The Decline of the Trophic Level Concept

Steve Cousins

The development of the trophic level concept[1] is described and the causes of its failure as a predictive model in ecology are examined. A defence[2] of and modifications to the trophic level concept are reviewed. A trend towards taxonomic food web analysis is identified leading to models that are independent of the trophic level approach.

There have been[3-6] and there still are[7,8] ecologists alarmed at the fundamental problems inherent in the trophic level concept. According to Murdoch[3], trophic levels are not state variables and therefore cannot be related to any quantifiable property of natural ecosystems (green plants excepted); Rigler[4] stated that 'classification by trophic levels has thrived on its inadequacy'. Other ecologists adopt the view that the trophic level concept *is* useful, for example in teaching. According to van Dobben and Lowe-McConnell[9],

> A concept may be useful even when it is not possible to relate it to quantifiable properties of natural ecosystems except in a general way. For instance the trophic level concept, however shaky in this respect, has nevertheless deepened our insight into the gross structure of ecosystems.

These ecologists were reporting on the trophic level based International

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Biological Programme (IBP), and would perhaps have had difficulty in arguing otherwise. But need ecology accept shaky foundations? It is significant that a recent study of hierarchical structure in ecosystems[10] excluded trophic levels on the grounds that they obscured rather than illuminated organizational principles of ecosystems. So does the trophic level concept help or hinder our insight into ecosystem structure and function?

Early work

The concept of a feeding system in which organisms of one species were dependent on another for energy can be traced[11] to Semper[12] in 1881. 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 mass of plants. The general idea of 'consumer layers' of plants, herbivores and carnivores was prevalent in the early 20th century. Elton[13] believed there to be only five or so consumer layers in what he significantly termed the food cycle. When the concept of the trophic level was first formally defined (Hutchinson in Ref. 1) it had the merit of being precise and simple; this facilitates examination of the properties of the concept today (see Box 1).

Thus the basic ingredients of the trophic level paradigm were in place before Lindeman's classic paper[1] of 1942, in which the trophic level concept was applied to the analysis of ecological succession. A central hypothesis of this paper was that succession in animal and plant communities is driven by improvement in energy transfer between trophic levels. In short, Lindeman suggested that the thermodynamics of energy transfers may provide the ultimate cause of ecosystem organization. Early research therefore sought to establish ecological efficiencies of various kinds and to determine whether progressive improvement in efficiencies did occur[14] both between higher trophic levels and during succession. The area has been seen as under-studied[15,16].

Initial difficulties and current concerns

Three quite distinct problems that currently concern 'trophic' ecologists have their roots in the Lindeman paper. The most well known problem is that individuals of particular species do not fit wholly into discrete trophic levels. Both Hutchinson and Lindeman saw that while species could be distinguished as plants and herbivores, carnivorous species could not often be slotted into discrete trophic levels. It is equally true that herbivores are sometimes difficult to distinguish[1,5] (Fig. 1). Various authors have proposed methods of allocating organisms to non-integer trophic positions[2,17-19]. However, the essential features of the trophic level model are retained (Box 1), and Murdoch's objection (above) applies equally to these continuous measures.

The second problem concerns detritus. Although Lindeman and other authors[2,20,21] place dead carcasses and dung at trophic level one, this is a quite separate and arbitrary convention[5,14]. The 'correct' procedure, extending Hutchinson's original definition, is to place material according to the number of acts of assimilation it has undergone since being part of a green plant. Dung, since it is unassimilated, is at the same level as the original food and carcasses at the same level as they were when alive[14,22-24]. When detritus is given this correct trophic level status then there are higher numbers of trophic levels in a system. This is caused by energy cycling through the food web prior to dissipation[25]. Patten *et al.*[25] note that the term food cycle[1,13] looks appropriate again for trophic interactions.

The third problem lies in the confusion between body size relations and the trophic level concept, a confusion present in Lindeman's paper and one that has become well estab-

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Box 1. Trophic classification by trophic levels

Hutchinson (see Ref. 1) viewed the dynamics of lake biota 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 as trophic levels, were energy categories.

Consider any stage Sn. Energy is entering the stage and is leaving it. The rate of change of the energy content Sn therefore may be divided into a positive and a negative part.

$$\frac{d\,Sn}{dt} = s_n + s'_n$$

[unit of S, gm-calorie/m² lake surface]

where s_n is by definition positive and represents the rate of contribution of energy from $Sn-1$ to Sn, while s'_n is negative and represents the sum of the energy dissipated by Sn and the energy handed on to $Sn+1$.[1]

Thus energy passes from S_1 (the plant) to S_2, S_3...Sn. We can be precise about the meaning of this definition.

A trophic level is a category in an *historical* model of energy flow in which all events are scaled by treating the plant as unity. There are three elements to the model[6]: (1) the only information preserved by the model is the historical description of the number of times each carbon molecule has been assimilated since it last constituted plant material; (2) all trophic events are treated as equal, i.e. a passage from one trophic level to the next; and (3) all plant material, or detritus, is subsumed as a single biomass or a quantity of energy.

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lished in ecological text books (see Ref. 7). Elton[13] had 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. The weight of all predators must always be much lower than that of all food animals and the total weight of the latter lower than the plant production'. In fact Elton's pyramid is converted to a pyramid of biomass by multiplying the number of individuals in a size class by their average mass. Lindeman did not propose this. Instead he erected the new classification of 'progressive energy relationships of food levels' and asks us to imagine these in the Eltonian pyramid of numbers. However, the feeding level (trophic level) and size classifications are mutually exclusive. A size class in Elton's pyramid of numbers contains organisms of all different trophic levels, while a trophic level in the pyramid of food levels contains organisms of all different sizes (Fig. 2).

Lindeman's application of energetics to feeding interactions was an exciting development, and it was natural that he should have introduced it against the background of the dominant Eltonian model. However, Lindeman did not apply energetics analysis to the Eltonian pyramid itself (something that was achieved only recently[26]) but instead applied it to a product of the 'consumer layers' tradition[1], the trophic level. Here lies the heart of the problem: Lindeman and Hutchinson structured their energy model upon *historical classes* (the levels) when energy transfer is ahistorical[6]. In short, the trophic level is a non-markovian model of a markovian process, whereas the Eltonian pyramid of numbers is markovian.

Lindeman exonerated?

Ulanowicz's recent defence[2] of the trophic level concept (entitled 'Lindeman exonerata') usefully defines what can be expected from the concept and by inference what cannot. Ulanowicz is attracted, as was Lindeman, to the trophic level concept because he feels that comparisons of ecosystems using the technique will reveal an ultimate thermodynamic cause of ecosystem organization. The basis of Ulanowicz's defence is that the trophic level provides a quantitative *description* of an ecosystem rather in the same way as a statistical description may summarize certain data. He is rigorous in his

application of the concept as a description of an ecosystem. He tackles the central issue of the trophic level approach by applying his analysis to a large multispecies ecosystem. This involves using a matrix manipulation to transform quantitative measurements of food flows between species in a marine food web into flows between trophic levels. The method (see also Ref. 17) allows an appropriate mass of each species to be allocated to the relevant trophic level. To do this, 'it is necessary only to abandon the notion that the mapping from taxa to trophic levels be discrete'[2]. But the consequences of this condition are far-reaching, since each trophic level contains organisms and parts of organisms that, as a unit, cannot function as a state variable of the system. Ulanowicz's technique invalidates models of ecosystems that treat trophic levels as real biological entities, as is the case where the stability or productivity of ecosystems is predicted to be a function of the number of trophic levels[20,27]. However, the latter models[20,27] may well have application to defined population interactions.

It is possible that ecosystem organization may be expressed in thermodynamic terms but it is unclear what the trophic level concept will contribute to this view. The trophic level concept excludes description of energy *availability* and the historical basis of the model (see Box 1) is at odds with the thermodynamic principle that energy does not retain its history. Thus in Fig. 2 the hawk eats birds irrespective of what the birds have eaten. With regard to energy availability, the variety of organic structures in the green plant are very differently available to herbivores even though all parts of the plant can be oxidized in a bomb calorimeter to measure the energy content of trophic level one.

Other recent modifications

Heal and MacLean[21] had the task of synthesizing the IBP energetics studies. In spite of the effort that went into IBP, they were unable to find suitable data for trophic levels. They instead developed a model of taxonomic-trophic categories, marking a watershed both in acknowledging the practical problems inherent in trophic level analysis, and in adopting a taxonomic solution to these problems. They classified species populations as microorganisms, invertebrates and vertebrates and identified trophic functions taxonomically also as herbivore, carnivore, microbivore and saprovore.
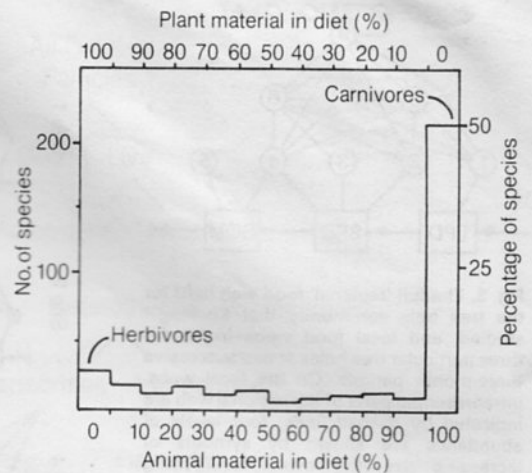

Fig. 1. The composition of the diets of 430 species of North American birds and mammals. The 33 herbivores include 14 coprophagous lagomorphs, 9 ruminants and 2 grouse, all of which act as secondary consumers of their own symbionts. *Redrawn, with permission, from Ref. 5.*

They then placed typical taxonomic groups of organisms into a hypothetical trophic level structure.

A more recent taxonomic-trophic hybrid approach has been proposed by Yodzis[28] with the concept of vertical structure in food webs measured as 'trophic height'. This model attempts to cope with the difficulty of applying trophic level ordering to food webs by setting all flows to zero except for the shortest path from any organism to the plant, on the grounds that the shortest path constitutes the important energy flow (but see Patten et al.[25]). He compensates for different growth efficiencies between different taxa by allocating different 'heights' to the vertices of the food web graph: height 1 for the plant and any invertebrate ectotherm, 1.5 for vertebrate ectotherms and 2 for vertebrate endotherms. Thus a caterpillar is at height 2 and a cow at height 3. He then used Briand's[29] food web data to test and reject the null hypothesis that there is no tendency for food chains to be longer over energy-efficient groups. He concludes that food chains are energy limited rather than dynamically limited. I am not further considering the food web literature,
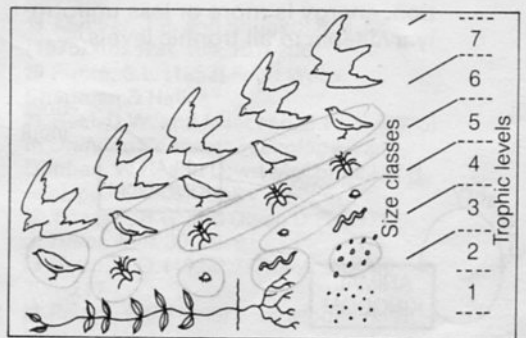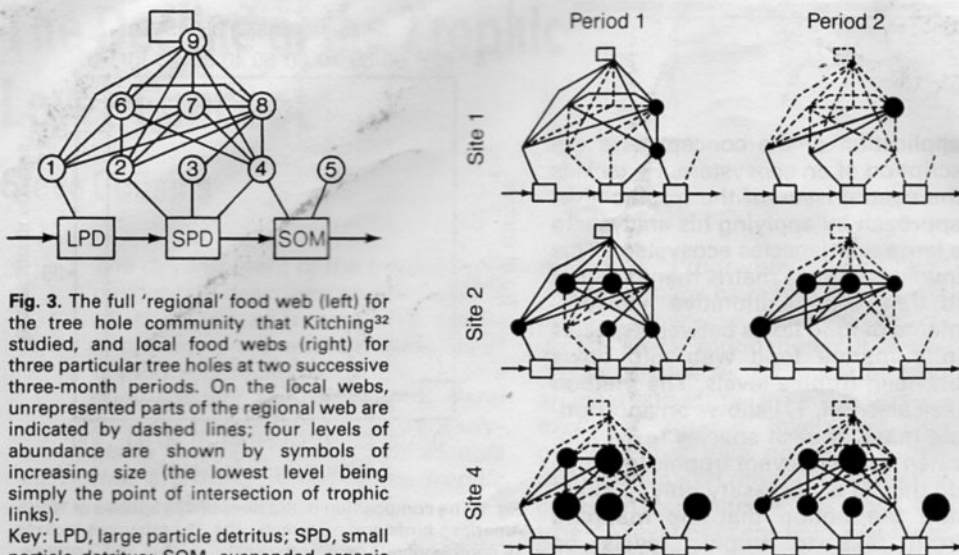

Fig. 2. The Lindeman and Elton models arranged so that they relate to one another: the individual hawk feeds at five trophic levels. *Redrawn, with permission, from Ref. 7.*

Fig. 3. The full 'regional' food web (left) for the tree hole community that Kitching[32] studied, and local food webs (right) for three particular tree holes at two successive three-month periods. On the local webs, unrepresented parts of the regional web are indicated by dashed lines; four levels of abundance are shown by symbols of increasing size (the lowest level being simply the point of intersection of trophic links).
Key: LPD, large particle detritus; SPD, small particle detritus; SOM, suspended organic matter; 1, *Prionocyphon niger* (Scirtidae); 2, *Clogdia* sp. (Psychodidae); 3, algophagid mites; 4, mosquito larvae; 5, ostracods; 6, *Anatopynia pennipes* (Chironomidae); 7, *Culicoides angularis* (Ceratopogonidae); 8, *Arrhenurus* sp. (Arrhenuridae); 9, *Lechriodus fletcheri* (Leptodactylidae). The full study comprised 11 tree holes for 1 year. *Redrawn, with permission, from Ref. 32.*

other than to note Cohen's[30] discovery that interval food web graphs are typical of sink webs and not source webs (the trophic level model being a source web, scaled on the green plant).

Patten[24] has attacked a variety of dogmas that have come to surround the trophic level concept. 'It is difficult to unlearn things learned. Traditional ecology teaches a number of principles to its students, for example, that energy does not cycle in ecosystems although matter does; that food chains are short' and so on. By studies of an intertidal oyster reef community he shows how energy can cycle through the system prior to dissipation through respiration. He shows that food chains are short and trophic levels are few because of modelling conventions of how detritus and carcasses are treated (that is, they are ignored or re-set to trophic level one). Patten *et al.*[25] have defined the latter as α-trophic level models, and ω-trophic level models are those that rigorously adopt the principle that energy changes its trophic level only when it is assimilated; ω-trophic dynamics show that, by network homogenization, energy is more or less uniformly available to all trophic levels.

Fig. 4. The taxonomic basis of observable trophic levels. No detritus flows are included.

Subtle changes

A subtle modification of the trophic level concept has been to modify the circumstances in which it is applied. Thus there has been a move away from using it for its prime purpose of the analysis of large multispecies ecosystems, where 'levels' have been difficult to observe, to the analysis of small subsets of the food web where discrete chains do exist. For example, the chain plant–caterpillar–predator–parasite[31] is fully observable. This set of species is *at* four trophic levels but the system itself does not provide a model *of* a four-level system except for cases where the ecosystem is limited to four species. In short, the observable species chain does not model the unobservable contents of real trophic levels as in Fig. 2.

Similarly, computer simulations of what purport to be trophic levels should be examined to see if the 'level' that is modelled is analogous to a species or to real trophic level categories. These three areas of research – computer simulation of trophic levels, few-species lab systems, few-species predator–prey or parasite–host systems – all reflect a narrowing of the range of applicability of the trophic level concept to situations where species can map more or less clearly onto particular trophic levels. While these systems are interesting and important in their own right, they are species-based phenomena and do not provide theories and predictions for trophic level phenomena of large ecosystems.

Kitching[32] attends to this question of spatial (and temporal) scale. Although studying naturally occur-

ing small scale systems, he contrasts 'local' webs, shaped by stochastic events, with full 'regional' webs for which plausible deterministic explanations are available. These studies have the virtue of replication in space and time and are represented (Fig. 3) using four classifications of abundance. His model includes non-feeding transfers[6] of food energy between detritus compartments, which is a further breach of orthodox trophic level representation.

On the number of α-trophic levels and animal size

Pimm[33] has addressed the cause of what he sees as the limit of 4–6 α-trophic levels in natural ecosystems. I use the term α-trophic levels because detritus, if modelled, is assigned to trophic level one. Pimm rejects the idea that the number of α-trophic levels could be limited by species size on the grounds that there have been larger extinct forms. What determines the largest species in a system is a legitimate question in itself and, like the elephant, independent of trophic level concepts. The smallest herbivore is important here, as Fig. 2 shows, since the number of 'levels' between the hawk and the plant is dependent on the route from the herbivorous bacterium. In this context the number of 'levels' in cases of carnivory is dependent on the average ratio of the size of predator to the size of prey. The question of how many levels there are can be better posed as 'why are predator–prey size relations as they are?'. This is a fertile area of research for community ecology, encompassing behavioural and spatial phenomena as well as population dynamics.

Resource and process models of food webs

One solution to the non-predictive nature of trophic level models[2] is to develop new model structures. For instance, there is a difference in the energy available from various plant parts. Seeds, leaves, wood and exudates provide one crude classification[6] of different resource types and a similar approach was recently adopted by Odum and Biever[34]. A number of resource categories of detritus have also been proposed[6,34,35]. For carnivory, however, resource quality is probably best described by the mass of the prey item because animal protein is of similar food value across taxonomic groups[36].

All feeding interactions are mediated by the feeder foraging for
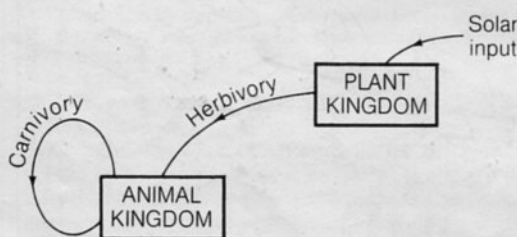
sources (prey). To be predictive, therefore, a model is required that can describe the resources in an ecosystem and the foraging processes that engage with them. A limited number of models have attempted to apply foraging theory to whole ecosystems containing many species[37,38].

Taxonomic models

Photosynthesis, herbivory and carnivory are often taken to be useful approximations to trophic level interactions. They are, however, *exact* taxonomic interactions between members of the plant and animal kingdoms (see Fig. 4). At this point I intended to ask readers to identify trophic level four in a local ecosystem, but a reviewer suggested that this was a trick question since levels one, two and three were fully observable. Notwithstanding the omnivory problem at lower levels, the trophic level classification 'feels' to break down at level four; this is simply because the taxonomic classification ceases to map approximately to trophic levels at this point. If there is only one message in this article it is this: when trophic levels appear to be observable (levels one, two and three) we are 'merely' observing taxonomic classes, i.e. the plant kingdom, animal kingdom and their interactions. Instead of treating this as a take-off point for trophic level four and above, we can further classify the animals taxonomically. Figure 5 shows a food web classification that divides taxa according to processes that are important to food web structure and function.

The number of taxonomic categories that food web researchers use depends on the purpose of their analysis. The framework of Fig. 5 can be used to compare the work of authors who have adopted different numbers of categories. Sheldon *et al.*[39] had only one category and did not distinguish any different types of particle in their description of marine particle size distributions. Later, some authors included distinctions between three functional groups, namely detritus, plant and animal particles[6,40,41]. Further taxonomic detail was required when changing diet with age or foraging styles were included in the analysis[38]. The inclusion of parasitism in a model requires creating species categories (since parasites are often host-specific) clearly showing how parasite–host models are not metaphors or simulations of whole ecosystems (as they are sometimes treated in trophic level analysis).
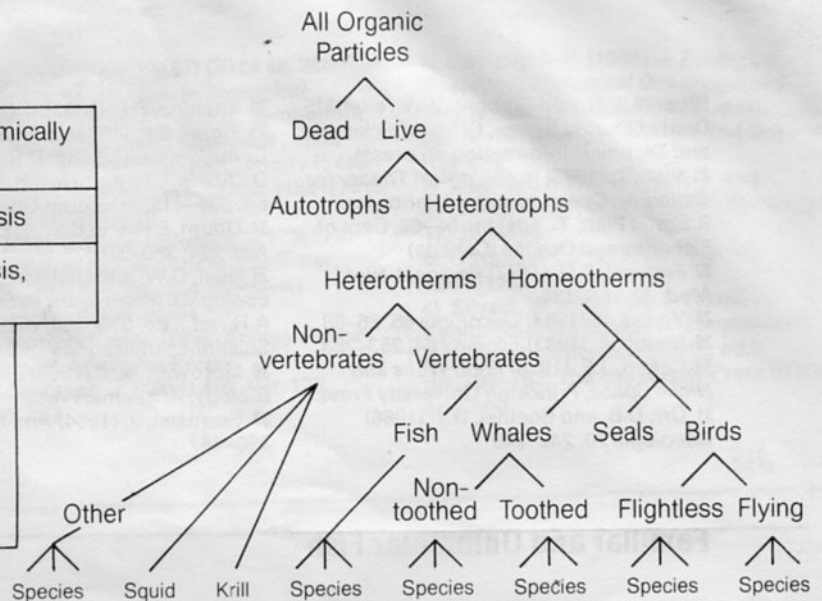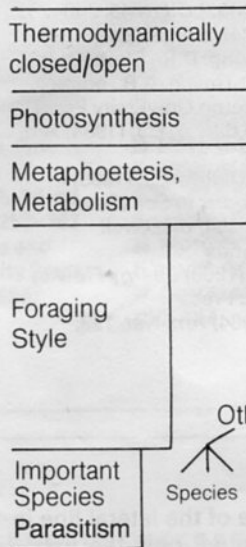

Fig. 5. Taxonomic classifications and their significance to functional food web factors in the Antarctic food web. When the category 'all organic particles' is successively partitioned into taxonomic categories, successive phenomena relevant to food web dynamics can be incorporated into an analysis or model. Metaphoetesis is the change of diet accompanying the growth of a predator. *Modified, with permission, from Ref. 38.*

Conclusion

The emergence of the trophic level as a tenet of ecological science was, I believe, an accident of history based on an invalid interpretation of thermodynamics. But whatever its shortcomings it did provide, through the International Biological Programme, the money to make ecology a medium, if not a big, science[11] – something from which we still benefit. Modifications to the trophic level concept have not overcome its basic flaws of historical energy classification scaled on the plant as unity. Recent work[2] establishes the trophic level as a descriptive and non-predictive model of ecosystems in which individual organisms or species cannot be wholly apportioned to a particular level. But as a description of large ecosystems, it will have to compete with models that describe observable flows of resources in real ecosystems. Above all, we need new models of large ecosystems into which we can place few-species subsystems without the spectre of either the superorganism, or single-species totipotency.

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