

A Trophic Continuum derived from Plant Structure, Animal Size and a Detritus Cascade

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(Received 23 January 1978, and in revised form 3 July 1979)

A new model of trophic interactions in large many species ecosystems is presented. This trophic continuum model is defined by organisms harvesting resources from an environment. Animal size classes, a classification of plant products and detritus initiates the resource descriptions of ecosystems. Strategic trophic models are reviewed. Trophic interactions are Markovian. The Lindeman trophic level concept is criticized for its dependence on the history of energy flow rather than an assessment of the present resource state. Criteria for a strategic model of ecosystem energetics are specified as the indivisibility of herbivore and detritivore chains; the non-equivalence of different trophic transfers; and that the plant is not a single reference point to scale trophic space. Elton's pyramid of number met these criteria. The trophic continuum model points to closer links between theories of energy flow, species diversity and ecosystem heterogeneity.

1. Introduction

Dale (1970) has emphasized the importance of accurately describing the parts of an ecosystem before attempting to measure the interactions between parts. He calls this the lexical phase of ecosystem analysis. This paper is concerned with the lexical phase of modelling trophic behaviour in large many species ecosystems. Sub-system models are not analysed.

If any system boundary is imposed on an ecosystem then flows of energy, information, nutrients, whole animals, etc. can be mapped across the boundary and inferences made about the parts which the boundary has separated (Margalef, 1968). Because making such measurements is expensive in time and effort system boundaries are not placed at random but where we believe they will yield the maximum useful information for the available effort. However where boundaries are placed determines what we can find out about the system.

Here the simple proposition that *organisms harvest food resources from an environment* is used to position system boundaries and thus define the parts

in a whole ecosystem trophic model. This model has affinities to that of Elton (1927) and Platt & Denman (1977) and will be compared to other trophic models particularly that of Lindeman (1942) and its developments (Darnell, 1961, 1968, Kozlovsky, 1968, Wiegert & Owen, 1971, Kercher & Shugart, 1975, Heal & MacLean, 1975) and the trophic web studies of Cohen (1978).

2. Partitioning the Trophic Model

(A) MAJOR BOUNDARIES

Initially let us distinguish between live and dead material. Of the live material let us distinguish autotrophs from heterotrophs. Thus all organic material of the ecosystem is partitioned into three spaces, detritus space, autotroph space and heterotroph space. The ecosystem is similarly partitioned by O'Neill (1976). These spaces are fundamentally distinct.

Instantaneously there is no difference between the two trophic states live and dead in the sense that a freshly killed animal or plant has the same resource value as the live form. Indeed it is a truism that all food must be dead at assimilation since food particles pass across the digestive surface as small or medium sized molecules. However if we view the two states after a period of time then each has different feedback effects on the ecosystem. With time, live organisms can feed and reproduce. Detritus will change its resource value with time. Detritus may be treated as a closed system which tends to disorder while live organisms are open systems which maintain order or increase order in themselves at the expense of disorder in the environment (Schrödinger, 1945).

The convention of distinguishing autotrophs from heterotrophs is based purely on the manner in which these organisms obtain energy for the processes of life. That convention is also consistent with the current lexical framework. The difference in physical structure of autotrophs and heterotrophs means that autotrophs represent a set of resources that are qualitatively different to heterotroph resources. Generally plants are plastic in shape, non-motile and depend on chemical and structural defence against herbivory. Chemical defences (Levin, 1976) are important in classifying plant resources. Heterotrophs are typically mobile, particulate, specific in form and have structural and behavioural defences against predation. Detritus, autotroph material and heterotroph material are now classified on the basis of the resource value they constitute to ingesting heterotrophs. Such a classification is simplest to apply to heterotrophs eating other heterotrophs.

(B) HETEROTROPH-HETEROTROPH INTERACTIONS

"Spiders do not catch elephants in their webs nor do water scorpions prey on geese" Charles Elton

In this expressive quote from Elton (1927) he points to an upper limit in the size of predator, size of prey relationship, namely that when prey become larger than a certain size the predator does not have the power or speed to catch and kill it. This upper limit can be extended by co-operation as in the case of wolves or army ants. A lower limit on the size of food taken may be considered to arise from the costs in time and energy of search, capture and chemical reassortment (Schoener, 1971) of prey; Ellis *et al.* (1976) have formulated a detailed diet selection model.

For any one organism the total system biomass per unit area is not of interest, merely the amount of energy available to that organism to ingest, e.g. available at the size of organism eaten. Resources above and below that range are not of interest. We may model this process in many species environments by considering energy transfers between size classes of organism. This set of system boundaries was first used by Elton in 1927 who described the ecosystem as populated by a very large number of small organisms and a progressively smaller number of larger organisms. Platt & Denman (1977) have recently formulated expressions for the transfer of energy and biomass between size classes of an ecosystem. Few systems have been described by size class biomasses, although examples are Williams, (1941), Ghilarov, (1944, 1967), Elton, (1973) and Janzen, (1973).

Recently there has been a revival of interest in properties dependent on animal size and size has been related to a whole variety of parameters according to the basic formula:

$$P = yW^X$$

where P is the parameter, W some measure of size, y and X are constants. Kleiber (1961) has shown many metabolic parameters to be a function of body weight to a power of the order of 0.75; Schoener (1968) has related the number of food items eaten, territory size and average prey weight to a function of body weight; Holling, Dunbrack & Dill (1976) predator morphology to prey size; Fenchel (1974) related the intrinsic rate of natural increase of a population to body weight and Bonner (1974) body length with inter-generation time. This latter pair of relationships was anticipated by Elton (1927) when he observed that it was the greater fecundity of the smaller organisms which sustained the predator-prey relationship. Hardy (1924) showed that herring of different ages and hence of different size classes had different food web interactions.

(C) PLANT STRUCTURE

Although the initial site of energy capture is the chloroplast the products of photosynthesis are translocated to all parts of the plant. This process of translocation and chemical transformation results in a great variety of forms of stored energy both in terms of different chemical compounds and in different concentrations and distributions of those compounds. The plant presents a variety of resources to heterotrophs.

Certain plant products such as seeds, storage organs and leaf drip are particulate in nature and provide an axis of resource concentration from large particles to soluble plant products which are free to disperse in the environment. Unicellular algae are also classifiable by size. However the bulk of plant biomass cannot be classified simply on the basis of particle size.

The empirical relationship between the size of the ingestor and the particle size of food taken was causally explained (Elton (1927), and Schoener (1971)) as a search problem and in terms of the predators power to capture. If we consider the ecosystem as a mixture of food particles in an environment of non-food then we may apply this search model to the plant since plant defence compounds, cellulose and lignin are non-foods for many species. The search problem is to find sugars within the leaf rather than finding the leaf itself.

TABLE 1
Autotroph states

1	Root mucilage and leaf drip
2	Woody tissue
3	Mature tissue: mature leaves
4	Young tissue: twigs, leaves, small roots
5	Growth sites: shoots, root tips, cork cambium
6	Storage organs: seeds and propagules

Considering Table 1 as a series of mixtures, soluble plant products which are free to disperse in the soil, create an intimate mixture with this 'non-food'. The mixture has low energy density. This contrasts with storage organs and propagules considered here to be the most energy dense, least mixed food source. Within that range I have ranked plant structures according to their degree of mixture with the 'non-foods' toxins, cellulose and lignins. This range of form of stored energy supports organisms from most taxa. As an approximation one might say that bacteria and fungi feed principally on 1-2, insects and invertebrates on 3-6 and vertebrates on 4-6.

(D) THE DETRITUS CASCADE

As has been observed all food is dead at the point of assimilation and that freshly dead material should have the same food resource value as live and occupy the same or adjacent point in trophic space. However on death, bacteria and fungi ever present in the organism's immediate environment proliferate and begin to digest it. Thus with time we may see the organism changing its position in detritus space as its resource value declines due to a reduced calorific content. In addition the dead organism may become fragmented and scattered; soluble products may also disperse in the environment. These processes together with the reduced calorific value change the organisms position in detritus space. This set of changes is here called a detritus cascade.

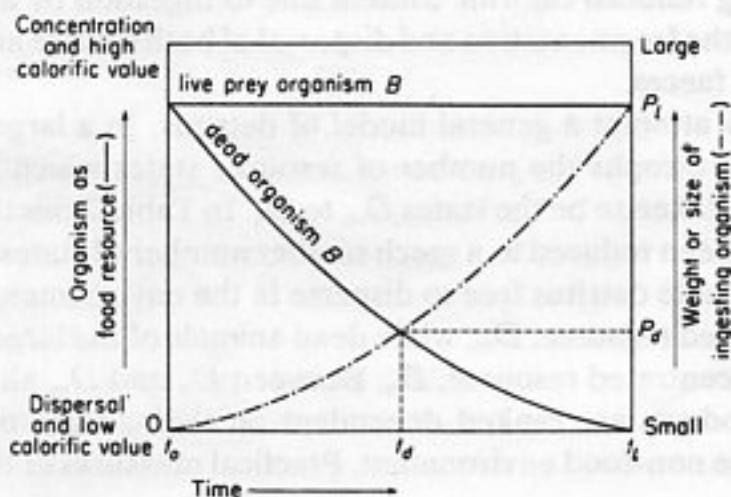


FIG. 1. A detritus cascade showing changes in heterotroph-detritus trophic interaction with time.

A model detritus cascade is shown in Fig. 1. The live prey organism, B , does not decrease in size or calorific value with time. Predators may have to reach size P_l before they can ingest B . When B dies it becomes prey to all sizes of heterotroph up to, say, P_l . Large predators are less abundant and will take longer to find their prey than small predators. Although the likelihood of meeting a large predator will increase with time, the prey will cease to constitute food for any organism larger than P_d after time $t_d - t_0$ since by time t_d a quantity of organism B will have already been digested. The activities of large and small organisms alike will fragment the dead organism; soluble products will be dispersed again reducing the size of the predator which will take the detritus as food. Janzen (1977) has suggested that selection will favour the production of toxins by detritivore bacteria in

order to make the food unpalatable to larger animals. This would affect the shape of the curves in Fig. 1.

This model presents the heterotroph-detritus interaction as being dependent on search limitations in the heterotroph. Dead plant products such as dehisced leaves do not appear to follow the same "search" relationship. Dead leaves are not difficult to find and often require the action of microbes and fungi before they become food for larger heterotrophs. As previously stated, for many species we may treat the leaf as a series of mixtures of food and non-food materials such as toxins, lignins and cellulose. Thus the palatable unit is not the leaf but its inner cell contents. The heterotroph may also be feeding on the microbial or fungal population of the leaf. This is the interaction between heterotrophs not involving detritus.

Faeces may also be treated as particles. With time, faeces become smaller in "size" having reduced calorific content due to ingestion by heterotrophs and also due to the fragmentation and dispersal of both soluble and insoluble portions of the faeces.

We may now attempt a general model of detritus. In a large ecosystem with many heterotrophs the number of resource states which the detritus present is large, taken to be the states D_m to D_n . In Table 2 this theoretically large array has been reduced to a much smaller number of states to initiate a description. Soluble detritus free to disperse in the environment represents the most dispersed resource, D_m , while dead animals of the largest size class is the most concentrated resource, D_n . Between D_n and D_m all other plant and animal products are ranked dependent on their "size" or degree of mixture with the non-food environment. Practical measures of this scale are discussed later.

TABLE 2

Detritus states

1	Urine and other plant and animal constituents in solution and free to disperse in the environment.
2	Faeces of different size classes.
3	Dead plants and plant debris of different classes.
4	Dead animals and animal debris of various size classes.

(E) INTEGRATING TROPHIC SPACE

Figure 2 shows how the various states in trophic space relate to one another. Each space is represented by a horizontal row. Each space has a different set of processes by which food changes state within that space.

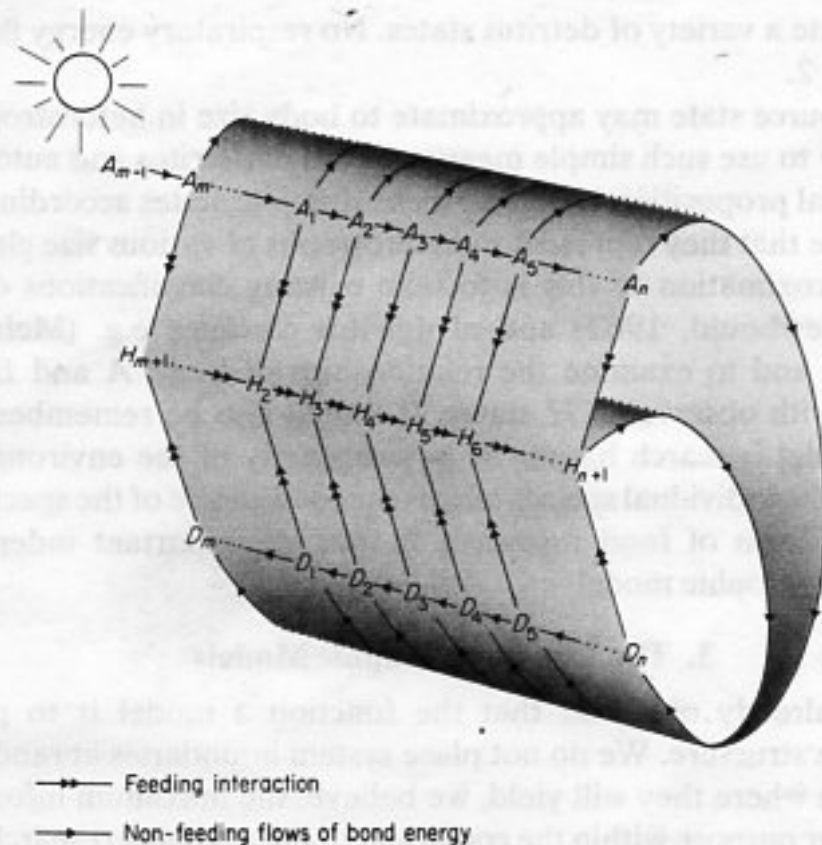


FIG. 2. A trophic continuum showing translocation and chemical transformation within the autotroph, heterotroph interactions and a detritus cascade.

Row *A* represents the resource states which the many plant species present to the rest of the ecosystem. State A_{m-1} represents all primary products of photosynthesis in all plants in the system. States A_m to A_n represent the different structural forms and chemical concentrations of the products of chemical reassortment and their distribution in the ecosystem. For example the states listed in Table 1 could be ranked from A_m to A_n ; A_n being seeds.

Each of these states may be fed upon by heterotrophs of sizes H_m (small) to H_n (large). Feeding interactions also occur between *H* states. With time individual organisms may change size and therefore change their state in trophic space.

Detritus in all its forms, Table 2, constitute the variety of states D_m to D_n . With time each item of detritus changes its position in detritus space towards greater dispersal D_m . These states are fed upon by heterotrophs H_m to H_n .

Figure 2 is simplified in that only 4 routes are shown for the transfer of energy at any one state. Organisms in H_4 for example may feed on H_5 , H_2 as well as H_3 , D_2 as well as D_3 and A_1 , A_2 , as well as A_3 . Any single *H* or *A*

state will create a variety of detritus states. No respiratory energy flows are shown in Fig. 2.

Whilst resource state may approximate to body size in heterotrophs it is less clear how to use such simple measurements of detritus and autotrophs. The theoretical proposition is to rank these resource states according to the resource value that they represent to heterotrophs of various size classes. A practical approximation to this is to take existing classifications of plant structures (Newbould, 1967) and of detritus cascades e.g. (McIntire & Colby, 1978) and to examine the relationships of these *A* and *D* states respectively with observable *H* states. It should also be remembered that since this model is search based the heterogeneity of the environment as perceived by the individual species affects the food choice of the species. The spatial distribution of food resources is thus an important independent variable in this trophic model.

3. The Choice of Trophic Models

We have already observed that the function a model is to perform determines its structure. We do not place system boundaries at random but position them where they will yield, we believe, the maximum information for a particular purpose within the constraint of the available research effort. Thus while no model structure can be said to be wrong, since flows may be measured across any boundary, models can vary in their efficiency at approaching a particular purpose. How efficient is the trophic level model in comparison to size phenomena at providing an overview of feeding relationships in whole ecosystems? Van Dobben and Lowe-McConnell (1975) claim that despite its drawbacks the model has "deepened our insight into the gross structure of ecosystems", a view which contrasts strongly with Rigler (1975) who in the same volume castigates the trophic level classification as a paradigm of ecological energetics, reminding us that "Classification is an essential arbitrary process whereby we simplify nature, fossilize our current world view and effect the probability of changing our theories".

The success of the Lindeman model can be measured in two ways, firstly by its efficiency at yielding information per unit effort for our purpose of analysing system structure and function; and secondly and more importantly by assessing if its role as a paradigm of ecological energetics restricts the development of other theories in ecology.

Lindeman's model is determinist. The history of feeding interactions is sought for all species in an ecosystem. These organisms are then positioned in the model taking the green plant as unity, taking each act of ingestion as unity, i.e. a change of one trophic level, and treating detritus either as unity

or (quite differently) it is placed at the trophic level from which the material came (Neess in Kozlowski (1968) and Batzli (1974). During the 38 years of the model's existence no large system has been analysed in that manner. The best the 10 year International Biological Program could produce was an analysis of "secondary" production (Heal & MacLean 1975). Details of whole system production and behaviour at trophic levels 3-5 are non-existent. Lindeman himself remarked on the difficulty of positioning species at higher trophic levels. It is clear that this model has not been efficient at describing whole system energetics certainly at levels 3 and above. We can perhaps say why.

If the trophic level of an organism cannot be identified from its present state behaviour either by an investigator or by a predatory heterotroph then we may say that the route by which the biomass of an individual reaches its present state will provide negligible information concerning the route by which it will leave. If the present state and not the previous states determine the state transitions then that state approaches the Markovian ideal. Suppose ecosystems are populated by organisms which are Markovian with respect to the probabilities of who they will be eaten by. Then any model which describes the present state in terms of its history, i.e. steps since the green plant will be enormously inefficient at detecting pattern or redundancy in interactions within an ecosystem. That trophic transfers are Markovian receives some support from Morowitz (1968) who has described the similarity of chemical constitution of living materials. Herbivores, detritivores and carnivores are virtually indistinguishable in their protein structure, carbon nitrogen ratio etc. There are no major nutritional distinctions to be made between these groups and hence it is the present food value not past feeding history which determines state transition properties. Dead material when assimilated becomes incorporated as live tissue. Since all food is dead after digestion it is impossible to tell from the nutritional state of the live organism if the food it lives on is killed before or after contact with the organism. The latter data has no predictive value for transition from its present state to becoming food for a predator. It follows directly that because these transitions are Markovian that there can be no separation of trophic models into detritus and herbivore chains. If a model is structured in that way it fails by the criterion of efficiency since information will be gained which does not contain sufficient redundancy.

The final criticism of the Lindeman model is that the categories "all plant life" and the category "all dead organic matter" do not provide single reference points to scale trophic interaction. The model which has been presented in this paper identifies ecological processes as ones of concentration of biomass into packets of different sizes or series of mixtures. The

process of concentration is achieved by ingestion in heterotrophs but other processes within the plant and disintegration in detritus are also important. The plant and detritus represent a range of resources just as the heterotrophs are a range of resources to each other. There is no way of treating the plant or detritus as unity in order to simplify heterotroph interactions. Similarly if we adopt a biomass concentration framework then trophic interactions are not equivalent but are dependent on the amount of biomass concentration they achieve. Conversely in the Lindeman model all acts of ingestion are equivalent as a change of one trophic level. The logical outcome is that strategic models should be modelled as a continuum both because the green plant is not a single reference point and hence cannot supply step functions in the model and because trophic interactions are not equivalent single unit step functions in a model of biomass concentration.

The criteria proposed for strategic models of ecosystems are:

- (1) no discrete herbivore and detritivore systems
- (2) the categories "all detritus" and "all plant material" do not form single reference points
- (3) trophic transfers are not equivalent.

Various whole ecosystem models are now examined with respect to these criteria. Heal & MacLean (1975) allocate all detritus to a single level and perceive trophic relations to be split into two distinct systems, a herbivore chain scaled on the green plant and a detritus chain scaled on "all detritus". They subdivide trophic levels into size class/taxonomic classes. Their taxonomic trophic categories do not meet criteria 1 and 2 but partially meet 3.

In terrestrial systems, decomposition occurs mainly at the soil surface and within the soil. This spatial separation has probably contributed to partitioning models into detritus and herbivorous chains. However, Coleman *et al.* (1977) point to the quantity of underground herbivory and plant respiration. They show that the soil ecosystem is a mixed herbivore/detritivore system as is the above ground system.

Neess (in Kozlowski, 1968), and Batzli (1975), Wiegert & Owen (1971), variously apportion detritus and heterotroph production to different levels dependent on how many acts of ingestion have affected it. All four authors do not separate detritivores from herbivores and so meet condition 1 but not 2 and 3.

Darnell (1961, 1968) partitioned trophic levels in a trophic-taxonomic scheme as has Heal & MacLean (1975). The Darnell trophic spectrum fits criterion 1 but not 2 and 3.

Kercher & Shugart's trophic continuum, in which each species has an effective trophic position, is scaled on the plant as unity. However their use

of a variety of trophic transfer efficiencies to position organisms in trophic space may effectively meet conditions 2 and 3. Condition 1 is met.

Elton's Pyramid of Number and Platt & Denman's (1977) use of particle size to determine state in the model each meet all 3 criteria. Ecosystem trophic studies based on the distribution of organisms of different sizes have been few. Examples from soil biology are Anderson (1975), Persson & Lohm (1977), and from pelagic systems, Sheldon *et al.* (1972).

Cohen's (1978) analysis of the properties of many different food webs examines whether food web graphs are interval or not. Community food webs describing composite habitats are not expected to be interval even if the component parts are. Problems of defining what is and what is not a habitat may limit this approach as a strategic model of whole ecosystems. The approach may provide interesting information on the topology of subsets of the whole system such as sink food webs. A similar criticism is applicable to Pimm and Lawton's (1977) conclusions about trophic behaviour. These may be appropriate to interactions in a trophic chain and thus to the topology of simple food chains but not the properties of trophic levels each of which contains species of many different sizes. Predator-prey interactions are not analogous to trophic level interactions.

Adopting a sized based model of ecological energetics promises to bring together previously isolated parts of ecological theory. A taxon occupies a much more limited position in trophic space in a size based model than it does in a trophic level model. The taxon is both a category for measurement of species diversity and an energetics (size) category in a trophic model, (Cousins, *in press*). Species size as a component of species diversity is investigated by Southwood (1978) and May (1978).

Since one of the bases of the trophic continuum model is the search for resources the spatial arrangement of those resources is important to their rate of harvest. Thus this model provides a framework in which to pose Weins' (1975) question of how spatial heterogeneity affects energy flow in ecosystems. Species diversity is also affected by spatial heterogeneity. Thus theories of species diversity, energy flow and ecosystem heterogeneity may be closely linked. Rigler's (1975) contention that the trophic level paradigm is one which has restricted the probability of our developing new theories must be investigated. But as he notes "Because it embodies our world view it is not easily discarded".

I thank Professor Mike Hussey and Howard Parkin of the Engineering Mechanics department at The Open University for much stimulating discussion on trophic matters and the following who have made many helpful comments on various drafts of this paper; Peter Evans, Paul Clark, Dennis Owen, David Thurling, John Hedger and Nick Polunin.

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