COENOSES 11(2): 73-76, 1996
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A THERMODYNAMIC INTERPRETATION OF SUCCESSION

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Keywords: Disorder; Dissipative structures; Entropy, Self-organization; Vegetation.

Abstract: An interpretation of ecological succession is outlined based on recent applications of non-equilibrium thermodynamics to living systems. From such a perspective it is suggested that phenomenological analogies between ontogeny, phylogeny and succession are not accidental but follow from patterns of self-organization in complex systems. Thereby Lotka's maximum power law and Prigogine's concept of self-organizing dissipative structures are seen as the common organizing principles. Consequences of such an interpretation are discussed in light of Darwinian theory and Gleasonian objections to holistic succession theories.

1. Introduction

Most ecologists would agree that terrestrial plant succession results from the manifold interactions among the various biotic and abiotic constituents of a system as a new site is colonized or a previously occupied one recovers from disturbance. Controversy exists, however, over whether a theory of succession should be sought at the species level (Drury and Nisbet 1973, Horn 1974, 1975, Pickett 1976, Connell and Slatyer 1976, Noble and Slatyer 1980, Huston and Smith 1987) or at the level of the system as a whole (Margalef 1968, Odum 1969, Schneider 1988, Weber et al. 1989). Whereas the former view is reductionist, stating that community properties are contained within species properties, the latter is holistic, claiming that system properties emerge as the community develops.

The parallels between patterns observed in vegetation succession and those in the phylogeny and ontogeny of living organisms led Clements (1916) to propose an organismic concept of plant communities. This concept held that plant communities were strongly integrated units with sharp boundaries and clusters of species tightly associating together. This view was simultaneously but independently attacked by Gleason (1926) and Ramensky (1926), based on the observation that changes in species abundance and presence occurred so gradually that a division of the vegetation into distinct associations was not justified. Clements' organismic view was further rejected on the grounds that a community had no continuity by descent reflecting its lack of a central control system or an inherited genetic message for the community as a whole (Cain 1947, Whittaker 1975). This "individualistic" concept, the antithesis to Clements' view in its most extreme formulation, would imply that the spatial distribution of plants is a "consequence of the individual, relatively uncoordinated responses of the species to the gradients in the physical environment" (Simberloff 1980, summarizing the work of Curtis and McIntosh 1951, Curtis 1955, 1959, Whittaker 1956, 1967).

This article reexamines the reductionist/holistic debate over community succession motivated by a suspicion that the parallels between succession, evolution and ontogeny are not purely accidental but are expressions of an underlying principle. Indeed, Wicken (1987) regarded the study of succession to be of particular interest because it "provides a tractable microcosm for evolution". Recent efforts to apply non-equilibrium thermodynamics to biological systems (Prigogine 1980, Brooks and Wiley 1986, Wicken 1987) have contributed insights that may have important consequences for succession theory and may be able to bridge the rift between reductionist and holistic approaches. Applications of thermodynamic theory to living systems suggest that analogies between developmental patterns of organismic growth and ecological succession are indeed non-trivial and can be interpreted as the result of patterns of energy flow. The phenomenon of succession is thereby placed into the larger context of systems development in general which makes its investigation worthwhile beyond its strict application to plant ecology alone.

2. Succession – a Thermodynamic Interpretation

Biological systems can be viewed as thermodynamic entities that survive as a result of processing matter and energy. According to the second law of thermodynamics the entropy of closed systems invariably increases over time, leading ultimately to an equilibrium state of maximal entropy where the parts of the system are arranged in a state of minimum order. In contrast to closed systems, living systems develop an increasing degree of organization and complexity during the course of ontogeny, phylogeny and succession. This apparent violation of the second law of thermodynamics can be explained by the fact that living systems are "open", i. e. constantly exchanging energy with the environment; thus, overall entropy increases although there is evidently a local decrease of entropy within the system.

As pointed out by Landsberg (1984) and Brooks and Wiley (1984), however, the lower entropy of a living system does not represent a decline, as such, but rather a departure from a potentially higher state of disorder (i. e. order = $H_{max} - H_{real}$). Viewed in this light there is no violation of the second law of thermodynamics in the living world. Although in developing systems order and organization will increase over time, there will be an absolute increase in entropy as they grow as result of the increase in the number of potentially available states (H_{max}). The increase in order and organization can be explained as a decrease in relative entropy, measured as the fraction of the number of actually occupied (H_{real}) to H_{max} (Landsberg 1984, Brooks and Wiley 1986).

Prigogine (1955) realized that living systems share this entropic property and other features with dissipative structures. Dissipative structures, e.g. hurricanes or Benard cells (structures forming on the surface of certain fluids as a result of convection due to a strong temperature gradient), are open systems that are able to maintain themselves away from equilibrium by exchanging energy with the outside world. Within a discrete range of energy input such systems tend to develop towards increasing organization, a feature termed "self-organization". Such systems are further characterized by increased internal cycling of energy as they mature (Morowitz 1968). Ulanowicz (1986), analyzing model flow systems, identified cycling as a key feature in developing systems; under certain conditions increased cycling would lead to an increase in total systems throughput as well as rises in the level of organization and complexity. The persisting flow of energy will prevent such systems from reaching thermodynamic equilibrium; instead the system will eventually settle down in a state of least dissipation, investing a maximum amount of the inflow in internal structure building (Prigogine 1980).

The concept of "dissipative structures" provides a framework for an explanation of succession and other time-dependent phenomena that lead towards increasing organization and complexity in the living world. Higher organization and complexity are achieved by minimizing dissipation from the system. This is realized by internal cycling of the available energy leading to an increasingly finer network of functional interactions accompanied by increased specialization and diversity.

The actions of Prigogine's principle of minimum dissipation also affect the stability of a system. Apart from increased cycling of energy, energetic efficiency can also be gained by the elimination of redundant system configurations. This has important consequences on the system's resistance to external disturbance since such redundant configurations are thought to be important in maintaining homeostasis in the face of external disturbance through compensatory flow pathways (Odum 1953). Concurrent with this decrease in resistance to external perturbation, development slows down and a state of dynamic equilibrium (homeostasis) is approached. Thus, with increasing age and declining redundancy, the system becomes more vulnerable to external disturbance while at the same time becoming more stable internally. These two properties have been used by Weber et al. (1989) to define the senescence of a system.

Thus, dissipative systems in their mature phases are characterized by an increasingly efficient use of resources within a constrained energy economy. Conversely, under the relatively unconstrained circumstances of early phases of development, an open system displays the tendency to maximize total system flow-through, resulting in system expansion, rather than those resources being used in the most efficient fashion. This "maximum energy principle", first recognized by Lotka (1922, p. 148) holds that "natural selection will so operate as to increase the total mass of the organic system, and to increase the total energy flux through the system so long as there is present an unutilized residue of matter and available energy".

The principles of Prigogine and Lotka are interacting tendencies, each prevailing at a different stage of development. According to Wicken (1986), the cooperative tension of the two will favour strategies that focus resources into the system, while at the same time stabilizing the web of energetic interconnections; hence dissipation will decrease and biomass/throughput ratios will increase. In his analyses of model flow networks, Ulanowicz (1986), showed that the system will seek an optimal configuration at a point of compromise between total throughput and internal organization.

From a thermodynamic perspective a reply to Pickett's (1976, p. 112) statement that "succession can be understood solely in terms of the interaction of evolutionary strategies without reference to a deterministic progression toward climax" would be that both evolutionary strategies and the deterministic drive toward climax follow from the same underlying causes, viz. Lotka's "maximum power" law and Prigogine's "minimum dissipation" principle. Thus, evolutionary strategies can be viewed as expressed microstates within ecosystem macrostate all of which are under the control of the same thermodynamic laws.

3. Consequences of a Thermodynamic Interpretation to Community Theory

It is obvious from the above that a thermodynamic interpretation of succession is a holistic one. The principal agent driving succession is identified as an overall energetic strategy of the system, a unifying principle directing the processes manifest on the level of individual populations and species. The thermodynamic scenario provides a plausible explanation for the undeniable similarities of the processes of succession, evolution and ontogeny, such as directionality towards increasing organizational complexity, energetic efficiency, and size. The common organizing principles thereby are Lotka's law of "maximum energy" and Prigogine's principle of "minimum dissipation", causing the expansion of the system and driving it towards higher organization and complexity. Such a view is ostensibly in close approximation to the Clementsian "superorganism" and will have to stand up to Gleasonian objections as well as to Darwininan theory.

There is generally little doubt that the distribution and abundance of species in a community result not only from the individual responses to the abiotic environment, but also from plant-to-plant interactions. Such interactions including competition for light, water and nutrients, as well as the allelopathic, mutualistic and parasitic relationships, have been explored by a host of experimental and descriptive studies (Tansley 1917, De Wit 1960, Goss 1960, Thurston 1969, Eis 1970, Sharitz and McCormick 1973, Connell 1972, Lubchenco 1980, Paine 1984, Grace and Whetzel 1981, Silander and Antonovics 1982). Turkington and Aarssen (1984) documented that biotic interactions may affect community structure even on an evolutionary timescale. Whereas Harper (1982) argued that interactions may be restricted to take place only between neighbouring plants, Eis (1970) reported that entire networks of trees and living stumps connected by intraspecific root-grafting, a result that led him to recommend a "modification of the generally accepted concept that individual plants are discrete physiological units" (p.29).

In light of this evidence it appears justified to conclude that plant communities have some degree of organization that goes beyond the description of the spatial occurrence of plants in certain areas. Therefore, properties at the level of the community (productivity, respiration, biomass, diversity, stability, etc.) are likely to be influenced by this organization as expressed through interactions. Furthermore, it is instructive to note that even though the thrust of the 1947 articles by Cain, Egler and Mason in Ecological Monographs (which led to a breakthrough of the "individualistic" concept) was directed primarily against the concept of communities as discrete entities and the taxonomic grouping of these into associations, no one claimed that a community had no reality in itself or was nothing beyond an assembly of unrelated objects. In fact, Gleason (1917, p. 473) himself wrote "... as soon as the ground is occupied competition restricts it [the species] to its proper proportions", and Egler (1947, p. 388) noted "...[the community] consists of a group of species reacting among themselves and with all their environmental factors, so as to attain a 'degree of integration' and organization".

It has to be added that the Clements-Gleason conflict was concerned mainly with plant-plant interactions which obviously comprise only a fraction of the total community interactions. As Ulanowicz (1986, p. 152) has noted, "organization is seen to exist over the total ensemble of transfers, and...the least likely place to discover it is where Gleason confined his search - among the members of the same trophic level".

Wicken (1987) discussed the holistic approach of thermodynamic community interpretation in light of current evolutionary concepts. Whereas neo-Darwinian theory regards natural selection to be the driving force of evolution, a thermodynamic interpretation goes one step further and identifies "fitness" as the ability to optimize patterns of thermodynamic flow, be it by maximizing the flux of energy in unconstrained situations or by increasing its efficient usage as a system matures. This principle acts on all levels of a biological hierarchy; individuals, populations and communities are all selected for their ability to maximize the efficient use of energy. System configurations of higher organization and complexity are thereby at a competitive advantage over lower order configurations; the higher their organization and complexity, the more efficiently systems are operating. In Wicken's interpretation this advantage constitutes the driving force of developmental processes, be it on the level of individual ontogeny, population evolution or community succession. While current evolutionary theory holds that selection acts only on individuals, a thermodynamic approach extends the process to include all the interactions among members of the community that influence energy flow. While each individual "is in business for itself exploiting energy sources for survival and reproduction, it is the ecosystemic cycle to which they contribute that makes these niches available" (Wicken 1987, p. 136).

Selection thus acts hierarchically, with higher-level parameters determining the adaptive possibilities of lower orders. Adaptive strategies are passed on in a top-down fashion because ecosystems have a higher level of autonomy than populations or individuals. Whereas ecosystems are constrained only by abiotic constituents (temperature, water, light, etc.), populations and individuals are additionally constrained by their functional relationships with other biotic elements of the system.

Polanyi (1969) clearly illustrated the notion of autonomy using an example from a literary composition: the highest level of autonomy belongs to the text as a whole; the rules of the text determine the choice of the sentences; words are chosen according to the rules of the sentence; finally, letters are strung together according to the rules of the words. Accordingly, constraints on units in an ecosystem increase the lower their location in the hierarchy.

Evidence of top-down hierarchical relationships in ecosystems may be seen in such properties as community biomass and respiration behaving according to relatively predictable patterns, whereas at lower levels in the hierarchy the behaviour of units (e.g. individual plants) becomes less predictable. This compares to the microstate/macrostate distinction in entropic systems (Layzer 1975). Whereas the specific configuration of the community is one of many alternatives, any one of which is difficult if not impossible to predict, among such alternatives the collective community properties will remain relatively stable.

Thus, a thermodynamic interpretation of succession appears to support the holistic tradition in ecology, although not in the sense of Clements' superorganism. Rather the thermodynamic view holds that development on all levels can be understood in common terms relating to patterns of energy flow.

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Manuscript received: June 1996