Three selected ecological observations interpreted in terms of a thermodynamic hypothesis. Contribution to a general theoretical framework

João Carlos Marques [a],*, Sven Erik Jørgensen [b]

[a] *Department of Zoology, Faculty of Sciences and Technology, Institute of Marine Research (IMAR), University of Coimbra, 3004-517 Coimbra, Portugal*
[b] *Environmental Chemistry Section, Institute A, Royal Danish School of Pharmacy, Universitetsparken 2, DK-2100 Copenhagen Ø, Denmark*

Abstract

Biology and ecology are, in many ways, lacking universal laws and predictive theory, and most biologists and ecologists have been feeling the need for a more general and integrative theoretical network that may help in explaining their observations and experimental results. Thermodynamics has been widely applied in ecosystem theory since input, output, and cycling of mass and energy constitute the basis of ecological processes without exception. In this paper, we try to show that it is possible to explain different empirical biological and ecological observations in terms of a comprehensive thermodynamic hypothesis, instead of interpreting results according to a number of non-universal generalisations (e.g. the optimal partition theory or the 'generalised niche model'). The intention is to contribute to the elaboration of a general theoretical framework in biology and ecology, of which the thermodynamic hypothesis could be a part. The proposed approach is shown to be robust enough to provide an integrated explanation for the selected set of observations, and the fact that it was able to explain field observations and experiments supports the hypothesis. A stepwise approach is employed in developing a consistent theoretical framework, considered necessary to build new horizons for biology and ecology.
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1. The rationale

The criticism that biology and ecology as a whole are lacking universal laws and predictive theory is frequent, and there are authors who even argue that theoretical biology and ecology concerned for instance with fitness and natural selection is not scientific (Murray, 2001).

Scientific observations carried out on nature usually give origin to possible explanations and, in a further step, intend to provide tentative generalisations that may comprehend the entire set of available information. Generalisations may be descriptive and inductive, like the Archimedes

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* Corresponding author. Tel.: +351-39-836386; fax: +351-39-823603
E-mail address: jcmimar@ci.uc.pt (J.C. Marques).

principle, deriving from observations carried out on observable characteristics (volume for instance), or become much more eager, constituting the base of deductive theories, like the quantum theory. In biology and ecology, we must recognise that there are basically no universal laws, and that in fact most explanations are inductive generalisations, without any deductive theory behind them. As a consequence, we may find a large number of non-universal tentative generalisations in biology and ecology.

Biology and ecology are more complex than physics, and it will, therefore, be much more difficult to develop an applicable, predictive ecological theory. Testing explanatory hypotheses by verification instead of doing it by falsification is perhaps the easiest way. But most biologists and ecologists probably feel inwards the need for a more general and integrative theory that may help in explaining their observations and experimental results.

In the last 20 or 30 years several new ideas, approaches, and hypotheses appeared in the field of systems ecology, which when analysed more deeply appear to form a pattern of theories able to explain the dynamics of ecosystems (Jørgensen, 1997). Due to the complexity involved, we probably need a number of different complementary approaches to explain ecosystem structure and function (Jørgensen, 1994a). Such ecosystem theories were only used in a limited way in ecological modelling, namely in the development of non-stationary models, able to take into account the adaptation of biological components (Jørgensen and Padisak, 1996; Jørgensen and De Bernardi, 1997a,b Jørgensen and De Bernardi, 1998 Jørgensen, 1986, 1992, 1994b, 1997). It is argued that to improve substantially the predictive power of ecological models it will probably be necessary to apply theoretical approaches much more widely (Jørgensen and Marques, 2001). Nevertheless, the question remains: is it possible to develop a theoretical framework able to explain the numerous observations, rules, and correlations dispersed in the ecological literature during the last few decades?

Although we may have no answer to this question, it has been argued (Jørgensen and Marques, 2001) that it should at least be possible to propose a promising direction for ecological thinking, and try to build some fragments of such a theoretical framework. Thermodynamics has been widely applied in ecosystem theory since input, output, and cycling of mass and energy constitute the basis of ecological processes without exception. Jørgensen and Marques (2001) selected a specific thermodynamic hypothesis to illustrate the possibilities of constructing an ecological theoretical framework, and provided a few examples of ecological observations that can be derived from the thermodynamic hypothesis by using models.

The goal of the present paper is to test the thermodynamic hypothesis from a different perspective, using it to interpret empirical ecological results provided by a set of selected ecological studies. The idea is to see if ad hoc (i.e. non universal) explanations provided by different authors about different ecological problems can be further enlightened according to the same theoretical approach.

2. A short review of the thermodynamic hypothesis

To ensure the existence of a given system, a flow of energy, or more precisely exergy, must pass through it, meaning that the system cannot be isolated. Exergy is a concept derived from thermodynamics that may be seen as energy free of entropy (Jørgensen, 1997; Jørgensen and Marques, 2001), i.e. energy which can do work. For instance, only approximately 98% of the solar radiation constitutes exergy, being able to produce work. A flow of exergy through the system is sufficient to form an ordered structure, or dissipative structure (Prigogine, 1980). If we accept this formulation, called the fourth law of thermodynamics by Morowitz (1992), then a question arises: which ordered structure among the possible ones will be selected or, in other words, which factors determine how an ecosystem will grow and develop? Jørgensen (1992, 1997) proposed a hypothesis to interpret this selection, providing an explanation for how growth of ecosystems is determined, the

direction it takes, and its implications for ecosystem properties and development.

Growth may be defined as the increase of a measurable quantity, which in ecological terms is often assumed to be the biomass. But growth can also be interpreted as an increase in the organisation of ordered structure or information. From another perspective, Ulanowicz (1986) makes a distinction between growth and development, considering these as the extensive and intensive aspects, respectively, of the same process. He argues that growth implies increase or expansion, while development involves increase in the amount of organisation or information, which does not depend on the size of the system.

According to the thermodynamic hypothesis, when a system grows it moves away from thermodynamic equilibrium and stores exergy in its dissipative structure. Exergy constitutes a measure of the distance between a given state and what the system would be at thermodynamic equilibrium (Jørgensen and Mejer, 1979). In other words, if an ecosystem were in equilibrium with the surrounding environment its exergy would be zero (no free energy), meaning that it would not be able to produce any work, and that all gradients would have been eliminated.

Structures and gradients, resulting from growth and developmental processes, will be found everywhere in the universe. Of course, second-law dissipation acts to tear down the structures and eliminate gradients, but to have dissipation the gradients to be dissipated must exist in first place. And thus an obvious question is: what determines the buildup of gradients?

In the particular case of ecosystems, during ecological succession, exergy is presumably used to build biomass, which is exergy storage. Structure and organisation may then be expressed in kJ, corresponding to the distance from thermodynamic equilibrium = exergy expressed in energy units. In other words, in a trophic network, biomass and exergy will flow between ecosystem compartments, supporting different processes by which Exergy is both degraded and stored in different forms of biomass belonging to different trophic levels.

Biological systems are an excellent example of systems exploring a plethora of possibilities to move away from thermodynamic equilibrium, and thus it is most important in ecology to understand which pathways among the possible ones will be selected for ecosystem development. Such knowledge would be the key to describing the processes characteristic of developing ecosystems and to predict their emergent properties. Taking into account the perspective defended in Jørgensen et al. (2000), it would be more appropriate to approach not the selection of the components and processes for an ecosystem's development, but rather the propensity (Ulanowicz, 1997) for directional development (Jørgensen and Marques, 2001). Jørgensen (1997) formulates the answer as a hypothesis.

If a system receives a throughflow of exergy (a) the system will utilise this exergy flow to move away from thermodynamic equilibrium, and (b) if more than one pathway is available to achieve this, the one yielding most stored exergy (measured in J m^{-2} or J m^{-3}) by the prevailing conditions, i.e. with the most ordered structure and the greatest distance from thermodynamic equilibrium, will have a propensity to be selected.

The three laws of thermodynamics cannot be proved by deductive methods, and thus the thermodynamic hypothesis can only be proved by inductive methods. This implies that it should be investigated in as many concrete cases as possible.

The thermodynamic hypothesis may also be seen as an extended version of 'Le Chatelier's Principle' (Jørgensen and Marques, 2001), with energy + nutrients = molecules with more exergy (free energy and organisation) + dissipated energy. If energy is pumped into a system in equilibrium, the system shifts in equilibrium composition in a way to counteract the change. The meaning of this, according to the 'Le Chatelier Principle', is that more molecules with more free energy and organisation will be formed. If there is more than one pathway, the one that uses most energy forming molecules with most embodied exergy will be the selected one, according to the hypothesis.

The stored exergy of an ecosystem can be approximately estimated by the following expres-

sion:

$$Ex = \sum_{i=1}^{n} \beta_i C_i$$

where Ex is the exergy, β_i is a weighting factor dependent on the amount of information that the components carry, and C_i is the concentration of the components $i = 1-n$. Exergy can be converted from detritus equivalents to kJ by multiplying by 18.7. The derivation of this equation can be found in Jørgensen et al. (1995), Jørgensen and Padisak (1996), Jørgensen (1997); Jørgensen and De Bernardi (1998); Jørgensen et al. (2000). This equation presumes that exergy from the ecosystem is found relatively to the same system at thermodynamic equilibrium at the same temperature and pressure. It means that exergy represents the energy that does work due to the free energy of the many organic compounds plus the information that the living organisms carry. Table 1 provides the β-values of different types of organised organic matter (organisms) relative to detritus, which for practical purposes is considered to have no information but only the free energy of the organic matter (on average 18.7 kJ g^{-1}) (Jørgensen et al., 1995). There is an obvious lack of discriminating power in the weighting factors given in Table 1, where organisms are considered at very high taxonomic levels. The estimation of more accurate weighting factors involves nevertheless practical difficulties that are still not fully understood and overstepped (Marques et al., 1997; Fonseca et al., 2000; Debeljack, 2002). Actually, the assessment of β-values constitutes a weak point, which may nevertheless be reduced in the future when we know more about the genes and their active expression, or in other words, how many amino acids can be directed by genes.

Despite the obvious uncertainty regarding the weighting factors, these have been used with a relative success to assess ecosystem health, and quite successfully in the development of structural dynamic models. This is probably due to the fact that calculations are robust in the sense that, in certain cases, it is not important that we know accurate weighting factors, although it is important that these be approximately correct. For

Table 1
Values for the weighting factors to estimate exergy related to organisms biomass for different groups of organisms

Organisms	Weighing factor
Detritus	1
Minimal cell	2.7
Bacteria	3.0
Algae	3.9
Yeast	6.4
Fungus	10.2
Sponges	30
Moulds	32
Plants, trees	30–87
Jellyfish	30
Annelid worms	50
Insects	70
Crustacean Zooplankton	30–46
Crustaceans (Decapods)	230
Gastropods	450
Bivalves	760
Echinoderms	260
Fish	287–344
Amphibians	800
Reptiles	1000
Birds	1100

Values of weighting factors are based on the number of information genes. The exergy content of the organic matter in the various organisms is compared with exergy contained in detritus. Estimations were carried out according to the method described by Jørgensen et al. (1995), based on analytical work (Fonseca et al., 2000) and on literature sources (Lewin, 1994; Li and Grauer, 1991).

instance, the differences between weighting factors of phytoplankton and zooplankton organisms is roughly a factor of 10. This factor could be 5, 8, or 15 without affecting calculations too much, meaning that it might not be exact as far as it is able to express a major difference between phytoplankton and zooplankton. But this would not be the case if one wanted, for instance, to develop a model of ecosystem health assessment where competition takes place between two similar species.

3. Tentative interpretation of ecological results in terms of the thermodynamic hypothesis

Three ecological studies have been selected to serve as examples of how empirical ecological results can be consistently interpreted in terms of

the thermodynamic hypothesis. The intention is to demonstrate this hypothesis as part of a more general theoretical ecological framework.

Example 1. Let us consider a first observation taking plants as an example. The patterns of biomass through the whole vegetative growth phase of three annual plant species, respectively, *Abutilon theophrasti*, *Chenopodium album*, and *Polygonum pensylvanicum* were examined along three separate gradients of resource availability (McConnaughay and Coleman, 1999). Individuals of the three species were grown in controlled greenhouse conditions across gradients of light, nutrients, and water to determine if the plasticity in the patterns of biomass allocation were consistent with the optimal partitioning theory, seen here as a non-universal tentative generalisation. According to the optimal partition theory, plants should respond to variation in the environment by partitioning biomass among various plant organs to optimise the capture of nutrients, light, water, and carbon dioxide in a manner that maximises plant growth rate. For example, plants exposed to reduced sunlight would be predicted to shift resources toward stem and leaf growth, and to pigments associated with light capture, instead of increasing the production of root biomass, carbohydrate availability for nutrient uptake, or enzymes associated with carbon fixation. Alternatively, factors that limit the acquisition of belowground resources relative to light and CO_2 should have the opposite effects.

Variable, or plastic, biomass allocation patterns may result from either ontogenetic drift in biomass allocation coupled with plasticity in growth rates (reflecting an apparent allocation plasticity), or from true plasticity in biomass allocation. In this case study, frequent harvests were used to determine the growth and allocation responses of selected species by analysing variation of root/shoot biomasses, and leaf area/biomass ratios. From growth analysis, each species exhibited a significant plasticity in growth rates and much ontogenetic drift in root/shoot and leaf area/biomass ratios along the resource gradients considered. Allocation of biomass to roots decreased and leaf area increased under low light and high nutrient conditions, which was basically in agree-

ment with the optimal partitioning theory. On the other hand, despite the fact that strong differences in growth rates were observed, the studied species did not show changes in biomass allocation in response to large variations in the water regime. Finally, most of the observed differences in biomass allocation were limited to a given time during growth and development. Thus, the authors concluded that for those rapidly growing species plasticity in biomass allocation patterns was only partially consistent with optimal partitioning theory, and that plastic responses were ontogenetically constrained.

Can the results obtained by McConnaughay and Coleman (1999) be interpreted in terms of the thermodynamic hypothesis? Plants, as all living things, are ordered (or dissipative) structures. Different plants exhibit growth processes along a gradient of light, nutrients, and water availability. According to the thermodynamic hypothesis, each one of the plants received a throughflow of exergy, which was used to remain at or move away from thermodynamic equilibrium by maintaining its structure and function (information) and growing (increasing exergy storage). In low light conditions, plants increased exergy storage by increasing leaf biomass and pigmentation, which also increased exergy capture (positive feedback). In high light conditions, since exergy capture is fully assured, allowing plants to keep structure and function (information) without constraints, exergy storage is then increased (augmenting distance to thermodynamic equilibrium) by building more structure through increase in root biomass (reserves).

If nutrient uptake is low as under nutrients limitation, plants increase exergy storage by increasing root biomass (reserves). The reason is they increase leaf biomass, and consequently the exergy capture (positive feedback) that would not be reflected in an optimisation of exergy storage, since due to nutrient limitation not all exergy captured could then be used to build more structure.

Finally, the water regime did not affect the biomass partition between roots and leaves because it just had an indirect effect on the balance between dissipation (keeping structure and func-

tioning) and exergy storage (building structure). Nevertheless, for extreme water conditions, it is predictable that plants would not be able anymore to keep or increase distance to thermodynamic equilibrium. In the long run, in nature, this would mean that the species present would not be the most efficient any more in keeping distance from thermodynamic equilibrium considering the new prevailing conditions. Consequently, those species would predictably be replaced through interspecific competition, leading to a shift in the community species composition.

Example 2. Another example regards the relationship between primary productivity and species richness in lake plankton communities, taking into account phytoplankton, rotifers, cladocerans, copepods, macrophytes, and fish (Dodson et al., 2000). Thirty-three lakes were surveyed for which there were available data on the six major taxonomic groups. Additionally, the effects of short term and long term whole-lake nutrient addition on primary productivity and planktonic richness were analysed. As a whole, in the survey, higher values of species richness of the six groups considered appeared consistently related with increased annual primary productivity, although the richness versus productivity relationship for phytoplankton and fish was strongly dependent on lake size. Species richness peaked at levels of primary productivity in the range of 30–300 g C m^{-2} per year, with obvious differences among taxa. Therefore, the highest values of species richness occurred at levels of productivity comparable to those of oligotrophic to slightly mesotrophic lakes, being likely to decline as lakes become eutrophic, which emphasised the potential threat of eutrophication to lacustrine biodiversity.

Short term (3 year) and long term experiments (21–24 year) allowed testing the response of individual lakes to whole-lake nutrient enrichment. Experimental addition of nutrients caused largely variable and unpredictable responses in species richness, probably due to transient dynamics and time lags, with effects of nutrient addition being taxon and lake specific. For instance, depending on the history of enrichment and recovery, phytoplankton exhibited quite variable relationships between species richness and

pelagic primary productivity. Moreover, in the experimental lakes, primary productivity had no effect on rotifer richness, and crustacean zooplankton were negatively correlated with primary productivity in both short- and long-term experiments. Several possible factors were suggested to explain the decline of richness at high productivities, namely (a) competition, at least in the short term and for some taxa, (b) predation, and (c) abiotic factors, such as reduction in nocturnal oxygen concentrations. Several different theories suggest, therefore, that the relationship between primary productivity and species richness is driven by multiple factors. In other words, a variety of factors might account for the absence of unimodal richness versus productivity relationships, including transient dynamics, lagged responses and possible shifts to new system states.

Let us now look into these comprehensive set of results from the thermodynamic hypothesis perspective. Why should species richness increase with productivity? Lake ecosystems, as all ecosystems, are complex ordered (dissipative) structures through which an exergy flow will be utilised to remain at or move away from thermodynamic equilibrium. Increased primary production, reflecting exergy storage at the primary producer level, represents more exergy available in the whole system, which potentially increases also the information in the system by supporting additional species and trophic levels. Thus, the probability of having more species and trophic levels in the ecosystem increases as a function of an increased exergy input. This explains why it was observed, that phytoplankton was already diverse in very low productive lakes (~ 1 g C m^{-2} per year) (see Dodson et al., 2000), and also why phytoplankton diversity reached a maximum in lakes where the productivity of the above trophic groups was very low (small to moderate size lakes) (see Dodson et al., 2000). Although herbivores were present in low productive lakes, they could only reach their maximum diversity in more productive lakes (moderate size lakes) (see Dodson et al., 2000, which possibly reflected the increase of available exergy between the primary producer and primary consumer levels. Finally, fish, as top consumers, showed maximum diversity in medium to large size

lakes at moderate levels of lake productivity (see Dodson et al., 2000). As a whole, this picture is pretty much consistent with the thermodynamic hypothesis.

Additionally, (Dodson et al., 2000) observed also that macrophyte (benthic primary producers) species richness usually attained the peak at higher lake productivity values than does phytoplankton richness. These observations are also consistent with the thermodynamic hypothesis, according to the following explanation: for a given level of sun radiation (exergy input), temperature, and nutrients, the specific net productivity of phytoplankton is higher than that of macrophytes because these have non-photosynthetic tissues that absorb exergy stored through photosynthesis.

Why should eutrophication decrease species richness? In a stress induced situation only a smaller number of species will be efficient enough in capturing exergy to take profit from nutrient enrichment, and those will win interspecific competition. These fast growing species will shade other species, avoiding them to capture exergy, and thus a probable shift of species composition in the system is predictable. In the long run, the system will loose information, and, therefore, will become closer to thermodynamic equilibrium.

Example 3. A third case study (Wilsey and Potvin, 2000) analyses a controversial problem: do reductions in species evenness affect ecosystem functioning in terms of energy flows and nutrient cycling in plant communities? The authors take as an example a plant community, considering three plots, with different dominant species. 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. Nevertheless, the effects of changes in species diversity were quite smaller compared with effects of changes in species composition. Since diversity has two components, species richness (number of species in a given area) and evenness (how well distributed abundance or biomass is among species from a given community), the authors decided to vary species evenness

and to identity of the dominant plant species in a field experiment. The basic idea was to separate the effects of species composition and evenness, testing if plant productivity would increase with increasing levels of evenness, and if relationships would be invariant in relation to species identity.

In the experiments, besides differences due to species identity, total plant biomass (above + belowground) increased with increasing levels of evenness. Moreover, this trend between evenness and biomass was always observed independently from the dominant species in the plots (evenness × species identity interaction). The separate analysis of aboveground and belowground biomasses showed that belowground parts increased linearly with increasing levels of evenness, while aboveground parts varied mostly as a function of species identity. Finally, there was a relationship between variations in plant height, but no relationship was found between variation in rooting depths and total biomass.

As a whole, results suggest that there is a direct relationship between diversity and plant productivity in such a way that diverse communities are more productive not merely because they have a larger probability of containing species with higher growth rates, and evenness appears to play a more important role than species richness. To explain these results, the authors adopted an hypothesis (again non universal) termed 'generalised niche model', according to which more diverse communities are more productive because a greater proportion of light is captured by the plant community as a whole, involving greater complementary use of resources in space and time, and thus a shift in community interactions from strong competition to weak competition or facilitation. Since total plant biomasses were related to plant heights but not to rooting depths, it was concluded that differences in the interception of light were probably more important than nutrient uptake in explaining the plant community response to evenness. This was considered to be most likely in communities where intraspecific competition for light is greater than interspecific competition, and especially in communities where there are differences in plant architecture among species. Nevertheless, the proportion of light captured during the

experiments was not measured directly and the authors recognise that further work would be necessary to test if the 'generalised niche model' is a sufficiently robust mechanism to explain their observations.

Let us see how these results could be interpreted according to the thermodynamic hypothesis. In a complex system like an ecosystem, evenness, as one of the components of diversity, constitutes part of the system information. Exergy capture allows to increase biomass and/or information, and the more information a system contains the farther it is from thermodynamic equilibrium. In the present study, the authors experimentally carried out a kind of information manipulation by increasing evenness. Such manipulation increased information and artificially moved the system further from thermodynamic equilibrium. As a result, a more efficient dissipative structure was created, optimising exergy capture (necessary to keep the structure at the new information level) and increasing exergy storage, namely as biomass. Despite quantitative differences depending on the species, this explains why, as a trend, total biomass increased as a function of increased levels of evenness. Moreover, this also explains why belowground parts increased linearly with evenness, while the response of aboveground parts was very much species dependent. In fact higher exergy storage (biomass reserves) in belowground parts is a result of a more efficient exergy capture, while exergy storage in aboveground parts depends on the different plant specific strategies (architectures) in optimising exergy capture, which depend on long term genetic adaptation and, therefore, will not undergo significant change as a function of evenness manipulation.

4. Discussion and conclusions

Biological and ecological explanations often appear isolated, and links between different observations, laws and/or rules are most often weak or nonexistent. To make real progress in a field requires a more general and integrative theory that may help in explaining biological and ecological observations and experimental results.

The general idea behind this paper was to demonstrate that it is possible to explain different biological and ecological observations on the basis of ecosystem theory, replacing a number of non-universal generalisations (e.g. the 'optimal partition theory' or the 'generalised niche model') by a broader one. As a theoretical frame, we tested a thermodynamic hypothesis that could be part of a general theoretical framework in biology and ecology.

It has been shown that the thermodynamic hypothesis is able to explain successfully the following observations/rules:

1) In view of a gradient of environmental conditions, plants will respond by partitioning biomass among various plant organs in such a way that they optimise the capture of nutrients, light, water, and carbon dioxide, maximising plant growth rates.
2) In oligotrophic to slightly mesotrophic lakes, species richness will increase as a response to increased annual primary productivity, but will tend to decline as lakes become eutrophic.
3) More diverse plant communities will be more productive, with evenness appearing to play a more important role than species richness.

The proposed approach has limitations, of course, but is revealed to be robust enough to provide an integrated explanation for the selected set of observations. It is a fact that the theoretical approach followed, although promising and intellectually challenging, is still a hypothesis. On the other hand, the fact that it was able to explain field observations and experiments may be considered to support to the hypothesis.

It is time to start developing a universal theoretical framework in biology and ecology; one anchored in general laws such as those from physics and chemistry. The understanding of complex systems, such as ecosystems, means following a stepwise approach, and the effort of many researchers over a long period of time will be necessary. Although this is not the easiest way, it will be necessary to build new horizons for biology and ecology.

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