



Review

Application of thermodynamic principles in ecology

Sven E. Jørgensen^{a,*}, Brian D. Fath^b

^a*Department of Environmental Chemistry, Royal Danish University of Pharmaceutical Sciences,
University Park 2, 2100 Copenhagen, Denmark*

^b*Biology Department, Towson University, Towson, MD 21252, USA*

Received 9 July 2004; received in revised form 22 July 2004; accepted 23 July 2004
Available online 30 September 2004

Abstract

Current developments in ecosystem theory to understand ecological complexity, particularly those incorporating and applying thermodynamic principles, are making it possible to integrate various ecosystem approaches into a consistent theoretical framework. The time, therefore, seems right to apply this theory to explain observations published in the ecological literature that typically lack linkages to ecological theory or other rule-based explanations. This paper presents the foundations of that theory of ecological complexity in eight observational principles and summarizes the results from a review of a number of papers using thermodynamic principles to explain ecological observations. The theory will continue to evolve and be modified as more test cases are made, however, here explanations of some published ecological observations are presented to illustrate how the ecosystem theory is applied.

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Keywords: Ecological modeling; Ecological theory; Ecological thermodynamics; Ecosystems

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* Corresponding author. Tel.: +45 35306281; fax: +45 35306013.
E-mail address: sej@mail.dfh.dk (S.E. Jørgensen).

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1. Introduction

The ecological literature is full of papers that are lonely islands in the sense that they present some ecological observations, which are most often treated statistically to determine a relationship between ecological variables, but lack linkages to an ecological theory or to general ecological rules. In this regard, ecology has progressed slowly as a theoretical science since each environment–organism complex is a unique nonreplicable situation unless the interesting aspects—those that characteristically make it a living system—are “controlled for” by artificially constructing the organism’s environmental habitat. We present here an attempt to formulate a theory based upon an integration of many contributions, which could be used to explain ecological observations (e.g., Jørgensen and Marques, 2001; Jørgensen et al., 2002a).

Attempts have been made to formulate general laws in ecology. For example, Lawton (1999) discusses three: thermodynamics, stoichiometry, and natural selection. Whereas, he emphasized the mesoscale issues of community ecology such as species composition, thus omitting important thermodynamic considerations, we deal primarily with thermodynamic implications of macroscale ecosystem processes. The hypothetical ecosystem theory we present here will of course be improved and expanded in the coming years with further research, but, although the ecosystem theory is in its infancy, its explanatory power has been demonstrated and will be reviewed in this paper. The time is ripe to apply this theory more widely and thereby bind the ecological literature together in a theoretical framework, as it is the case in physics, chemistry and even biochemistry. We hope that by presenting the theory here others will apply it in their own studies. The

application of the ecosystem theory may fail from time to time, but this will inevitably lead to new ideas about how to do it. This is how basic theory improves in science.

The next section presents the basic observational principles of a proposed ecosystem theory. Several of these principles have been taken from other disciplines and some have been widely accepted by ecologists but not applied very often in a theoretical context. References to where these principles are applied are given after presentation of each principle.

The more controversial ones, which deal with ecosystems moving further from thermodynamic equilibrium by increasing throughflow of energy and storage of exergy, will be explained in more detail in the following section. After this presentation, we give an overview of papers that have published explanations of ecological observations by use of the proposed and presented theory. We do not repeat the complete reasoning for each application, but one detailed explanation will be presented as an illustration to how the ecological observations and rules have been used. For the selected illustration, ecological models, based upon observations, are used in combination with the proposed ecosystem theory.

2. Basic observational principles of ecosystem ecology

“*Hierarchical organization* and the characteristics of *open systems* are fundamental principles of living nature... the advancement of theoretical biology will depend mainly on the development of a theory of these two fundamentals” (von Bertalanffy, 1952).

Biology in general, and ecology specifically, are still struggling to fully understand and apply the ramifications of living systems as complex, open, hierarchical, granular systems (Allen and Starr, 1982; Ulanowicz, 1999). These important considerations form the beginning context of ecosystems and provide the starting point for the basic principles of ecology. Altogether, we present eight principles, which can be divided into three main classes: environmental context, ecological elements or parts, and ecosystem processes. Several of the principles are generally known and accepted, but they are rarely applied as a consistent theory on which ecology is based. The last principle—regarding the storage of exergy—successfully explains many ecological observations, but is still hypothetical and even controversial at this point. Therefore, the examples presented later in the paper will focus mainly on this more controversial principle.

Environmental context

1. All ecosystems are open systems embedded in an environment from which they receive energy–matter input and discharge energy–matter output. From a thermodynamic point of view, this principle is a prerequisite for the ecological processes. If ecosystems would be isolated without boundary source of low-entropy energy and boundary sink for high-entropy energy, they would approach thermodynamic equilibrium without life and without gradients.
2. Ecosystems have many levels of organization and operate hierarchically (Allen and Starr, 1982). This principle is used again and again when ecosystems are described: atoms, molecules, cells, organs, organisms, populations, communities, ecosystems, and the ecosphere.
3. Thermodynamically, carbon-based life has a viability domain determined between about 250–350 K. It is within this range that there is a good balance between the opposing ordering and disordering processes: decomposition of organic matter and building of biochemical important compounds. At lower temperatures the process rates are too slow and at higher temperatures the enzymes catalyzing the biochemical formation processes decompose too rapidly. At 0 K there is no disorder, but no order (structure) can be created.

Order (structure) creating processes increases at increasing temperatures, but the cost of maintaining the structure in the form of disordering processes also increases.

Ecological elements/parts

4. Mass, including biomass, and energy are conserved. This principle is used again and again in ecology and particularly in ecological modeling.
5. The carbon based life on earth, has a characteristic basic biochemistry which all organisms share. It implies that many biochemical compounds can be found in all living organisms. Therefore, organisms have almost the same elementary composition and can be represented by a relatively small number (~ 25) of elements (Morowitz, 1996). This principle is used when stoichiometric calculations are made in ecology, i.e., an approximate average composition of living matter is applied.
6. No ecosystem organism exists in isolation but is connected to others. The theoretical minimum unit for any ecosystem is two populations, one that fixes energy another that decomposes and cycles waste, but in reality viable ecosystems are complex networks of interacting populations. This principle has been used in numerous ecological network papers (e.g., Higashi and Burns, 1991).

Ecosystem processes

7. All ecosystem processes are irreversible (this is probably the most useful way to express the Second Law of Thermodynamics in ecology). It is widely used in ecology that living organisms need energy to cover the maintenance of the life processes. This energy is lost as heat to the environment which is in agreement with the Second Law of Thermodynamics.
8. Biological processes use captured energy (input) to move further from thermodynamic equilibrium and maintain a state of low-entropy relative to its surrounding. After the initial capture of energy across a boundary, ecosystem growth and development is possible by an increase of the physical structure (biomass), an increase of the network (more cycling) or an increase of information embodied in the system. All three growth forms

imply that the system is moving away from thermodynamic equilibrium and all three growth forms are associated with an increase of 1) the exergy stored in the ecosystem, 2) the energy throughflow in the system (power). Corollary: furthermore, an ecosystem receiving solar radiation will attempt to maximize exergy storage or maximize power such that if more than one possibility is offered, then in the long-run the one which moves the system furthest from thermodynamic equilibrium will be selected.

The first seven principles apply basic thermodynamic principles and biochemical knowledge regarding ecosystems. All seven principles have been accepted in ecology, which can be seen from their wide application. These applications are touched on above for each principle. The 8th principle and its corollary have good support from many ecological observations and models, and as the most controversial and novel principle will be discussed in detail in the next section.

The formulation that we give the eight principles is probably slightly different than that which other ecologists would have used, but the basic concepts would be similar. For example, Salthe (2002) uses what he calls a developmental-infodynamic-thermodynamic theory (DITT), while Odum (2002) uses maximum power, which is based on flows of useful energy (exergy), and there is a close relationship between the distance from thermodynamic equilibrium and the energy throughflow (power) that the system component can support. Our goal here is to aggregate and then distill the key features governing ecosystem behavior based on these thermodynamic principles.

Another question is whether or not these eight principles are sufficient to explain ecological observations either directly or indirectly by rules which can be derived from them. We do not propose that the theory is closed to further refinement, and it is clearly necessary to apply these principles more widely and to challenge them to a broad range of empirical observations before they can be fully accepted to describe the behavior of complex ecological phenomena. However, we have to start to try to construct a theoretical framework for ecological observations, particularly those related to ecosystem growth and

development, if we want to develop ecology in a more theoretical direction.

3. Ecosystem growth and development

The thermodynamic principles of ecology are proposed to explain growth and development observed in ecological systems. In general, growth means an increase in system size, while development is an increase in organisation independently of system size. In thermodynamic terms, ecosystem growth and development means moving away from thermodynamic equilibrium. At thermodynamic equilibrium, the system cannot do any work. All its components are inorganic, have zero free energy (exergy), and all gradients are eliminated. Everywhere in the universe there are structures and gradients resulting from growth and development processes cutting across all levels of organization. A gradient is understood as a difference in an intensive thermodynamic variable, such as temperature, pressure, altitude, or chemical potential. Growth is defined as an increase in a measurable quantity, often taken in ecology to be biomass, but an ecosystem can grow and develop in four different ways (Fath et al., in press):

- I. *Boundary input*: The system takes input low-entropy energy or biomass across its boundary. This is the initial condition requirement for growth in open systems.
- II. *Structural growth*: The physical quantity of biomass retained within the system boundary increases by increasing the amount, size, or number of components in the ecosystem.
- III. *Network growth*: The ecosystem network develops such that the number of components, connections, and thereby feedback in the system increases (Odum, 1969). This implies that mass and energy cycle more and the total system throughflow increases. Network growth continues up to a point after which pruning or articulation of these connections can also occur as ecosystems develop which leads to the last growth category.
- IV. *Information growth*: System information increases, which means that the system organization becomes more energetically efficient, typically associated with an increase in genetic

complexity. See also the relationship between Kullback's measure of information and exergy presented below.

4. Explanation and discussion of the thermodynamic principles of ecosystems

Boltzmann (1905) proposed that "life is a struggle for the ability to perform work", which is in accordance with the definition of exergy (Szargut et al., 1988). The difference between free energy and exergy, is the ability with exergy to select a case-dependent reference state. Ecological (and biological) growth and development deal with the organization of material into ordered structure, and work must be done to create this order out of the background (reference state) of less order. Teleology is frequently mentioned in the discussion of the origins of order, but we are not seeking nor advocating a final end state for these dynamic systems, but rather are interested in the expressions that track the direction of these ordering processes. Objective functions, goal functions, optimization criteria, extremal principles, and orientors are examples of criteria that have been used to track ecosystem growth and development (e.g., Müller and Leupelt, 1998). Maximizing exergy storage is one such goal function, or in Aristotelian terms, a "final cause."

Exergy is a measure of the useful work a system can perform when brought into equilibrium with its surrounding. In the case of ecosystems, it is beneficial to select a reference system where all the components are inorganic at the highest oxidation state, i.e., the free chemical energy is zero—the reference is like the ecosystem but at chemical equilibrium where all the chemical energy has been used up. To distinguish the exergy calculations with the above defined reference state for biological systems from the exergy calculations applied in engineering which uses the environment as a reference state, we call the exergy we are using eco-exergy. Eco-exergy is used throughout this paper whenever we use the concept of exergy. This is a useful construct, particularly in ecological applications because it allows for consideration of constraints that are embodied in the system. Strictly speaking, it was designed to quantify energy quality as the system's energy that is available to do work, however, for biological systems this has been extended to include

both the energy that can be turned into work (stored biomass) and the biological information which separates the organism from its surrounding. Here, we calculate biological information as the organism's stored genetic information (Marques et al., 1998; Fonseca et al., 2002). There are some limitations to this approach (Debeljak, 2002) namely that it considers the genome as the sole source of embodied information and that it assumes that organisms' genome information scales linearly to ecosystem-level information. Other approaches have been proposed to measure biological information (e.g., Collier, 1990; Ulanowicz and Abarca-Arenas, 1997; Brooks, 2001), however, if anything the genomic approach used herein underestimates the importance of information. Technically, there is also a small contribution of exergy due to the temperature and pressure differences between the system and the reference environment, but this assumed to be minor since the chemical energy embodied in the biomass and the genetic biological structure contribute most to the exergy content of the system. Under these circumstances we can calculate the exergy content of the system as coming entirely from the chemical energy of the biomass

$$\text{Ex} = \sum_c (\mu_c - \mu_{c0}) N_i \quad (1)$$

This represents the chemical exergy, where $(\mu_c - \mu_{c0})$ is the difference in chemical potential between the ecosystem and the same system at thermodynamic equilibrium, and N_i is the amount of the i th component. This difference is determined by the concentrations of the considered components in the system and in the reference state (thermodynamic equilibrium), as it is the case for all chemical processes. We can measure the concentrations in the ecosystem, but the concentrations in the reference state (thermodynamic equilibrium) can be based on the usual use of chemical equilibrium constants. If we have the process

component A \leftrightarrow inorganic decomposition products

it has a chemical equilibrium constant, K

$$K = \frac{\text{inorganic decomposition products}}{\text{component A}}$$

The concentration of component A away from thermodynamic equilibrium is difficult to find, but we can find the concentration of component A at chemical

equilibrium from the probability of forming A from the inorganic components.

Using these equations, we find the exergy of the system compared with the same system at the same temperature and pressure but in form of an inorganic soup without any life, biological structure, information or organic molecules. As $(\mu_c - \mu_{c0})$ can be found from the definition of the chemical potential replacing activities by concentrations, we get the following expressions for the exergy:

$$\text{Ex} = RT \sum_{i=0}^n C_i \ln \left(\frac{C_i}{C_{i,0}} \right) \quad (2)$$

where R is the gas constant (8.317 J/K mol = 0.08207 l atm/K mol), T is the temperature of the environment, while C_i is the concentration of the i th component expressed in a suitable unit, e.g., for phytoplankton in a lake C_i could be expressed as mg/l of biomass or as mg/l of a nutrient. $C_{i,0}$ is the concentration of the i th component at thermodynamic equilibrium and n is the number of components. $C_{i,0}$ is of course a very small concentration (except for $i = 0$, which is considered to cover the inorganic compounds), corresponding to a very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium. $C_{i,0}$ is even lower for the various organisms, because the probability of forming the organisms is very low with their embodied information which implies that the genetic code should be correct. Nonetheless this value is calculable as the exergy content of the system. We furthermore wish to calculate the exergy due to the information (genetic) in the system. It is possible to distinguish between the biomass and information exergy (Svirezhev, 1998) using a new variable, p_i , defined as C_i/A , where

$$A = \sum_{i=1}^n c_i \quad (3)$$

is the total amount of matter in the system. This gives a new equation for the exergy

$$\text{Ex} = ART \sum_{i=1}^n p_i \ln \left(\frac{p_i}{p_{i,0}} \right) + A \ln \left(\frac{A}{A_0} \right) \quad (4)$$

As A approximates A_0 , exergy becomes a product of the total biomass A (multiplied by RT) and Kullback

measure of information

$$K = \sum_{i=1}^n p_i \ln \left(\frac{p_i}{p_{i,0}} \right) \quad (5)$$

where p_i and $p_{i,0}$ are probability distributions, a posteriori and a priori to an observation of the molecular detail of the system. It means that K expresses the amount of information that is gained as a result of the observations. If we for instance observe a system, which consists of two connected chambers, we expect the molecules to be equally distributed in the two chambers, i.e., $p_1 = p_2$ is equal to 1/2. If we, on the other hand, observe that all the molecules are in one chamber, we get $p_1 = 1$ and $p_2 = 0$.

The ability of a species to perform work in an ecosystem, its exergy or free energy, is thus proportional not only to its information content, but also its biomass. Margalef (1968), Straškraba (1979, 1980) and Brown (1995) have all proposed the use of biomass as an ecological goal function.

Lotka (1956) proposed maximum power as a goal function for energy systems. Power is work per unit time. Maximum power refers to maximum work performed per unit of time, which requires evolution of appropriate transformations within and between different energy forms (Odum, 1983). The transformation of energy to perform work is correlated with the amount of exergy available (stored or in passage) in the system. The more exergy stored, the more is available to be drawn on for work at a later stage, which requires conversion from storage to through-flow. In order to achieve storage, however, there must first be boundary flows (inputs) to sequester. A nice link between exergy storage and work performance was demonstrated for two lakes with significantly different levels of eutrophication by Salomonsen (1992). He showed that the exergy/maximum power ratio was approximately the same in both cases.

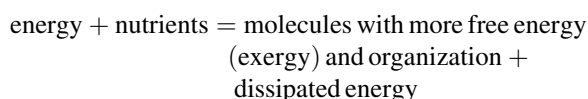
Second-law dissipation acts to tear down the structures and eliminate the gradients, but it cannot operate unless the gradients are established in the first place. Structure and organization can be expressed in different units, such as number of state variables, number of connections in an interactive web, and kJ of exergy which corresponds to distance from thermodynamic equilibrium. Biological systems, especially, have many possibilities for moving away from

equilibrium and it is important to know along which pathways among possible ones a system will develop. This leads to the following hypothesis (the formulation is in accordance with Jørgensen et al., 2000):

If a system receives an input of exergy, it will utilise this exergy to perform work. The work performed is used to maintain the system far from thermodynamic equilibrium whereby exergy is lost by transformation into heat. If, after maintenance, additional exergy is still available, then the system moves further away from thermodynamic equilibrium, reflected in growth of gradients. *If there is more than one pathway away from equilibrium, then the one yielding the most useful work (exergy) which ultimately moves the system furthest from thermodynamic equilibrium under the prevailing conditions will tend to be selected.* The result is a system with the most ordered structure. Or expressed differently: among the many ways for ecosystems to move away from thermodynamic equilibrium, the one maximising dEx/dt under the prevailing conditions will be selected.

This is a restatement of the corollary expressed above and an expansion of Jørgensen and Mejer (1977, 1979). The formulation is also consistent with an expanded version of Le Chatelier's principle. According to Le Chatelier's Principle, if energy is put into a

reaction system at equilibrium the system will shift its equilibrium composition in a way to counteract the change. This means that more molecules with more free energy and organization will be formed. If more pathways are offered, those giving the most relief from the disturbance (displacement from equilibrium) by using the most energy and forming the most molecules with the most free energy will be the ones followed in restoring equilibrium. Therefore, biomass synthesis can be expressed as the following chemical reaction:



Note also, the caveat of prevailing conditions in the above statement. We recognize that environmental inputs are variable even in response to the modification of the system parts themselves. This coevolutionary interplay feedback is what makes this not a smooth optimization problem. Just as it is not possible to prove the first three laws of thermodynamics by deductive methods, so too can the above hypothesis only be "proved" inductively. Below we present, a number of concrete cases, using models and observations, that contribute generally to the support of the hypothesis.

Table 1

Sixteen ecological phenomena explained using the presented eight thermodynamic principles of ecology

-
- (1) Water flow velocity in a marine environment decreases the impact of both competition and predation with the final effect of increasing local biological diversity.
 - (2) Disturbance disrupts the fronds of the superior competitor between two similar seaweeds allowing both to survive in areas scoured by waves.
 - (3) Effect of removing a strongly competitive C3-grass from perennial grassland is increased species richness of C4 grasses.
 - (4) Plants allocate biomass to minimize limiting factors.
 - (5) There are fewer species and lower biodiversity in higher latitude.
 - (6) When regional diversity is reduced (i.e., agriculture) predators switch to alternate food with less prey–predator oscillations.
 - (7) A stable parasite population does not overload bird physiology and helps sustain the host population.
 - (8) Species richness of lakes peaks in the range of 30–300 gC/y m².
 - (9) Reduction in species richness implies a decline in some ecosystem processes and a lower level of primary production.
 - (10) Increased evenness implies increased capacity for information and that the ecosystem moves further away from thermodynamic equilibrium.
 - (11) Forcing functions determine the ecosystem conditions and the conditions determine the species composition.
 - (12) Lower mammal mortality leads to later offspring weaning.
 - (13) Lower mortality implies later first birth with reduced risk.
 - (14) Exploitive competition can be explained by a higher growth to mortality ratio.
 - (15) Ecotoparasites have relatively high early stage mortality.
 - (16) Founder density is higher when the mortality is relatively high at an early stage.
-

5. Application of the thermodynamic principles of ecology

A list of some of the phenomena explained in the literature is given in Table 1. The detailed explanation of one of such instance is given at the end of the section as an example, whereas in most cases only an overview is given. Those interested in the detailed explanation are referred to the papers cited.

In addition, three other examples: (1) genome size, (2) organic matter oxidation sequence, and (3) cycling are presented immediately below. They are included as particularly illustrative examples taken from Jørgensen (2002a) and Jørgensen et al. (2002a) because they have a straightforward explanation based on the eight ecosystem principles given above. Additional examples can be found in these references.

5.1. Genome size

In general, biological evolution has been towards organisms with an increasing number of genes and diversity of cell types (Futuyma, 1986). If a direct correspondence between free energy and genome size is assumed, this can reasonably be taken to reflect increasing exergy storage accompanying the increased information content and processing of “higher” organisms.

5.2. Organic matter oxidation sequence

The sequence of organic matter oxidation (e.g., Schlesinger, 1997) takes place in the following order: by oxygen, by nitrate, by manganese dioxide, by iron(III), by sulphate, and by carbon dioxide. This means that oxygen, if present, will always out-compete nitrate which will out-compete manganese

dioxide, and so on. The amount of exergy stored as a result of an oxidation process is measured by the available kJ/mol of electrons which determines the number of adenosine triphosphate molecules (ATP's) formed. ATP represents an exergy storage of 42 kJ per mol. Usable energy as exergy in ATP's decreases in the same sequence as indicated above. This is as expected if the exergy-storage hypothesis were valid (Table 2). If more oxidizing agents are offered to a system, the one giving the highest storage of free energy will be selected. In Table 2, the first (aerobic) reaction will always out compete the others because it gives the highest yield of stored exergy. The last (anaerobic) reaction produces methane; this is a less complete oxidation than aerobic oxidation.

5.3. Cycling

If a resource (for instance, a limiting nutrient for plant growth) is abundant, it will typically cycle faster. This is a little strange, because cycling is not needed when a resource is not limiting. A modeling study (Jørgensen, 2002b) indicated that free-energy storage increases when an abundant resource cycles faster. This is also consistent with empirical results (Vollenweider, 1975; see Fig. 1). Of course, one cannot inductively test anything with a model, but the indications and correspondence with data tend to support in a general way the exergy-storage hypothesis.

6. Review of papers using the ecosystem principles to explain ecological observations

Salthe (2002) introduces a general theory of ecology that combines information theory and thermodynamics. The main application of the theory is ecosystem

Table 2
Yields of kJ and ATP's per mol of electrons, corresponding to 0.25 mol of CH₂O oxidized

| Reaction | kJ/mol electrons | ATP's/mol electrons |
|---|------------------|---------------------|
| CH ₂ O + O ₂ = CO ₂ + H ₂ O | 125 | 2.98 |
| CH ₂ O + 0.8NO ₃ ⁻ + 0.8H ⁺ = CO ₂ + 0.4N ₂ + 1.4H ₂ O | 119 | 2.83 |
| CH ₂ O + 2MnO ₂ + H ⁺ = CO ₂ + 2Mn ²⁺ + 3H ₂ O | 85 | 2.02 |
| CH ₂ O + 4FeOOH + 8H ⁺ = CO ₂ + 7H ₂ O + Fe ²⁺ | 27 | 0.64 |
| CH ₂ O + 0.5SO ₄ ²⁻ + 0.5H ⁺ = CO ₂ + 0.5HS ⁻ + H ₂ O | 26 | 0.62 |
| CH ₂ O + 0.5CO ₂ = CO ₂ + 0.5CH ₄ | 23 | 0.55 |

The released energy is available to build ATP for various oxidation processes of organic matter at pH = 7.0 and 25 °C.

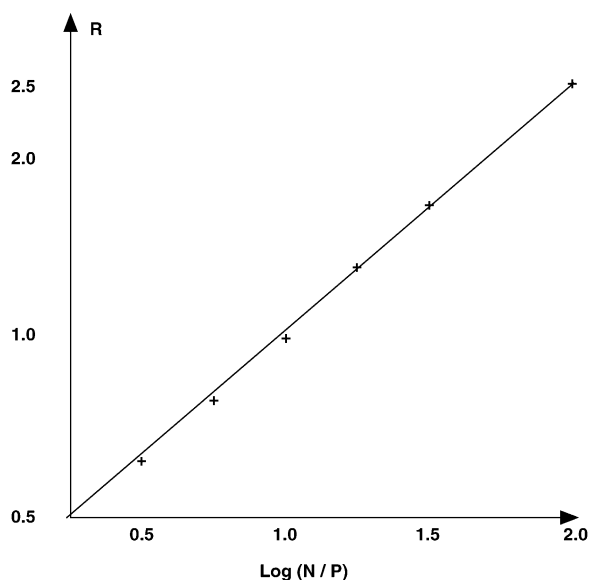


Fig. 1. Log–log plot of the ratio of nitrogen to phosphorus turnover rates, R , at maximum exergy vs. the logarithm of the nitrogen/phosphorus ratio, $\log N/P$. The plot is consistent with Vollenweider (1975).

development, so he calls it the developmental-infodynamic-thermodynamic theory (DITT). He views development as a response to thermodynamic potentials either to reduce energy gradients or to produce entropy. In this manner, he views the Second Law of Thermodynamics

as a key organizer of ecosystems because the imperfect energy transactions ensure that no single entity in the system consumes all the energy in a gradient. Salthe divides development into two sequences, the *development of immature systems* guided primarily by maximizing specific energy throughflow for growth, and *system senescence* during which gross energy throughflow is maximized for system maintenance. In the paper, he applies the DITT to a series of 39 recent papers in the ecological literature ranging from general development perspective, to immature and senescent systems. His conclusion is that the DITT can serve as an organizing framework for many current ecological studies.

Reynolds (2002) proposes that ecosystem structure, function, and pattern emerge from the interactions of individuals and populations and how they respond to cohabitating in a continuously variable environment. He introduces thermodynamic concepts by considering the individual organism's energy harvesting potential. Obviously, the maximum standing crop is reached when the potential energy harvest is equal to the maintenance costs. Below this intersection, the organism is growing; after maintenance exceeds energy intake, the organism is losing biomass, or entering senescence. He then continues to show how the thermodynamic ecosystem theory can be applied to eight previously published community assembly rules (Reynolds et al., 2000; Reynolds, 2001—repeated here

Table 3

Proposed rules of community assembly, modified after Reynolds et al. (2000) and Reynolds (2001)

- (1) Provided that species are present in substantial numbers and local conditions are adequate to meet their minimal requirements, then they will grow wherever and whenever the opportunities are fulfilled.
- (2) Of the species present, the most prominent will be those bringing structure that is most ordered and furthest from thermodynamic equilibrium (i.e., that store the most exergy).
- (3) In environments with unfilled resource and processing-flux capacity, assembly is biased towards adaptive traits favouring rapid acquisition and transformation, i.e., *r*-strategists predominate in early succession (Odum, 1969).
- (4) Pending constraints on resource acquisition and processing, growth raises the aggregate ability of the developing assemblage to harvest and store exergy. More species operate in benign environments: the richer the species representation, the more complex the network of energy flow and the greater is the information content.
- (5) Ascendant development brings “self-imposed” constraints upon resource availability or the opportunities to process them. There is a progressive change in the environmental conditions and these alter the organismic traits that are beneficial to the maximization of growth. Species-specific tolerance of resource stress (Grime's (1979) *S*-strategists) or disturbance (*r*-strategists) becomes selectively decisive.
- (6) Habitat deficiencies bias in favour of particular species traits. Organismic preadaptations and facultative adaptabilities of individual species determine their relative competitiveness and influence the species survival and the functional operation of the residual structure.
- (7) The more severe the constraints, the more selective its impact and the more robust is the direction of assemblage ascendancy. However, the succession of events and their emergent outcome is increasingly predictable from the attributes and performance limits of the species available: the fittest survive.
- (8) Emergent outcomes are always subject to overriding, environmental resetting, and structural reorganization through the intervention of external forcing, loss of unsustainable biomass, and a sharp return towards equilibrium conditions. Habitat opportunities are opened to post-disturbance exploitation.

in Table 3). For example, he considers the effect of latitudinal gradients on species diversity particularly regarding the models Taylor and Gaines (1999) use to relate the diversity decrease with latitude to the larger territories of species at higher latitude, and also the effect of range size on populations of bats and marsupials (Lyons and Willig, 2000). He also applies his theory to issues of optimality theories, structural thresholds, and diversity. He concludes with the statement that ecosystem structure emerges from the controlled dissipation of energy which moves the system further from thermodynamic equilibrium in the face of a continuously variable non-living environment.

Odum (2002) uses his energy circuit diagrams and the maximum empower principle (similar to maximum energy throughflow) to explain 12 phenomena in the current ecological literature. For each case he provides an energy circuit diagram. Examples of the case studies he examines are the allocation of biomass to maximize early growth (McConnaughay and Coleman, 1999), variation in number of species with latitude and area (Lyons and Willig, 2000), effect of chemical substances on food benefits to herbivores (Schmidt, 2000), increase in net productivity by increasing species evenness (Wilsey and Potvin, 2000), adaptive mechanisms connecting harrier predators and herbivorous voles to an ecosystem simplified by agriculture (Salamolard et al., 2000), and intraspecific competition regulates the flea concentration on host birds (Tripet and Richner, 1999). For example in response to Lyons and Willig's (2000) observation, H.T. Odum shows how there is less energy available in higher latitude for species interactions and niche separation necessary to prevent competitive elimination; and in the case off the ectoparasite (Tripet and Richner, 1999), the energy system diagram shows how a stable parasite population does not overload the bird's physiology and helps sustain the host population's role in the ecosystem. Odum concludes with the comment that systems diagramming forces investigators to see how ecological observations fit into and receive support from the larger system they are part of, and that since most researchers do not want their work to be diagrammed by others, encourages all ecologists to take up this practice.

Marques and Jørgensen (2002) use the maximum exergy principle, principle 8, to explain three selected case studies. In the first example they show how the

plant resource allocation findings of McConnaughay and Coleman (1999) already mentioned above are consistent with maximizing exergy. Second, they address the study by Dodson et al. (2000), which looks at the relationships between primary productivity and species richness in 33 lakes. Using the maximum exergy storage principle it follows that greater exergy storage at the primary producer level would allow for additional exergy available in the whole system resulting in a positive feedback in which storage increases at all levels. However, when stress of eutrophication occurs only a few species are efficient enough to capture the exergy input and benefit from the elevated nutrient levels. In the long run such a system experiences a decrease in information and moves closer to thermodynamic equilibrium. Finally, they address the controversial problem posed by Wilsey and Potvin (2000): does a reduction in species evenness affect ecosystem functioning in terms of energy flows and nutrient cycling in plant communities? Several studies carried out in experimentally established communities showed a decline in some ecosystem processes following the reduction in species richness and also that species-poor communities usually have lower levels of primary productivity, as well as plant cover and biomass, than species-rich communities. In a complex system like an ecosystem, evenness, as one component of diversity, constitutes part of the system's capacity for information. Exergy captured allows the biomass or information to increase and the more information a system contains the farther it is from thermodynamic equilibrium. In the present study, the evenness was increased by a kind of information manipulation. Such manipulation increased information and artificially moved the system further away from thermodynamic equilibrium. As a result, a more efficient dissipative structure was created, optimizing the exergy captured and increasing the exergy storage as biomass.

Jørgensen et al. (2002b) model exergy storage to explain the observed structure of functional feeding groups of aquatic macro-invertebrates. They selected five case studies from a large Dutch database EKKO, and in each case assessed the growth rates based on the observed size of the various functional feeding groups. It is difficult to generalize based on only five cases, but provided these five cases represent typical communities, they conclude that it is possible to use the

maximum exergy principle and a model to explain the composition of a community when the conditions are known. The following hypothesis can be formulated as a result: *The forcing functions or external factors determine the conditions of an ecosystem and the conditions determine the species composition.* This hypothesis is often used when an ecological model is developed because the state variables reflect the forcing functions. In some cases, there are two solutions (structures) that are equally valid for a given set of conditions, but the species composition is still determined by the conditions that are determined by the forcing functions. The hypothesis may be considered a consequence of the presented ecosystem theory.

In another paper, Jørgensen et al. (2002a) use a model to examine structural changes in an estuary and come to the same conclusion, namely that the maximum exergy principle can be used to determine a structure when the environmental conditions are given.

Jørgensen (2002a) again uses ecological models and the maximum exergy principle to show the validity of four specific observations published in the ecological literature. In each case, the observed phenomena can be explained by the following thermodynamic pattern: gradients increase as the system captures solar radiation, initiating a rapid rise in exergy degradation, gradients increase further by accumulating stored exergy which moves the overall system further from equilibrium. These cases include the following: lower mammal mortality leads to later offspring weaning (presented in detail below); lower mortality implies later first birth with less risk; exploitative competition relation to higher growth rate to mortality ratio; and, high early stage mortality in ectoparasites (Table 1 #12–16). The last phenomena, presented by Tripet and Richner (1999), has been explained differently by the maximum power principle and an energy system diagram by H.T. Odum.

Li and colleagues have also used fundamental thermodynamic principles as those discussed above to explain specific empirical ecological phenomena. For example, Li and Charnov (2001) used a Markov model of energy allocation and the fluctuation–dissipation relation to derive scaling rules of species number and population variability. They concluded that the balance of nature promotes diversity, and therefore the diversity–stability relationship may be an ener-

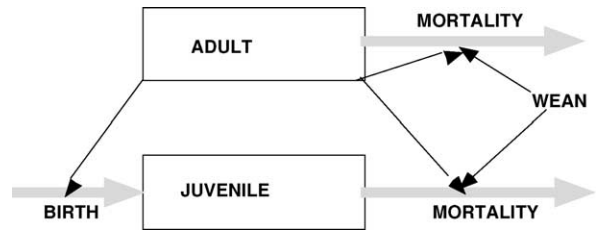


Fig. 2. Conceptual diagram of the model used to show that the lower mammal mortality leads to later offspring weaning.

getic consequence of ecosystems near equilibrium. In another study, Li (2002) considered phase transitions, which occur when thermodynamic parameters are changing, as a way to measure ecological vegetative succession. This approach also relies on the principle that as the system moves away from thermodynamic equilibrium a non-equilibrium phase transition occurs resulting in a new stable non-equilibrium state with more structure than the previous state. Using informational fractal patterns derived from aerial photos to measure far from equilibrium development, he found that the fractal dimension, and thus, woody vegetation increased over time.

7. Example: lower mammal mortality leads to later offspring weaning

One final specific example is given to show how ecological phenomena can be explained by the ecosystem theory and the application of models. A simple ecological model was developed based on

Table 4
Model equations using STELLA software which accompanies Fig. 2

| |
|--|
| Adult (t) = adult ($t - dt$) + ($- mortad$) $\times dt$ |
| INIT adult = 1000 |
| OUTFLOWS |
| Mortad = $0.0075 \times \text{adult} \times (1 + 100 \times \text{wean})$ |
| Juvenile (t) = juvenile ($t - dt$) + ($\text{birth} - \text{mortju}$) $\times dt$ |
| INIT juvenile = 0 |
| INFLOWS |
| Birth = $0.8 \times \text{adult}$ |
| OUTFLOWS |
| Mortju = if ($5 \times \text{juvenile} (1 - 100 \times \text{wean} \times \text{adult} / (1 + \text{juvenile})) > 0$), then ($5 \times \text{juvenile} (1 - 100 \times \text{wean} \times \text{adult} / (1 + \text{juvenile}))$) else (0) |
| Total = adult + juvenile |
| Wean = 0.00015 |

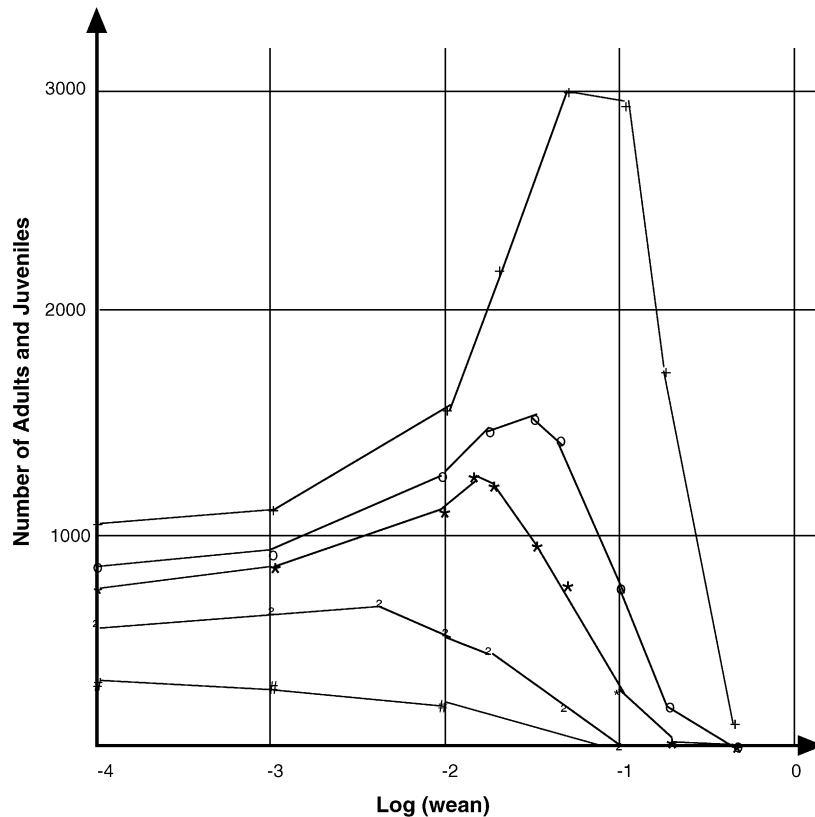


Fig. 3. The model results are used to set up a graph for wean time (log) in years vs. the number of adults and juveniles for five different mortality rates of adults from 0.001 (1 per year) indicated with + to 0.075 (75 per year) indicated with #.

observations using STELLA software to simulate the typical life history of a representative mammal species (Fig. 2). The model equations are given in Table 4. By running the model at different combinations of mortality and offspring wean times, the results in Fig. 3 are obtained. As seen, the most biomass (greatest exergy) follows the pattern that the longer wean time is associated with a small adult mortality. Therefore, by searching the model results for the condition in which exergy storage is maximized, we are able to reproduce the observed ecological phenomena that lower mammal mortality leads to later offspring weaning.

8. Conclusions

The presented ecosystem theory encompasses eight basic principles of open, thermodynamic, hierarchical

systems to ecosystems, including a principle that ecosystems move further from thermodynamic equilibrium by increasing both energy throughflow and exergy storage. We do not submit that these thermodynamic principles of ecology are the final words for ecosystem theory. They are in fact a tentative first step, and will most likely be amended in the coming years. New principles may be added or others may be modified. We therefore cannot conclude whether the tentative ecosystem theory presents the sufficient and necessary principles for a comprehensive and satisfactory ecological theory. However, the principles presented in this paper do capture many important features and emphasize already accepted thermodynamic principles. Like any theory, its value comes from its explanatory power, and we conclude that the tentative system theory can be used to explain observed ecological phenomena. We demonstrate this with the examples and findings presented in the papers

reviewed in this paper. A better ecosystem theory can only be achieved by gaining more experience in its application. Therefore, we recommend a wider application and use of the ecosystem theory in order to construct and advance a theoretical framework in ecology.

Acknowledgements

The authors wish to thank Robert Ulanowicz for his useful comments on the manuscript. B.D. Fath was visiting research scientist with the Dynamic Systems Project at the International Institute of Applied Systems Analysis while preparing the first draft of the manuscript.

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