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Evolutionary Processes Which Organise Ecological Systems as Nested Hierarchies

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ABSTRACT

The aims of this paper are to investigate the evolutionary processes that lead to the hierarchy's formation and examine the role of natural selection in it. The approach used was critical analysis of key references to identify important processes in the formation of the hierarchy and then examine the role selection plays. First, the structural organisation of the ecological system was examined, and then processes that created the structure were identified. Third, the causal relationship between non-equilibrium thermodynamics and key processes was articulated. Fourth, the important processes were then incorporated into a general model to explain how they generate and maintain the ecological hierarchy. Finally, the model provided the conceptual framework in which to examine selection's role in the formation of the nested ecological hierarchy. The arguments in this paper showed that two key processes in the formation of the hierarchy are self-organisation and integration. Self-organisation creates the structure, whereas integration stabilises it. The iterative process adds levels and complexity to the nested hierarchical structure. The analysis showed that natural selection affects the structure within levels as well as at the level immediately above the target of selection.

Key Words: Biological Organisation; Thermodynamics; Self-Organisation; Cooperation; Integration; Specialisation; Division of Labour; Natural Selection

INTRODUCTION

The role of natural selection in evolution as viewed by Darwin and Neo-Darwinists has been challenged. The Neo-Darwinist view is that variations occur by chance and natural selection acts upon that variation and those which are better adapted to the environment leave more progeny to future generations (Darwin 2009, Monod 1972, Dawkins 1991). This perspective of the role of natural selection in evolution was largely accepted while it dealt with how organisms adapted to their environment. In the Neo-Darwinist school of thought, the nested hierarchical structure of ecological systems was taken as a given. Most Neo-Darwinists did not delve into how the ecological hierarchy formed (e.g. Fisher 1958, Monod 1972, Dawkins 1976, 1991). An exception is Maynard-Smith and Szathmáry (1995), who dealt with evolutionary transitions to individuality using a gene-centred approach, but they did not consider self-organisation as a major source of variation for natural selection to act upon. Their view is consistent with Monod's idea of evolution being "chance caught on a wing" (Monod 1972).

In contrast, Kauffman (1993) argued that self-organisation, and not chance, provides much of the variation on which natural selection acts, but it was clear that he did not consider what caused self-organisation. It was another group of researchers, who argued that non-equilibrium thermodynamics provides a theoretical reason for self-organisation at a molecular level (Prigogine et al. 1972a, b), and at macro levels of biological organisation (Wicken 1987, Johnson 1988, Schneider and Kay 2006).

This is the conceptual landscape in which one may consider Reeve and Keller's (1999) two important questions that remain current in theoretical and empirical research: i) how does natural selection among lower-level biological entities create a nested hierarchy? and ii) given that there are multiple levels of selection in the nested hierarchy, how does natural selection at one level affect selection at lower or higher levels?

The aim of this paper is to address Reeve and Keller's first question as a part of the more fundamental question; what are the evolutionary processes that lead to the development of nested ecological hierarchies? Some of the key articles (Kauffman 1993, Maynard-Smith and Szathmáry 1995, Buss 1987, Michod 1999a, Prigogine et al. 1972a, b) representative of the literature on the topic were selected and analysed for models about how the ecological hierarchy evolved. Only when the processes involved have been identified, could their respective roles be addressed. This is an appropriate approach because there may be more processes involved than natural selection. Understanding how the ecological hierarchy is formed can clarify the role of natural selection in evolution and provide insights into the dynamic relationships between different levels of the hierarchy that are crucial for answering Reeve and Keller's second question successfully.

This paper is organised in the following way. First, it analyses how the ecological hierarchy is organised because it reveals insights into the processes that generated it; second, it examines the causal connection between non-equilibrium thermodynamics and self organisation, one of the key processes in the formation of the ecological hierarchy; third, it presents a model describing the role of key processes in generating the ecological hierarchy. The model is based on the results of a critical analysis of key papers in literature presented in the first two sections; the paper concludes with an examination of natural selection's role in the evolution of the ecological hierarchy by analysing how the process of selection affects the key processes in the model presented in the third section.

BIOLOGICAL ORGANISATION

Ecosystems provide the environment in which biological entities evolve (Hutchinson 1965), and provide many of the selection pressures (Loreau 2002). The nested hierarchical structure of an ecosystem is significant because articulating how it forms can improve our understanding of the role selection plays in evolution. For the purposes of this paper, the ecological hierarchy has the ecosystem at its apex.

The structure of the ecological hierarchy can be viewed as a nested hierarchy of networks (Conrad 1997, Hulsman et al. 2011). An ecosystem consists of the abiotic environment and the network of populations of different species with specific ecological functions, e.g. different species occupy various trophic levels in a food web. Each population consists of a network of individual organisms, each organism consists of a network of organs and tissues made up of specialised cells, and each cell consists of a network of organelles and macro-molecules (Conrad 1997, Hulsman et al. 2011). The entities that function as integrated wholes can be considered as being modular in structure, e.g. cell, multicellular organism. Where the modular structure is repeated at each level in the hierarchy, the higher level entities are effectively modules of modules and so on (Leigh Jr. 1999). Effectively, biological entities, such as macromolecules, cells, individual organisms, are in fact groups of smaller entities. This decomposability feature of biological entities enables Systems Theory to be applied to biological organisation (von Bertalanffy 1969). Therefore, considering biological entities as groups may be useful approach to use when dealing with natural selection and the problem of defection of constituent components from the group.

In considering what organises ecological systems, some researchers have proposed that natural selection creates order in an otherwise chaotic environment (Monod 1972, Dawkins 1991, Dennett 1995). On one hand, some argue that natural selection has a dual role; not only does it select, but it is also a source of the variation that it will later act upon. On the other hand, others argue that natural selection does not organise (Endler 1986, Kauffman 1993), but that biological entities have self-organising capabilities (Kauffman 1993) and the laws of thermodynamics facilitate that organisation (Wicken 1987, Johnson 1988, Schrödinger 1992). Resolving this issue is central to determine the evolutionary processes that lead to the development of nested ecological hierarchies.

Evolutionary change is manifested at population level through different combinations of the same genes (Jablonka and Lamb 2005), or changes in gene frequencies (Dobzhansky 1951, Fisher 1958, Mayr 1963) and as a result those individuals that are better adapted to their environment leave more progeny that survive to breed successfully. Evolution can occur via genetic drift (Wright 1931) or natural selection (Darwin 2009, Dawkins 1976, 1982, Mayr 1963). Darwin (2009) argued that adaptation by natural selection is driven by competition, but competition decreases the chances of survival and reproduction of both competitors (Morin 1999, Campbell et al. 2012). Therefore, competition seems to pose a problem for the formation of a nested hierarchy that depends upon its constituent entities working together, i.e. cooperating.

There is a vast literature on evolutionary transitions, and much of it centred on dealing with altruism and the problem of defection stopping cooperation and disrupting macro-level biological organisation (Buss 1987, Maynard Smith and Szathmáry 1995, Michod 1999a, Gardner and Grafen 2009, Akçay and van Cleve 2012). Although it is an interesting question, the significance of defection may have been overemphasised (Calcott 2008). Kin selection is but one of five different mechanisms by which cooperation can evolve. The other four mechanisms include three types of reciprocity (reciprocity, inverse reciprocity and network reciprocity) and group selection (Nowak 2006).

Group selection involves selection between groups of entities (Nowak 2006). This is the mechanism of interest because as was argued earlier, all biological entities from macromolecules upwards can be to be considered groups. For example, a macromolecule is a group of atoms, a cell is a group of macromolecules and organelles and a multicellular organism is a group of specialised cells. From this perspective, group selection appears to be a feasible mechanism for developing cooperation between biological entities (or groups) at different levels within the ecological hierarchy. Defection is not likely to be a major issue for group selection as it is for altruism and the reciprocity mechanisms of cooperation. The reason is that group selection is a win-win situation for the participants and the penalty for defection is loss of fitness. The fitness is increased by the greater variability amongst the members of the group which increases its capacity and flexibility to deal with changes in the environment, as well as its evolvability, that is the capacity to change. Specialisation in specific functions by the cooperating entities stabilises the cooperative structure (Michod 1999a) because it increases the interdependence between members of the group for their survival.

In this section, it has been argued that cooperation between biological entities increases the fitness of the co-operators and that specialisation in particular functions stabilises the cooperative structure. What factors facilitate cooperation which is often manifested as self-organisation in biological systems? Kauffman (1993), who championed self-organisation as a source of variation on which selection acted upon, did not delve into why biological entities self-organise. A number of other researchers (Lotka 1922, Prigogine et al. 1972 a, b, Wicken 1987, Johnson 1988, Schrödinger 1992, Schneider and Kay 2006) explored why matter self-organises. However, a clear explanation of the mechanism by which thermodynamics promoted self-organisation has not emerged. This will now be addressed.

THERMODYNAMICS AND HIERARCHICAL STRUCTURE

Thermodynamics is about energy flows through systems (Schneider and Kay 2006) and energy flows through biological systems (Lotka 1922, Wicken, 1987, Johnson 1988). The Laws of Thermodynamics provide theoretical reasons why self-organisation occurs and why the complexity of a system can increase over time, if the system is not disturbed. The First Law of Thermodynamics is the conservation of energy, which states that energy can be neither created nor destroyed, but can change form (Feynman 2008). The Second Law states that entropy of an isolated system never decreases. This occurs because an isolated system does not receive any inputs of energy or matter from elsewhere and therefore evolves spontaneously towards thermodynamic equilibrium, i.e. where energy is so diffuse that it cannot do any work (Crofts 2007). However, biological systems are not isolated, but open and highly ordered systems. This makes energy flows central to understanding biological organisation. Therefore, non-equilibrium thermodynamics, which accounts for order being created out of chaos, applies to biological systems (Schrödinger 1992).

Energy is a core concept in biological organisation, but no one knows what energy is (Feynman 2008). Apparently, this situation has not changed in the 50 years since Feynman made this statement. Energy is something that is observed indirectly and it has different forms: radiant energy, magnetic energy, electric energy, thermal energy, mechanical energy, sound energy, nuclear energy and it is contained within mass ($E = mc^2$) (Feynman 2008). Energy is measured by the amount of work that it can do, and work can be usefully defined as the change of energy in the system (Sexl 1981). This definition encompasses the more commonly encountered definitions of work (W) such as it equals force (F) (i.e.

mass * acceleration) times the distance the force moves the object (d) i.e. W = F * d. This definition is limited in its application since it does not cover cases where force is applied to an object that does not move but energy is expended.

The formation and maintenance of self-organised systems are compatible with the laws of physical chemistry (Prigogine et al. 1972a, b). Non-equilibrium thermodynamics provides the theoretical framework in which these processes occur. To be more precise, non-equilibrium thermodynamics informs us what cannot happen, therefore by default it reveals what is possible. The availability of free energy enables energy flows which facilitate chemical interactions that create order. For example, the free energy supplies the activation energy for chemical reactions to proceed. However, it is the characteristics of the chemicals that affect how they interact, and consequently, the characteristics of the order that emerges from those interactions. Many of these reactions dissipate energy. When energy stored in chemical bonds is released the inefficiency of the energy transfer generates heat which quickly diffuses rendering it incapable of doing further work, i.e. it increases entropy outside the open system (Stoner 2000). Thus, when available free energy does work it creates order as well as increases the rate of entropy production (Johnson 1988). In this case, the order is at the molecular level.

The same reasoning that applies to chemical reactions also applies to the biochemical reactions that occur within organisms. The reactions are catalysed by enzymes and the available free energy facilitates the initiation of those reactions that create order. In this process of energy transformation, heat is generated and is quickly dissipated and lost to the system. Under these conditions, reactions that when coupled are self-catalytic are favoured. That is, reaction ‘A’ converts its starting chemical ‘X’ into ‘Y’ which is the starting chemical of reaction ‘B’ which converts ‘Y’ into ‘X’. Therefore the two reactions when coupled provide the resources for each other (Maynard-Smith and Szathmáry 1995). These reactions are self-catalytic when they can replicate at least one of the input chemicals which maintains the supply enabling the reactions to continue indefinitely in the presence of available free energy (Maynard-Smith and Szathmáry 1995). The repeated coupling of self-catalytic reactions occurs spontaneously (i.e. it is self-organising); they persist because they fuel themselves in the presence of free energy and through this process may create a metabolic network. This is consistent with its modular structure evident in the coupling of three separate reactions in an aerobic cell: glycolysis, Citric Acid Cycle and Oxidative Phosphorylation.

The processes that apply at the molecular level are the same as those that create structure above the molecular level. Cells and multicellular organisms are dissipative structures (Lotka 1922, Prigogine et al. 1972a, b, Wicken 1987, Johnson 1988). That is they take in energy, store it and use it which provides a flow of energy through the system. Autotrophs (e.g. plants) capture energy from the sun and store it as food which they access for nutrients and energy that powers their metabolism. Heterotrophs (e.g. animals) obtain their nutrients and energy from their food and store it in tissue as well as in ATP. They dissipate energy when they access the energy stored in ATP or their tissue and that energy powers metabolic reactions necessary for maintenance, growth, activity and reproduction. Thus, the ecological hierarchy is the hierarchy of biological entities that obtain energy and nutrients from their environment to create, maintain and replicate themselves (Eldredge 1985).

There is a causal connection between thermodynamics and evolution. Thermodynamics provides the explanation for: why an external source of energy and an external energy sink are necessary to maintain the flow of energy through the system, and why free energy facilitates self-organisation which is a property of matter. The characteristics of the matter, in this case biological structural entities, affect how they interact with one another which in turn affects the emergent structures and their characteristics. This relationship between free energy and self-organisation applies at different levels of biological organisation from the molecular level through to macro-levels of organisation. Adding levels of organisation in the system increase its complexity (Simon 1962). Thus, the theory of non-equilibrium thermodynamics provides the direction for evolution and promotes self-organisation which is a major source of the variation upon which natural selection acts.

GENERAL MODEL

From their studies of evolutionary transitions to individuality, Buss (1987) and Michod (1999a) developed explanations of how the nested ecological hierarchy formed. Buss (1987) focussed on conflict between selection at different levels in the ecological hierarchy, specifically conflict between cell and multicellular organism levels. Michod (1999a), building on

Buss' work, specified four conditions necessary for a nested hierarchy to form:

i) the entities at a lower level in the hierarchy cooperate with one another;

ii) this cooperation may lead to conflict, and if it does, then

iii) there must be some means of mitigating that conflict. In situations where conflict is not controlled, it would disrupt cooperation between entities and prevent a new individual being formed or persisting (e.g. cancer - the uncontrolled growth of cells kills the multicellular organism);

iv) entities specialise in reproductive and non-reproductive functions.

However, Michod's fourth condition cannot be a necessary condition for a general model of the formation of any nested hierarchical system because physico-chemical entities form nested hierarchies, but they do not have the capacity to reproduce. The general model presented in this paper shares the first three conditions with Michod's (1999a) model. However, it has a variation of the fourth condition, it does require specialisation in function to inhibit defection, but none of the specialisations have to be reproductive.

A nested hierarchy forms via the application of the same processes at each level, but the reiterative application of the same processes at each level produces a different outcome at each level. This is because the entities at each level have different characteristics and these affect how the entities interact with one another, i.e. organise themselves. The entities at the lowest level in the hierarchy (level 1in Figure 1) aggregate and still operate as individual entities until they become functionally interdependent. In the case of the ecological hierarchy, macro-molecules such as DNA, RNA (e.g. m-RNA, t-RNA and r-RNA), proteins, and organelles such as endoplasmic reticulum, cell membrane, nuclear membrane, Golgi body, mitochondria, and cytoplasm can be at level 1 of the hierarchy (Figure 1). These different entities, each of which have different functions, form a structural and functional network; which is a eukaryotic cell represented as level 2 in a nested ecological hierarchy (Figure 1). The cell is an emergent entity, and can be considered to be a modular construction (Leigh Jr. 1999), that functions as an integrated whole. Figure 1 shows the aggregations of lowest level entities between levels 1 and 2. These aggregates of sub-cellular entities are transformed into an emergent entity at level 2 via division of labour that creates the interdependency between them.

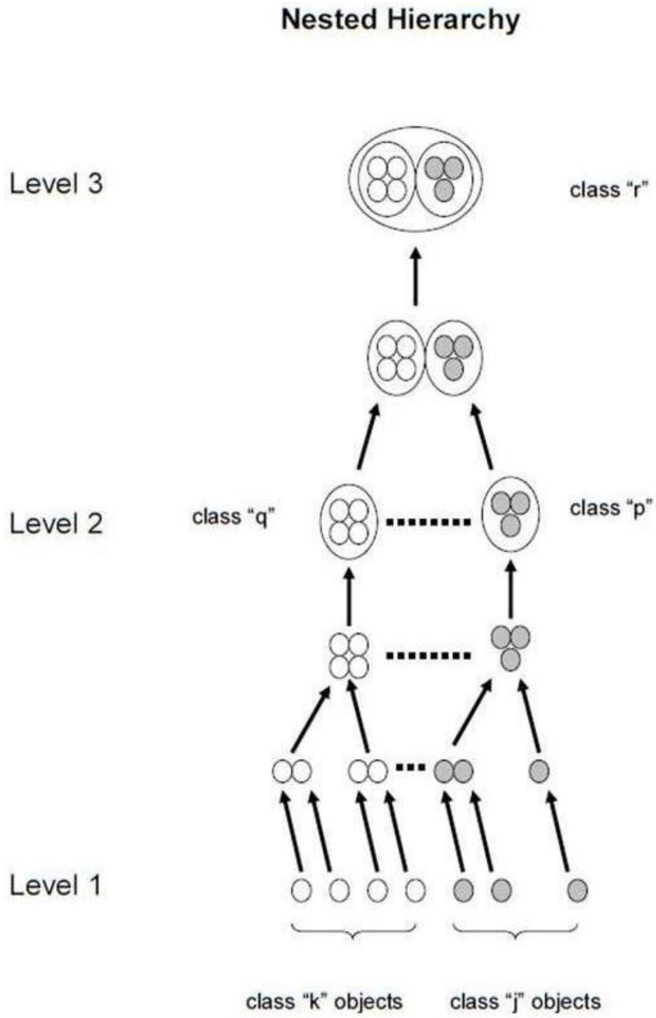

Figure 1. A diagrammatic representation of the formation of a nested hierarchy. Lowest level (level 1) objects "k" and "j" (e.g. macromolecules) initially form aggregations but the interdependency creates an emergent entity represented at level 2 by class "q" and "p" objects (e.g. cells), and these in turn form aggregations but interdependency creates an emergent entity depicted as class "r" at level 3 (e.g. organs, tissues etc.). Repeating the process would give rise to other emergent entities at level 4 (e.g. multicellular organism) and so on creating a nested hierarchy.

The integrative role of division of labour has been recognised previously by Weismann (cited in Michod 1999b) and others (West-Eberhard 1975, Michod 1999a, Szathmáry 1999). The process is repeated on the emergent entities (level 2, e.g. cells) and produces composite entities at level 3 in the hierarchy, such as organs and tissues. The process can be repeated on the entities at level 3 and produces composite entities at level 4, e.g. multi-cellular organisms.

The development of a hierarchy of levels of selection arises from the creation of modules or integrated composite entities at different levels in the hierarchy. The specialised entities depend on one another for survival. For example, at the cellular level excretory cells specialise in ridding the body of metabolic wastes. However, excretory cells are essential for the survival of the other specialised cells, e.g. nerve, lung, heart etc. This interdependency between specialised cells involves the loss of autonomy to interact with other entities as individuals because they now have an integrated structure, and thus behave as an individual or modular entity. This new modular entity at the next level in the hierarchy will be a target of selection provided its fitness is greater than the average fitness of the individual entities comprising it (Okasha 2006). When this occurs there is a hierarchy of selection. Therefore, evolution progresses via a mix of individual and group selection. This means that if the cell were an example of individual selection, then a multicellular organism would be an example of group selection, as would a colony of social insects. However, the choice of which biological entity is the individual is arbitrary since they are all groups of their constituent entities.

Advantages of a modular structure are increased speed with which the hierarchy can evolve and increased stability (Simon 1962). Modularity increases the speed at which evolution occurs because ready-made modules can replace, or be added to others to expand a specific level. In addition, modularity increases the relative stability of the hierarchy since a module can be replaced by another with similar function thereby avoiding major changes flowing on through the system (Simon 1962). An example of this would be a species being replaced by another at the same trophic level and the overall structure of the ecosystem remains stable.

In the general model presented in this paper, self-organisation is a major source of variation among the composite entities that it produces. This does not preclude mutation from being an important source of variation. The variation that self-organisation creates depends on the characteristics of the entities that are interacting with one another. For example, a population of organisms may consist of organisms that will not cooperate and those that are predisposed to cooperating with one another. The relative abundance of each type of organism will affect how the population is organised. A population numerically dominated by non-cooperating organisms would have fewer cooperative groups of organisms than a population dominated by organisms that work together. This is where natural selection plays a role, in that it acts on the variation that self-organisation generates among the emergent entities.

In summary, two critical processes are necessary for the formation of a nested ecological hierarchy: self-organisation and integration. Self-organisation creates aggregations of entities and is responsible for adding new levels of aggregations to the system. Integration transforms an aggregate of entities into a new functional entity via division of labour. Thus, integration adds new levels of functional entities to the system. This is the context in which the role of natural selection in the formation of the ecological hierarchy is examined.

ROLE OF NATURAL SELECTION

The approach used to examine the role of natural selection in the formation of the ecological hierarchy is to explore how selection affects the two critical processes of self-organisation and integration. According to both Lotka (1922) and Wicken (1987), natural selection favours entities in a system that: i) obtain energy and other resources from the external environment and use them to create, maintain and replicate themselves; and ii) increase the energy flow through themselves and thus the system. Based on these two criteria, natural selection will determine which entities persist in a hierarchy (Figure 2, NS1 and NS2 acting on emergent entities). In such a case, natural selection is constructive because it increases the functional efficiency at each level within the hierarchy. Although natural selection is not responsible for the initial organisation, it can affect the internal organisation of the hierarchy because the characteristics of the entities that remain in the system at any level affect the emergent entity at the next level. Thus, natural selection subtly influences the organisation of a nested hierarchy within a level and the level above the target of selection.

Evolution is an opportunity for biological entities to explore new options in time and space wherein they become better adapted to their environment (Wicken 1987). In most cases, competition disrupts any cooperation between competitors. There are circumstances in which competition could promote cooperation, but it would not be between rivals. Natural selection driven by competition (NS1) could provide the impetus for rivals to explore cooperating with other entities and by doing so gain a competitive advantage. Consider the case of two competitors, A and B. Competitor A is at a compe-

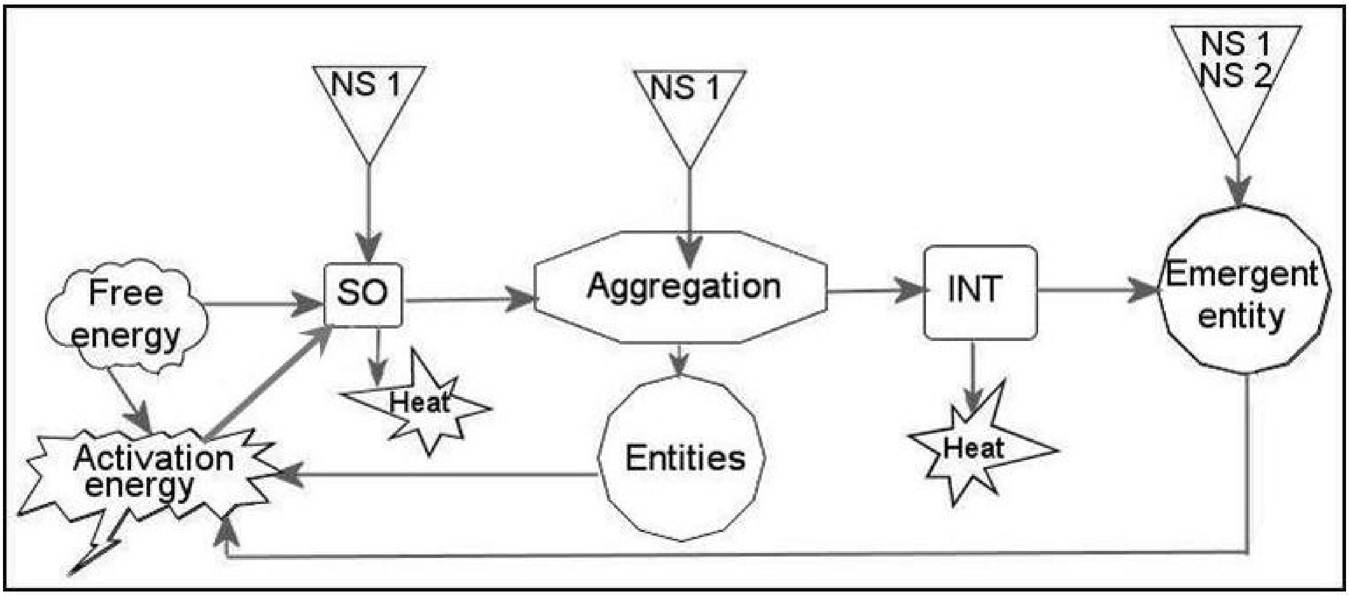

Figure 2. Diagrammatic summary of the thermodynamic and evolutionary processes that organise ecological systems as nested hierarchies. The free energy is supplied by an external source and heat is lost to an external sink. The iterative nature of the process is represented by the arrow from the emergent entities back to the activation energy which is necessary to promote self organisation. NS1 = natural selection driven by competition,; NS2 = natural selection without competition; SO = self-organisation; INT = integration. NS1 may act directly on the individual entities in the aggregation breaking it up and they are then available to form an aggregation with a different array of entities.

titive disadvantage and explores, perhaps by trail and error, cooperating with other entities (Figure 2, NS1 acting on self organisation). Some combinations may increase its capacity to compete. The impetus for cooperation provided by competition may lead to A becoming a new entity A^1 that has a competitive advantage over its rival B. In response to these changed conditions, B may explore cooperating with other entities and be transformed into a new entity B^1 that has a competitive advantage over its rival A^1. If this process continues to repeat itself, then it could lead to what is effectively an "arms race" between the two competitors. In this way, competition would contribute to the emergence of new composite entities in the hierarchy by promoting self-organisation.

In contrast, natural selection without competition (NS2) cannot be a source of variation. For example, in the absence of competition when one entity is more efficient than another, it will leave more progeny, eventually outnumbering the less efficient one (Dobzhansky 1951). Under these circumstances, there is no mechanism by which this type of selection could influence the initial organisation of entities. Therefore, this type of selection has the subtle effect on the organisation of the hierarchy by determining the structures that persist in the system (Figure 2, NS2).

There is a pronounced difference between the effects of selection driven by competition and selection without competition. Both types of selection determine which entities will persist in the system. However, selection driven by competition has two additional functions. It could accelerate the rate at which the preferred entities spread in the population and it could promote self-organisation. Thus, they could play different roles in the formation of the nested ecological hierarchy.

Natural selection driven by competition could affect the organisation of the nested hierarchy of an ecosystem in another way. That is, if entities of different functions within an aggregation (or group) compete with one another, then that would disrupt cooperation between them and break up the aggregation (or group) (Figure 2). Those entities could be available to interact with a different set of entities and form different composite entities in which there is no competition. This specific role of natural selection may be considered a type of creative destruction, i.e. by destroying one structure it releases its constituent components providing them with the opportunity to cooperate with other entities and so create new structures that in turn would be acted upon by selection.

The effects of selection on self-organisation have been considered, but whether selection affects the second key process, integration is yet to be considered. Integration affects which entities become targets of selection. If the aggregation of entities at a specific level do not transform into a functional integrated whole, then they remain an aggregate of entities (Figure 1) and an aggregate is not a direct target of selection. Therefore, integration determines the entities upon which selection directly acts in the hierarchy (Figure 2). In this manner, the different types of selection have an indirect effect on integrative process.

CONCLUSIONS

In this paper, we have shown how thermodynamics contributes to self-organisation at the molecular level and this mechanism can be applied to higher levels of biological organisation. Biological entities such as cells, individual organisms, populations and ecosystems are dissipative structures that require a flow of free energy to create, maintain and replicate themselves.

It was argued that there were two key processes that create the ecological hierarchy; namely self-organisation and integration. These two processes operate in tandem creating emergent structures that add new levels to the hierarchy. Selection acts on the emergent structures and determines which ones persist in the ecological hierarchy. Self-organisation provides variation in the targets of selection, whereas integration provides the targets of selection. The system's structural and organisational complexity increases as these processes add new structural levels and the accompanying functional organisation to the system.

The arguments presented show that natural selection may play several roles in the process of evolution. First, it may select what has already been organised within a level and thereby affect the nature of the entities that emerge at the next level. Second, selection driven by competition may in some circumstances promote self-organisation. Third, selection driven by competition may promote creative destruction. Through these three different roles natural selection affects structures within a level of the hierarchy (horizontal effect), which has flow on effects on the structures that emerge at the level immediately above the target of selection (vertical effect).

Essentially, the formation of an ecological hierarchy involves the interplay between three processes: self-organisation, integration and natural selection. Future research could test i) whether non-equilibrium thermo-dynamics and the propensity of matter to self-organise provide a theoretical reason for increased complexity developing when uninterrupted over evolutionary time; ii) whether factors which disrupt self-organisation prevent a simple system from developing into a more complex one; iii) how selection at one level affects adaptation at that and the other levels in the hierarchy; iv) whether group selection is the most common mechanism for the evolution of cooperation in biological systems because biological entities are in fact groups.

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