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Fundamental Components in Ecology and Evolution: Hierarchy, Concepts and Descriptions

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In a review /1/ of two recent and seminal books on the theory of evolution /2,3/ the evolutionist Ghiselin points to limitations at the root of ecological science, "Ecologists are most unclear about the nature of their fundamental units, and about what such units do". This is a useful challenge to ecologists and one that can be answered at least in part. It is also interesting from a further aspect as it illustrates the value of interdisciplinary contact which may hold some lessons for the future collaboration of biologists and physicists under the banner of Ecodynamics. Thus in this paper I shall try to address the question of fundamental components in particularly in ecology and where possible make connections to concepts in physics. If this makes for a rather strangely structured paper then at least the reason for it is clear.

You might ask why Ghiselin's criticism of ecology should be found in a review of two books on evolution. It arises because Eldredge and Salthe have attemped to define the fundamental components involved in evolution while expanding the conventional synthesis (see /2/) of evolutionary theory to include ecology more explicitly. The stimulus to re-examine the synthesis came from observations /4/ suggesting that evolution occurs in rapid bursts which follow (punctuate) long periods of stasis or equilibrium. This punctuated equilibrium theory has become a focus of evolutionary debate in the 70's and early 80's. In the search for a mechanism for punctuated equilibrium Eldredge and Salthe /5/ have proposed two interacting hierarchies of fundamental components. These are hierarchies of replication (genes make more genes, species make more species etc) and a hierarchy of energy and matter transfer (enzymes, ecosystems etc). We first consider hierarchy itself.

Hierarchy

The pursuit of fundamental biological components has often been associated with the construction of hierarchies of these components. Rowe /6/ traces the history of the use of hierarchy in ecology. He acknowledges Comte as classifying the sciences in a hierarchy according to levels of inclusiveness and Kant's distinction between logical classification and physical classification. Combining these approaches, Rowe sees a logical classification of biological sciences in a hierarchy: Ecology - morphology - anatomy - physiology, which parallels a physical hierarchy of objects: Ecosystem - organism - organ - cell. However in the search for mechanism we are interested in the physical hierarchy of objects or fundamental components. Although this distinction between the conceptual hierarchy of biological sciences and the hierarchy of objects appears clear in this case (possibly with the exception of ecosystem as an object) many of the important debates concerning evolution are predicated on whether something is a concept or an object; for example, treating species as classes (concepts) or as individuals (objects) /7-9/.

Although I am mainly concerned with Eldredge and Salthe's proposals for a dual hierarchy, another group of workers, O'Neill et al /10/ have adopted a dual hierarchy of ecological phenomena first suggested by MacMahon et al /11/. Each of these views has significant implications for ecology; Salthe's /3/ deduction that species are not entities in ecosystems has far reaching effects on current debates in ecology. Resolving the dual hierarchy of O'Neill et al may require a change in how ecosystem is defined. Rejecting the case for Eldredge and Salthe's dual hierarchy rests on showing how important taxonomic categories (eg phyla) are as classes of functional organisms in food webs /12/. As a result a single hierarchy can be constructed in which evolution may be studied and suggesting new priorities for research.
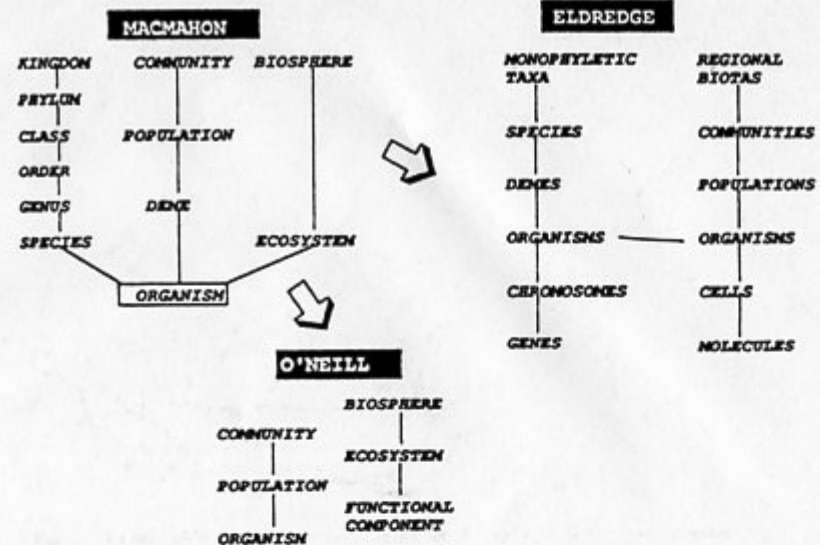

Fig. 1 Recent hierarchical approaches to ecology and evolution.

We will trace the origin of and examine these dual hierarchy proposals to see if a single hierarchy of biological objects is possible. The following terms are used i) Class - a group or set which is not itself an entity or object, ii)Entity - a thing defined in space and time with a cybernetic system of parts.

In recent times the origins of these hierarchical approaches stem from MacMahon et al /11/ figure 1. They proposed four hierarchies involving the individual organism, with the organism given a special status or importance. One hierarchy is contained in the organism, organ - cell - molecule etc while the others contain the organism. Somewhat ironically in my view, the phylogenic hierarchy is separate from two ecological hierarchies. Ironic because phylogeny can describe classes of biological machine active in the 'ecosystem', the basis for this lies in the ecological importance of body size and with these allometric relationships holding most precisely within taxonomic groups /12/. As MacMahon et al note their greatest departure from tradition comes in removing community and population from the biosphere and ecosystem hierarchy. This is required by their adoption of the definition of ecosystem as 'a set of organisms and inanimate entities connected by exchanges of energy and matter'. Thus since the community - population - deme hierarchy only includes organisms a separate hierarchy is required by those authors.

MacMahon et al acknowledge that the terms community and ecosystem do not represent bounded objects . The boundaries must be supplied, they say, by the observer. O'Neill et al take a similar approach "the ecosystem comes to look more like an abstraction with spatiotemporal properties that can be specified only within the context of an observation set. The ecosystem as an independent discrete entity begins to look less tenable." We are left with ecosystem as a viable concept but not as a fundamental component or entity.

Before proceeding further we need to attend to the problem of entity in the ecological hierarchy. What would such an ecological hierarchy look like? Certainly organisms and the biosphere qualify as entities which also provide the lower and upper boundaries to the hierarchy. However, candidate intermediate levels such as populations, communities, ecosystems, trophic levels, and food webs all fail the test as ecological entities because they are unbounded in space and time.

An ecosystem entity

The hierarchies of O'Neill and MacMahon are conceptual and explicitly
subjective. Eldredge and Salthe have instead tried to define real entities in
ecological and the evolutionary process. The search for ecological entities has
typically focussed on finding discrete ecosystems. These are usually cases
where some spatial discontinuity leads to a change in the type of ecosystem
found. Rowe /6/ sees these boundaries as minimum interaction surfaces as may
characterise the boundaries of a pond or lake. These boundaries are not
produced as a consequence of ecological interactions, they are externally
imposed on the ecology. Ponds can be discrete water bodies but are they single
ecosystems? Is the Atlantic a single ecosystem? Even the pond ecosystem can be
differentiated into several zones leading to the arbitrary definition of the
pond as being either one or several ecosystems.

By adopting Salthe's definition there is a candidate for such an entity in the
energy-matter transfer hierarchy. I call this a food-web entity which is
defined as the set of organisms comprising the food web of a single individual
of the largest predator in a location. This entity has a given size, the
foraging area of the largest predator; is distinct in space from similar
foraging areas by behavioural mechanims and distinct in time by birth and death
of the predator; the food web has a dynamical cybernetic structure. This
definition also meets the test of containment, the smaller organisms and their
feeding interactions are spatially contained within the foraging area of the
largest creatures. This containment is statistical. The membership of the
food-web entity is probabilistic in that any individual organism within the area
enclosed by the entity may emigrate, die of causes other than predation, or be
predated. The fact that membership of the food-web entity is statistical does
not alter the possibility of calling it a real object or entity. Similarly, an
organism is made up of protein molecules etc. which have a much shorter
membership of the organism's body than the lifetime of the organism.

It remains an important question to ask if there are any other entities between
the food-web entity and the biosphere. There are interactions between top
predators for example when pack hunting is undertaken or when young are raised
co-operatively by parents. Clearly there are also flows of organisms from one
food-web entity to another. Do these flows themselves create some larger entity
which is not the biosphere? How indeed does the effect of human industrial and
social activity interact with the biosphere or the food-web entity?

A clue to the solution of this problem may be provided by how species are to be
treated in the proposed hierarchy. Sexually reproducing species have well
differentiated parts eg male and female. These parts interact and it is argued
/7,8/ that these interactions and the offspring produced mean that species are
real entities which can therefore act as causal agents in evolution. However,
while the reproductive pair constitutes an entity, the set of pairs which
constitute the species can be seen as additive and not constituting an
interacting set of parts of an entity. While I have used the word pair I wish
this social entity to cover any social grouping such that a species is a set or
class which is the sum of social groups (entities) of organisms which share the
same specific-mate recognition system /13/.

It is now possible to propose a single hierarchy of evolutionary phenomena. We
can define the largest naturally occuring ecological entity as the ecosystem
trophic module (ecotrophic module) which is the food web of the social group of
largest predators in a location. This entity has a given size, the foraging
area of the social group; is distinct in space from other such groups by
behavioural means and is distinct in time due to the origination and extinction
of the social group; the food-web entity has a dynamical cybernetic structure. Note
that the ecotrophic module is a lineage which is therefore capable of evolution.
This definition of the ecotrophic module supercedes the exploratory definition
/14/. Figure 2 shows the spatial boundaries of such ETMs, the clans of hyaenas
in the Ngorongoro crater, each clan contains between 30 and 80 hyaenas /15/.
Although spatially well defined these clans are lineages and have a lifetimes
longer than the individual hyaenas which compose them.

The suggestion that the reproductive or social unit is a feature of the
ecotrophic module could at least in principle be extended to human society.
However in present day ecology observability is to me of vital importance and so
the impact of human society on ecotrophic modules is perhaps the best measure we
have of the existence of some human ecological object. This impact could be
measured by size and numbers of predators active in a human impacted ecosystem
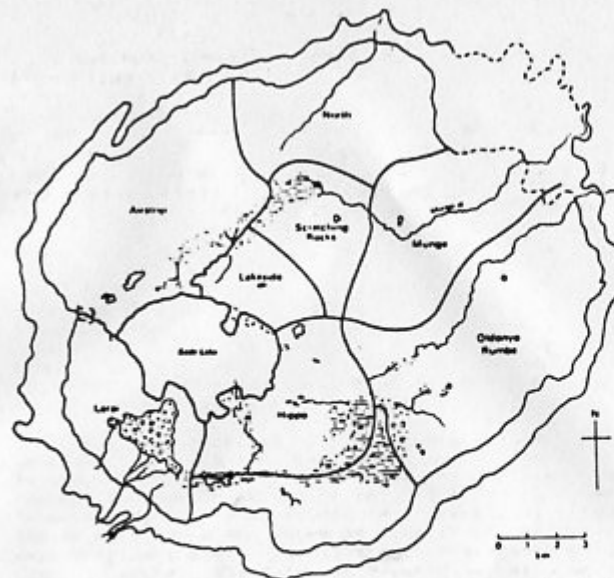

Fig. 2   Ecotrophic modules formed by clans of Hyaenas in the Ngorongoro
Crater, Tanzania /15/.

relative to a reference size and density typical of that biome. Human
intervention in the ecosystem tends to eliminate top predators and therefore
fragments the largest biome ETMs into numerous smaller ETMs based on the
predators present in the human impacted ecosystem. A large human population in
the Ngorongoro crater would almost certainly radically alter the observed ETM
structure.

Other flows between ecotrophic modules such as migrations can be considered to
be caused by some climatic effect which is properly considered to be part of the
biospheric entity.

Single hierarchy

To further explore the evolutionary process and in the interests of parsimony I
propose the following single hierarchy of levels, figure 3.

There are many kinds of entity at each level in this proposed single hierarchy;
many kinds of molecule - proteins, DNA and so on; many kinds of organism -
different castes, sexes, different species, different taxonomic sets of
organisms. It is a condition of hierarchy theory that entities engage in
interactions at the same hierarchical level /16/ and in so doing create the
(emergent) properties of the entities at the next level and are constrained by
the interactions at that level also. Thus molecular interactions create the
metabolic patterns of the cell organelles, DNA together with other molecules in
the metabolic and transcription pathways, replicate the DNA, sub-cellular
structures, which include genetic structures and organelles which form the cell.
Perhaps the most controversial aspect of the proposed hierarchy is the omission
of species as entities and their treatment as sets of organisms. Species as
sets are here treated as names we give to similar organisms. Species are not
treated as causal agents in their own right. I take the view that species are
types of organisms which share the same mate recogniton system /13/ and thus
sets of organisms, the species members, have a potential to breed at some future
time. Although species are observable (countable) at any one time, they are not
countable through time except by convention.

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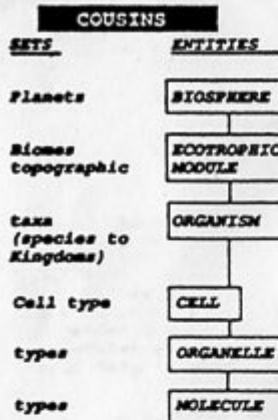| SETS	ENTITIES
Planets	BIOSPHERE
Biomes topographic	ECOTROPHIC MODULE
taxa (species to Kingdoms)	ORGANISM
Cell type	CELL
types	ORGANELLE
types	MOLECULE

Fig. 3 The proposed single hierarchy of biological entities.

My reluctance to accept the proposed separate genealogical and ecological hierarchies is that below the level of organism the entities are components interacting at the molecular organelle and cell levels; the existence of different types of entity being a necessary condition for hierarchy theory and not reason for the creation of separate hierarchies. Above the level of organism I follow Grene /17/. Grene excludes taxa above the species level as being entities in the present even though they are linked through history by descent. I extend her view to the species itself while placing the interactions of species parts (eg the male female interactions) into the framework of the ecotrophic modlule.

There are certain consequences of the definition of ETM for the definition of ecosystem itself. First the geographical or topographical descriptions of ecosystem (pond, ocean, prairie, forest) become classes of trophic modules. That is, they become the names we give to different types of real objects the ecosystem trophic modules. Second, the definition does not mention the interaction with environment or the cyling of nutrients. These are essential prerequisites for the operation of ecosystems which may determine the type of ecosystem trophic module found at a location but are not a necessary part of the definition of an ecological entity. In a similar way, sociologists may define social systems without specifying the air needed to breathe or other essential aspects of bio-geological flows needed for society's operation. Flows of nutrients are from the hierarchy viewpoint too low in the hierarchy to occur in the definition of ecosystem or society.

Concepts

Concept formation is the step in science said to precede the formation of theories and laws. Ecology is often perceived as a young science and the view taken as suggested by physicists at the Ecodynamics conference, that concept formation and exploration is particularly appropriate in ecology. There is no doubting the much longer experimental and mathematical tradition of physics which does indeed make ecology look young by comparison. However it can be shown /18/ that aspects of ecological science date from earlier than Haekel's definition of ecology in 1869. In particular making species distribution atlases /19/ follows a clear line of descent from 17th century descriptions of national or local flora and fauna /20/.

Certainly there is a perception by some ecologists that ecology is coming out of its youth into early middle age. Youth in science is characterised by a proliferation of concepts which are not coherently interrelated. Concepts are indeed welcome but they must be justified by their contribution to the development of an integrated theory of ecology. Concepts should be clearly identified as ideas rather than as pieces of reality. Progress in science obviously also occurs by rejecting concepts in the search for theories and laws or better concepts. The rapid rise and the slow decline /12/ of one of

ecologies most cherished concepts, the trophic level /22/ is perhaps an interesting example.

Lindeman and Hutchinson /22/ viewed the population dynamics of lake organisms as a problem in energy transfer. Beginning with photosynthesis in phytoplankton energy would be transferred to herbivorous zooplankton and from there to carnivorous organisms. These stages, S, renamed by Lindeman trophic levels, were energy categories. Thus energy passes from S1 the plant to S2,...S3..Sn. The concept of a feeding system in which organisms of one species were dependent on another for energy can be traced to Wallace /21/ and Semper /23/. Semper explicitly described a 10% rule in which an ecosystem comprised a mass of carnivores ten times less than the mass of herbivores which in turn weighed ten times less than the weight of plants. Thus the basic ingredients of the trophic level paradigm were present before Lindeman's classic paper in 1942. What Lindeman added was the hypothesis that succession in animal and plant communities is driven by improvement in energy transfer efficiency between trophic levels. In short, Lindeman invoked the second law of thermodynamics and suggested that the improvement of the efficiency of energy transfers may provide the ultimate cause of ecosystem organisation.

But there were problems with Lindemans's view. Energy transfer efficiencies were not uniformly improved during succession as is illustrated by the inclusion of homiothermic predators on heterothermic prey. One important problem with the concept and one which can be related to thermodynamic concepts is the confusion between body size and trophic level concepts. Elton /24/ had earlier described the animals in an ecosystem as constituting a pyramid of numbers in which there were very many small organisms and progressively fewer larger organisms. Lindeman wrote " The Eltonian Pyramid may also be expressed in terms of biomass ". This is very simply done by multiplying the number of individuals in a size class by their average weight, however, Lindeman did not propose this. Instead he erected the new classification of "progressive energy relationships of food levels" and asks us to imagine these as the pyramid of numbers. However feeding level (trophic level) and size class are mutually exclusive. A size class in Elton's pyramid contains organisms of different trophic levels while a trophic level contains organisms of different sizes. The claim that the second law of thermodynamics was being applied when the trophic level methodology was being used was convincing enough to almost totally displace the Eltonian method of ecosystem analysis. It was not for 50 years that the energetics of the Eltonian pyramid was worked out /25/ or the principles of body sized based mechanisms of predation, reproduction, movement and animal abundance more comprehensively described /26/. Physicists (now marine biologists) have added to this subject area papers on spectral analysis of ecosystems /27/ and dimensional analysis in ecology /28/.

It was natural that Lindeman should have introduced his concept against the background of the then dominant model of Elton. However Lindeman and Hutchinson had structured their model upon historical energy classes when energy transfer is dependent on the present state and not previous states. In short the trophic level model is a non-Markovian model of a Markovian process whereas the Eltonian pyramid does provide a Markovian description.

In Lindeman's model energy transfers are limited to respiration, egestion and ingestion. Respiration of some of the energy ultimately collected by the plant is used for growth either in the plant or animal or other kingdoms. However, we may however consider energy transfer as a thermodynamic problem which is posed in a way consistent with Elton's model.

Entropy and food particle size

Suppose we take a uniform food item and break it into smaller parts and scatter them over an ecosystem. This act produces a calculable change in the entropy of that food item.

Let the food item be broken into n particles of equal size and scattered over an ecosystem which is itself partitioned into m boxes each of the size of the food particles. Then the change in entropy, ΔS is given by,

$$\Delta S = -k \cdot \ln W \tag{1.1}$$

where k is the Boltzmann constant and W the number of ways of rearranging n particles in m boxes.

$$W = \binom{m}{n} \qquad (1.2)$$

Thus, taking 10^7 particles and scattering them over an ecosystem of 10^0 boxes of the same particle size then,

$$\Delta S = -k \frac{10^{8!}}{(10^8 - 10^7)! \; 10^{7!}} \qquad (1.3)$$

$$\Delta S = 1.4 \cdot 10^{-20} J/K \qquad (1.4)$$

We may in general consider the ecosystem to be populated by statistically unlikely occurances of local high energy dense states which are the organisms themselves. These arise in a uniform distribution of energy in the form of sunlight incident on the ecosystem. Thus different sized organisms can be seen as differently likely states while growth in size occurs as a result of predation (ecological collision). In this model the plant can also be considered as a variety of energy states, ranging from simple to complex molecules present in different densities ranging from soluable sugars found in leaf drip to energy dense nuts and seeds /29/.

Descriptions

Ulanowicz /30/ and O'Neill et al /10/ stress that any system boundaries can be drawn on a system and measurements made on the parts that have been created. Ulanowicz's defense of the trophic level is that it provides a quantitative description of an ecosystem rather in the same way as a statistical description may summarize certain data. The system boundaries implied by the trophic level concept cannot in that sense be right or wrong but merely more or less efficient than other methods for a purpose. But there is the danger that we are therefore left to evaluate concepts without the prospect of refutation.

An abstract # concept has to be operationalised by making measurements on, or, by counting observable entities. In the trophic level case a measure of the biomass, B, of the number Ni of creatures weight i provided by records of feeding behaviour such as stomach contents.

$$B = \sum_i n_i W_i \qquad (2.1)$$

But we know from the entropy discussion that different particle sizes are not equivalent and so the same biomass can have different entropy values. Thus instead of B, we need to keep the data in the form of a distribution, n,

$$n(w) \qquad (2.2)$$

If we wish this description to have a predictive value then we need to take into account that at t=1 two particles may have the same mass while at t=2 one particle may have grown (eg a juvenile organism) while the other which was an adult of a different species had stayed the same weight. For predictive purposes therefore, we need,

$$n(w, w_\infty, t) \qquad (2.3)$$

where, w_∞ is the assymptotic weight to which the particle is growing, w is its present weight at time t. The w_∞ variable is also characteristic of each species; each animal species has a characteristic adult weight.

Different taxa have different bauplans which give them different properties in the ecosytem; warm-bloodedness, flight, photosysnthesis etc. Thus a whole ecosystem model can be created to any degree of complexity by subdividing all biota into taxonomic number distibutions, ni, giving for all heterotrophs,

$$\sum_i n(w_i, w_\infty, t) \qquad (2.4)$$

By adopting number distributions, ni, for each species rather than each higher taxon, and since each species has a characteristic w_∞ , then the biota is described by

$$\sum_i n(w_i, t) \qquad (2.5)$$

The time dependent change of this distibution due to internal causes of predation and respiration can be found from a set of partial differential equations for predation, starvation, growth and reproduction /31,32/. The complexity of the latter model can be reduced by setting delay terms (caused by prey handling times) to zero and by treating the model as a series of single species interactions. Then distributions of type 2.5 rather than type 2.4 can be used.

Conclusion

The case for a single hierarchy of biological objects has been made against a prevailing tendency towards dual or multiple hierarchies. In an attempt to find an ecological object intermediate between individual and biosphere a new ecological entity has been defined, the Ecosystem Trophic Module. The ETM is located within the pyramid of number and not the trophic level approach. A possible framework for the application of thermodynamics to the Eltonian pyramid is proposed. Finally the role of concepts in ecology has been highlighted by the difficulty of appraising concepts once they become widely used. The trophic continuum model of the Eltonian pyramid can be applied at a variety of levels of complexity showing that simple versus complex model debate need not be polarised into models with different general structures.

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