be established just what is the significance of the phrase compatible with the constraints which [...] modifies the maximum principle enunciated."

This caution and others (Lotka 1922b, 1924 pp. 357–358) about inferring that evolution maximizes an energy flux was largely ignored by Odum, as was the recognition of the importance of other constraints. Odum's ideas thus differ dramatically from the original intent of Lotka.

Because the development of Odum's work is more fragmented than many ecologists realise, one object of this paper is to provide a thorough analysis of his conjectures about thermodynamic principles which he claims to be relevant to ecological theory. To be of benefit, criticism should be constructive; we have therefore made a particular effort to extract what seems to be scientifically useful in Odum's ideas. We have adopted the methodology of O'Neill et al. (1986, p. 74), who propose several tests to evaluate a new ecological theory; the theory must: (i) be internally consistent; (ii) not be adopted simply because of success in other fields; (iii) agree with known properties of ecosystems and (iv) be capable of producing new and testable hypotheses. In our analysis we have constrained ourselves to ideas which concern ecology, arguing that the remaining assemblage of Odum's hypotheses on economics, sociology and technology lie outside the scope of this discussion.

The paper broadens out the argument and looks at the problems of using energy as a universal currency in ecology. Energy plays many important but different rôles in ecosystem production and consumption: in this paper we concentrate on the consumptive part of the ecosystem and in particular animal ecology. Such a separation is motivated by the fact that global production is dominated by photosynthetic systems, in which the primary conversion is from light energy (high-energy photons) to chemical energy, whereas consumption is dominated by transformations of one form of chemical energy into another, and from chemical energy into thermal energy and radiation (low-energy photons) (Lehninger 1971).

The interaction of photons with matter in photosynthetic processes has special characteristics which require a different treatment.

A theoretical framework

Without a coherent terminology and theory, scientific analysis is virtually impossible. The intent of this section then is to clarify some of the concepts and terms which are essential to the biological and ecological application of thermodynamics. We particularly look at the physical concepts which Howard T. Odum relates to thermodynamics in his ecological ideas of systems ecology (Odum 1983).

We first discuss the ideas of using a resource concept, for example *useful energy*, as a means to allow an *agent* to reach a specified *goal* or set of objectives. The utilization of diverse, sometimes general, resource concepts as a basis for the development of theories and descriptions has had a long history in ecology (Hutchinson 1957; MacArthur and Wilson 1967; Tilman 1982); this interest has focused mainly on resources in limited supply. Pomeroy and Alberts (1988) trace the ecologist's preoccupation with limiting factors back to Liebig (1855). As they point out, it is generally recognised that at the ecosystem level the idea of a single limiting factor is too simplistic; rather, the normal situation is one in which several resources embody limits with important interdependencies and spatio-temporal characteristics.

In economics, the central concept of value is encapsulated in the term *numeraire*. This signifies the function of money as a common, universal currency, a measure of value or a unit of account. From this perspective, it is easy to see why ecologists would be tempted to speculate on a physical concept, for example *useful energy*, to play the same rôle in ecology. As we shall see, this is one of the main ideas of Odum's systems ecology.

Useful energy occurs in many forms and to differing degrees according to agent, objective and situation. An animal moving into the sunlight may achieve the same heat gain as an animal oxidizing carbohydrates from its food, but the latter process can also release energy for locomotion. Because the concept of useful energy differs for producers and consumers, an ecological theory based on this concept will not be internally consistent; it will also be non-general or incomplete, and will thus fail the first criterion proposed by O'Neil et al. (1986).

Ecological resources – A physical perspective

Every animal has a resource base which has to be partitioned amongst its many different needs: this base can be described in terms of physics, chemistry and biology, e.g., the number of available reproductive partners. Although many resources are in limited supply, only a few are relevant to an organism at any one time. In physics, thermodynamics is the most important theoretical framework for describing and analysing resources and their utilization. Thermodynamics is built around quantitative measures of materials and energy; whenever a thermodynamic framework is used, energy is automatically considered.

In biology, the resource space is denoted by the term niche (Hutchinson 1957; Whittaker and Levin 1975). Originally Grinnell (1917) used the idea of a nîche to describe the habitat space and habits of birds as a subdivision of the environment, whereas Elton (1927) saw the nîche as the animal's rôle in the community, defined in relation to its position in the food web and its enemies. Gause (1934) introduced the idea of competition between species with overlapping resource demands in the ecological debate, but it was Hutchinson (1957) who formally put these ideas together. He said that ideally the activity range of each species could be defined in an infinite-dimensional space, where every measurable feature of the environment, including physical, chemical and biological features such as availability of prey species or the potential for other species to provide background camouflage, was given a co-ordinate. The region in this space where the fitness of an individual was positive represented that individual's niche. If there were *n* dimensions, then the niche was defined in an *n*-dimensional space. It is already clear by this stage that any one-dimensional representation of this *n*-dimensional entity leads to a significant loss of information.

Overlap of niches, the measurement of the breadth (the variety of resources used) and the height (the level of activity attained) has remained a key element in community ecology for many years (Pianka 1974; Schoener 1989). But our ability to define a niche does not go hand in hand with measuring it; niche co-ordinates are usually ambiguous, and it is not known how the addition of dimensions might shrink or expand their intersection. Resources are often mixtures of continuous and discontinuous variables, so that as Roughgarden (1972, 1974, 1979) and others have pointed out, there is no direct relationship between the resource utilization of populations of individuals and those of the entire species.

One way out of these problems might be to adopt a more dynamical approach to studying ecosystems, so as to be able to define such features as stability, resilience and basins of attractivity to understand the long- and short-term changes in ecosystem functions (Johnson 1981; Hogg et al. 1989; Yodzis 1989; Rand et al. 1992). Individuals within an ecosystem use resources opportunistically to achieve certain sets of goals: if resources become scarce either these goals or the agents themselves will tend to change. As a physical resource theory can express the agent, the means and the goals within one language, this could lead to a dynamical extension of the niche concept. But the *modus operandi* is still that of mathematics and physics, so care must be taken in the use of physical concepts to analyse systems falling outside these areas.

Thermodynamic numeraires

This section is meant to highlight some key issues pertaining to the use of thermodynamic concepts such as energy or work as numeraires in ecological theory. Our exposition is closely related to the conceptual frameworks of Reif (1965), Woods (1975), Denbigh (1981), Moran (1982) and Eriksson et al. (1987).

Thermodynamics in its classical[1] form is a phenomenological theory based upon observations of common experience. It is usually formalized by four thermodynamic laws, and from these the rest of thermodynamics can be deduced, given a set of conventions for specification of reference levels to enable appropriate quantifications.

The *zeroth* law is vital for the formalization and operationalization of the property *temperature*. The temperature concept typically involves two reference levels set by convention.

A common formulation of the *first* law states that when a closed system undergoes an adiabatic process (i.e. a process without transfer of heat), the amount of work depends on the initial and final states of the system only; it is independent of the details of the process. This formulation leads to a clear definition of the *energy* concept, but it is nevertheless necessary to assign a specific value to some reference state, in order to be able to calculate absolute energy values for any state. Classical thermodynamics does not indicate how such a reference state should be chosen[2].

Except in rare cases processes are not reversible; there is always some loss of a quality associated with the constant quantity, energy; the energy is dissipated. The thermodynamic formalization of this phenomena is the *second* law, and the associated concept is *entropy*. The related *third* law of thermodynamics, which is based on microscopic theory and statistical mechanics, defines an absolute scale for entropy. In simple terms, entropy can be seen as a measure of disorder, but it is only in the framework of the microscopic basis of thermodynamics that such a linkage can be given a precise meaning. If energy passes the boundary of a system, which is typical for a living system, then the energy in the system need not be constant; furthermore the entropy of the system may decrease.

The two basic axioms of thermodynamics are very simply put: (i) energy is conserved for all systems, (ii) in a closed system the entropy increases to a maximum. These axioms give us two important perspectives on energy. The first focuses on the amount of energy a system contains, which is often divided into the type of energy involved (e.g. kinetic, potential, chemical, thermal), whilst the second focuses on the potential of that energy to be turned into some kind of *work*. In thermodynamics, work is usually defined in terms of the fundamental, physical concepts of mechanical force and distance. Work is a distinctive energy form in that it is associated with zero entropy.

A generic model of both classical thermodynamics and statistical mechanics consists of a system embedded in an *infinite* reservoir. The system delivers mechanical work to a work reservoir through reversible processes mediated by a converter. The use of a system with constant intensive thermodynamic variables is an important limitation in the derivation of all free energy concepts. Obviously no such system occurs in nature.

In a particular situation, energy may be wholly or partly in a form incapable of delivering any chemical, mechanical or other work; thus, one of the first questions to be asked is just how much work a system can deliver. Today, there are several kinds of maximal work or free energy measures in use. Typically each of them is used extensively by a certain scientific or technical discipline for which it has convenient properties.

Free energy. In biology, the most common maximal work measure is probably the Gibbs free energy, G. It is often used in chemistry, since it measures the maximal work output, which equals the difference in G between initial and final state, ΔG, of a closed system where isobaric and isothermal chemical reactions occur. In general, determining ΔG for a particular reaction involves the so-called *standard free-energy change* for the chemical reaction, which is defined on the basis of the values of the chemical potentials of the reactants and products in a particular chosen *standard state*; Denbigh (1981) elucidates the key conventions. As Battley (1987) and others have pointed out, the conventional standard state in aqueous solution is often unsuitable for the calculation of energy changes in biochemical reactions, mainly because such states are too far away from those actually encountered under natural conditions.

For processes inside a single, practically isothermal, organism, the use of Gibbs free energy as the basic free-energy concept is a natural and often reasonable approach. However, when the processes involving interactions with the organism's environment are important, we need a more appropriate free-energy concept which takes the rôle and properties of the environment into account.

Exergy. Limitations of the traditional free-energy concepts have led to the search for a more general measure of a system's maximal work yield. Really the measure

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[1] We need only deal with classical thermodynamics here. However, one should note that the derivation of conventional non-equilibrium thermodynamics assumes that, locally, the systems behave like equilibrium systems; it is based on a division of the system into small volume elements that are assumed to be close enough to equilibrium, i.e., assuming *local thermodynamic equilibrium* (LTE). The irreversible processes are confined to the boundaries between the volume elements, sometimes with the exception of irreversibilities in chemical reactions. For the LTE approach to be valid several conditions on the temporal and spatial characteristics of the system and the processes must be fulfilled, see, e.g. the discussions by Woods (1975) and Westerhoff and van Dam (1987). The theory based upon the assumptions of LTE and of linear relations between the thermodynamic flows and forces was to a large extent completely developed by the early 1960s [see e.g. de Groot (1952) and de Groot and Mazur (1962)]. There then followed attempts to apply these ideas to biological systems (see e.g. Katchalsky and Curran 1965), but it soon became clear that this theory was only of limited value in this context. One reason for this is that for coupled chemical reactions the range where the linear approximations are valid is quite small. In spite of these problems, linear chemical non-equilibrium thermodynamics is a major source of inspiration for H.T. Odum's general approach

[2] This can only be found from first principles in the context of statistical and quantum mechanics

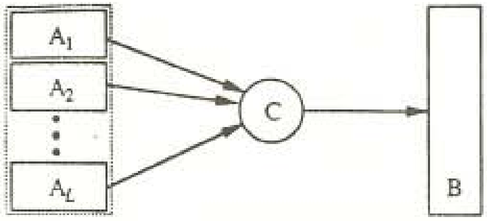

Fig. 1. A schematic model for a derivation of exergy. The system *A* consists of *L* finite subsystems $A_1, \ldots, A_L$, each in *internal* thermodynamic equilibrium, which may interact *reversibly* through the converter *C*, delivering mechanical work to the work reservoir *B*

needs to be applicable to more general processes, involving interactions, either internally or with other systems. The most general measure to date, and thus the prime candidate for use as energy numeraire in ecological theory, is to be found in the concept of *exergy*[3].

To find the exergy in an arbitrary system, A, we need to know the maximum amount of work that can be delivered to a work reservoir, B, in connection with reversible internal processes in A (see Fig. 1). One important operational consideration is that the exergy in this general sense is never negative. In contrast to energy, exergy is not conserved. It is lost in every process through various forms of irreversibilities. For example, as the chemical exergy fixed by the plants is distributed through the food web, it is dissipated and destroyed until next to nothing remains: peat bogs and petroliferous sediments, for instance, retain a very small proportion of this total energy.

The problem in Fig. 1 is easily solved if all the energy transfers occur via matter (Eriksson et al. 1987). There are still unresolved problems, however, when it comes to the interaction of radiation with matter, as in photosynthesis, partly because the exergy of radiation is a complicated subject in itself (Karlsson 1982). Unfortunately, in ecology energy flows in the form of radiation are the norm rather than the exception (see Table 1); to complicate matters further, the spectrum is typically significantly different from that of black-body radiation. Furthermore, ecological systems are rightly notorious for their resistance to the kind of compartmentalization presumed in Fig. 1.

Perhaps the most significant problem in applying the exergy concept in any of its forms to ecology is that it is often based upon a specific *reference environment*, often appropriately denoted *dead state*, which has to be in internal thermodynamic equilibrium. This is not the case for natural systems. One way of handling this difficulty is to construct a hypothetical reference system whose properties are those that the actual system would acquire if it were to go to equilibrium reversibly, delivering maximal work to a work reservoir [see Ahrendts (1980); Sussman (1980); Szargut (1980); Morris and Szargut (1986); review by Gallo and Milanez (1990)]. Construction of such a reference system may be impossible in some situations.[4]

Postulated or derived reference states are ubiquitous in thermodynamics in general and in useful-energy analysis in particular. In fact, all usage of extant energy concepts involve several more or less arbitrary choices of standard values. It should now be clear that exergy is inherently context-dependent.

From this we can see that though exergy is the best energy numeraire, there are major hurdles in the way of its application within ecology. Before ending this review, it must be stressed that there is no question about the existence of the exergy value for any system – it is implied by the first law. The main point here is that to actually determine it quantitatively in a particular situation may be impossible, and this has a direct bearing on the possibility of verifying any hypothetical evolutionary principle involving exergy.

Thermodynamics and ecology

Thermodynamics has been widely used in areas of ecology such as productivity studies, trophic analysis and food web analysis, and to some extent this has been fruitful (Ulanowicz 1986; Baird et al. 1991); but such successful applications have tended to overshadow the inherent limitations of the theory.

Classical thermodynamics deals with macroscopic concepts and phenomena that result from the behaviour of large numbers of interacting microscopic entities such as photons, electrons, atoms and molecules. The reduction in the number of quantities taken into account when going from the molecular-dynamic to the thermodynamic description is based on the assumption that systems usually consist of large numbers of particles which either behave identically, behave coherently, or do not change at all within the relevant time scale. There are thus limits

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[3] The term exergy has been accepted in science as denoting the most general attainable-work or free energy concept, embracing all others as special cases. Various terms have been used to denote exergy: available energy, availability, énergie utilisable, and technische Arbeitsfähigkeit are a few examples. The term was derived by Rant (1956), with the objective of finding a word which has the correct etymology (ex ≈ out of; ergon ≈ work) and would fit semantically with other thermodynamic terms, e.g. energy and enthalpy

[4] One difficulty arises from the fact that the relevant geophysical systems e.g. the atmosphere, hydrosphere, geosphere etc., are subject to the incessant forcing of solar radiation, which keeps them out of thermodynamic equilibrium. Another difficulty is to define the reference state so that negative values for the exergy are avoided. Construction of a reference system is usually based upon thermodynamic data, often tabulated using an arbitrary reference datum, e.g. pure elements in their most stable state at 298.15 K (25° C) and 101.325 kPa (1 atm). For many thermodynamic calculations this particular choice of reference state is unimportant, since only certain differences enter the calculations. However, it may be inappropriate for exergy calculations. The few attempts that have been made to define general geophysical reference states, e.g. Ahrendts (1980), have neglected radiation. For ecology, this is a fundamental flaw, both because photon energy is of paramount importance for all photosynthetic organisms and because radiative heat exchange with the environment is an important component of the energy budget for all animals (see Table 1). Another obvious gap in current examples is the absence of organic compounds

to the possible representation of the complexity of a system. Ecology, by contrast, deals almost entirely with objects which have highly individual behaviours and physical characteristics. To represent these with one or a few thermodynamic variables, e.g. energy, is an extreme form of reductionism. Also, since far from all of the processes allowed by the thermodynamic laws are available to living beings, some extra information must for this reason alone be included in the theory.

Materials in ecosystems. Another aspect of thermodynamics which impinges upon ecology, apart from *energy*, is *material* flow and chemical change (Hutchinson 1948; Smerage 1976; Waring 1989). Strictly speaking, both matter and energy obey conservation laws, which are often absolute for many elements found in ecosystems. In fact, the conservation laws for some elements can be used to define ecosystem boundaries. The elemental mass conservation laws provide more than 90 relevant balance relations for ecological systems, including isotopic discriminations. Since it is a straightforward procedure to measure the amounts of some of the elements with reasonable precision, any suggestion that the analysis should be carried out only in terms of an aggregated, and experimentally elusive, variable such as "energy" needs ample justification.

In some ecosystems one or more essential elements can become important limiting factors. Through residence times element limitations can influence the dynamics of an ecosystem, including the definition of niches, and the exclusion of species from different areas (O'Neil et al. 1989). Indeed some material constraints, e.g. water availability, affect the ecosystem so severely that energy input can become more of a problem than a resource. Furthermore, as a result of the configurations of elements inside living material, it is in most ecosystem analyses not one but several resources that are limiting. Odum in particular equates materials as scarce resources with energy, but it is unclear what the exact relation between scarcity and energy is supposed to be. Thermodynamics establishes that exergy is needed to extract materials from the environment and to transform them but no general relationship between material scarcity and exergy can be found.

Energy in ecosystems. As shown in the comprehensive treatments of Gates (1980) and Miller (1981), almost any conceivable form of thermal, chemical, electromagnetic and gravitational energy appears in ecology (see Table 1). Also, it is clear that the temporal characteristics of the energy flows have important effects on the biological energy transformation processes. On a global scale, the energy intake and loss of the Earth occurs almost entirely through radiation, and the energy content of the biosphere does not vary significantly with time. Similarly, the entropy content of the Earth is practically constant and entropy is only carried away by the terrestrial electromagnetic radiation. At the biogeographical region level, heat transport is dominated by atmospheric and oceanic processes mediated by the hydrographic cycles, and at the local level, the dominant radiative heat exchange occurs through individuals, moderated by size. Finally at the molecular level, photosynthesis and catabolism are the dominant processes.

Table 2. Overview of energy inflows to an animal. A similar list can be constructed for the outflows of energy. Among the radiative flows, and in terms of crude energy per time unit (power), the prominent flow is A; note though that in terms of exergy this flow is most likely to be insignificant. There are clearly drastic effects of only taking ingestion of chemical energy (F) into account in an analysis of the animals' energy income, and neglecting all other terms

D	Direct sunlight; the spectrum is modified during the passage of the atmosphere
S	Sunlight scattered reflected in the atmosphere
R	Sunlight reflected from ground and vegetation
A	Atmospheric radiation; essentially a composition of black-body radiation
V	Radiation emitted by other animals or by vegetation
F	Food ingestion
G	Radiation emitted from the abiotic environment
C	Energy added through convection processes, including conduction

The heat balance of vegetation is determined mainly by its environment, therefore the temperature of plant tissue can only be influenced to a limited extent by the organisms itself (e.g. Woodward 1990). On the other hand, many animals can control body temperature either by adjusting metabolic heat production and evaporation rates (e.g. homeotherms) or by changing their radiation balance e.g. by moving in or out of shade.

In ecology, energy conservation can be equated with a time-average balance in the energy budget of animal. Table 2 indicates the kinds of energy "income" that may be involved in such an energy budget. The most striking feature of this description is that several forms of energy, besides chemical energy, are involved and play important rôles. This impression is further enhanced if one includes the outflow components of the energy budget.

Physical time, as measured by clock mechanisms governed by regularly recurring physical events, is assumed to conform to a uniform scale; it provides one frame of reference for change. Physiological or ecological rates of change are variable and individual. For example, the energy or exergy input at the basic photosynthetic level of most ecosystems oscillates, with a dominant frequency corresponding to the day/night cycle. Energy input at other levels or in other forms may also show regular behaviour, but it is more likely to be intermittent. These different temporal scales make aggregation difficult, impossible or meaningless.

Porter and Gates (1969) claim that, generally, a six- or seven-dimensional space of descriptive variables is necessary to treat the problem of interaction between an animal and its environment. This is probably an underestimate. Their assertion that the energy concept can be used to reduce the effective dimensionality of the problem rests upon implicit restrictions on exactly the kind of system one is attempting to analyse. The necessity of a multidimensional description becomes evident when one attempts to define "useful energy" as discussed above. Clearly, what is useful depends on the perspective employed (useful for whom, for what, when and for how long?), and no particular perspective can claim universal priority. What it comes down to is that it does make a difference whether a unit of energy is acting in the system in the form of radiation or as chemical energy. Different forms of energy have qualities that are essentially different, and which have to be taken into account.

Odumania

H.T. Odum has proposed a body of ideas called systems ecology (Odum 1983), which is stated as being a new paradigm for ecological research, and also of such generality as to be successfully applicable to every other science, particularly economics. As indicated by Taylor (1988), the strong connections between ecological and social concepts advocated by Odum dominated the prevailing systems approach of the 1950s when the main parts of his thesis were developed. This influence can be seen in terms of Odum's scientific tradition, undoubtedly inspired by the ideas of von Betalanffy (1968).

A paradigm may be described as a set of accepted examples of actual scientific practice, including law, theory, application and instrumentation, that gives rise to models from which spring a particular coherent tradition of scientific research (Kuhn 1962). In creating such a set of examples, Odum makes prolific use of analogies and metaphors that have been successful in other fields, particularly in engineering sciences. Odum's systems ecology is dominated by the view of organisms as machines, and ecosystems as factories, and he discusses ecosystems in terms of their design features (see Table 3). It is also obvious that the language and models of electrical engineering of the 1950s provided the formalism; for example, the energy circuit language was defined originally as a generalization of passive analogs.

Odum's framework is to a large extent a paradigm involving a particular optimality model (*sensu* Krebs and Houston 1989), with the following three main components: (i) decision assumptions, (ii) currency assumptions and (iii) constraint assumptions. The second of these, which is used to evaluate alternative choices of currency, has been chosen a priori as some kind of energy flow variable. The third mainly involves thermodynamic constraints as given by the first and second laws, as well as the fact that the rate of total inflow of energy from the sun is finite. The decision assumptions are formulated in terms of how the energy budget should be partitioned into maintenance, growth, and so forth.

Table 3. Taken from H.T. Odum (1983): "Design features of ecosystems"

- A set of driving energy sources constituting an energy signature
- A web of components that includes feedback loops
- Convergence of successive energy transformations to form a chain of quality
- Increase of time constant and spatial size along the quality chain that can absorb various frequencies of energy flow and filter variation
- Pulsing of system controlled by oscillatory period of the terminal consumer phenomena
- Storage of mass and information
- Recycle of materials
- Feedback control systems of a switching nature, including temporal and spatial programs
- Interactions of energy flows of different quality so as to maximize power and reward those components that contribute
- Parallel units that can adjust their relative loading for maximum power
- Coupling of producers with consumers

The conjectures

The keystones of Odum's framework can be reduced to five main conjectures, although there are many more sub-conjectures or corollaries.

Conjecture 1. All significant aspects of ecosystems can be captured by the single concept, energy.

Ecosystems are classified on the basis of type and level of gross energy flow; as E.P. Odum (1975, p. 15) states: "Since energy is an important common denominator in all ecosystems [...] it provides a basis for what might be called a 'first-order' classification. As will be detailed [...] energy is always a major forcing function". The use of energy as a numeraire is also claimed to be a revolutionary step in the development of ecological theory:

> "The first edition of *Fundamentals of Ecology*, written in collaboration with my brother, Howard T. Odum, and published in 1953, was revolutionary in two respects: (i) principles were presented in a whole-to-part progression with consideration of the ecosystem level as the first rather than the last chapter, and (ii) energy was selected as the common denominator for integrating biotic and physical components into functional wholes (E.P. Odum 1977)".

Conjecture 2. The formalism of an energy circuit language is sufficient for a holistic approach to be developed.

A key to the conjectures is the special symbolic language, the *energy circuit language*, that Odum invented. Each symbol represents a particular *linear* mathematical relationship. The diagrams are meant to entirely replace expressions formulated using the conventional symbols of mathematics: one can "use the diagrams without the redundancy of writing equivalent equations since the diagrams are rigorous as equivalent expressions" (Odum 1983, p. xi). Since there are some 12 symbols in the energy circuit language this amounts to the assertion that all mathematical formulae (at least those relevant for ecology) can be written with this very small number of symbols. Many ecologists will have seen diagrams using the circuit language, but are unaware of the underlying assumptions implied by certain symbols; many other ecologists have used the symbols, without paying much attention to the way in which Odum claims that they could or should be used. There are also examples where similar symbols are used as a shorthand to describe the types of sources and sinks in cycling of elements, such as carbon, but the origin of these diagrams does not rely on Odum's paradigm (e.g. Ulanowicz 1986; Baird et al. 1991).

Conjecture 3. Systems evolve so that "power" is maximized, i.e. according to the maximum power principle.

Odum's systems ecology paradigm relies totally on the universal validity of the maximum power principle. He has given several different formulations of it, e.g. using different definitions of "power".

The influence of engineering on Odum's ideas comes out in the general view of the dynamics of ecosystems, in which they are considered as self-stabilizing, predictable, and controllable. In this picture, the self-stabilization is achieved through various forms of feedback. The predictability is due to the claimed existence of a general-maximization objective, the maximum power principle. The controllability rests upon the idea that the static and dynamic properties of every active part in an ecosystem can be precisely described; thus, the outcome of any human action can be predicted, and the development of an ecosystem is completely under human control.

Conjecture 4. Hierarchical structures, system boundaries and compartments can always be deduced and taxonomically resolved.

According to one version of the maximum power principle, the flows of energy in an ecosystem evolve into characteristic webs of energy pathways; "Ecosystems,.... and possibly all systems are organized in hierarchies because this design maximizes useful processing" (Odum 1988). Thus he sees that an environmental system is a network of component parts and processes operating on the scale of the environment, and states that there are similar laws of function and mechanism operating at all levels of scale and size.

Odum takes the idea of evolution one step further in his ideas about taxonomic hierarchies, which he sees as an energy spectrum of evolution. "The species is thus a smaller unit with faster time constant that processes energy necessary to generate the next higher taxonomic category, the genus etc." (Odum 1983; p. 342). Dividing up the energy spectrum, and assuming that selection for the maximum power will generate energy transformation hierarchies, implies that system boundaries and compartments can be simply deduced.

Conjecture 5. Ecological succession is due to the maximum power principle applied to ecosystems. It culminates in stabilized systems with maximum biomass and symbiotic function between organisms per unit of available energy flow.

Deviating from the perspective that at later stages of succession, the same biomass can be maintained for less production (e.g. see Margalef 1963; Odum 1969), Odum states that:

> "As structure is accumulated, biomass is added in those situations where biomass facilitates power maximization. There is, however, a curve of diminishing returns in the addition of biomass and other structure as the energy required for maintenance of the structure becomes equal to the gross production and other energy incomes that can be induced. The key measures in succession, therefore, may be the gross production and total respiratory metabolism (not net production or biomass). Total metabolism is a measure of the total structure and of the dissipation rate for the low-entropy structure being maintained. Where organic inputs are small, gross production is a measure of maximum power. Increases in these total measures are observed in succession to climax." (Odum 1983, p. 459).

A critique of the conjectures

H.T. Odum's claim to a revolutionary new paradigm for systems ecology lies primarily on the assumption that energy is an appropriate currency with which to describe system function and evolution. The problems of using energy as a numeraire were discussed in the first part of this paper, where it was concluded that the types of energy and their spatio-temporal partitioning in real ecosystems are too diverse to support the argument for a single currency to describe ecosystem dynamics. The severe problems with relating material scarcity to energy were also noted. It should also be added that no matter how generous an interpretation one gives to the use of a single numeraire to invent a new language for defining values in an ecosystem, we consider it virtually impossible to support the drastic reinterpretation, reduction and loss of information concerning ecosystemic form and function within Odum's approach. Indeed, he inadvertently and implicitly admits that his paradigm involves a redefinition of many thermodynamic concepts (Odum 1987). This is especially true for the thermodynamic terms energy, work and power. The most important and surprising gap in Odum's version of thermodynamics is that the pivotal concept *energy* is not defined properly, and is even circular: "energy is defined and measured by the heat that is formed when energy in other forms is transferred into heat. All kinds of energy can be converted into heat. *Heat* is the energy of molecular motion" (Odum 1983, p. 6). The word 'useful' is involved in several definitions. One of the most basic concepts in the framework is what is called 'useful energy'. But again, this is also an elusive concept whose definition varies widely in the key text (Odum 1983), partly because of the instrumental dimensions inherent in the word 'useful', and partly because of the many synonyms for 'energy' (some of which are metaphorical). In most cases 'useful energy' seems to denote a one-dimensional entity related to the amount of work which can be or is performed. As we have shown above, there are several such concepts in thermodynamics, but it is unclear which ones (if any) are involved in this approach.

Another example of problems relating to terminology concerns the treatment of the thermodynamic concept of *heat*; here there is an attempt at a revival of some version of caloric thermodynamics. Whereas physicists today agree that it is improper to speak of the heat 'contained' in a system[5], such a caloric or substantive view on heat is very convenient for Odum's formulation of ecosystem components involving storage. A similar situation occurs for power, and hence for the maximum power principle. The term 'power' is in physics usually defined as the time rate of doing work. Odum however extends the definition to a much wider class of entities.

In view of the difficulties described above, it is perhaps not surprising that the problems associated with defining a set of thermodynamic reference levels that could be suitable for an ecological context are consistently ignored. One effect of this is that the energy numeraire is unworkable.

The second conjecture refers to the derivation of a special energy circuit language to describe the fluxes and flows of energy. Odum claims that all phenomena in ecosystems can be described in terms of this language (e.g. Odum 1983, p. 5). We have found no supporting argument for this assertion. On the contrary, a close inspection of the definitions of the energy circuit language symbols, in particular including their relations to dynamical systems, shows that linearity assumptions are invoked to such an extent that very few nonlinear expressions could be represented with these symbols, and even in those cases in an exceedingly clumsy fashion. This is regarded as an unimportant shortcoming of the language, since "[m]ost of the natural world's flows are covered by one of the two linear laws and thus the linear pathway definitions of the energy circuit language apply to most systems" (Odum 1983, p. 11). We would conclude that the formalism of the energy circuit language is at best poorly contrived and unnecessary, and at worst highly misleading.

Concerning the third conjecture, perhaps the most famous statement of Odum's systems ecology school is found in the key paper by Odum and Pinkerton (1955): here the main argument is based upon weak analogies with some pieces of linear non-equilibrium thermodynamics. The paper introduces one of the prototypical examples (*sensu* Kuhn 1962) of Odum's framework (Odum 1983, p. 116), which comes via a simple mechanical model (see Appendix). In view of the importance of this model for the introduction of the maximum power principle, it is surprising that no explicit expression is given for 'power output'. The definition used is neither self-consistent, nor consistent with the definition of dissipation and losses. As shown in the Appendix, there are a number of rather specific problems associated with this example, not least of which is the calculated value beyond which the efficiency of conversion of useful input power at the level of maximum power output cannot be exceeded. One can still see mindless invocations of these results, and a persistence of the incorrect value (see for example Wiegert 1988).

In view of the fundamental importance of the maximum power principle to Odum's framework, it should be discomfiting to its proponents that the mechanisms which are supposed to result in the maximization of power remain to be elucidated. Given the simplicity introduced through the pervasive use of linearity assumptions, one would have thought that such mechanisms would have been found.

The next problem refers to that of compartmentalisation and the raison d'être for taxonomic hierarchies. Traditionally, measurements at the ecosystem level have been centered upon changes or declines in the various species contained within the chosen boundaries. However, ecosystems can be highly complex and are not necessarily decomposable. Indeed, different investigators have different ideas about complexity: for example Ashby (1973) pointed out that the complexity of a sheep's brain depended much on whether one was a butcher or a neurophysiologist.

Ecosystem measurements have varied according to the predilection of the investigator. The schools that have existed include one based on number and size (the Eltonian paradigm) and another on taxon and transformation (the Lindeman-Odum paradigm). To measure flows of energy and materials, as in Odum's formulation, requires that divisions be made either at the trophic or functional size level. But as Fenchel (1987) has pointed out, Odum's attempt to describe ecosystems in terms of energy flow is at best a descriptive approach, and at worst a strongly deceptive approach if used as a predictive or analytical tool to state how other unstudied ecosystems might function. Indeed, it is not yet clear how any of the widely used macroscopic features of ecosystems such as trophic status, ascendency or biodiversity really articulate with individual characteristics such as genetic and physiological status. Certainly, Odum's approach towards compartmentalisation is unlikely to contain the answer, for as Fenchel (1987) has said "to make analogies between non-equilibrium thermodynamics and ecological systems, such as equating species diversity of communities with 'negative entropy' of chemical systems [...] is a fundamentally false analogy [...] [Odum's approach has] had an appeal for some time, I suppose, only because it was sufficiently obscure and incomprehensible to appear profound." We can see from the previous sections that there are indeed severe problems in obtaining a genuine understanding of the divisions within ecological systems based on an evolutionary context of efficiency in terms of maximization of energy conversion. What is more disturbing is the idea that taxonomic hierarchies are the energy spectrum of evolution: species are smaller units with faster time constants that process energy to generate the next higher taxonomic category. This appears to be a statement connected to a static world where species are only represented through their association with a genus, and in some sense are only acting to promote the genus. However, taxonomy is a human construct used to delineate kinship and genetic relatedness. To extend the underpinning of systematics to imply that classificatory procedures in fact reflect a scheme of energy is something for which we have no evidence in molecular biology and genetics.

When we turn to devising indices of ecosystem status,

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[5] Once inside a system it is not possible to determine whether a certain amount of energy came from heat transfer or work transfer: it is simply internal energy

we find key elements missing, i.e. the processes affecting individuals, such as growth and physiological ageing. This is of course consistent with classical thermodynamics, where it is not necessary to make reference to microscopic entities to define macroscopic properties: and in classical biological terms this would relate to the resolution of phylogenetic relationships (*sensu* Hennig 1966). But more recently body size has been seen as a paramount characteristic that can overshadow its taxonomic form (Elton 1927; Haldane 1928; Platt 1985). In more general terms Hemmingsen (1960) and Kleiber (1961) document the regularity with which respiration rates vary with body size. Fenchel (1974) generalized this allometric formula for respiration to include the fact that generation time was also a function of body size, and Platt and Silvert (1981) and others (e.g. T.D. Iles, Biological Research Station, St. Andrews, N.B., Canada personal communication) have gone further to argue that there exists a universal size-related time scale in organisms according to which all processes could be expressed in a simple way.

Supposing then that an organism's physiological rates are directly related to body size, and the distribution of size classes in an ecosystem is known; then by integrating over the range of all sizes, one should be able to estimate ecosystem features such as gross respiration or total primary and heterotrophic production. These characteristics would be central to a thermodynamic analysis of a community. Thus Peters (1983) would be correctly optimistic in thinking that allometric and particle size models are the most appropriate starting points for a predictive ecology, in contrast to the approach discussed here.

The final part of this critique refers to the oscillatory behaviour of ecosystems and its rôle in succession. Biology abounds with examples of periodic or aperiodic oscillations on the microscopic scale of internal processes in organisms (e.g. heart beat), to the macroscopic scale of cycles in populations and epidemics. In population dynamics, one prototypical example is the Lotka-Volterra model, which in its simplest form exhibits regular periodical oscillations. Since oscillatory phenomena are so pervasive, it is natural to enquire whether oscillatory behaviour is advantageous according to the maximum power principle or not; in the usual linear formulation of the principle, all oscillations should die out as the system approaches the steady state which maximizes power. If no real advantage can be found, this would constitute a major challenge to the principle.

One way of testing such a hypothesis is to compare the effectiveness of utilization of a physical resource, for example power in the sense of exergy flow, in two typical states or modes of system behaviour, namely the steady state and the periodic oscillation. In virtually every population dynamics model which generates periodic oscillations as a solution to the equations of motion, there is at least one steady-state solution. Given the different rates of energy turnover of different organisms, population oscillations will unavoidably result in power oscillations. They do not have to be invoked separately, as suggested by the statement that the "Maximum power implies ecosystems develop mechanisms for their own pulsing" (Odum 1983, p. 450), and that this happens because "the maximum power principle causes systems to store and pulse their feedback services to the system of which they are part, thus maximizing their roles in useful work and control at that size scale" (Odum 1983, p. 444).

Indeed for the oscillatory mode the relevant entity is not the instantaneous power flow, but the time-average over one period. In the situation where the steady state is unstable, the system dynamic will be oscillatory. The validity of the maximum power principle requires that this oscillatory mode is *always* favorable in terms of power output. This general requirement can be easily tested for a special class of periodically oscillating systems, namely those where the oscillating mode appears through a Hopf bifurcation. This kind of problem was investigated in another context by Månsson (1985). The conclusion as to which mode is favorable in terms of power is determined by whether the Hessian matrix of the power output is positive or negative definite. This points to a fundamental flaw of the maximum power principle in the context of oscillating systems, since there is no a priori rule or fundamental reason for the matrix to be either negative or positive definite. In fact, it is easy to construct model examples in which both cases occur, i.e. where the maximum power principle is invalid.

According to the maximum power principle conjecture, the power (however this is defined) output of an ecosystem will gradually evolve towards the state of maximum power output, a maximum implied by the first and second laws of thermodynamics. This description is of course very convenient for two popular ecological concepts, namely succession and the climax community: the first relates to the evolution of an ecosystem, and the second is the final state, in this case thermodynamically, and hence physically, defined! In discussions of succession, adaptation at the community level has always been explicitly assumed (e.g. Paine 1980). Yodzis (1989) tried to model the effects of an energetic constraint on the possibilities of introduction of new species into a food web: in his model, species with a superior energetic (or more properly, exergetic) efficiency have an evolutionary advantage. However, the effect turns out to be highly sensitive to the basic assumption of adaptation in the model. Yodzis therefore found that almost any variation of the model gave different results, particularly those made to make the model more closely resemble real ecosystems. But Odum claims that ecosystems are organized into energy hierarchies because such a design is optimal according to the maximum power principle. He states that: "In time through the process of trial and error, complex patterns of structure and process have evolved, the successful ones surviving because they use materials and energies well in their own maintenance, competing well with other patterns that chance interposes. ... The engineering of new ecosystems designs is a new field that uses systems that are mainly self-organizing" (Odum 1983, p. 17).

The question thus remains of which point the maximum power principle pertains to in succession, if as Odum says the maximization of power involves a rise and fall of power levels when stored and renewable resources are being drawn in. From an evolutionary standpoint, Odum puts the self-organizing principle of systems which retain units and mechanisms to meet contingencies before Darwinian selection. He is therefore in the position where virtually any configuration is admissible. For example, we are told that circular succession is simply a changing climax where one state produces another until eventually the first state recurs, but we are unable to discern when to expect circular succession or whether it has an advantage over non-circular succession, simply that it is a another pulsing mechanism.

If the usefulness of an ecological theory is to be evaluated on the basis of its internal consistency and ability to yield new insights and testable hypotheses, then Odum's framework fails. The admissability of virtually any system configuration, together with the incorrect reasoning behind the maximum power principle are incompatible with what we have learnt from deriving other theories and laws in the natural sciences.

Confrontations with ecological reality

In this final section of the paper we evaluate whether or not Odum's systems ecology can be used as a form of phenomenological reasoning for observations of ecological reality. To begin with, we examine whether Odum's systems ecology agrees with the known properties of ecosystems, and then move on to animal ecology.

Ecosystems analysis and animal ecology

In 1942, Lindeman attempted to describe the energy flow of an entire community. He chose for his work Cedar Bog Lake, Minnesota, and estimated energy flow from the harvestable net annual production at three trophic levels – primary producers, primary consumers and secondary consumers (Lindeman 1942). The animals and plants collected at the end of each growing season made up the net production of the trophic level to which the various species were assigned. Lindeman then estimated the energy dissipated through respiration from ratios of respiratory metabolism to the measured production. Lindeman considered that predation on secondary consumers was insignificant. The gross annual production of primary consumers and the annual consumption of primary consumers by secondary consumers were calculated in a similar way. To calculate the gross annual primary production Lindeman assumed that the secondary consumers had an assimilation efficiency of 90%, and that the assimilation of herbivores feeding on plant material was 84%; the annual estimate obtained was 1,114 kcal m^{-2}.

In 1957, H.T. Odum published estimates of a similar small aquatic ecosystem called Silver Springs, Florida (Odum 1957). Gross production of aquatic plants was estimated by gas exchange rather than by harvesting of the plants and an estimate was made of the inflow of energy in the form of detritus from the surrounding land. The gross annual primary production was 20,810 kcal m^{-2}, a significantly higher than the more northerly bog lake investigated by Lindeman. Odum (1956) asserts that these differences arise from Lindeman's definition of production. However, it is not clear that the distinction between production as the rate of synthesis of organic matter at the primary trophic level and production in the sense of energy intake in the consumer trophic levels can be resolved by simply assigning different symbols, as in Odum's diagrammatic formulation.

Indeed, the real problem is that the combination of various species into trophic levels will cause a wide variation in the estimates of energy flows between the various sub-compartments of seemingly similar ecosystems (Slobodkin 1960, 1962). A further complication is brought up in the case of Silver Springs, which Odum uses as an example of pulsing, the argument being that as a result of the maximum power principle a system stores and pulses its feedback services to maximize their rôle in useful work. The steady productivity that Odum cites as a key feature or a pulsed system comes from the convergence of many short pulses which accumulate along the energy chain to produce oscillations of larger amplitude giving rise to the observation of a high productivity peak in spring and summer. But in real systems the seasonal peaks can often be missing as a result of physical structuring or lack of light and nutrients; in this case it is not clear that the maximum power principle could be used to evaluate the presence or absence of pulses in any testable way. For example, in a recent paper by Baird et al. (1991), the flows of carbon, and therefore by extension energy, in six marine ecosystems were compared. The results were contrary to what Odum has suggested, in that the aggregate amount of cycling was an indication not of maturity but rather of the type of dynamics and levels of stress. This could arise from the fact that perturbations often affect the higher-level species (e.g. fishes and birds) to a greater extent, such that the homeostatic response of the less-disturbed lower-level trophic components or microorganisms is to retain the resources released from larger organisms through recycling the materials amongst themselves in short intense loops. Adaptation will therefore not necessarily result in the consistent decrease with time of the production-to-biomass ratio, as suggested by E.P. Odum (1969). The authors conclude that as a system matures, the qualitative changes that we should expect to see are (i) increasing numbers of cycles; (ii) longer cycles; (iii) greater specificity of predator-prey interactions; and finally (iv) a topological structure that can withstand large perturbations in resources through time. Contrary to H.T. Odum's ideas, the development of a climax ecosystem results in intensification of existing parts of the ecosystem network.

One of the main problems in testing Odum's conjectures is that much of the data is impossible to collect. However, in the fields of limnology and oceanography it is relatively easy to acquire data on particle size distributions (PSDs) of planktonic communities in the range 2–250 μm using a Coulter counter, and of fishes and mammals using side-scanning sonar. From studies based on size as an organising principle. Sheldon et al. (1972) discovered that the PSDs of planktonic communities in the oceans were relatively flat and lacked structure, an observation which Platt (1985) showed to be a natural consequence of a simple transformation on the Eltonian pyramid. As research into size distributions continues, it is becoming clear that in fact it is the picoplankton which are of great importance in determining the ocean's productivity and hence energy uptake and cycling (Pomeroy 1974; Johnson and Sieburth 1979; Platt et al. 1983). And indeed, we do not seem to find the hierarchical structures in the oceans we expect to find through application of Odum's ideas about the climax resulting from the maximum power principle.

The question is how to translate the various living components of primary productivity into the uptake of materials and energy throughout an ecosystem. Some animals consume small members of their own species, whilst some live off the excreta of others. How much of this autotrophy effects heterotrophic production at macroscopic scales remains to be seen, but most agree that there is a high degree of cycling and dissipation within the microbial loop (Goldman 1984). Thus the construction of ecosystems based on Odum's approach cannot account for the observations on size distributions of organisms in the oceans.

On the single organism level, the discussions in Westerhoff et al. (1983), Westerhoff and van Dam (1987) and Battley (1987) not only demonstrate that there are several equally legitimate ways of defining output power, but that there also exist real microbiological systems which do not maximize power output in any of these senses. An important aspect of their discussion concerns the reasons for failure of the maximum power principle, which in most cases is due to constraints from several independent factors, not only by free energy limitations.

The generally accepted view at the individual level is that the exergy which an animal has assimilated is expended in four different ways: growth, reproduction, maintenance, and storage (plus support of other organisms, e.g. symbionts and parasites). Maintenance here includes not only basal metabolism but also metabolic expenditures for activity or thermal regulation. The stored and accumulated exergy may be used for any of the other three, or may be utilized by other organisms. Blaxter (1989) carried out a very refined and detailed analysis of the energy flows and transformations in the context of a single animal. One important observation was the difficulty associated with defining precisely the ecological/organismal energy categories, for example maintenance energy. A complete energetic analysis must involve ingestion, assimilation, egestion, respiration, growth and death rates as well as numbers and biomass: each of these must be translated into energy (flow) values. Thus an analysis of maintenance energy from a physical perspective is profoundly affected by both physical and chemical details, and will be quite specific to the system under study, with only a few aspects open to generalization (Pimm and Kitching 1987). This is clearly the case in many studies of foraging behaviour, cooperation, sexual selection, reproduction and the trade-off of gonadic versus somatic growth (see for example papers in Clutton-Brock 1988).

Conclusions

We can now examine Odum's system ecology in the light of the four test criteria proposed by O'Neill et al. (1986). The main failing of the first test is the contradiction between the aim of applying a holistic perspective in the study of ecosystems and the inherent and far-reaching reductionism in the conceptual framework, e.g. using energy as a numeraire. Although the existence of nonlinearities is recognized, the entire framework is based on linear assumptions and formulations. Further it is accepted that ecological systems are in thermodynamic nonequilibrium, but not that they may be outside the range of validity of the local thermodynamic equilibrium approach. Thermodynamics is not used in a self-consistent way, nor as it has been developed in other scientific fields: the framework is thus not internally consistent.

The second criterion refers directly to the rôle of physics as a source of concepts, theories and methods for ecologists. In spite of its fundamentally reductionist ideology, some concepts from physics have played an important part in the development of ecological theory. But the rôles of energy as conjectured by H.T. Odum, e.g. energy as an ecological numeraire or as a gauge of evolutionary success, are now wholly discredited, both in terms of their theoretical plausibility and in terms of empirical verification.

Our inquiry indicates that the relations between thermodynamics and ecology are intricate and demand much more sophistication than the simplistic energy concepts of Odum's paradigm. In particular, the recently suggested concepts "emergy" and "transformity" (Odum 1988) are both inoperational since the actual quantities are almost entirely arbitrary; e.g. they can have practically any values for any particular substance. Furthermore, they cannot even in principle be established for a nonclimax (non-stationary, nonequilibrium) system; they are wholly dependent upon the maximum power principle.

On the third test, we have shown that the maximum power principle is contradicted by both ecological data on energy flows, and by the results emerging from models which capture essential aspects of the dynamical behaviour of ecosystems. Likewise, the principle does not correctly describe evolutionary processes.

As to the fourth test, H.T. Odum's ideas have really only generated the original testable hypothesis of the maximum power principle. The ecological version of the principle is a version of Lotka's hypothesis. Perhaps the ultimate problem is that even though the generality and universality claims can be overlooked, the absence of a single correct derivation makes it impossible to establish characteristics of the hypothetical class of systems for which it is valid.

In view of the recognition awarded to H.T. Odum's ideas, it is striking that we have been able to show that they fail all four test criteria. Note that rather than a simple negation, we have tried to offer something constructive, by describing exergy as the best conceptual tool for "useful energy" studies that thermodynamics has on offer – but we have shown that even this is unable to play the rôle in ecology envisaged by H.T. Odum. Although the prospects look dismal, we should in fairness note that the question of whether or not it will be possible to formulate an exergy concept that is applicable at the ecosystem scale remains to be resolved.

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Appendix

One of the basic ideas of H.T. Odum's conjectures is the trade-off between rate (output power) and efficiency. The origin of this idea is the commonly held view that a reversible process must proceed at practically zero rate, in which case the system does not deliver any output. This particular compromise has been known to engineers for more than a century, and was closely connected to the scientific development of thermodynamics. In more general terms, Hero of Alexandria, around 62 A.D., had already recognised that what is gained in force is lost in speed. In engineering thermodynamics and in the thermodynamics of processes carried out in finite time (Andresen 1983), it is well known that the losses may be reduced with a minor cost in rate of output.

The paper by Odum and Pinkerton (1955) introduces one of the prototypical exemplars (*sensu* Kuhn 1962) of Odum's paradigm, a simple mechanical model involving two weights, called the Atwood machine. Although this model is the basis of the maximum power principle conjecture, no explicit expression is given for "power output", nor is it clearly defined in words anywhere in the paper. The definitions that are given are meant to comply with a non-equilibrium thermodynamic framework. Through studies of later works of H.T. Odum, one can deduce that the definition "power output $= mgh/\tau$" was used, where m is the mass of the smaller weight, g is the gravitational "constant", h is the distance that the larger weight falls, and τ is the time the fall takes. Those familiar with the history of physics will recognize that he works within the framework of Aristotelian mechanics. The kinetic energy of the weights is totally neglected, even though it can easily be converted to "power output" in the above sense. The possibility of conversion between kinetic and potential energy is recognized in Odum (1983), but the consequences for the treatment of the Atwood machine example are not considered. Thus, this definition of power output is not self-consistent; nor is it in fact consistent with the definition of dissipation and losses used later in the paper.

Odum and Pinkerton (1955) state: "Atwoods machine. Efficiency is equal to the force ratio. As one can demonstrate in a physics laboratory, the optimum arrangement for maximum power-output is at 50 per cent efficiency." We should here note that this is incorrect. Later (see e.g. H.T. Odum 1971, 1983), but again using this very odd definition of power output, a correct value for the optimal ratio is given, namely:

$$\frac{\sqrt{5}-1}{2} \approx 0.62,$$

i.e. the golden mean. The correct value for this generic example of the Odum school is in obvious conflict with the value (optimal ratio $= 0.5$) that the rest of the paper attempts and claims to establish as a *universal* value.

Trade-offs between efficiency and power are well investigated in thermodynamics. Here, we may note the significance of the model of Curzon and Ahlborn (1975), a Carnot engine with the simple constraint that it is linked to its reservoirs through finite heat conductances. The maximum efficiency of their engine is of course $1 - T_L/T_H$, obtained at zero rate. When this machine is operated to produce maximum power, the efficiency is

$$1 - \sqrt{\frac{T_L}{T_H}}$$

Clearly, different temperatures in the hot (T_H) and cold (T_L) reservoir will yield different efficiencies in the range 0 to 1, not the simple 0.5. Many similar results in the literature show that Odum and Pinkerton's claim of universality is fallacious.

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