An alignment of diversity and energy models of ecosystems

Thesis

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AN ALIGNMENT OF DIVERSITY AND
ENERGY MODELS OF ECOSYSTEMS

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The work for this thesis first began as background research for the animal ecology section of a course on Human Ecology under the chairmanship of Mike Hussey, Professor of Engineering Mechanics at the Open University. I thank him for the intellectual stimulation which he has given me over many years and for the practical support he offered me by providing a research assistantship and later a fellowship in his department.

I would also like to thank Howard Parkin for his collaboration on the mathematical model, and the sheer amount of effort and thought put into bringing that research to a successful close. I also thank him for his advice and friendship.

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I conclude with a quote, not about biology, from Howard Parkin

"Where modelling ends, life begins".

Howard, I hope you're right!
Abstract

In this work the problem of incompatibility between diversity and energy models of ecosystems is investigated. Compatible models are developed by using species density measures for species diversity measurement and by adopting a new model of ecosystem energetics, the trophic continuum, based on plant structure, animal size and a detritus cascade. A combined, compatible measure is developed. This is the species density of a size class of a taxon. In generating the trophic continuum model an extensive critique of the trophic level concept is undertaken.

Four published papers form the basis of the thesis and these are linked by a commentary. The commentary details how the papers are related. Paper 1 examines the properties of sample size independent measures of species diversity and concludes that sample size dependent measures, such as species density, are preferable for compatibility with energy models. Paper 2 develops a new model of ecosystem energetics, the trophic continuum, applicable to large (that is, many species) ecosystems. The model is defined by organisms harvesting resources from an environment. Thus the model has strong affinities with optimal foraging theory. This is developed in appendix 2. Animal size classes, a classification of plant products and of detritus, determine the resource state boundaries used in the trophic continuum. Paper 3 combines the approaches developed in papers 1 and 2 to examine the species density distribution of birds of different size classes using data from the UK atlas of breeding birds. This work shows that large birds are predominately found in the north of Britain and so has implications for the structure of food webs in different geographical areas. Paper 4 considers species density and species size distributions over a hypothesised gradient of environment patch size. It examines the distribution of birds and snail species of an urban area. Average species size declined towards the centre of the area as predicted. Papers 1, 3 and 4 adopt the species density measure at different scales.

In the commentary, possible counter examples to the trophic continuum are discussed, including the phenomenon of parasitism and the group behaviour of animals. Significant differences in the species diversity relationships between predators and prey compared to parasites and hosts are identified. Future research is indicated by appendices containing currently unpublished papers on Bergmann's rule as applied to an avifauna (appendix 1) and a mathematical model of the trophic continuum for large ecosystems (appendix 2). A poster paper illustrating the seed size distribution of part of the UK flora (appendix 3) shows biogeographical changes in one aspect of the plant structure sector of the trophic continuum model.
The following four papers and written commentary form a submission for Ph.d by published papers under the Open University rules for higher degrees. The four papers are as follows:


These papers are located in a pocket in the rear cover of the submission.
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1.0 INTRODUCTION

The study of the flow of energy through ecological systems and of the diversity of the component species of ecosystems are dominant themes of synecology. They are also separate themes. Each may be used independently to explain the same ecological phenomena. Moreover there is little understanding of how species diversity and energy models are related. The subject of this submission for PhD is to investigate aspects of that relationship. Such an aim could encompass much of the material of modern ecology and indeed the approach taken is a broad one. Thus it is necessary to keep in mind the general structure of the submission and its key conclusions. The most important conclusion is that the green plant cannot be used as a simple scalar for the feeding interactions between animals. Significantly the thesis can therefore be regarded as forming a critique of the trophic level model of ecosystem energetics. An alternative model is proposed in which energy transfers occur between animal size classes. From this alternative model of ecosystem energetics comes the opportunity to establish a relationship with species diversity models.

This submission for a PhD by publication is structured around four published papers concerning ecosystem energy flow and species diversity. In this first section of the submission I discuss the reasons for choosing the area of research and why it is relevant to ecological theory. I then describe the historical background of the data sets used in the empirical part of the papers. The next section presents a short summary of each of the four papers and of three unpublished appendices. The following sections show how the papers are related, review the current literature and indicate directions for future research.
1.1 Origins of the research

The subject of the thesis stemmed from observations on two practical problems. The first concerned the measurement of species diversity. Murton and Westwood (1974) published a paper where they claimed to show that if hedgerows were removed from farmland then the bird diversity of that land was not adversely affected even though the abundance of birds declined with hedge removal. However, the diversity index they used, Williams $\alpha$, is independent of sample size (Williams, 1964). Thus even as the number of birds on a 'farm' approached zero the diversity index can remain high.

At the time I was interested in the question whether high species diversity might or might not create stability in ecosystems. In particular would stability be enhanced by energy flowing through a variety of pathways, that is, via a variety of species. This hypothesis could not be examined if diversity, as measured, remained high while the capacity of the bird population to affect the energy flows of the system approached zero. My first task was therefore to examine the commonly used diversity indices to try to find an index which behaved 'correctly' with respect to the supply of energy to the system. This amounted to investigating indices for sample size independence and comparing them with diversity measures per unit area, such as species density. This work forms the first paper.

The second problem again came from trying to apply the diversity-stability hypothesis to bird populations. I tried to calculate the bird species diversity of each trophic level and to examine the relationship between that functional form of diversity measurement and the stability of the bird populations. However I found that I was unable to identify the trophic level at which species fed; even if common foods could be identified it was by no means always clear at which level the food was itself unless the food was plant material. I therefore began an examination of
the Lindeman (1942) model and of the modifications to it which other authors had proposed.

Thus the thesis grew out of two problems. First, the inappropriateness of sample size independent measures of diversity for the examination of the variety of energy flow pathways in ecosystems. Second, the inability to identify the trophic levels of species in order to calculate bird diversity at different trophic levels. Consequently the focus of my research shifted from the diversity-stability problem to finding compatible models of species diversity and ecosystem energetics and to examining their theoretical relationship.

1.2 Theory and practice

Although I have given some indication of how and why I have adopted this particular research area there needs to be some consideration of whether it is desirable to link diversity and energy models of ecosystems. To put the discussion in context, May (1974) has argued that the phenomena of ecology are so varied that a variety of approaches to the subject should be expected and encouraged. This pluralist view of ecology can be distinguished from Southwood's (1977a) aim of a unified ecological theory. Clearly there are contrasting views concerning the feasibility or desirability of achieving a unified ecological theory. This is summarized by Levins and Lewontin (1980) who question whether ecological generalisations reveal deeper levels of reality or destroy the richness of nature.
However where it has been possible to create unified approach in ecology the benefits have been substantial. An example is given by Hill's (1973) theoretical work on diversity indices.

The comparison of the properties of various diversity indices was the subject of intensive ecological debate during the 1960's and 1970's. The debate was based on both theoretical and empirical work (Pielou, 1975). Hill demonstrated that the debate was largely sterile. This was because the indices involved could be shown to belong to a single mathematical family. Although differently sensitive to rare or common species the indices produce the same, or very similar, ordinations between sites. Further, Hill's conclusions indicate that if a relationship is found between energy flow and one measure of species diversity, for example species density, then the relationship to other indices such as Shannon's H' and Simpson's D will also be known. Hill's work on diversity contrasts with current research in ecosystem energetics.

Unifying theories in ecosystem energetics have not been so successful (May, 1979). This could account for the recent enthusiasm for empirical studies of trophic webs, exemplified by Cohen (1978) and Paine (1980). However the results of these empirical studies require theoretical evaluation to see whether it is appropriate to predict similar results in other environments or indeed to see if the experiment should be repeated and the data collected in a different way.

Paine's demonstrations of the effects of removing various species from food webs have been dramatic. He has shown that in the littoral (coastline) ecosystem the local removal of a single species can result in several other species becoming locally extinct. However the littoral ecosystem is a highly stressed system which lacks many of the 'buffers' that are present in the ocean and terrestrial systems that the littoral system separates. It is possible that these other systems have food webs which
behave in different ways and therefore Paine's work should be
generalised from with caution.

Cohen's empirical discovery that food webs from fourteen
different ecological communities have remarkably similar ratios
of predators to prey says, I believe, more about the data
collection process than it does about the properties of food
webs. Cohen acknowledges this possibility. The ratio which he
finds is $\frac{3}{4}$ prey types to predator types. However it is
necessary to recognise that all live organisms other than plants
are predators in that they derive their food from eating other
organisms or by being supplied by others. Normally only once in
their lives do these 'predators' become 'prey'. Given that even
top carnivores have parasites then all species in a food web,
excepting plants and detritus, are both predators and prey. Thus
a food web, if it excludes plants and detritus, can only have a
'predator-prey' ratio of one and if it includes plants or
detritus, of less than one. Consequently Cohen's observed
predator-prey ratio of 1.33 is suspect.

This discussion of these two recent and significant studies by
Paine and Cohen illustrates that empiricism cannot be applied
without caution. By contrast Hill's endeavour to create a
unified approach to diversity indices has been beneficial. The
stance taken in this thesis follows Hill's example and is
primarily theoretical rather than empirical. I shall not call
upon Feyerabend's (1975) 'anything goes' for further support for
this type of research but instead I quote Giddens (1976), writing
of Popper,

"Popper attempts to break free from the perspective
according to which science is founded upon the dull
discipline of careful fact-gathering, and replaces it with
the thesis that science advances above all through bold and
daring conjectures of implausible hypotheses that are
readily open to potential falsification."
1.3 Ecology as a young science

Before discussing the origins of the data that I use to examine particular hypotheses it is relevant to consider to the idea of ecology as a young science. Krebs (1974) characterises a young science as a chaotic assembly of observations and relationships without a strong theoretical framework to link them. More recently, McIntosh (1980) has reviewed authors who believe that ecology could soon approach a relative maturity. This maturity would be identified by the existence of coherent theory.

The perception of ecology as a young science is encouraged by its relatively recent identification as a distinct discipline. Ecology was first defined by Haeckel in 1869 (cited in Krebs, 1974) as,

"the total relations of the animal to both its organic and inorganic environment."

So in some ways ecology can be said to date from 1869. However, this definition and Margalef's (1968) definition below, make it clear that ecological science was being undertaken much earlier.

"...the study of ecosystems at a level in which individuals or whole organisms may be considered elements of interaction either among themselves or with a loosely organised matrix".

In both definitions, although perhaps more obviously in the latter, it is clear that identifying and listing the organisms in the 'matrix' is the first step to establishing any interactions. The data used in this thesis is of the 'species list' type. Cataloguing the species in different geographical areas may be considered as a form of ecological research undertaken well before 1869. The historical roots of these data lists are now considered.
1.4 Species distribution atlases and their history

The experimental work for the thesis comes from the analysis of published data on species distributions in the British Isles. Three atlases of animal species distributions are used; The atlas of Breeding Birds in Britain and Ireland (Sharrock, 1976), The atlas of the non-marine mollusca of the British Isles (Kerney, 1976) and The atlas of breeding birds of the London area (Montier, 1977). The other data set I use is the BTO Common Birds Census (CBC). This has affinities with atlas studies as the CBC is also based on a mapping technique. Maps are made of the territory of each pair of birds breeding on the census plot. Indeed, the CBC can be considered as almost the limiting case of the bird distribution map.

What are the origins of bird distribution mapping? Not only is this question interesting in itself but it also illustrates that ecology is not a young science in a literal sense. Ecologists who today use computer aided techniques to record lists of species found in 10x10 km squares are pursuing an activity which is no different in kind from the work of naturalists or scholars of the 16th century whose sampling frame was the national or county boundary.

Fisher (1939) has made a study of early ornithology dating it from 8000 BC with cave paintings in Spain where some 8 species may be identified; Egyptian frescos of 3000 BC provide another set of very early records. Aristotle c. 400 BC listed 200 species of bird with notes on their physiology and reproduction. From then until the 16th century lists of known organisms were primarily made for purposes of taxonomy. However in 1577 Harrison gave a list of British birds in his Description of Britain. A little later Carrew published a list of Cornish birds in 1602 and Merrett a list of British birds in 1667. Monographs on the birds of all the British counties appeared during the next two centuries.
The county as a primary recording unit was retained unchanged until 1850 when Watson rearranged the county units into vice-counties for the purpose of recording species distributions. Vice-counties were obtained by aggregating smaller counties into single units and partitioning larger counties to give 110 units of approximately equal area covering the whole of Britain. Watson's recording units remained in use for a century.

In Britain the adoption of a grid system for the organised record of species distributions waited until 1950. The stimulus for change was the British participation in data collection for an atlas of European flora which used a 50 x 50 km lattice. However data could be recorded on a finer scale in Britain and a 10 x 10 km lattice was adopted. Some 1500 botanists listed the plant species found in each of the 4900 10 x 10 km squares to produce the **Atlas of the British Flora**, (Perring and Walters, 1962). This publication has acted as a watershed with county floras, for example, Dony's (1975) *Flora of Hertfordshire* being produced using an even smaller scale, 2 x 2 km, and the production of similar atlases for various taxonomic groups such as the **Bedfordshire Bird Atlas** (Harding, 1979). It is estimated (Ferguson-Lees, in Sharrock 1976) that Sharrock's atlas of British birds is the outcome of the fieldwork of some 10,000 - 15,000 ornithologists between the years 1968 and 1972.

This brief history of species list making shows that the process of identifying the organisms present in a locality has gone on in a similar way for a very long period. What has changed is the technology used to record the data. We have literally come from the cave wall, oral and written traditions to the printing press and the computer. The printing press appears to have proved a strong stimulus to this type of recording as has the availability of computers in the 1960's. Indeed the production of species atlases by ecological research centres which is in full spate today is exactly analogous to the surge of national and local monographs produced in the 16th to 19th centuries.
The activity of recording the species present in an ecosystem is central to Haeckel's and Margalef's definition of ecology. Therefore I conclude that ecology is not a young science in the literal sense as its activities have been pursued for centuries. The emergence of ecology as a mature discipline will come not from the simple passage of time but from unifying the subjects theoretical base.
2.0 SUMMARY OF PAPERS

The set of papers around which the thesis is structured are summarized in an overall way below. The papers are then individually summarized and presented in this section with copies of the papers concerned.

The first two papers are methodological. In paper 1 BTO Common Birds Census data is used to examine how diversity is measured and to select a methodology, species density measurement, for this purpose. In paper 2 I examine how energy flows are measured and construct a new model based on energy flows between organisms of different sizes.

The next two papers use species atlas data to examine species size distributions. Paper 3 demonstrates the relationship between species density and animal size by the spatial distribution of species densities of birds of different sizes in Britain. Paper 4 uses species atlas data to investigate species size distributions on a local scale in response to ecosystem heterogeneity.

Summaries of three appendices follow the four papers. Two of these appendices are joint work and are included at the end of the thesis. In appendix 1 species size distributions are examined from the viewpoint of Bergmann's rule as applied to a fauna (as yet unpublished). Appendix 2 restates the energetics model as a set of equations which explicitly show the model to be based on optimal foraging theory applied to large ecosystems, (joint paper with Howard Parkin and as yet unpublished except in this thesis). Appendix 3 shows the seed size distribution for 81 forb species in Britain, (joint poster paper with Steve Smith).
2.1 Summary of paper 1


Data from a national census of birds on farmland are used to investigate properties of species diversity indices. In particular the choice of indices appropriate to monitoring environmental change is examined by comparing the behaviour of sample size dependent and sample size independent indices. Shannon's $H'$ and the related index, $J$ are shown to be algebraically and empirically dependent on sample size. It is noted that these indices have been commonly used without reference to the size of sample.

The desirability of sample size independance as a characteristic of diversity indices is questioned where the indices are used for monitoring environmental change.

It is observed that since the solar energy supply to the system is available per unit area then the number of species and individuals in an area determine the magnitude and variety of the pathways through which that energy is dissipated. Species density measurements are made at four different scales $625m^2$, 10ha, 20ha and 40ha. When these densities are calculated half the individuals found at the edge of the plot should be excluded from the data. This number can be considerable and in some samples approaches 40% of the total species recorded.

By using species density as a measure of species richness and Fager's NM as a measure of species evenness these two aspects of species diversity can be kept distinct. The use of a variety of scales from which to observe species density does not force a definition of what is an ecological community thereby allowing a neutral description of the species in a collection.
2.2 Summary of paper 2


This is the central paper of the thesis. It forms a critique of the Lindeman trophic level model and proposes an alternative. The recent use of trophic level concepts and of other trophic models are reviewed.

The Lindeman model is defined by a simple set of system boundaries. I adopt the approach that the specification of a set of system boundaries, in order to investigate energy flows, cannot be refuted but merely shown to be inefficient or inappropriate for a particular purpose. The purpose ascribed to the Lindeman model is that it provide some practical and theoretical basis for the comprehension and exploitation of the processes of energy flow in ecosystems. In a significant paper on ecosystem energetics Ulanowicz and Kemp (1980) claim,

"Perhaps no other idea pervades the body of modern ecological thinking more than Lindeman's (1942) exposition of the trophic-dynamic aspect of ecology."

I show, however, that there are numerous and fundamental problems in both the theory and practice of the Lindeman model and an alternative model is proposed. At each stage it is shown where this new model differs from the trophic level approach. It is suggested why the new model is likely to be more efficient both in providing new theoretical insights and by being useful in practical situations.
The paper sets out to deduce, from first principles, where to place system boundaries in a general model of ecosystem energetics. Lindeman used the boundaries that A is separated from B and B from C because A has eaten B which in turn has eaten C. Instead the proposed trophic continuum model is derived from Schoener's (1971) work on foraging strategies and an attempt is made to describe the availabilities of resources in their environment. Thus the model can be considered as an initial classification of plant, animal and detritus resources in the ecosystem so as to be able to make albeit limited predictions of change in those resource distributions in time and space.

The trophic continuum classification begins by distinguishing live and dead material since these states affect the resource value of the material at later times. Plant and animal material are also classified separately because of their chemical, structural and behavioural differences each of which affect their value as a food resource. Live animal, live plant and dead material define the three major system boundaries of the model.

Change in resource availability is seen to occur both within and between these three major boundaries. If we first consider animals eating other animals then body size is an effective parameter of resource availability in most species. An upper limit on the size of prey available to a predator is dependent on the power of the predator to catch and kill the prey, a lower limit is defined by the cost in time and energy of searching for the prey. Energy transfers which take place across the weight class boundaries in the model occur as a result of growth as well as the trophic relations of predation and parasitism.

The terrestrial green plant is seen as presenting a variety of resources to heterotrophs. Over evolutionary timescales species of plant have become toughened or in some way toxic to herbivores. A preliminary classification of plant resources is given. Treating the plant as a range of resources rather than as
a single entity is a major departure from the Lindeman model where the plant is treated as unity and used to scale all the other trophic interactions in the ecosystem. During growth, chemical change in the plant alters the plant's resource availability to heterotrophs just as animal growth alters the availability of that animal to predators. Both for plants and animals biological material is able to change its position in the trophic model without being eaten which is again a major departure from the Lindeman model.

The detritus part of the trophic continuum is analogously structured to the other two parts of the model in that material can change state without being ingested. It is noted that in an ecosystem detritus represents a wide variety of resource states. Again this is unlike the trophic level model where detritus is treated as a single state.

The full trophic continuum in the form of a cylindrical graph integrates the three sub-models. It is significant to note that the direction of energy flow in the detritus cascade, row D, is in the opposite direction to the live part of the system, rows A and H. This is another departure from the Lindeman model.

The paper now returns to the idea that a set of system boundaries cannot be 'wrong' or refuted, but merely inefficient. On page 615 paragraph 2 it is argued that the organism's current mass determines the probability of its trophic transition rather than the organisms feeding history. Organism mass provides a Markovian descriptor of trophic transfers. This leads to a proof that herbivore and detritivore food chains cannot be separated other than where they are spatially 'isolated', for example, in Benthic and Pelagic systems. The soil system is included in this generalisation. Coleman et al (1977) shows the below ground ecosystem to be a mix of herbivory and detrivory just as the above ground system.
Finally the observation is made that predator-prey interactions or parasite-host interactions are not analogous to trophic level interactions. The application of the model is anticipated to lie in relating previously isolated parts of ecological theory concerning species diversity, energy flow and ecosystem heterogeneity.
2.3 Summary of paper 3


This paper combines the method of species diversity measurement selected in paper 1 with the species size classification of the trophic continuum model. A map of breeding bird species density over the whole of the UK and Ireland is produced, together with three similar maps showing the species density of different size classes of bird. The greater number of small species in Southern Britain and of larger species in the North shows that bird diversity is differently distributed in the Eltonian pyramid dependent on latitude.

Although the current paper contains a summary of the trophic continuum model it is developed in two respects. First it makes the case that the direction of trophic interaction between organisms is one which favours the concentration of biomass into larger 'packets'. That this process can occur by means other than ingestion is a point made more explicitly here than in paper two.

Secondly, the mode of measurement used in Lindeman's model is discussed. The sentence on page 1052, paragraph 3, "The variety of energy states in the green plant have different entropies and (so) cannot be summed to give a reference point for the interactions of heterotrophs" could benefit from some amplification here.

Georgescu-Roegen (1971) places great emphasis on the use of ordinal as opposed to cardinal measurement for the study of processes which conform to the second law of thermodynamics.
Ordinal numbers, 1st, 2nd, 3rd etc relate to a ranking in a series and they may not be added or subtracted as can cardinal numbers 1, 2, 3 etc. As an illustration suppose we wish to add two masses of the same material, one weighing 2y g which is at the temperature T°A, and the other weighs y g and is at 2T°A. Both have the same calorific content and cardinal measurement may be used to add the quantities of heat according to the first law of thermodynamics ie

\[ 2y \cdot T \text{ cals} + 2T \cdot y \text{ cals} = 4Ty \text{ cals} \]

However the entropies of the two bodies are different. Given a heat sink at less than T°A the mass at double the temperature can do more work than twice the mass at half the absolute temperature. If we are trying to measure the capacity of the bodies to do work it is necessary to describe the two bodies in terms of the number of calories at a particular temperature. This is an ordinal mode of measurement, the quantities are ranked in a particular manner, in this case according to temperature.

Consider now a geological example where two pieces of ore contain the same quantity of an element, Q, then the total quantity present is plainly 2Q using cardinal measurement. If however the ores are present in different concentrations then the value of the two pieces of ore will not be in proportion to 2Q. The element will have different costs of extraction from the ores. Here it is necessary to describe the weight of ore at a particular concentration or price.

In this second example the existence of different concentrations is analogous to different entropy states but the ores are not physically at different entropies. A similar caveat has to be placed on the 'scattered bread' example used in the present paper. The analogy does not minimise the importance of using ordinal measurement however.
Ordinal classifications are continuous; temperature gradients, concentration gradients, etc., and where they cease to be continuous cardinal measurement becomes possible again. Thus it is possible to add meaningfully two quantities of material at the same concentration using cardinal numbers. Because ordinal measurement is continuous it is usual to treat the continuum as a stepped gradient where, between specified limits, the quantities concerned are treated as cardinal variables. In the economic system the quantity of a resource, say oil reserves, is given as the number of barrels at certain prices, ignoring the continuum of price.

Returning once more to the summary, changes in concentration are treated, by analogy, as changes in entropy and as a consequence Elton's model of trophic relations, the trophic pyramid, can be seen as being consistent with the second law of thermodynamics. What is particularly significant about Elton's model is that it is an ordinal one, as is required by Georgescu-Roegen (1971) for systems which exhibit change analogous to change in entropy. The mass or number of individuals of particular size classes is specified in Elton's pyramid and the size classes can be changed at will.

Prey size is some indicator, relative to the size of predator, of the availability of the prey to the predator. Since members of the same phylum are of similar size for mechanical reasons (Thompson, 1916) they therefore inhabit similar positions in trophic space.

Finally, four observations are made on the species size distribution maps before drawing the principle conclusion that by adopting the trophic continuum model certain taxonomic groups occupy much more limited position than was possible in the trophic level model.
2.4 Summary of paper 4


This paper examines the potentially close relationship between energy flow, spatial heterogeneity and species diversity which was suggested by the trophic continuum model described in paper 2. The choice of an urban ecosystem as the environment in which to test this relationship came after an unsuccessful attempt to design experimental ecosystems to fulfill that purpose.

I first tried to design a set of experimental environments which had the same level of resources each and yet were qualitatively different. Such a set of environments might be thought of as a multi-coloured chessboard where each coloured square was 'different' but had an equal quantity of available food material. One hypothesis which could be tested here is, given suitable species, there would be no difference in the animal productivity of any of the squares. However this would require that species were available for the experiment that were perfectly adapted to the 'difference' of each square. Clearly this is an untestable hypothesis.

It can be noted that if the patch types (colours) are non-overlapping and of equal area, as indeed they are on a chessboard, then the greater the number of colours the less is the area occupied by each colour. In this form, mean patch size is a function of the number of patch types.

If we pursue the chessboard analogy a little further a useful simplification becomes apparent. From the viewpoint of any one
species, adapted to a single colour (blue), the board can be represented as two states: blue and not blue, regardless of the number of other coloured squares on the board. Suppose blue covers 10% of the board area then for the blue adapted species patchiness can be defined by the manner in which the 'blue' is distributed over the board eg in 5 patches or 500 patches and, not considered here, their arrangement. At some scale of patchiness the blue adapted species will go extinct.

In the laboratory altering the patch size inhabited by single species until they go extinct is of little interest. However variation in patch size can provide a simple hypothesis to test in multispecies 'natural' ecosystems where the outcome is less predictable.

This then is the approach taken in paper 4. Urban areas are hypothesized to present a gradient of declining 'green' patch size towards the urban centre. Small bird species are predicted to survive in urban centres because they require smaller territories. Analysis of a London bird atlas shows that average species size per 100 km² does decline towards central London. No such relationship is found for land snails and it is suggested that water relations may determine the snails' survival. Trophic structure based on size of feeder and size of food 'packet' size is affected by any factor which influences organism size. Human food wastage creates a subsidy of large food 'packets' which may favour larger non-territorial birds.
2.5 Summary of appendix 1

Cousins, S.H., Bergmann's rule as applied to an avifauna: its relevance to trophic structure. Unpublished.

In 1849 Bergmann published the evidence for his theory that larger homoiotherms would be found in cold climates relative to the size of homoiotherms in warm climates. The rule is perhaps the only well-known allometric phenomenon in ecology. It is therefore appropriate to apply the trophic continuum model to the analysis of this rule if, as is claimed, animal size is an important aspect of ecosystem energetics.

One immediate and interesting problem arises when the trophic continuum is applied to the analysis of Bergmann's rule. When one passes from the tropics to the arctic the solar input available for photosynthesis declines and ambient temperatures fall. Thus the food requirements of homoiotherms for thermogenesis are raised as the total energy entering the trophic pathways falls. If, additionally, as Bergmann's rule requires, homoiotherms are larger in colder climates then this has considerable implication for the shape of the trophic pyramid, the energy flows between size classes in an ecosystem and possibly community stability.

However we must first establish that Bergmann's rule applies to homoiotherms as a whole. It is clear from James' (1970) translation of Bergmann's original work that Bergmann expected the rule to hold between species in a genus. By summing this behaviour over all land bird genera we would expect the rule to apply to an avifauna. The recent practice of using the rule to only examine intra-specific variation with latitude has occasioned James to redefine it as the Neo-Bergmannian rule when
used in that way.

The paper first establishes that species size is positively correlated with latitude for the British land-avifauna. Migrants do not follow this trend however. This fact is used to introduce the concept that body size is the resultant of energy supply as food and the energy costs of existence including body heat maintenance, \( \text{(Searcy (1980))} \). However Searcy overlooks one important factor. Since very little is known of food availability at different latitudes then even if the birds heat demand can be estimated at those latitudes the outcome of the balance of energy supply and demand is not presently calculable. Another implication of this balance is that the abundance of individuals, ie of feeders, is of interest as well as of food abundance.

Data from 80 Common Birds Census plots which recorded the abundance of individuals showed the median individual by weight of the census plots correlated only weakly with latitude. However the median individual weight could not be shown to differ from the median species weight. This allowed a broader interpretation of the species size map, figure 1, indicating that the distribution of size of mean individual would follow that of the mean species size. If the relationship between median species and median individual is confirmed for other data sets then an important empirical connection between energy and diversity models would have been indentified. (See also 5.2.1)

I am able to conclude that Bergmann's rule holds for resident land bird species but not for migrants. Body size in migrants would fit Searcy's broader energy supply and demand model. However the migrants refute his prediction that consideration of both the supply and demand for energy would favour larger homiotherms at higher latitudes thereby supporting Bergmann's rule.
2.6 Summary of appendix 2


This appendix takes the trophic continuum model developed in paper 2 from the lexical stage, where the system boundaries were defined, to a mathematical description of the exchanges across those boundaries. The purpose of this second stage is to show that the trophic continuum concept is based on quite well understood parts, such as growth curves, assimilation efficiencies, foraging strategies and a body weight dependent food demand. In the context of differentiating the trophic continuum model from the trophic level model it is particularly important to note that in the continuum feeding is controlled by a foraging strategy.

During the construction of this mathematical model certain developments to paper 2 were made. The emphasis on foraging strategy has already been stressed but terrestrial plant growth is also modelled. The main difference between this description of the plant and the description given in paper 2 is that energy captured by the leaves is partitioned to both higher assimilable fractions, such as, seeds and to lower assimilable fractions for example, wood.

Since size is a continuous variable, the model 'state' is defined at any time, \( t \), by graphs of the number of individuals against weight for each of four trophic categories of animal. Plants and detritus do not normally exhibit 'size' in the same way as animals and so are defined as biomasses at different assimilabilities. Initially it is assumed that assimilability is a function of the plant's chemistry, not that of the herbivores' digestive systems, and so each plant material has a single assimilation fraction.
Figure 1a shows the number distribution of herbivores of each weight, \( w \), in the system ranging from single cells to some upper size limit specified by the modeller. This number distribution, \( n_2(w, w_0, t) \) is a function of the herbivores' current weight, \( w \), and its asymptotic adult weight, \( w_0 \), to which it is growing, and time see figure 1b. The \( w_0 \) parameter is vital for realistic model behaviour as it prevents plankton growing into whales, or flies into eagles. The adult weight parameter can be used to identify particular 'species' and to define which are to be included in a run of the model.

Changes in the herbivore number distribution, \( n_2 \) figure 1a, are caused by losses to carnivores, losses to the detritus distribution due to starvation, and by increases due to growth of individuals and the recruitment of young via the reproduction term.

\[
\frac{dn_2}{dt} = \left( \frac{dn_1}{dt} \right)_{\text{carnivores}} + \left( \frac{dn_2}{dt} \right)_{\text{starvation}} + \left( \frac{dn_2}{dt} \right)_{\text{growth}} + \left( \frac{dn_2}{dt} \right)_{\text{reprod}}.
\]

A similar set of partial differential equations is used to change the carnivore \( n_3(w, w_0, t) \) and detritivore distributions, \( n_3(w, w_0, t) \) and \( n_4(w, w_0, t) \). Plant detritus and dung
are fed upon by detritivores \( n_3 \), while carcasses, \( n_D \), are fed on by detritivores \( n_A \). Carcasses are minor components of the model but their inclusion is necessary to complete the flow network. \( n_D(w,t) \) is a function of current carcass weight, \( w \), and not \( w_0 \) since growth has obviously ceased.

\[ \frac{\partial m_A}{\partial t} = \left( \frac{\partial m_A}{\partial t} \right) \text{herbivory} + \left( \frac{\partial m_A}{\partial t} \right) \text{graze} + \left( \frac{\partial m_A}{\partial t} \right) \text{litter} \]

In open ocean systems the plant may be described as a number distribution \( n_A(w,w_0,t) \) of phytoplankton, figure 2a. On land the plant takes a different form. Figure 2b shows the distribution of biomass of different assimilable fractions, \( v \), of the plants in a terrestrial ecosystem. The three part division into photosynthetic (leaves) and non-photosynthetic (wood and seeds); into annual (leaves and seeds) and perennial (wood) materials defines the components of the plant growth and litter sub-model. Changes in the plant biomass distribution \( m_A(v,t) \) of figure 2b are given below,
The overall model structure is shown in figure 3. For terrestrial systems the five number distributions and the two biomass distributions describe the state of the model at any instant. For open marine systems $m_A(v,t)$ is replaced by $n_a(w,w_0,t)$.

The central feature of the interactions between the distributions is an equation for carnivory incorporating an optimal foraging strategy. This is generalised to cover herbivory and detritivory. The equation for carnivory is given in discrete form as equation 20 and in continuous form as equation 24 in Appendix 1.

At first sight the model may look unwieldy and inherently untestable. However as I hope I have shown the structure of the model is regular and quite simple. Moreover the behaviours of
the parts from which it is made are quite well understood and may constitute a minimum system characterisation. The model offers the opportunity to examine the behaviour of the whole when these parts are coupled together. Knowledge of such behaviour will in turn allow the replacement of the trophic continuum concept by some simpler theory or the identification of key variables in the continuum where data collection and further research should be concentrated.
2.7 Summary of appendix 3

Cousins, S.H. and Smith, S. (1982) Biogeographical variation in seed size of a flora. Poster presentation at the British ecological society seed ecology meeting held at the Open university.

Data from the *Atlas of the British Flora* (Perring and Walters, 1962) are used to construct a map of the UK distribution of 81 species of forb found in the Sheffield region. A second map indicates that large seeded forbs have survived at higher latitudes and altitudes.
3.0 THE RELATIONSHIP BETWEEN THE 4 PAPERS

In this section I discuss the relationship between the four papers and the appendices. Some general linkages between diversity and energy models will be found in section 5.

The first paper is a methodological one which investigates the question what diversity is and how it should be measured. The number of species in a collection is central to concepts of species diversity. Thus the paper is based around the species area, or species number curve (Gould 1980), viz, as the number of individuals collected or the size of area sampled is increased then the number of species collected is also increased. Although these curves can be distinguished in a truly sample size independant fashion, by their exponents, they can also be identified by the number of species found per unit area. This latter measure contains more information and is some parameter of the variety of the pathways through which the energy flows occur in that area.

The second paper is again predominately methodological. An attempt is made to answer the questions; what are energy flows in the context of ecosystems and how should such flows be measured? The approach taken is to recognise the different availabilities of energy sources in the ecosystem and to initiate a set of resource descriptions to describe these availabilities. Animal size appeared an important parameter affecting both the size of food eaten and the size of species for which the animal would in turn be food. In addition to defining availability and hence the direction of flows in the system body size also defined the energy demand of the organism and can therefore indicate the magnitude of the energy flows.

Several relationships with species diversity could also be found. First, May (1978) had shown that there are many small and
progressively fewer larger species in a taxon. This parallels the decline in number of individuals with increasing size found in Elton's pyramid. Second, since the availability of food items is affected by the environment in which they are placed then the heterogeneity of the environment becomes a parameter of the energy flow model. Further, as species diversity is thought to be strongly affected by the heterogeneity of the environment here, a second relationship between energy and diversity models could be identified.

Paper 3 combines the methodologies developed in papers 1 and 2. The species density of different size classes of bird is mapped over Britain and Ireland. Developing this type of compatible methodology for diversity and energy flow measurement is one of the primary aims of the thesis.

Paper 3 further develops certain aspects of the trophic continuum, namely the concept of energy availability, the measurement of energy at different availabilities and the explicit inclusion in the continuum model of changes in energy availability which are not caused by ingestion. The paper combines the species density measure of species diversity selected in paper 1 with the animal size classification of the trophic continuum energetics model of paper 2. The combined measure is applied to the breeding bird atlas for the United Kingdom to create maps of species density of size classes. The predominance of large species in the North and small species in the South of the United Kingdom lays the basis for considering Bergmann's rule in appendix 1 and also indicates where diversity is distributed in the trophic pyramid.

Paper 4 tackles the central questions posed by the trophic continuum model developed in paper 2. How does heterogeneity affect energy flows between size classes and how does it affect the species diversity in the system? This particular paper showed
that a gradient in patch size was correlated with a decline in mean species size and lower species diversity. Bird species behaved as predicted while snail species did not.

In the context of the thesis the purpose of appendix 1 is to examine the abundance of individuals in different size classes rather than the abundance of species of different sizes. For this I used the CBC data of paper 1 which showed only a weak correlation of individual size with latitude in the UK. However the data did allow the comparison of the medians of the distribution of individuals of different sizes and of species of different sizes. These could not be shown to differ. This is of interest as an empirical link between diversity and energy models. It is also of practical importance in this case as the map of species size in Britain could be interpreted as a map of mean size of total population of breeding birds in Britain.

Appendix 1 is more detailed than paper 3 as it deals with land feeding species only and it distinguishes migrants from residents. Both the abundance of species and abundance of individuals of different sizes is studied in order to test Bergmann's Rule. The trophic continuum model developed in paper 2 is shown to be particularly relevant to this phenomenon. If as it appears larger homiotherms are selected in colder climates, that is, in ecosystems with lower energy inputs from the sun, then the operation of Bergmann's rule is likely to considerably effect the structure of the food web.

Appendix 2 further develops the trophic continuum model in a system. The objective of this joint manuscript with Howard Parkin is to generate equations as a basis for computer simulation of the continuum.

The paper develops the trophic continuum in several ways. It adopts an approach in which foraging strategy is specifically incorporated into the model. It develops the plant model into an
operational form in which green tissue, reproductive tissue and support tissues are distinguished. Finally the expression of the trophic continuum in a mathematical and therefore computable form makes the theory useful in a practical way for the first time. Potential applications are as a management tool for multispecies fisheries, such as in the North Sea, the Whale-krill-plankton fishing problem and modelling toxin effects on multispecies ecosystems. The latter could include radioactive toxins.

The role Appendix 3 in this thesis is to investigate at least one aspect of the plant component in the trophic continuum. The distribution of seed size will be significant to graznivores. Thus this example indicates that plant materials are differently available over space.

3.1 The themes running through the four papers

i) There is a deliberate attempt to examine species density phenomena at different scales. These range from 625 m$^2$ to 40 ha in paper 1, and 100 km$^2$ in paper 4 to 2500 km$^2$ in paper 3. Each of these scales of observation has revealed phenomena of interest which would not necessarily have been observable at different scales. This is particularly important given Pielou's (1973) insistence on the asymptotic measurement of $H'$ as the principle measure of diversity. It can now be seen that this technique limits the investigator to a single scale of observation.

ii) The species abundance or species area curve offers a perfectly smooth link between species diversity measured on a local scale up to any larger scale. Linking microscopic to macroscopic (Orians 1980) is also possible in energy modelling. The trophic continuum model since it is based on the search for
resources by animals in an environment offers an ecosystem scale energetics model which is based on the micro-ecological principles of foraging strategies. Thus there is no need for a separate phenomenology to be invoked to distinguish between the energetics of single species and large collections of species.

iii) A final theme has been to reappraise the Lindeman model and bring the trophic continuum into good currency. However during my research for the thesis, research by other workers on the effects of body size has established a field of interest in allometrics per se. This may have deflected attention from the plant and detritus parts of the trophic continuum model. It is these parts, together with animal size element, which establishes the need to reappraise the Lindeman model.
4.0 REVIEW

It is useful to begin this review section with an analysis of the ways in which Lindeman's work has been subject, I believe, to some misinterpretation. Next I examine the relationship between trophic levels and size classes in order to make the distinctions between models based on the two classifications quite clear. Then, ecological phenomena which appear not to fit the trophic continuum model are discussed. The section is concluded with a review of recent publications relevant to the thesis and not mentioned elsewhere.

4.1 In defense of Lindeman

It is quite common for papers on trophic structure to begin with a homage to Lindeman (1942). Ulanowicz and Kemp (1979) have already been quoted in the Summary of paper 2; Kercher and Shugart (1975) begin their paper with the statement,

"The trophic dynamic concept (Lindeman 1942) has become a dominant construct in ecological theory (Odum 1968)"

Perhaps the importance ascribed to Lindeman's 1942 paper can be judged by the fact that the history and correspondence surrounding its initial rejection and subsequent acceptance by Ecology is the subject of a substantial article in Science (Cook 1977). Cook notes that after its acceptance Lindeman's paper

"became the foundation for much future work concerning the dynamic flow of energy in plant and animal communities" (my italics).

Lindeman died at the early age of 27 and his celebrated paper was published posthumously. There was therefore no opportunity for
him to develop or modify his trophic-dynamic concept. However it is quite clear from his paper that the trophic level concept is extensively attributed to Hutchinson (unpublished). Lindeman's original contribution lay in applying Hutchinson's trophic level idea to the dynamics of species replacement in a community, that is to succession. Lindeman (1942), begins,

"Recent progress in the study of aquatic food-cycle relationships invites a reappraisal of certain ecological tenets. Quantitative productivity data provide a basis for enunciating certain trophic principles, which, when applied to a series of successional stages, shed new light on the dynamics of ecological succession.

A chronological review of the major viewpoints guiding synecological thought indicates the following stages: (1) the static species distributional viewpoint; (2) the dynamic-species distributional viewpoint; and (3) the trophic-dynamic viewpoint."

This latter viewpoint included succession,

"The trophic-dynamic viewpoint as adopted in this paper, emphasises the relationship of trophic, or energy availing relationships within the community unit to the process of succession."

Thus Lindeman hypothesised that an increasing efficiency of energy transfer between trophic levels was the motive force driving succession. Not only did energy become more efficiently used at higher trophic levels, but the efficiency of each level would be higher at later stages in succession.
My defense of Lindeman is that he wrote a highly stimulating paper about the principles of succession in lakes using Hutchinson's concept of energy flow through trophic levels. Thus it is to Hutchinson that we should look for the refinement of the trophic level concept.

4.2 Trophic level and size class boundaries

The relationship between the trophic level and allometric classifications is shown in figure 4. By ranking herbivores in order of size (left to right) and applying the simple rule that predators are larger than their prey then trophic levels map onto size classes as shown. Parasites are discussed in section 4.3.
The three columns represent three different approaches to whole ecosystem energetics.

From column 1 it can be seen that a variety of species are found at each trophic level and the same species are also present at different trophic levels. Identifying the biomasses at and flows between these trophic levels was the major aim of the International Biological Programme.

Column 2 represents the study of a selected food chain as a model of the whole system. The validity of this approach requires that the whole system lacks generalist feeders. It also requires that there is no feedback between the selected chain and the rest of the system and that the other chains in the system are also independent.

Column 3 represents the allometric model. In this size classes can be varied at will. These form a trophic model by using weight specific appetites, size of predator to size of prey regressions and other allometric relationships.

The comparison of these models of ecosystem energy flow has been the subject of much of this thesis and I shall not reiterate them here. However in the context of the origin of these approaches it is interesting to which 'columns' Hutchinson adopted as a research framework.

In 1959 Hutchinson published a joint paper with MacArthur describing a theoretical model of size distributions among animals. This particular work on the Eltonian Pyramid does not mention the concept of the trophic level. While in his seminal paper on diversity, Hutchinson (1959) refers to the 'Eltonian' form of predator chain in which each feeding organism was larger than its prey. Hutchinson (1959) defined a term, metaphoieszis, by which organisms changed their trophic position in a continuous way as they grew. The example he gives is of fish growing from 1
to 150 cms in length. A further allometric aspect of trophic interactions is given by Hutchinson's observations of character displacement in the size of trophic apparatus in mammals and birds.

Hutchinson's trophic level notation used by Lindeman (1942) has now been published (Hutchinson, 1978). He expresses the view that the trophic level represents the common sense application of 2nd law of thermodynamics to Eltonian pyramid.

Inspite of inventing the trophic level formalism Hutchinson's research was orientated to the properties of animal size rather than trophic levels. As has been seen, many features of the trophic continuum were present in this earlier work. However in, paper 3, I draw the opposite conclusion to Hutchinson with regard to the application of the second law of thermodynamics to the Eltonian pyramid.

4.3 Data which do not fit the trophic continuum theory

Every theory starts out life fresh and with some promise and then with time accumulates a collection of provisos and refutations until eventually it becomes transformed, passed over, or rejected. The instances where body size is not a sufficient descriptor for interactions in the trophic continuum are now discussed.

4.3.1 Water relations, Patches and Reproduction

One of the most obvious shortcomings of the theory of the trophic continuum is that it assumes energy flows to be the sole cause of body size distributions in biological communities. Certainly water relations were not considered as a parameter that would affect the body size distributions of insects as has been shown
by Schoener and Janzen (1968). These authors discovered that larger insects were found in drier areas. Similarly James (1970), studying the intra-specific variation of birds in the USA, showed that larger birds were found in drier areas. From James' work, a combination of humidity and air temperature factors, as measured by wet-bulb temperatures, gave the most significant correlation with body size. Rosenzweig (1968a) suggests that evapotranspiration (AE) rates are better predictors of mammalian body size than latitude and temperature variables. Elsewhere Rosenzweig (1968b) indicates that AE rates can be used to predict plant productivity. It should also be noted that, in Britain, bird size is positively correlated with rainfall for resident species and negatively correlated for migrants. This was shown in appendix 1.

The above discussion suggests that the relationship between body size and water regime of an ecosystem is complex involving plant productivity as well as water losses from animal body surfaces. However important body size is in the trophic relations of the ecosystem body size also has a very great impact on the life history strategy of organisms. Large body size is correlated with greater longevity and lower reproductive output per unit time*. Life history phenomena do not represent a problem in the trophic continuum because the processes of growth and reproduction are specifically included in the model. Organisms change their position within the model as they grow or reproduce. Equations for these processes are given in appendix 2. But an evolutionary ecologist viewing the species size distribution of appendix 1 might interpret it as a distribution of reproduction rates rather than of avian energetics.

*As Fenchel (1974) points out this is not summarized by the concept of r and K reproduction strategies which he only finds meaningful after the effect of body size has been 'factored out' from comparative data between species.
Paper 4 showed the effect of human settlement density on the distribution of species size and with opposite results for bird and snail species.

Body size can therefore be seen as the resultant of many selection pressures. If trophic structure is genuinely a function of the size of feeder and size of food then any of these causes will have an effect on that structure. This was seen for example in the case of Bergmann's rule. Although this phenomenon is explicable in terms of body size the distribution of size runs counter to the axis of ecosystem productivity. Thus it appears that adherence of species to Bergmann's rule has a substantial impact on the trophic structure. Bergmann's rule itself represents an embellishment of the initial model of the trophic continuum.

4.3.2 Parasites, Herbivores and Herds

The most common objection raised with regard to the trophic continuum is that the largest animal in the world, the Blue whale, eats a small organism, krill. Another comment concerns parasitism, that is, small organisms eating larger ones. Put together there may appear to be little sense in constructing a trophic model based on animal size. May (1979) has made another criticism of the trophic continuum that in addition to parasites and predators there are parasitoids which are the same size as their prey. Further questions are raised by herbivores which can be of any size from bacteria to elephants (Orians, 1980).

Let us first deal with these problems in the broad sense and then in the particular. The trophic continuum is, like the Lindeman trophic level model, no more than a set of system boundaries. Thus there is no problem in having energy passing in both
directions across the boundaries, that is, from small to large and from large to small. All that is required is that there exist clear relationships to model the flows in either direction. What then are these relationships which determine the size of the ingestor organism relative to its prey or for herbivory the size of herbivore and the type of food resource?

i) Parasitism and predation

The strongest theoretical result to be produced from the trophic continuum is indicated by the difference in system properties when energy passes across the weight class boundaries of the trophic continuum in the direction large eats small as opposed to small eats large. The role of species diversity and environmental heterogeneity is important to this result.

The mechanisms of predation and parasitism are quite distinct. Predation requires some method of locating the prey and then relies on the superior power of the predator to 'handle' (Pyke et al 1977) the prey and ingest it. Parasites must also locate their prey. They cannot overpower their prey but instead must find some particular way of defeating the prey's defences. To do this it appears that parasites have become highly specialised, attacking only a single or closely related group of species. Ectoparasites are less host specific than endoparasites.

Energy can pass readily from small species to large by predation. For energy to pass in the opposite direction such specialisation is required on the part of the parasite that a tight coupling is created between the parasite and host species. This in turn leads to a set of system properties which are quite distinct from those of predation. The high intrinsic rate of reproduction of parasites as compared with their prey can lead to local extinction of prey. Models of parasitism are therefore critically sensitive to spatial heterogeneity where refugia of unaffected prey can survive. Thus we may say that the high
diversity of parasitic species and the importance of spatial heterogeneity characterise parasitism as a class of trophic interactions.

Species diversity seems to play almost the opposite role in the diet of predators making the spatial heterogeneity of the environment far less significant to the predator. The spatial heterogeneity of the environment is made trophically homogeneous by species diversity if species exist in each 'patch' which can form a sufficient part of predator's diet. This transforms a patchy environment into a relatively homogeneous one with respect to predation. This also indicates why the model in appendix 2 is, with one exception, homogeneous.

A consequence of this argument is that the phenomena of parasitism and predation are quite different and one does not provide a good model of the other. This is particularly important with reference to the trophic level model.

ii) Herds

There is no doubt that trophic relations are altered when either the predator or likely prey species aggregate together. In a model characterised by the size of predator and size of prey the size of an ant or a hyaena is known but what size do we consider a column of army ants or a pack of hyaenas? Some way would have to be found to quantify the increase in predatory power that the group behaviour gives them. A second herding problem comes in the form of the whale - krill interaction where the huge baleen whales feed upon shoals of the shrimp Euphausia superba. Again there is a difficulty in choosing the representation of the prey as the size of the shrimp or the size of the shoal.
iii) Herbivory

Given the importance of the direction of flow of energy through the trophic continuum to the diversity and heterogeneity relationship it is necessary to classify herbivory as parasitism, or predation or as neither. Ricklefs (1973) suggests that the majority of herbivores are parasites rather than predators, the exception being when the herbivore devours a whole plant, for example, a seed, or kills the plant as a result of feeding on it. The more normal form of herbivory is one where the host plant continues to live while the herbivore feeds on it. The diversity of herbivores associated with any plant host appears to be a function of the plants size and structure (Hutchinson 1959, Lawton and Price 1979) and of the distribution of the plant in time (Southwood 1961) and space (Southwood 1977b). Where the herbivore is host specific heterogeneity can be expected to be important due to the distribution of the host plant as has been shown by (Dodd 1959) for Opuntia/Cactoblastis distributions. High species diversity in herbivores can be seen as a function of host specificity induced by plant defense strategies.

The relationship between plant and herbivore body size is as yet unclear.

4.3.3 Taxonomic differences

Within the trophic continuum as currently described, an organism is only identified by its mass. However many organisms have equal weights but behave differently to each other in nature. For example there are ecosystems in which could be found of birds, bats, lizards, rodents, frogs and snails which have the weight 15g. The phyla from which these species come possess distinct allometric relationships for their energy requirements of existence which would require inclusion in the continuum model.
Phillipson (1981) has reviewed the relationships of bioenergetics to taxonomy (phylogeny). To quote Phillipson,

"Not subject to debate is the fact that all living organisms expend energy to survive and reproduce".

However the way in which energy affects survival is, I suggest, through the medium of the organism as an energy (or information) processing machine. The different taxa, in this case phyla, have distinct gross mechanical structures such as similar skeletons which give the organisms in the phylum a similar capacity for movement and hence for the capture and ingestion of food as distinct from other phyla with their different anatomies. At a sub-cellular level micro-anatomical features affect biochemical processes which in turn affect allometric energy relationships. Phillipson classifies animals into three groups, warm-blooded animals, multicellular cold-blooded and single celled cold-blooded animals on the basis of these different weight dependant metabolic rates.

4.3.4 Summary of section 4.2

The abundance of organisms of different sizes in a community is the resultant of many different selection pressures. Of these, water relations, ambient temperature, reproductive strategy and environmental heterogeneity are certainly important. However, these factors may affect different taxa in different ways and affect parasites differently to predators. The resulting distribution of body size will be further shaped by the feeding relationships between those functional and taxomic groups.
4.4 Recent literature

Most of the recent literature which is relevant to the thesis has already been discussed. However there are specific areas which require review.

Of the literature on diversity indices I shall refer to Alatalo (1981) and Routledge (1979) who have commented on Hill (1973) and to the work of Wolda (1981) and Howmillar and Scott (1977) who use information derived from species identity in their indices.

Alatalo shows that the evenness component of diversity, $J'$, is frequently used in spite of its dependence on species richness. Alatalo confirms the use of Hill's ratio $E_{1,0}$ as a measure of evenness independent of species richness. Routledge debates the relative merits of various of Hill's ratios and by so doing undermines the coherence introduced into the field by Hill.

Howmillar and Scott and Wolda discuss indices which compare species collections according to whether they share or lack the same species rather than whether they have similar species abundance curves irrespective of species identity. The latter approach is used in Hill's ratios or similar indices. Wolda is particularly concerned with sample size effects whereas Howmillar and Scott test their index as a discriminant of pollution in a marine bay. These approaches make far more use of the information contained in a species list than do the conventional diversity indices as is raised in the conclusion of paper 1.

On relating energy to diversity models I am aware only a single, though pertinent, publication (Brown, 1981). Brown reviews the two decades of research into diversity which have followed since Hutchinson's (1959) paper "Homage to Santa Rosalia".
Brown says of Hutchinson,

"his basic message is that to understand the diversity of life we should investigate how usable energy is acquired by and apportioned between species....During the last two decades most of the ideas in the 'Homage' have been explored by theoretical ecologists but the central importance of energetics has been largely ignored. The reason for this appears to have much to do with personalities..."

Brown goes on to describe the formation of the two schools of ecological thought, viz the 'ecosystem ecologists' concerned with energy flow following Lindeman's tradition and the 'evolutionary ecologists' who are concerned with the interactions between species as explanations for species diversity. These starting points are common to this thesis.

Although presenting no solution to the problem of unification of these schools Brown does point to the promise of large ecosystem optimal foraging models and to the success of the MacArthur-Wilson (1967) model of island biogeography as potential areas for providing a basis of unification. The optimal foraging approach is adopted in Appendix 2.

The recent literature on organism size is more extensive. At an abstract level allometric properties are seen (Platt and Silvert, 1982) as a consequence of dimensionality. This is typified by the changing ratio of the surface to the volume of spheres of different sizes. The power of larger creatures to catch their prey can be deduced from dimensionality, Platt and Denman argue, as can the similarity of structure of many animals (Gunther and Morgado 1982). Economos (1981) has postulated a limit to animal size from gravitational effects. From an empirical standpoint Humphreys (1981) has found a useful relationship between a new index based on live-weight and biomass to production and
assimilation in animal populations.

A second group of papers (Smith, 1980, Sweet, 1980 and Harvey 1982) have concentrated on the accuracy of logarithmic transformations which are regularly used in allometric comparisons. Sweet suggests that attention should be given to outliers in allometric data sets. White (1981) has applied allometric methods to plant population dynamics and (Kira, 1976) has applied allometry to the growth of certain tree species.

A recent synthetic work on the importance of body size at the species level has been edited by Townsend and Calow (1981). The book is concerned with 'resource aquisition and allocation' and how this changes with the 'age and size' of animals. This single species approach is complementary to the multi-species one developed in appendix 2.

A third group of papers are relevant to the theories of the structure of large ecosystems. These include Yodzis (1981) random assembly of organisms in a community. He argues that the set of species assembled must satisfy rules, such as, there being an adequate food supply. In essence this is an allometric model. That it is stochastic may be a reflection of the scale at which the system is observed. Systems viewed at a sufficiently local level appear stochastic whilst in a larger frame they are ordered or deterministic. However Yodzis concept of the random assembly is an interesting one.

A model giving an overview of ecosystem processes comes from Ulanowicz (1980) who follows Lindemans tradition of examining succession as a function of energy flow characteristics. An original alternative in which the system is viewed from the standpoint of component species is provided by MacMahon et al (1981). The theoretical properties of species at different trophic levels has been investigated by Kirkwood and Lawton (1981) and of trophic efficiency by Colinvaux and Barnett (1979).
5.0 CONCLUSION

The discussion of the theoretical and practical issues raised by energy and diversity measurement has uncovered some of the current difficulties in those fields and gone some way to the resolution of certain of those difficulties. In conclusion I shall indicate what these contributions have been, including how as a result of this work how the species diversity of an ecosystem may be related to the energy flows though that ecosystem. Finally I discuss where future research may be useful.

5.1 Contributions

Formally I am required to indicate where academic contributions have been made in the published papers of the Phd submission. These I suggest can be listed as,

1) putting the case for measuring species diversity as species density where environmental monitoring and comparison with energy studies are required

2) describing a new model of energy flows in ecosystems, the trophic continuum, the model not being scaled by the green plant, but by a resource classification of plant products, detritus and animals of different sizes

3) the indication that Bergmann's rule is a phenomenon of community ecology which has potential importance for trophic interactions

4) the demonstration of new phenomena in urban ecology and of the usefulness of urban environments for research on spatial effects in community ecology
5) the demonstration of links between diversity and energy models including the difference in the importance of diversity and spatial heterogeneity according to the direction of energy flow through the trophic continuum, that is, between parasitism and predation.

5.2 Energy and diversity

In this final discussion I want to try and synthesise as much as possible of the empirical and theoretical relationships between energy flows in ecosystems and their species diversity. As we have seen the ability to point to these relationships has come from new classifications*. There have been many indications here that species size is important to both diversity and energy flow classifications.

5.2.1 Relations between S and N

The flow of energy through animals in an ecosystem is some function of the number of animals, \( N \) and their size. The species diversity of the collection of those animals is in some way represented by the total number of species in the collection, \( S \). Thus the relationship between energy and diversity models should be explicable in the relationship between \( S \) and \( N \). Williams' (1964) index \( \alpha \), \( \alpha = f(S,N) \) is therefore of considerable interest.

* It is tempting to agree with Pantin (1965) that science is about classification rather than measurement.
If we partition the collection of individuals into large and small individuals and species then we may calculate two values of $\alpha$,

$$\alpha_{\text{small}} = f(S_{\text{small}}, N_{\text{small}})$$

and,

$$\alpha_{\text{large}} = f(S_{\text{large}}, N_{\text{large}})$$

It was shown in appendix 1 that the 80 CBC data sets did not have different medians for species size and individual size. Thus the median individual divides the species and individual weight distributions into two halves each containing the same number of individuals and species respectively. It follows that,

$$\alpha_{\text{small}} = \alpha_{\text{large}}$$

Although it would be quite wrong to take this single result too far it does suggest that the number of species could be simply a function of the number of individuals irrespective of the individuals size. Thus the number of very small species is explicable in the number of very small individuals. This was first suggested by Hutchinson (1959). He used the same argument to explain the low species diversity in arctic regions which he suggested was due to low populations of individuals.

5.2.2 Energetics, Water relations and taxonomic groups

A perfect understanding of the relations between diversity and energy flow would allow the prediction of one from the other. The mathematical model of the flows of energy in the ecosystem, Appendix 2, may go some way towards this by predicting the number of herbivores and predators of different sizes. But since parasitism and, in particular, plant diversity mechanisms are not included in the model this source of diversity is not accessible to it.
What has become apparent from section 4 is the importance of the phylum as an additional variable in allometric phenomena of large ecosystems. The importance of water relations has also been identified. Holdridge (1947) has classified plant biomes on the basis of ambient temperature and water relations. The same scheme could be used to characterise species size and size abundance distributions of various phyla.

There are very many opportunities for further research in this field. Species distribution atlases have been produced for many phyla for Britain, Europe and other parts of the world. These atlases should indicate the effect of climatic variables on the species size distributions of these major taxa including representatives of the seven groups identified by Humphries (1981) as having distinct production efficiencies. Also to be investigated are the distribution of plant and animal parasites and the distribution of whole plants, plant parts (see Appendix 3) and plant defense compounds. In this way the structure of different ecosystems could be determined.

5.2.3 Predators, parasites and patchiness

In section 4.3.2, I drew upon the well established observation that parasites tend to be host specific and therefore to be very sensitive to any patchy distribution of their hosts. By contrast predators are less sensitive to the distribution of single prey species. Predators will feed on any species available if it is not actively distasteful and provided it falls in their optimal diet as defined by a foraging strategy Pyke et al (1977).

Therefore one important item of further research would be to examine the stability of a system where parasites including plant parasites and hyper-parasites are sensitive to spatial
heterogeneity while predator species are assumed to have broad diets and are not sensitive to spatial heterogeneity.

5.2.4 Species diversity, energy flow and patchiness

The decline of species density towards central London, paper 4, could be accounted for, at least in part, by the species area curve since the area of green space declines towards the centre. It is interesting that the mean size of bird also declines towards the centre. Earlier it was postulated that if the number of patch types at a given scale increased and if the patches were non-overlapping then patch size must fall. The distribution of species size over an environment with declining patch size is thus an analogue of increased patchiness although in the latter case species diversity should rise. Thus increased patchiness should, from the empirical and theoretical model provided by the urban distribution, decrease the size of individuals found in that environment. Small size is characterised by a lower position in the Eltonian pyramid.

5.2.5 Information theory and allometry

Future research at a more fundamental level could be directed towards trying to understand the energy flow through the trophic pyramid as an information processing problem. This has been an unspoken theme though the submission. The search for food in an environment is an information processing problem for parasite and predators alike. The parasites relationship to the host and the host's to the parasite are informational problems. Furthermore the environment varies in time as well as space thus the organism can be treated as an information processing unit in a noisy environment in almost a classic manner (Ashby 1952). As many allometric phenomena seem important to trophic dynamics this could indicate a fundamental relationship between an organism's size and its information processing capacity. Species size
distributions should on this basis be different in environments which have different degrees of patchiness, disturbance or 'noise'.

5.4 Old Monographs, new Atlases

The discovery of the importance of body size phenomena in trophic ecology is also the rediscovery of the importance of taxonomic ecology. Allometric relationships appear to hold most precisely within taxonomic groups for essentially mechanical or structural reasons (Thompson 1916). The relationship between the number of individuals and the number of species, which is the essential relationship between energy and diversity models, is therefore appropriately examined within the taxon.

The theoretical perspectives raised in this submission have now been brought to the point where further empirical input is required. It is to my own surprise that this unification of theory points to the future adoption of the methods first used by the sixteenth century monographers (section 1.3) and away from the trophic level approach and Shannon-Wiener $H'$ statistics which characterise modern community ecology.

The early monographers who described the number of species of a phylum in an area, usually a country or county, were measuring the species density of a taxon. The same approach, albeit on a grid square basis, is now needed is to examine the species density and species size distribution of functionally distinct taxonomic groups over large geographical areas. The range of available and soon to be available species distribution atlases for plants, parasites, homiotherms and heterotherms of many taxa make this data readily accessible.
these atlas studies certainly provide one route by which we may understand the structure of large ecosystems. But while a theory of large ecosystems is desirable in itself and has significant applications, such as multi-species fisheries and pollution problems, the large system is also something in which the small or local system is embedded. Thus, it would be wrong to end with an emphasis only on the large scale. Consideration of the direction of energy flow through the trophic continuum points to further research into the stability of quite simple predator, parasite, host systems with these trophic groups being differently sensitive to spatial heterogeneity. These large and small scale applications are consistent with my theme throughout the submission which has been to link diversity and energy models at a variety of spatial scales.
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7.0 APPENDICES

7.1 Cousins (1982)
Bergmann's rule as applied to an avifauna: its relevance to trophic structure.

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The definition, empirical validity and theoretical basis of Bergmann's rule have all been recently challenged \(^1\-^4\). Although based on general dimensional principles that heat is generated from the body mass and heat transfers occur at the body surface the rule has been used almost exclusively to study the intra-specific variation of body size \(^1\). Here the hypothesis that the mean or median species of a land avifauna is larger at higher latitudes is tested using species distribution data for Britain\(^5\). The distribution of different sized homiotherms at different latitudes has importance for the structure of food webs. Resident species show significant correlation with latitude (\(+ve\)), altitude (\(+ve\)) and mean July C (\(-ve\)). However summer migrants refuted the hypothesis by having correlations of opposite sign. Migrants are mainly insectivorous. That they differ from residents is consistent with Searcy's \(^4\) model of optimal body size as a function of food supply and weight dependant energy demand. Bergmann's rule is further tested using the BTO Common Birds Census which indicates that the median individual in a community is larger at higher latitudes.
Here land birds are defined as being directly dependent on the land for food thus excluding marine, estuarine and fresh water feeding species. From figure 1 average species weight is greater at higher latitudes and to the west of Britain with its higher altitudes. Species means in southern England are almost exclusively in the range 115g–153g compared to the range 191g–271g in Scotland. Table 1 shows that both the median and mean species size are strongly correlated with latitude but even more so with altitude and (negatively) correlated with mean July temperatures. Mean January temperatures correlated least well with the variables chosen. However data are from a breeding season survey and so do not relate directly to winter distributions. This is both because of the presence of summer migrants and the movement of birds during the winter. When migrants, as defined by O'Connor, are distinguished from resident species radical differences between the two groups become apparent. The signs on the correlation coefficients are opposite for each variable tested. While residents have a distribution consistent with Bergmann's rule, migrants do not; larger migrants are found in the warmer southern latitudes.

The mean size of the 37 migrant species is also much lower, at 85.2 g than that for the 121 residents at 323.0 g. Taken in isolation this would appear to support Bergmann's rule were it not for the spatial distribution of migrants. Small birds will remain below the limit of thermo-neutrality for considerable periods of time during the summer, thus small species should preferentially adhere to the rule if it is valid. However the arrival of migrants in Britain cannot be divorced from the seasonal availability of insect biomass. In Searcy's model optimal body size is seen as maximising the difference between energy gained from foraging and the energy cost of maintenance, including body surface losses. Unlike Searcy I am unable to predict that the outcome of this balance at different latitudes will be consistent with Bergmann's rule since, as well as change in the ambient temperature, the abundance of food of a
suitable size or type will vary with latitude. Indeed, a logarithmic decay in the biomass of larger organism sizes has been found both on land and in the oceans. Thus more food may be available to the smaller of two species (or individuals) even though the food demand per unit mass is higher for the smaller bird. Similarly from comparison between latitudes there is also evidence that smaller insects are found at higher latitudes.

Two factors emerge here. First, because of the range of food 'sizes' there is no single optimal size for the homiotherm at different latitudes, but an optimal distribution of species sizes dependent on the ambient temperature and the available food resources. This meets Scholander's argument that Bergmann's rule did not hold because the range of species sizes is broadly the same in the arctic and the tropics. Instead we should expect the mean or median species size to be greater in the arctic if the rule is valid. Second, because Searcy's theory of Bergmann's rule now includes the availability of food resources then the number of individuals competing for, or using, those resources is a factor in determining the individuals survival. Therefore Bergmann's rule can be usefully examined by finding whether the mean or median individual of a set of homiothermic species is greater at higher latitudes. This hypothesis is now tested.

Data for land birds are taken from the Common Birds Census for farmland, 1973. The CBC records the abundance of all species breeding on a census plot by using, where appropriate, a technique for mapping breeding territories. The 85 plots ranged in size from 11 ha to 98 ha with a mean of 40 ha but were mainly located in Southern England. Species weight data exclude any intraspecific variation. The median individual weight of the total of land birds on the farm is correlated with latitude (r=0.21, p=.03). However Weins cautions against using numerous local surveys to infer biogeographical trends and a more general approach is taken. For a
community, if the median individual and median species of the bird weight distribution are the same then the median individual partitions the bird weight distribution into two halves each containing the same number of species. Of the 85 distributions 5 had equal species and individual medians, 39 had species medians below the individual median and 41 above. A CHI\(^2\) test \((v = 84, \text{CHI}^2 = 77.8)\) indicated no evidence of any difference between the expected equal distribution of species and that observed. Using Spearman's rank correlation coefficient the median individual was positively correlated with median species weight \((r=0.70, p>0.001)\).

If the median species weight and individual weight in a community are closely correlated this is a result which empirically relates diversity and energetics phenomena\(^1\). Here it allows us to say that if the median species size is correlated with latitude as has been established, then the median individual also increases in mass with latitude.

Here are undoubtedly many causes of body size selection\(^1,17\text{--}19\). Additionally the structure of different habitats influences foraging strategies\(^20\) and so may affect species (size) selection. However a general problem arises from the distribution of larger endotherms at higher latitudes. The solar energy input to the ecosystem ultimately determines both the ambient temperature and the level of primary productivity. At higher latitudes the energy demand per bird rises, due to larger body size and the costs of thermogenesis, while the gross supply of energy declines. The importance of body size in mechanisms of predation\(^21\) and the significance of latitudinal changes in both the demand for energy and the environments capacity to supply it place Bergmann's rule at a focal point in comparative food web studies.
References

06 Hickling, R.A.O. ed The British Trust for Ornithology Jubilee Volume (Poyser, Berkhampstead, in the press).
Figure 1

Title

Mean species weight of the British breeding land-avifauna.

labels

115.8 g - 153.0 g

153.0 g - 191.3 g

191.3 g - 229.1 g

229.1 g - 266.9 g

Caption

The presence or absence of the 158 breeding species of land bird species breeding in each of the 90 contiguous land areas of 2500 km² covering Britain was determined from Sharrock. Data are for 1968 - 1973; each area may contain more than 25 10 x 10 km squares if the latter extend beyond the coastline. The mean species weight of the set of species in each area was calculated using a single weight for each species: no intra-specific variation was examined. Data were interpolated and displayed using SYMAP. The contour level is given by number (1-4) at the centre of each area.
Table 1

Title

Correlations of species size with environmental parameters.

Caption

The number of species $S$, found in each of the 90 areas of figure 1, the mean and median weight of the set of species in each area were correlated, using Spearman's rank coefficient, with environmental data means for each square calculated from the overlay maps of Sharrock.
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7.2 Parkin and Cousins (1981)
TOWARDS A GLOBAL MODEL OF LARGE ECOSYSTEMS: EQUATIONS FOR A TROPHIC CONTINUUM

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Abstract

Equations are presented for a previously described non-mathematical model of whole ecosystem trophic behaviour based on organism size. The model is specified at any time by number distributions of carnivores, herbivores and detritivores of different sizes and by biomass distributions of autotroph and detritus materials of different resource states. Dynamic events are determined by a weight dependent appetite function, an optimal foraging strategy, growth, reproduction and detritus decay terms. Global modelling of large ecosystems is discussed. It is held to be useful as a framework for detailed studies and to have practical value for ocean fishery management and whole ecosystem toxin impact assessment.
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10. Recapitulation
11. Discussion
1. Introduction

Modelling whole ecosystem trophic behaviour using the trophic level concept (Lindeman, 1942) has been criticised by various authors (Rigler 1975, Platt and Denman 1977, Cousins 1980) and its demise as a central tenet of ecological energetics has been anticipated by Yodzis (1978) and Orians (1980). Here we attempt a mathematical description of the trophic continuum of Cousins (1980) as applied to a spatially homogenous ecosystem. The trophic continuum is a model of biomass concentration which occurs by a number of mechanisms including feeding. In the model trophic transfers are not equivalent as a change of one trophic level but are dependent on the degree of biomass concentration achieved, that is, dependent upon the size of feeder and size of food. Other mechanisms which create changes in biomass concentration are animal growth, translocation and chemical transformation in the plant and disintegration in detritus. The plant and detritus are treated as distributions of biomasses at different concentrations, referred to as resource states. Herbivory and detritivory are simply food flows to herbivores and detritivores of various sizes from the live plant and from detritus of various resource states.

The model is defined by the number distribution of heterotrophs of different sizes and by a biomass distribution of living plant materials of various resource states and a distribution of detritus of various resource states. Asymptotic animal growth curves, a simple plant growth model and a logarithmic detritus decay curve determine the non-feeding biomass flows across the model's weight class and resource state boundaries. Food flows to heterotrophs are determined by an appetite function dependent on the animals' weight (Fenchel 1974) and by an optimal foraging strategy (Krebs 1978).

Modelling whole ecosystem behaviour using animal size as the central parameter although initiated by Elton (1927) has only recently been revived in a mathematical form by Platt and Denman (1977, 1978) and Silvert and Platt (1978, In Press). Ellis et al (1976) have also
proposed an ecosystem trophic model driven by an organism weight dependent appetite function and which incorporates a feeding strategy sensitive to food abundance. In this paper we pass from the lexical phase (Cousins 1980) to a mathematical description of the interactions of the trophic continuum. The next stage, not considered here, is the investigation of the model's behaviour on a computer. We justify omitting this step at present on three grounds, to enable discussion and criticism of the model structure, to allow the collection of a set of allometric data from a single ecosystem with which to test the model, and last but not least, brevity.

2. Modelling strategy

All flows across system boundaries in the model are required to satisfy the principle of conservation of energy. However, the model's chief system properties are determined by the availability of energy as well as its quantity. The availability of a biomass of organic tissue to a heterotroph species or weight class is affected by the food's fragmentation and dispersal. For instance the availability of prey to a given carnivore depends crucially upon prey size and prey density. There is a correspondence between ecological availability and thermodynamic availability. Traditionally ecologists have limited the discussion of entropy change to photosynthesis and respiration (Morowitz, 1968). Small but calculable changes in entropy are associated with food dispersal and concentration (Cousins, 1978).

It may be possible in future to derive ecosystem structure and dynamics from principles analogous to those of thermodynamics for example to determine an optimal foraging strategy and to allocate assimilated food so gained to maintenance, locomotion, growth and reproduction. In the absence of such a grand simplifying theory we content ourselves with piecing together plausible, isolatable model elements. Where choice is necessary elements have been chosen here for their global properties rather than the level
of local resolution they achieve. An instance of this is where we have isolated the internal metabolic processes of assimilation, growth and reproduction from feeding interactions in the ecosystem. Thus an appetite function and constant assimilation fraction tied to a rigid growth curve does not allow second order system behaviours where growth is accelerated or retarded due to prey availability. However the global relationships between food supply and population number is retained by the possibility of starvation if the food requirements of growth are not met. Additionally the identification of all individuals with particular asymptotic growth curves prevents individual members of any weight class growing indiscriminately large. The latter is both a plausible and essential global feature.

In modelling a large ecosystem our dilemma has always been marrying the local and global properties. Our preference for the global automatically leads to some over-specification in the absence of a more profound theoretical synthesis. Whilst we have made every effort to minimise over-specification a residual amount seems to us inevitable and requires the introduction of an extra and thus unnatural degree of freedom. In our case this is achieved by instantaneously neglecting certain metabolic rate constraints within the organism. When energy stores are depleted, so for example, growth continues at a healthy rate until death by starvation intervenes.

3. Structure of the mathematical model

The model is completely specified at any instant in time, t, by a set of seven distribution functions. The total rate of change in time of each distribution is expressed as the sum of the partial rates of change, one for each of the model elements. Since we are considering a homogenous ecosystem the seven distributions are totals for the whole ecosystem area or volume under study. \( m_A(v,t) \) is the distribution of the plant biomass over resource value variable, v. The resource value, v, of plant tissue is defined in terms of its assimilable fraction relative to the assimilable fraction of the same biomass of animal flesh. \( v_m^A \) is thus the flesh equivalent biomass distribution of the plant. That is, the biomass assimilated when a carnivore digests \( v_m^A dv gm \) of animal flesh is the same as that assimilated when a herbivore digests \( v_A(m) dv gm \) of plant tissue at resource value v.
The equation for the plant (autotroph) is

\[ \frac{\partial m_A}{\partial t} = \left( \frac{\partial m_A}{\partial t} \right) \text{herbivory} + \left( \frac{\partial m_A}{\partial t} \right) \text{growth} + \left( \frac{\partial m_A}{\partial t} \right) \text{litter} \quad ... (1) \]

where the herbivory term represents the rate of change of \( m_A(v) \) due to feeding herbivores; growth is similarly the rate of change of \( m_A(v) \) due to photosynthesis, translocation and transformation of its products; losses to litter include leaf-fall and natural death of all or any plant part.

\( n_1(w,w_0,t) \) is the population distribution of carnivores over their current weight, \( w \), and their asymptotic adult weight, \( w_0 \).

The equation for carnivores is

\[ \frac{\partial n_1}{\partial t} = \left( \frac{\partial n_1}{\partial t} \right) \text{carnivory} + \left( \frac{\partial n_1}{\partial t} \right) \text{starvation} + \left( \frac{\partial n_1}{\partial t} \right) \text{growth} + \left( \frac{\partial n_1}{\partial t} \right) \text{reproduction} \quad ... (2) \]

where carnivory is the reduction \( n_1 \) due to ingestion by other carnivores; the starvation term generates losses in \( n_1 \) when food requirements are not met; growth is the change in \( n_1 \) due to the growth into and growth out of the infinitesimal weight class \( n_1 \text{dw} \); births are allocated to small weight classes in the model and are driven by the reproduction term.

Similarly \( n_2(w,w_0,t) \) is the population distribution of herbivores \( n_3(w,w_0,t) \) is that of detritivores of dead animals and \( n_4(w,w_0,t) \) is that of the detritivores of dead plant material and dung of all origins.

\[ \frac{\partial n_2}{\partial t} = \left( \frac{\partial n_2}{\partial t} \right) \text{carnivory} + \left( \frac{\partial n_2}{\partial t} \right) \text{starvation} + \left( \frac{\partial n_2}{\partial t} \right) \text{growth} + \left( \frac{\partial n_2}{\partial t} \right) \text{reproduction} \quad ... (3) \]

\[ \frac{\partial n_3}{\partial t} = \left( \frac{\partial n_3}{\partial t} \right) \text{carnivory} \quad ... (4) \]

\[ \frac{\partial n_4}{\partial t} = \left( \frac{\partial n_4}{\partial t} \right) \text{carnivory} \quad ... (5) \]

\[ \text{† The use of a slightly non-standard notation for the terms on the right of equations 1-7 is to improve the clarity of presentation through the text.} \]
Note that the carnivory term is retained in each case as this refers to the reduction in the number distribution caused by carnivores feeding.

\[ n_D(w,t) \] is the number distribution of carcasses or carcass fragments

\[
\frac{\partial n_D}{\partial t} = \left( \frac{\partial n_D}{\partial t} \right)_{\text{detrivory}} + \left( \frac{\partial n_D}{\partial t} \right)_{\text{carcass}} + \left( \frac{\partial n_D}{\partial t} \right)_{\text{fragmentation}} \quad \text{(6)}
\]

where detrivory is the change in the distribution due to feeding by detrivores; the carcass term is the increase in the distribution due to heterotroph starvation and natural death although the latter is not included in the current model; the fragmentation term models both putrifaction and fragmentation itself, with the carcass biomass conserved as a larger number of smaller particles. Exuviae are not considered.

\[ m_D(v,t) \] is the distribution of detritus biomass of resource state, v, defined exactly as for the live plant. Thus \( v m_D \) is the flesh equivalent biomass distribution of detritus.

The distribution of detritus biomass of plant and dung is given by

\[
\frac{\partial m_D}{\partial t} = \left( \frac{\partial m_D}{\partial t} \right)_{\text{detrivory}} + \left( \frac{\partial m_D}{\partial t} \right)_{\text{plant}} + \left( \frac{\partial m_D}{\partial t} \right)_{\text{dung}} + \left( \frac{\partial m_D}{\partial t} \right)_{\text{decay}} \quad \text{(7)}
\]

where the detrivory term is the loss due to feeding by detrivores; the plant detritus term raises the distribution due to addition of plant litter; 'dung' is the increase in \( m_D \) due to defaecation by animal populations; and decay is the movement of biomass to lower resource states caused by putrifaction.

In the proceeding sections these 7 basic equations will be discussed term by term. The carnivory equation, equation (2), is taken first as the modelling of predation is subsequently generalised for herbivory and detrivory.
4. Change in the number of carnivores

4.1 Carnivory

We propose to develop a generalised model of predation which will be applicable to herbivory, detritivory as well as carnivory. It is developed in three stages, the first takes account of travelling time only, the second includes handling time and the third includes optimal foraging. What we call travelling time (Krebs 1978) has been called foraging time (Silvert and Platt, 1978, In press). Our use of the term is defined as the fraction of time spent neither eating or resting where resting includes all non-feeding activities.

To clarify the continuous equations for predation it is simplest to first discuss carnivory for a discrete case with a finite number of prey classes.

4.1.1 Predation with travelling time only

The simplest assumption is that a single predator's encounter rate with prey is proportional to the number of prey present within the given system. This assumption gives the Lotka-Volterra result that the predation rate for the rth prey is \( P_r N_r \), where \( N_r \) is the number of individuals in the rth weight class and \( P_r \) the predation coefficient, a constant for the given system and is the predator - prey encounter rate per unit prey. Under Lotka-Volterra assumptions eating is instantaneous and thus encounter and predation rates are equal.

With \( L \) prey classes in the system the total encounter rate of a single predator with prey of any type is \( \sum_{r=1}^{L} P_r N_r \).

Unit travelling time is defined as the time between encounters which for 1 predator, 1 prey type is \( \frac{1}{P_1 N_1} \), and, \( \frac{1}{\sum_{r=1}^{L} P_r N_r} \) for 1 predator and 1 prey types.
4.1.2 Predator with travelling time and handling time only

In this section we derive an expression for the flesh equivalent feeding rate of a predator on a prey class.

Unit prey handling time for the rth prey is $H_r$. The fraction of all encounters when the rth prey are predated will be

$$\frac{P_{Ni}}{\sum_{i=1}^{\ell} P_{iNi}}$$

so mean unit prey handling time with $\ell$ prey types is,

$$\sum_{r=1}^{\ell} H_r \cdot \frac{P_{Ni}}{\sum_{i=1}^{\ell} P_{iNi}}$$

Then mean unit predation time, that is, mean unit travelling time plus mean unit handling time is given by

$$\frac{1}{\ell} \cdot \frac{\sum_{r=1}^{\ell} H_r P_{Ni}}{\sum_{r=1}^{\ell} \sum_{i=1}^{\ell} P_{Ni}} = \frac{1}{\ell} \left(1 + \sum_{r=1}^{\ell} H_r P_{Ni}\right)$$

thus the net predation rate is

$$\frac{\ell}{\sum_{r=1}^{\ell} H_r P_{Ni}}$$

and the predation rate on the kth prey is

$$\frac{\sum_{i=1}^{\ell} P_{iNi}}{\sum_{r=1}^{\ell} H_r P_{Ni}} \cdot \frac{P_{Ni}}{\sum_{i=1}^{\ell} P_{iNi}} = \frac{P_{kNi}}{\sum_{r=1}^{\ell} H_r P_{Ni}}$$

For a parallel definition of equation (9) see Silvert and Platt (In press).

These interactions for a carnivore can be generalised for herbivory and detritivory by considering biomass flows. Some instances of herbivory are exactly analogous to carnivory e.g. where herbivores forage for discrete high food value items such as fruit or seeds or
where detritivores forage for carcasses. However, for non-discrete food items further definition of the predation coefficient is required. In order to achieve this we will re-examine the carnivory equation.

For a carnivore the fraction of the time spent travelling is,

$$\frac{1}{\sum_{i=1}^{\lambda} P_i N_i \left( \sum_{i=1}^{\lambda} P_i N_i \right) + \sum_{r=1}^{\lambda} H P N_r \left( \sum_{i=1}^{\lambda} P_i N_i \right)}$$

\[ \text{... (10)} \]

The fraction of time spent handling the sth prey is

$$\frac{H P N_s}{\sum_{i=1}^{\lambda} P_i N_i \left( \sum_{i=1}^{\lambda} P_i N_i \right) + \sum_{r=1}^{\lambda} H P N_r \left( \sum_{i=1}^{\lambda} P_i N_i \right)}$$

\[ \text{... (11)} \]

So, \frac{\text{fraction of time spent handling the sth prey}}{\text{fraction of time spent travelling}} = \frac{H P N_s}{R_s} = R_s, \text{ say.}

Since neither H, P, or N depend upon \lambda, this result is independent of the number of prey types, \lambda, and gives an empirical definition of the predation coefficient \( P_s \) which can be extended to herbivory or detritivory.

If \( h_s \) is the handling time of unit biomass of the sth prey, then

\( H_s = w_h h_s \) where \( w_s \) is the mass of the sth prey.

So, \( R_s = w_h P N_s = h P M_s \) \[ \text{... (12)} \]

where \( M_s \) is the total biomass \((N_s w_s)\) of the sth prey type.
Equation (12) is now in a general form suitable for application to carnivory, herbivory and detritivory.

\[
\frac{\text{Fraction of time spent handling any biomass}}{\text{Fraction of time spent travelling}} = \sum_{s=1}^{\ell} \frac{h_{PM}}{s}
\]

\[
\frac{\text{Fraction of time handling + fraction of time travelling}}{\text{Fraction of time travelling}} = 1 + \sum_{s=1}^{\ell} \frac{h_{PM}}{s}
\]

So fraction of time spent travelling is

\[
\frac{1}{1 + \sum_{s=1}^{\ell} \frac{h_{PM}}{s}}
\]

From (12) the fraction of time spent handling the kth biomass is

\[
\frac{h_{PM}}{k} = \frac{1}{\sum_{s=1}^{\ell} \frac{h_{PM}}{s}}
\]

If all the time were spent handling the kth biomass with no travelling time then the biomass feeding rate is given by \( \frac{1}{h_k} \)

But the fraction of time spent handling the kth biomass is given by the preceding expression.

So the actual feeding rate on the kth biomass by a single predator is

\[
\frac{h_{PM}}{k} \cdot \frac{1}{\sum_{s=1}^{\ell} \frac{h_{PM}}{s}} = \frac{P_{MK}}{k} \cdot \frac{1}{\sum_{s=1}^{\ell} \frac{h_{PM}}{s}}
\]

.... (13)

The flesh equivalent feeding rate for the kth biomass is

\[
\frac{v_{kPM}}{k} \cdot \frac{1}{\sum_{s=1}^{\ell} \frac{h_{PM}}{s}}
\]

.... (14)

where \( v_k \) is the resource value of the kth biomass. \( v = 1 \) for flesh and is \( 0 < v \leq 1 \) for plant and detritus materials.
4.1.3 Predation with an optimal foraging strategy

To implement feeding relations in the model using equation (14) would result in the rth predator feeding on all prey where \( P_r \) is non-zero. Here we adopt one of several possible foraging strategies, one which maximises assimilated energy flow to a predator. We define a subset of food types which maximises the rate of flesh equivalent biomass flow to the predator. To simplify the notation for the following proof let, \( x_k = v_k P_k M_k \) then from equation (14) total flesh equivalent flows to a predator is

\[
F = \frac{\sum_{k=1}^{l} x_k}{1 + \sum_{s=1}^{n} \left( \frac{h_s}{v_s} \right) x_s}
\]

We assume we have found the subset of \( n \leq l \) food classes which maximises \( F \). If necessary we could rearrange the food class subscripts such that the optimal diet is indexed \( 1 \) to \( n \). Addition of one food class will by definition reduce \( F \) whilst subtraction of one class will also reduce \( F \) or leave it unchanged.

The following inequalities can be deduced.

\[
\frac{y - x_p}{1 + z} \leq \frac{y}{1 + z} \quad \text{...... (15)}
\]

and,

\[
\frac{y + x_q}{1 + z} \leq \frac{y}{1 + z} \quad \text{...... (16)}
\]

where \( y = \sum_{s=1}^{n} x_s \) and \( z = \sum_{s=1}^{n} \frac{h_s}{v_s} x_s \)

and \( 1 \leq p \leq n < q \leq l \)

Inequality (15) reduces to

\[
\frac{h_p}{v_p} \leq \frac{1 + z}{y} \quad \text{...... (17)}
\]

and inequality (16) reduces to
\[
\frac{h_p}{v_p} < \frac{h_q}{v_q}
\]  \quad \text{\ldots (19)}

This result shows that \( \frac{h}{v} \) for each class in the optimal diet, is less than that of any class excluded from it. This simple result allows us to choose the required subset of classes from the \( 2^\ell - 1 \) possible non-empty subsets of \( \ell \) classes.

Note that \( \frac{h}{v} \) has an empirical interpretation. Since \( h \) is the handling time for 1 g of food of resource value \( v \) and \( \frac{1}{v} \) is by definition that mass of food equivalent to 1 g of animal flesh, \( h \frac{1}{v} \) is the unit flesh equivalent handling time of food at \( v \).

The strategy for the optimal diet of a predator in our model is to first rank foods according to \( \frac{h}{v} \) then starting with minimum \( \frac{h}{v} \) add successive food classes until \( F \) reaches a maximum where addition of a further class would reduce \( F \). The flesh equivalent biomass flow rate to an optimally foraging predator is thus,

\[
F_{\text{opt}} = \sum_{k=1}^{n} \frac{v_k p_k m_k}{1 + \sum_{s=1}^{n} \frac{h_s p_s m_s}{s}} \quad (n \leq \ell) \quad \text{\ldots (20)}
\]

The relative abundance of foods in different food classes can influence the number of food classes in the diet but from (19) all food classes with \( \frac{h}{v} \) less than the maximal \( \frac{h}{v} \) in the optimal diet will be included irrespective of their abundance.

Paradoxically it is possible to demonstrate that if a diet contains more than one class of food the class which has lowest \( \frac{h}{v} \) doesn't necessarily contribute to the diet at the greatest rate although it is necessarily a member of the optimal subset.
4.1.4 Satiation, Starvation and non-feeding time

A predator may or may not reach satiation when feeding at the rate $F_{opt}$ dependent on the availability of prey at any instant in time. However the optimal foraging rate can be compared to the weight dependent food demand rate, $K$.

If, $F_{opt} \geq K$ then death rate due to starvation = 0
if, $F_{opt} = 0$ then death rate due to starvation = $D_{opt}$

The starvation rate $D$ is the death rate of heterotrophs of a particular mass in the complete absence of food.

Then for $0 < F_{opt} < K$ assuming a simple linear relationship between death rate and degree of satiety then the death rate due to starvation is given by

$$D(1 - \frac{F_{opt}}{K})$$  .... (21)

This is one instance where we have relaxed the condition of model homogeneity since failure to do this results in all members of a weight class dying simultaneously. The present approach implies a statistical (i.e. patchy) distribution of food shortages.

Heterotrophs continue to forage optimally until their appetite is satisfied they then rest from feeding. The final form of the flesh equivalent biomass flow to a given predator is

$$\min \{F_{opt}, K\}$$  .... (22)

From equation (9) the number of individuals of the kth class eaten by a predator is

$$\frac{P_{kN_k}}{1 + \sum_{s=1}^{n} w_{s} h_{s} P_{sN_s}}$$

without satiation and with satiation

$$\frac{P_{kN_k}}{1 + \sum_{s=1}^{n} w_{s} h_{s} P_{sN_s}} \cdot \frac{k}{F_{opt}}$$
the two cases can be combined to give the number of prey class \( k \),
eaten by a single predator in unit time

\[
\frac{P_k N_k}{1 + \sum_{s=1}^{n} w_s h_s P_s N_s} \min \{F_{opt}, K\}
\]

Observe that expression (22) can be regained from (23) by multiplying
by \( w_k \) and summing over \( k \).

4.1.5. The continuous carnivory model

Any large ecosystem will contain carnivores of many different masses.
Over a short time interval carnivores of different masses may be
preying upon other heterotrophs, be starving or be being predated upon
by other carnivores. A continuous model allows the simultaneous
operation of these processes as the total rate of change of population
number is given by the sum of the partial rates, equation (2). We
shall now determine \( \frac{\partial n_1}{\partial t} \) carnivory, using equation (23).

The number of individuals of all ages in an infinitesimal weight class
is given by \( n_1(w,w_0,t)dw_0dw \). Note that subscript 1 refers to
carnivores, 2 to herbivores and 3 and 4 to detritivores. The set of
predation coefficients, \( P \), becomes a function \( p_1(\tilde{w},w) \) where \( \tilde{w} \) is the
weight of the ingester carnivore and \( w \) the weight of the carnivore
ingested. Similarly the unit biomass handling time, \( h \), becomes
\( h_1(\tilde{w},w) \). Appetite, \( K \), becomes \( k(\tilde{w}) \) and \( F_{opt} \) becomes \( f_1(\tilde{w},t) \). To
simplify the notation \( \tilde{P}_1 \) is used for \( p_1(\tilde{w},w) \) similarly \( \tilde{F}_1 \) for
\( p_1(\tilde{w},w) \) and \( \tilde{F}_1 \) for \( f_1(\tilde{w},t) \).

From equation (20) putting \( v=1 \) and \( M_k = w_k \frac{N_k}{k} \), for carnivores,

\[
F_{opt} = \frac{\sum_{k=1}^{n} P_k w_k N_k}{1 + \sum_{s=1}^{n} h_s P_s w_s N_s}
\]
which in continuous form is

\[
\bar{f}_1 = \frac{\int_{-\infty}^{\beta_1} \bar{P}_1 \bar{h}_1 \bar{P}_1 \int_{-\infty}^{w} (n_1 + n_2 + n_3 + n_4) \, dw \, dw}{1 + \int_{-\infty}^{\beta_1} \bar{P}_1 \bar{h}_1 \bar{P}_1 \int_{-\infty}^{w} (n_1 + n_2 + n_3 + n_4) \, dw \, dw}
\] ...

(24)

Notice \( N_k \) becomes \( \int_{-\infty}^{\infty} (n_1 + n_2 + n_3 + n_4) \, dw \) which is the number of heterotrophs of masses which lie between \( w \) and \( w + \, dw \) irrespective of their age.

The optimisation procedure here reduces to optimising the domain of the integral over prey weight classes. This is achieved by selecting prey of lowest \( h_1 \) (since \( v = 1 \)) for each \( \bar{w} \) and progressively adding those of greater \( h_1 \) until \( \bar{f} \) reaches a maximum. Figure 1 shows the optimal domain \( \alpha_1(\bar{w}) \) to \( \beta_1(\bar{w}) \) for a single value of \( \bar{w} \).

![Figure 1](image)

Here the curve \( h(\bar{w}, w) \) has only one minimum and where there is a single interval of integration only. This appears to us a realistic assumption about \( h_1 \) but the optimisation procedure carries through for any \( h \) function giving possibly more than one interval in the range of integration. The \( \alpha_1, \beta_1 \) terms are a function of time as they respond to changes in prey abundance.

We now derive the actual rate of change in \( n_1 \) taking into account the condition of carnivore satiation. The continuous form of equation (23) is

\[
\min \left( \bar{f}_1, \bar{k} \right) \frac{\bar{P}_1 \left( \int_{-\infty}^{w} (n_1 + n_2 + n_3 + n_4) \, dw \right) \, dw}{\bar{f}_1 + \int_{-\infty}^{\beta_1} \bar{P}_1 \bar{h}_1 \bar{P}_1 \left( \int_{-\infty}^{w} (n_1 + n_2 + n_3 + n_4) \, dw \right) \, dw}
\]

which is the rate of decline of all heterotrophs of size \( w \) to \( w + \, dw \).
due to predation by a single predator of mass $\bar{w}$. But here we wish to know only the rate of change of population of carnivores whose mass is between $w$ and $w + dw$ and who will, if not predated, asymptotically attain an adult mass lying between $w_0$ and $w_0 + dw_0$.

The required rate of population change is

$$\frac{-\min \{\bar{r}_1, \bar{k}\} \bar{p}_1 \bar{n}_1 \bar{w}_0 \bar{w}}{1 + \int_{\bar{w}}^{\bar{w}} \bar{h}_1 \bar{p}_1 \left( \int_{\bar{w}}^{\infty} (n_1 + n_2 + n_3 + n_4) dw_0 \right) dw} \quad .... (25)$$

The number of predators that lie between $\bar{w}$ and $\bar{w} + d\bar{w}$ is

$$\left( \int_{\bar{w}}^{\infty} \bar{n}_1 dw_0 \right) d\bar{w} \quad .... (26)$$

The product of expressions (25) and (26) integrated over all predators $\bar{w}$ is,

$$\int_{\bar{w}}^{\infty} \bar{n}_1 dw_0 \quad .... (27)$$

So,

$$\frac{3n_1}{\partial t} \text{carnivory} = \left( \frac{3n_1}{\partial t} \right) \text{carnivory} dw_0 dw$$

Where $\phi_1(\bar{w},w)$ is defined such that

$$\phi_1(\bar{w},w) = 1 \text{ if } \alpha_1(\bar{w}) \leq w \leq \beta_1(\bar{w})$$

otherwise

$$\phi_1(\bar{w},w) = 0$$

The inclusion of this function $\phi_1$ ensures that prey populations are only reduced when they fall within predators' diets as defined by optimal foraging. This is illustrated in figure 2 where the predation domain for all weight classes is shown. The minima of $\bar{h}_1$ occur along the dotted line.
4.2 Starvation

From expression (21) we immediately arrive at the continuous form of the death rate due to starvation

\[ d(1 - \frac{f_j}{k}) \text{ if } f_j < k, \text{ and } 0 \text{ if } f_j \geq k \]

Which can be combined as

\[ d \max \{0, 1 - \frac{f_j}{k}\} \]

where \( d(w) \) replaces \( D \) as the death rate per individual per unit time in the absence of food.

So,

\[ \left( \frac{\partial n_1}{\partial t} \right) \text{ starve} = -n_1 d \max \{0, 1 - \frac{f_j}{k}\} \quad \ldots \quad (28) \]

4.3 Growth

Growth in our model is the movement of individuals into and out of an infinitesimal weight class in the direction of increasing \( w \). A simple asymptotic growth curve for an individual growing to weight \( w_0 \) is given by,

\[ w = w_0 \left(1 - e^{-t/\tau}\right) \quad \ldots \quad (29) \]

\( \tau \) is the time to grow to half adult weight divided by \( \ln 2 \) where \( \tau(w_0) \) is a constant for each \( w_0 \). From equation (29)

\[ \frac{\partial w}{\partial t} = -w_0 e^{-t/\tau} \left( -\frac{1}{\tau} \right) = \frac{w_0}{\tau} e^{-t/\tau} \]

But,

\[ w_0 e^{-t/\tau} = w_0 - w \]

so,

\[ \frac{\partial w}{\partial t} = \frac{w_0 - w}{\tau} \quad \ldots \quad (30) \]
We consider now the change in the number of carnivores which have current weight \( w \) to \( w + \, dw \) and which will have adult weights between \( w_0 \) and \( w_0 + \, dw_0 \) in the time interval \( dt \). From figure 3,

\[
\begin{align*}
\text{net increase in number of carnivores in the shaded area} &= \text{carnivores which grow in} - \text{carnivores which grow out} \\
\frac{\partial n_1}{\partial t} \text{ growth} \, dw_0 \, dt \, dw_0 \, n_1(w) - \frac{\partial w}{\partial t} (w + \, dw) \, dt \, dw_0 \, n_1(w + \, dw)
\end{align*}
\]

So,

\[
\frac{\partial n_1}{\partial t} \text{ growth} = \frac{-\left(\frac{\partial w}{\partial t} \cdot n_1\right)(w + \, dw) - \left(\frac{\partial w}{\partial t} \cdot n_1\right)(w)}{dw}
\]

\[
\frac{\partial w}{\partial t} = \frac{3}{2} \left(\frac{w}{w_0} \frac{w_0^{1/3} - w}{\tau}\right)
\]

from (30)

\[
\frac{\partial w}{\partial t} = \frac{3}{2} \left(\frac{w - w_0^{2/3} w_0^{1/3}}{\tau}\right) n_1
\]

The more sophisticated Bertalanffy growth equation (Bertalanffy, 1957)

\[
w = w_0 \left(1 - e^{-\left(\frac{t + c}{\tau}\right)}\right)^3
\]

may be substituted if required. In this case

\[
\frac{\partial w}{\partial t} = \frac{3}{2} \left(\frac{w^{2/3} w_0^{1/3} - w}{\tau}\right)
\]

and,

\[
\frac{\partial n_1}{\partial t} \text{ growth} = \frac{3}{2} \frac{\partial w}{\partial w} \left(\frac{w - w_0^{2/3} w_0^{1/3}}{\tau}\right) n_1
\]

4.4 Reproduction

Given the present state of the model, since the population distribution \( n_1 \) is only a function of weight and adult weight, only a single reproductive strategy is possible for each adult weight. This limitation could be partly met by having separate general equations for heterotherms and homiotherms, the latter with parental care included in the equation. Here we neglect parental care. Fertility and size of offspring are assumed to be single functions of adult weight only.
For a given adult weight class, \( w_0 \), the fertility \( r(w_0) \) is the number of offspring per individual of reproductive age per unit time. The reproductive weight is defined as \( w_0 \gamma(w_0) \). Note that \( \gamma(w_0) \) is the fraction of the adult weight at which reproduction begins. \( b(w,w_0) \), the birth distribution, is a Gaussian function of \( w \) defined such that the fraction of offspring born of weight class, \( w_0 \), whose weight lies between \( w_1 \) and \( w_2 \) is

\[
\int_{w_1}^{w_2} b(w,w_0) \, dw
\]

Note that

\[
\int_0^{\infty} b(w,w_0) \, dw = 1 \text{ for all } w_0
\]

The number of reproductively active individuals in an interval \( dw_0 \) at \( w_0 \) is

\[
\left( \int_{w_0}^{w_0} n_1(\overline{w},w_0,t) \, d\overline{w} \right) dw_0 \quad [\overline{w} \text{ is the parent not offspring}]
\]

So,

\[
\left( \frac{\partial n_1}{\partial t} \right) \text{reproduction} = b r \int_{w_0}^{w_0} \overline{n}_1 \, d\overline{w} \quad \ldots (33)
\]

Where \( \overline{n}_1 = n(\overline{w},w_0,t) \).

5. Change in the number of Herbivores

To determine the distribution of herbivorous heterotrophs we now find the expressions for the right hand side of equation (3).

5.1 Carnivory

The change in the number of herbivores due to ingestion by carnivores is given from equation (27) as
5.2 Starvation

To find the starvation rate we first have to calculate the rate at which herbivores can feed. In section 4 we generalised carnivory such that the concepts of handling time, travelling time and optimal foraging can be applied to herbivory. Equation (12) is now the defining equation for herbivory where the heterotroph feeding interaction term $P$ is now the herbivore feeding interaction term.

We go directly to the continuous form of the feeding equation (20) which becomes

$$f_2 = \int_{\alpha_2}^{\beta_2} \frac{v P_2 m_A dv}{1 + \int_{\alpha_2}^{\beta_2} h_2 P_2 m_A dv} \quad \ldots \quad (35)$$

where $f_2(w,t)$ is the flesh equivalent biomass feeding rate under the optimal foraging strategy of an individual herbivore. No bars are needed in this situation as the feeders have weights, $w$, whilst the food is defined by biomasses of plant state $m_A$ of resource value $v$. The herbivory coefficient, $P_2$, is a function of $w$ and $v$, $P_2(w,v)$ and similarly for $h_2(w,v)$ the handling time per unit plant biomass.

Thus the corresponding equation to (28) for starvation of herbivores is

$$\left( \frac{\partial n_2}{\partial t} \right)_{\text{starvation}} = -n_2 \frac{d}{dt} \max \{0, 1 - \frac{f_2}{k} \} \quad \ldots \quad (36)$$
5.3 Growth

The corresponding equations to (31) and (32) are

\[
\frac{\partial n_2}{\partial t} \text{ growth} = \frac{\partial}{\partial w} \left( \frac{w - w_0}{\tau} \cdot n_2 \right) \quad \ldots \ldots (37)
\]

\[
\frac{\partial n_2}{\partial t} \text{ growth} = \frac{\partial}{\partial w} \left( \frac{(w - w^{2/3})^{1/3}}{\tau} \right) \cdot n_2 \quad \ldots \ldots (38)
\]

5.4 Reproduction

The corresponding equation to (33) is

\[
\frac{\partial n_2}{\partial t} \text{ reproduction} = b \gamma \int_{w_0}^{\infty} \tilde{n}_2 \, dw \quad \ldots \ldots (39)
\]

6. Change in the number of detritivores

Again the distribution of detritivorous heterotrophs is provided by finding the expressions on the right hand side of equations (4) and (5).

6.1 Carnivory

The change in the number of detritivores due to ingestion by carnivores is given from equation (27) as

\[
\frac{\partial n_3}{\partial t} \text{ carnivory} =
\]

\[
- n_3 \int_0^\infty \frac{\min \{\tilde{f}_1, \tilde{k}\}}{\tilde{f}_1} \cdot \tilde{p}_1 \left( \int_\tilde{w}^{\infty} \tilde{n}_1 \, dw_0 \right) \, d\tilde{w}
\]

\[
1 + \int_{\alpha_1}^{\beta_1} \frac{\tilde{w} \cdot \tilde{h}_1 \cdot \tilde{p}_1 \left( \int_{\tilde{w}}^{\infty} \left( n_1 + n_2 + n_3 + n_4 \right) \, dw_0 \right) \, d\tilde{w}}{\alpha_1}
\]

Similarly

\[
\frac{\partial n_4}{\partial t} \text{ carnivory} = -n_4 \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots (41)
\]
6.2 Starvation

To calculate the starvation rate we must first find \( f_3(w,t) \) the biomass feeding rate upon carcasses by an individual detritivore from equation (24)

\[
\bar{f}_3 = \frac{\int \frac{\beta_3}{\alpha_3} w \ n_D \ dw}{1 + \int \frac{\beta_3}{\alpha_3} \ n_3 \ n_D \ dw}
\]

(42)

The starvation rate for detritivores of plant material and dung requires the calculation of \( f_4(v,t) \) the flesh equivalent biomass feeding rate of an individual detritivore.

\[
f_4 = \frac{\int \frac{\beta_4}{\alpha_4} v \ p_4 \ m_D \ dv}{1 + \int \frac{\beta_4}{\alpha_4} h_4 \ p_4 \ m_D \ dv}
\]

(43)

So starvation, from equation (28), is given by

\[
\left( \frac{\partial n_3}{\partial t} \right)_{\text{starvation}} = -n_3 \ d \ \max \{0, 1 - \frac{f_3}{k}\}
\]

(44)

Repeat this expression replacing subscript 3 by 4 for \( \left( \frac{\partial n_4}{\partial t} \right)_{\text{ starvation}} \).

6.3 Growth

The corresponding equations to (31) and (32) are

\[
\left( \frac{\partial n_3}{\partial t} \right)_{\text{growth}} = \frac{\partial}{\partial w} \left( \frac{w - w_0}{\tau} \cdot n_3 \right)
\]

(45)

\[
\left( \frac{\partial n_3}{\partial t} \right)_{\text{growth}} = 3 \frac{\partial}{\partial w} \left( \frac{w - w_0^{2/3}}{\tau} \cdot n_3^{1/3} \right)
\]

(46)

With similar expressions for \( n_4 \).

6.4 Reproduction

The corresponding equation to (33) is

\[
\left( \frac{\partial n_3}{\partial t} \right)_{\text{reproduction}} = br \int_{w_0}^{w} n_3 \ dw
\]

(47)

and similarly for \( n_4 \).
7. Change in the plant biomass distribution

Our model of autotroph behaviour is not as detailed as the heterotroph models presented above. We have attempted the simplest model which appears to us to establish the global properties of an autonomous plant mediating the solar energy supply to the food demands of herbivores which is perhaps not a botanist's view of the world.

7.1 Herbivory

The change in the plant biomass distribution is derived from the predation equation (27) with plant biomass substituted for heterotroph prey thus,

\[
\left( \int_{\nu}^{0} \left( n_1 + n_2 + n_3 + n_4 \right) dw \right) \frac{dW}{dw}, \text{ becomes, } m_A \frac{dW}{dv}
\]

and subscript 2 replaces subscript 1 since herbivores are the feeders not carnivores, then

\[
\frac{\partial m_A}{\partial t} \text{ herbivory } = -m_A \int_{0}^{\infty} \frac{\min \{ f_2, k \}}{f_2} \cdot \frac{p_2 \int_{w}^{\infty} n_2 \ dw \ dw_0}{1 + \int_{\alpha_2}^{\beta_2} h_2 \ p_2 \ m_A \ dv}
\]

\[
\phi_2(w, v) = 1 \text{ if } \alpha_2(w) \leq v \leq \beta_2(w)
\]

\[
\phi_2(w, v) = 0 \text{ otherwise}
\]

where \( \alpha_2(w) \) and \( \beta_2(w) \) are the limits on the range of plant resource states, \( v \), in the optimal diet of a herbivore of weight \( w \).
7.2 Growth

In our representation of plant growth we distinguish between photosynthetic and non-photosynthetic parts of the $m_A(v)$ distribution. In addition we distinguish seasonally replaced and non-seasonal portions of $m_A(v)$. A distribution of plant biomass for all $v$ states is given in figure 4 showing the parts of the plant which are distinguished above.

where $M_B = \int_0^{V_G} m_A$, $M_G = \int_{V_G}^{V_Y} m_A$, $M_Y = \int_{V_Y}^{1} m_A$

where $M_G$ is the photosynthetic biomass, $M_G + M_Y$ the seasonally replaced biomass and $M_B + M_Y$ the non-photosynthetic biomass. In nature this approximates to the distribution of woody tissue (brown), leaf tissue (green) and high resource value seeds and storage organs (yellow).

For $0 < V < V_G$, let the fractional rate of increase of woody biomass,

$$C_B = \lim_{\Delta t \to 0} \frac{\Delta m_A(v,t)}{\Delta t} = \frac{1}{m_A} \left( \frac{\partial m_A}{\partial t} \right)_{\text{growth}} \quad \ldots \ldots (49)$$

and for $V_G \leq V < 1$, let the fractional rate of increase of non-woody biomass,

$$C_{GY} = \lim_{\Delta t \to 0} \frac{\Delta m_A(v,t)}{\Delta t} = \frac{1}{m_A} \left( \frac{\partial m_A}{\partial t} \right)_{\text{growth}} \quad \ldots \ldots (50)$$

Our further assumption is that $C_B$ and $C_{GY}$ are only a function of $t$ and not $v$.

Under conditions of light saturation of a closed canopy the energy per unit time captured by the photosynthetic biomass in the ecosystem is given by $S$. Whilst the upper canopy photosynthesis may be limited by
factors other than light availability the plants or plant parts in
the lower canopy will through phenological changes or self-shading
experience conditions of light deprivation.

When herbivory reduces the photosynthetic mass a lower level of energy
fixation will occur given by $eM_{G}$, where $e$ is the rate of solar energy
fixation per unit biomass of photosynthetic material. Allowing for
saturation the total energy fixed in the ecosystem is given by

$$\min \{S, eM_{G}\} \quad \text{..... (51)}$$

which is available for maintenance and growth of the plant. We assume
that $M_{B}$ has no maintenance cost so the total maintenance energy cost is
$y(M_{G} + M_{Y})$ where $y$ is the energy consumption to maintain unit biomass for
unit time. $M_{B}$ will however have a growth energy cost given by

$$x_{B} \left( \frac{\delta M_{B}}{\delta t} \right)_{\text{growth}}, \text{where } x_{B} \text{ is the energy cost of adding 1 unit of biomass.}$$

Similarly $x_{GY}$ is the energy cost of adding 1 unit of seasonally replaced
biomass.

Thus,

$$x_{B} \left( \frac{\delta M_{B}}{\delta t} \right)_{\text{growth}} + x_{GY} \left( \frac{\delta (M_{G} + M_{Y})}{\delta t} \right)_{\text{growth}} + y(M_{G} + M_{Y}) = \min \{S, eM_{G}\}$$

So,

$$\left( \frac{x_{B} \partial \left( \int_{0}^{V} m_{A} \partial v \right)}{\partial t} \right)_{\text{growth}} + \left( \frac{x_{GY} \partial \left( \int_{V}^{1} m_{A} \partial v \right)}{\partial t} \right)_{\text{growth}} + y(M_{G} + M_{Y}) = \min \{S, eM_{G}\}$$

now using equations (49) and (50)

$$x_{B} C_{B} \int_{0}^{V} m_{A} \partial v + x_{GY} C_{GY} \int_{V}^{1} m_{A} \partial v + y(M_{G} + M_{Y}) = \min \{S, eM_{G}\}$$

So substituting for the integrals and putting $M_{G} + M_{Y} = M_{GY}$ we have

$$x_{B} C_{B} M_{B} + x_{GY} C_{GY} M_{GY} + yM_{GY} = \min \{S, eM_{G}\} \quad \text{..... (52)}$$
In order to solve for $C_B$ and $C_{GY}$ we require another relationship between them. This is provided by the following continuity condition for $m_A$ at $v_G$

$$C_B m_A(v_G) - D_B m_A(v_G) = C_{GY} m_A(v_G) - D_{GY} m_A(v_G)$$

whence

$$C_B - D_B = C_{GY} - D_{GY} \quad \text{..... (53)}$$

where $D_B$ is the death rate of unit non-seasonally replaced biomass and $D_{GY}$ for the seasonally replaced biomass. Under temperate conditions for example $D_{GY}/D_B$ is the average age in years at death of an individual plant.

Condition (53) ensures that if $m_A$ is continuous at $v_G$ it will remain so in the absence of herbivory. Without such a condition the standing crop of green plant could increase without a corresponding increase in supportive tissue.

We can now solve for $C_B$ and $C_{GY}$ and substitute them in equations (49) and (50) to yield our plant growth term.

$$\left( \frac{\partial m_A}{\partial t} \right)_{\text{growth}} = \left( \frac{\min \{S, \epsilon_{M_G} \} - y_{M_{GY}} + x_{M_{GY}} (D_B - D_{GY})}{x_B M_B + x_{M_{GY}} M_{GY}} \right) m_A$$

for $0 < v < v_G \quad \text{(54)}$

$$\left( \frac{\partial m_A}{\partial t} \right)_{\text{growth}} = \left( \frac{\min \{S, \epsilon_{M_G} \} - y_{M_{GY}} + x_B M_{GY} (D_{GY} - D_B)}{x_B M_B + x_{M_{GY}} M_{GY}} \right) m_A$$

for $v_G \leq v \leq 1$.  

It is instructive to investigate a few implications of these equations in order to confirm that the autotroph dynamics are behaving in a globally plausible manner.

The specific growth rates in the absence of herbivory are given by

\[
C_B - D_B = \frac{\min \{S, eM_G\} - yM_G - x_M D_G - x_M D_B}{x_M + x_G M_G} = C_{GY} - D_{GY} \tag{55}
\]

At steady state in the absence of herbivory we can equate these expressions to zero to obtain

\[
C_B = D_B \text{ and } C_{GY} = D_{GY}
\]

thus for these conditions growth exactly compensates for natural death and litter production, and,

\[
yM_G + x_M D_G + x_M D_B = \min \{S, eM_G\} = s \text{ here (see below)} \tag{56}
\]

that is the maximal solar input is entirely devoted to maintenance and litter production with no net increase in standing crop. So plant growth is limited by solar input as is desired.

The dynamic behaviour of the autotroph biomass distribution in the absence of herbivory can be investigated by assuming a mathematically simple distribution \(m_A(v, t) = \xi(t), \quad 0 < v \leq 1\)

Then for \(\xi < \frac{s}{e(v_y - v_G)}\),

\[
\min \{S, eM_G\} = \min \{S, e\xi(v_y - v_G)\} = e\xi(v_y - v_G)
\]
And by (55)

\[
\frac{dl}{dt} = \frac{e^{(v_Y - v_G)} - \gamma(1 - v_G) - x_{GY}(1 - v_G)D_G - x_{GV}D_V}{x_{G}V_G + x_{GY}(1 - v_G)} \cdot \lambda \ldots \ldots (57)
\]

The numerator of this expression (including \( \lambda \)) represents the solar input less the total maintenance cost and less the energy to replace biomass loss to detritus (each term is measured in unit time) and so the numerator must be greater than zero away from the steady state. Equation (57) then represents a situation of exponential growth of plant biomass.

If \( \lambda \geq \frac{S}{e^{(v_Y - v_G)}} \min \{S, eM_G\} = S \)

and by (55)

\[
\frac{dl}{dt} = \frac{S}{x_{G}V_G + x_{GY}(1 - v_G)} = \left(\frac{y(1 - v_G) + x_{GY}(1 - v_G)D_G + x_{GV}D_V}{x_{G}V_G + x_{GY}(1 - v_G)}\right) \cdot \lambda \ldots \ldots (58)
\]

Thus under conditions of light saturation \( m_A = \lambda \) is approaching a limiting value \( \lambda_{\text{max}} \) from below, where,

\[
\lambda_{\text{max}} = \frac{S}{y(1 - v_G) + x_{GY}(1 - v_G)D_G + x_{GV}D_V} \ldots \ldots (59)
\]

Rearranging equation (59) we recover our steady state equation (56).

Our choice of \( \min \{S, eM_G\} = S \) in equation (56) now becomes clear.

Finally we observe that our plant growth term equation (54) is responsive to overgrazing (low \( M_G \)) which produces reduced growth and, in extremis, unnatural plant death.
7.3 Litter

In calculating the losses to detritus we distinguish between seasonally and non-seasonally lost plant parts. We treat woody tissue as being part of the heterotroph until the whole plant dies.

Losses to detritus are

\[
\left( \frac{\partial m_A}{\partial t} \right)_{\text{death}} = -D_B m_A \quad \text{for} \quad 0 < v < v_G
\]

= 0 otherwise \hspace{1cm} \ldots (60)

\[
\left( \frac{\partial m_A}{\partial t} \right)_{\text{litter}} = -D_{GV} m_A \quad \text{for} \quad v_G \leq v \leq 1
\]

= 0 otherwise \hspace{1cm} \ldots (61)

8. Change in the carcass distribution

The distribution of dead animal tissue by particle size, \( w \), is determined by the terms in equation (6). We first consider change in the \( n_D \) distribution caused by detritivores feeding on carcasses.

8.1 Detritivory

By analogy with equation (27)

\[
\left( \frac{\partial n_D}{\partial t} \right)_{\text{detritivory}} = -n_D \int_0^\infty \phi_3 \cdot \frac{\min (\tilde{f}_3, \tilde{K})}{\tilde{f}_3} \cdot \frac{\bar{\tilde{n}}_3}{1 + \frac{\tilde{\beta}_3 \tilde{w} \tilde{h}_3 \bar{\tilde{n}}_3}{\tilde{\alpha}_3 \tilde{P}_3 n_D \tilde{w}}} \hspace{1cm} \ldots (62)
\]

Where \( \phi_3 \) is defined as,

\[
\phi_3 (\tilde{w}, w) = 1 \quad \text{if} \quad \alpha_3 (\tilde{w}) \leq w \leq \beta_3 (\tilde{w})
\]

and \( \phi_3 (\tilde{w}, w) = 0 \) otherwise

and where \( \alpha_3 (\tilde{w}), \beta_3 (\tilde{w}) \), are the limits on the range of carcass particle size, \( w \), in the optimal diet of a carcass detritivore of weight, \( \tilde{w} \).
8.2 Carcass supply

Carcasses are added to \( n_D \) as a result of heterotroph starvation. Natural death is not included in our current model but could be incorporated without difficulty as in equation (60) for the plant. From equation (28):

\[
\left( \frac{\partial n_D}{\partial t} \right)_{\text{carcass}} = \sum_{i=1}^{4} n_i \int_{\mathbb{W}}^\infty \max \{0, 1 - \frac{f_i}{k}\} \, d\mathbb{W} 
\]

\[
\ldots (63)
\]

8.3 Fragmentation

At the moment of a heterotroph's death the likelihood of its carcass being ingested is dependent only on the weight of the carcass and detritivore abundance. With time however the carcass becomes fragmented (Sih 1980) and suffers putrification. We model both these processes as fragmentation, which is defined here as the carcass changing weight class with time but conserving biomass. Janzen (1977) has suggested that the production of toxins by small detritivores effectively allocates the food resource to them only. We model this process of putrification by considering the carcasses with time to be progressively fragmented by toxins and so to fall within the foraging range of increasingly small detritivores.

Let us assume a fragmentation rate \( dw/dt \) of \(-C_Fw\).

Where \( \Delta_{1/2}(w) \) is the time taken for a carcass to fragment to half its weight

\[
C_F = \frac{\Delta_{1/2}}{\Delta_{1/2}}
\]

By an exact analogy to the derivation of equation (31) but conserving biomass rather than the number of individuals

\[
\left( \frac{\partial (wn_D)}{\partial t} \right)_{\text{fragmentation}} = - \frac{\partial}{\partial w} ((-C_Fw)(wn_D))
\]

so,

\[
\left( \frac{\partial n_D}{\partial t} \right)_{\text{fragmentation}} = \frac{1}{w} \frac{\partial}{\partial w} (C_Fw^2n_D)
\]

\[
\ldots (64)
\]
9. Change in the detritus biomass distribution

The distribution of detritus biomass over resource states, \( v \), is now considered by expanding equation (7).

9.1 Detritivory

By analogy with equation (48) the consumption of detritus by detritivores \( n_4 \) is given by

\[
\left( \frac{\partial m_D}{\partial t} \right) \text{detritivory} = -m_D \int_0^\infty \phi_4 \frac{\min \{f_4,k\}}{f_4} p_4 \left( \int_0^v n_4 \, dw \right) \, dw \\
1 + \int_{\alpha_4}^{\beta_4} h_4 p_4 \, m_4 \, dv 
\]

(65)

Where \( \phi_4 \) is defined as,

\[
\phi_4(w,v) = 1 \quad \text{if} \quad \alpha_4(w) \leq v \leq \beta_4(w) \\
\phi_4(w,v) = 0 \quad \text{otherwise}
\]

and \( \alpha_4(w), \beta_4(w) \) are the limits on the range of detritus resources, \( v \), in the optimal diet of a non-carnivorous detritivore of weight, \( w \).

9.2 Plant detritus

At death or leaf fall plant biomass of resource value, \( v \), is assigned to the same \( v \) state in the detritus distribution.

\[
\left( \frac{\partial m_D}{\partial t} \right) \text{plant detritus} = \left( \frac{\partial m_L}{\partial t} \right) \text{death} + \left( \frac{\partial m_D}{\partial t} \right) \text{litter}
\]

from equations (60) and (61)

\[
\left( \frac{\partial m_D}{\partial t} \right) \text{plant detritus} = \begin{cases} 
D_B m_A & \text{for } 0 < v < v_G \\
D_G m_A & \text{for } v_G \leq v < 1
\end{cases}
\]

(66)
9.3 Dung

All heterotrophs generate dung which can be defined as the non-assimilated fraction of ingested food materials. Thus dung production is dependent upon, \( v \), the food resource value. Our earlier definition of \( v \) is not convenient, as it stands, for comparison with available data from the literature. The resource value, \( v \), was defined such that \( m \) g of biomass at \( v \) are equivalent to, i.e. (give rise to the same assimilated biomass as) \( vm \) g of heterotroph flesh.

Let \( a_j \) be the assimilated fraction of flesh consumption, \( v = 1 \)
let \( a_v \) be that of a biomass at \( v \) consumed
Then \( m \) g of biomass at \( v \) produce \( a_v m \) g assimilated and \( mv \) g of flesh produce \( a_j mv \) g assimilated. So according to our definition

\[
a_v m = a_j mv
\]

so \( a_v = a_j v \) and \( v = \frac{a_v}{a_j} \) \( \ldots (67) \)

Thus digestion of mass \( m \) g at \( v \) gives \((1 - a_v)m\) g of dung. However, empirical input is required to determine the resource state, \( v' \), of this mass of dung. A summary of assimilation fractions \( a_v \) is given in Heal and Maclean (1975) from which we may estimate \( v \) values for the main trophic groups using equation (67). In the absence of more precise information known to us we assume the very simple functional relationship between \( v \) and \( v' \) namely that \( v' = v r_D \) where \( r_D \) is a constant. Values of \( r_D = 0.33 \) appear plausible as \( r_D \) lies between \( \frac{v_D}{v_C} \) and \( \frac{v_D}{v_H} \) i.e. between .25 and .44

*Heal and MacLean give the following values of assimilation; for carnivores \( a_C = .8 \), for herbivores \( a_H = .45 \), for detritivores \( a_D = .2 \)
So \( v_H = .56 \), and \( v_D = .25 \) and by definition \( v_C = 1 \).
$$\frac{\partial m_v}{\partial t} \text{dung} = \left( \frac{\partial m_v}{\partial t} \right) \text{carnivore} + \left( \frac{\partial m_v}{\partial t} \right) \text{herbivore} + \left( \frac{\partial m_v}{\partial t} \right) \text{detritivore}$$

$$\frac{\partial m_D}{\partial t} \text{carnivore} = g(1 - a_1) \int_0^\infty \min \{f_1, k\} \int_w^\infty n_1 dw_0 dw \quad ... \quad (68)$$

where $g(v)$ is a normalised Gaussian function whose maximum value is $g(r_D)$ and $(1 - a_1) \min \{f_1, k\}$ is the mass of dung produced in unit time, by a carnivore of weight, $w$.

$$\frac{\partial m_D(v)}{\partial t} \text{herbivore} = - \frac{1}{r_D} \left( \frac{\partial m_D(v)}{\partial t} \right)_{\text{herbivory}} \left( 1 - a_1 \frac{v}{r_D} \right) \quad ... \quad (69)$$

where the increment in the quantity of dung at $v$ is purely a function of herbivory, equation (48), at $v$-state $v/r_D$. Similarly for detritivores from equation (65) with a term for carcass detritivores analogous to (68),

$$\frac{\partial m_D(v)}{\partial t} \text{detritivore} = - \frac{1}{r_D} \left( \frac{\partial m_D(v)}{\partial t} \right)_{\text{detritivory}} \left( 1 - a_1 \frac{v}{r_D} \right) + g(1 - a_1) \int_0^\infty \min \{f_3, k\} \int_w^\infty n_3 dw_0 dw \quad ... \quad (70)$$

For equations (69) and (70) since $0 < v \leq 1$ implies $0 < \frac{v}{r_D} \leq \frac{1}{r_D} > 1$, it is necessary to artificially extend the domain of herbivory and detritivory by setting them equal to zero for $1 < v \leq \frac{1}{r_D}$.  

9.4 Decay

In the model the process of decay is characterised by movement of biomass towards the origin ($v = 0$) at a rate proportional to its displacement from the origin. By direct analogy with the derivation of equations (31) and (64) we get,

$$\frac{\partial m_D}{\partial t} \text{decay} = - \frac{3}{\partial t} \left( - C_D v m_D \right)$$

$$= \frac{3}{\partial t} \left( C_D v m_D \right) \quad ... \quad (71)$$
10. Recapitulation

We have now completed the description of the seven equations of the trophic continuum. It is inevitable that in making a mathematical model some changes in the original description (Cousins, 1980) will result, although the changes are minor.

The solar input which generates the initial products of photosynthesis now connects with the autotroph over the whole of the photosynthetic region of the plant. Plant products are then translocated and transformed chemically to both higher and lower resource states. The only other change of any magnitude arises from a natural limit on the size of the smallest heterotroph in the system. Because there will be a limit to the size or dilution of food taken by that heterotroph there will be a pool of unusable food in the system. We predict this for all ecosystems not just aquatic ones where it is already well known.

Other changes in the model which appear marked are in fact less so. The use of two detritus equations rather than one is simply because we have not succeeded in modelling organisms which eat both dead plant and animal material. Similarly omnivory is included in the original continuum description of heterotrophs but not in this paper. Detritivory, herbivory, and carnivory flows were also shown in the original model but the calculation of these flows requires that the number of heterotrophs of weight $w$, be disaggregated into carnivores $n_1(w)$, herbivores $n_2(w)$, and detritivores $n_3(w), n_4(w)$. We should perhaps stress that identification of these trophic groups in a weight class is not a recourse to trophic level concepts.
11. Discussion

Ecosystems are apparently comprised of loosely connected elements. Perhaps for this reason alone ecological research has been successful at the level of the single species, taxon or habitat. There are however a few applications which require analysis of much larger ecological groupings. These include whole system effects of radioactive or biochemical toxins or taking a different example, ocean fishery management (May et al 1979).

Global models have other uses too. The choice of variables investigated at the local level is influenced by the global model held by the investigator. Thus a global model focussed on body size suggests questions to be asked at the local level and also allows local models to fit with each other. Whilst global models have local implications the converse is also true. Optimal foraging strategies studied at the local level of the single species have important implications for global energy flows and biomass distributions. Optimal foraging theory is still at an early stage of development (Krebs, 1978) and what is to be optimised is still a subject of speculation and investigation. Ellis et al (1976) identify rate of energy gain, feeding time minimisation and nutritional balance as candidates. Evans (1976) presents a taxonomy of weather factors which affect prey availability and the energy cost of predator activity which together determine a foraging strategy. It is clear from our trophic continuum model that choosing different parameters to be optimised will generate different whole ecosystem structures. Viewed in reverse, observed whole ecosystem structures may indicate which foraging strategies are consistent at the local level.

Having identified some of the reasons for making global models we now briefly discuss the nature of global models themselves with particular reference to ecological examples. The joint interaction of many subsystems so as to produce structure and function on a macroscopic scale has been identified by Haken (1977) and others as a coherent field of study irrespective of system type. This study of the emergent properties of systems may be considered as the study of global...
models per se and our concern here. Behaviours which are of interest in this context include the system's trajectories over domains of attraction, whether there are stable equilibria, bifurcations and catastrophic changes between modes. These behaviours allow us to examine global models relevant to ecosystem dynamics. Clearly the predator-prey limit cycle is a good example of an emergent property of a simple but global ecosystem model. (May 1974). A two species model showing catastrophic change is given by Jones (1975) for the spruce budworm and by Bazin et al (1978) for microbial predation. A two species predator-prey model admitting spatial heterogeneity (Stenseth 1980), demonstrates multiple stable points.

Our sphere of interest is large multicomponent ecosystem. Examples from ecology are Platt and Denman (1977, 1978), Silvert and Platt (1978, In Press), Ellis et al (1976) and Innis (1978). Paradoxically the world models of Forrester (1968) and Meadows et al (1974) do not study global system properties as such but are concerned only to extrapolate the present state of the system in an integrated way. In order to study the global properties of a world model it would be necessary to investigate system trajectories from many starting points and over many timescales appropriate to whole system behaviour. The Forrester model was not structured for this purpose nor is that its function.

Of the large multi-component ecosystem models the most highly developed is the ELM model of the US Grassland Biome study of the International Biological Program (Innis 1978). In that model the abiotic, producer, consumer, decomposer and nutrient subsystems are interactively linked. By the nature of the system being studied the ELM modellers have the advantage that perturbation experiments can be carried out both on the model and on the ecosystem itself. This is in contrast to Forrester's world dynamics where only the model can be perturbed. Like Forrester, ELM uses the SIMCOMP simulation language based upon difference equations. Once again distinctions must be drawn between investigation of the integrated behaviours of the model over the region for which it has been constructed and the set of truly global behaviours. Finite difference equations are not well suited to the latter application.
Three problems in this respect are (i) the global behaviours of difference
equations deviate from those of the corresponding differential equations.
Whilst quantal processes are more accurately modelled using difference
equations, where the level of observer resolution is such that a
statistical description is all that is possible, then it is differential
equations that best provide the system's functional description (Wiegert,
1975). (ii) rounding errors of the computer simulation can propagate
and in the absence of the underlying functional description may do so
without the knowledge of the modeller. (iii) difference equations do
not allow the investigation of the unstable parts of the system
trajectory and so cannot easily detect catastrophic changes. We
should stress that we are not trying to criticise ELM which is the most
thorough computer model of an ecosystem to date, but only
to distinguish model strategies. In this respect Platt and his
co-workers and our own work, though at a more rudimentary stage, attempt
a truly continuous description of whole ecosystems.

Platt and Denman (1977, 1978) working on pelagic marine ecosystems give
an equation for the steady state biomass distribution of organic particles
by weight. Their result is in good agreement with the empirical findings
produced equations for biomass distributions of marine ecosystems
derived from entropy considerations only. Such steady state solutions
may be considered as referring to the equilibrium point in the system's
principle domain of attraction. Dynamic equations are required to
investigate behaviours away from the equilibrium point. Silvert and
Platt (1978, In Press) attempt a dynamic model and investigate its
response to a perturbation in the biomass distribution.

The formation of a global model from isolatable parts is completely
specified by the interactions between parts. In the present model
these interactions reduce to predation interactions and an energy
allocation strategy within the particular plant or animal. Considering
heterotrophs the choice is between allocating energy to growth,
reproduction, fat deposition and locomotion (McNab 1980). In our model
these activities are time invariant functions of food supply to
heterotrophs, their current weight and adult weight. We exclude many
of the interaction terms of McNab (1980).
At any instant in time the sum of energy expended may be more or less than the assimilated energy intake. In nature this is made possible for the organism by the presence of energy storage, figure 5. For the modeller the energy stores are decoupling points of the system which permit the isolation of the model elements essential to the modelling process. Although short term energy imbalances occur in nature, long term imbalances do not. Again in our model long term imbalances are prevented by starvation using empirical values for both appetite and the starvation rate. Decoupling also occurs between the biotic and abiotic parts of the ecosystem, for example, atmospheric oxygen may be considered as a store or buffer sufficient that it is not rate limiting for respiration.

Our model could be further developed in a number of ways. Detailed modelling of the organisms' energy stores (figure 5) and the energy allocation process would produce greater precision. Calow (1976) has for example modelled the relationships between fat storage, growth and reproduction. The role of stored fat may be particularly important for some pesticide studies. The organism's energy allocation strategy would also have to be allowed to vary if the continuum model were used to investigate change over evolutionary time. Structural change in the model may also be required if different foraging strategies are incorporated. Model developments and specialisations are legion; parental care, parasitism, omnivory, homiothermy, heterothermy, above and below ground ecosystems, seasonality, nutrient limits and spatial heterogeneity.

Now let us discuss the mathematical structure of the model and how one might solve the equations. Few equations of interest for the behaviour of ecosystems can be solved explicitly and recourse to numerical methods for their solution is essential. Numerical methods free us to model the system as faithfully as possible rather than attempting to reapply more familiar but less appropriate equations. It is not common for example to include integrals in the modelling of feeding interactions although Cushing (1977) reviews and extends their use to model delays in population dynamics. It is inherently because of delays caused by handling that integrodifferential equations are used in our predation terms. We should also note that delays due to reproduction and growth are directly incorporated into our model by the inclusion of juvenile stages in the
specification. One concern in using integrals is whether their repeated calculation at every step in the algorithm will generate errors. However the control of error bounds presents fewer problems for numerical integration than in numerical differentiation (Davis and Rabinowitz, 1975).

The solution of equations 1-7 is an initial-value problem in that given the state of the system at any instant in time its future is completely determined. The specification of the initial state requires inputting number and biomass distributions. Running the model from many initial states allows the study of its global properties. A numerical solution will require using predictor-corrector methods (Lapidus and Seinfeld, 1971). Unlike the Runge-Kutta method, which cannot be used here, a predictor-corrector solution needs an additional numerical technique to calculate initial values of rates of change of the distributions. This additional step would not be a trivial one for a simulation from any particular initial state. However we believe that initialisation errors will not pose a problem if whole ecosystems exhibit strong domains of attraction.
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Acknowledgements

We would like to thank Dr. F. Holroyd and Dr. P. Evans for detailed and constructive comments on earlier drafts of this paper.
CAPTIONS

Figure 1: The optimal foraging domain of a carnivore, \( \tilde{w} \).

Figure 2: Predator carnivore - prey carnivore domains of interaction for carnivores of all weights.

Figure 3: (No caption)

Figure 4: The plant biomass distribution.

Figure 5: Energy allocation in the individual organism.
ingestion \rightarrow \text{assimilated fraction} \rightarrow \text{defecation} \rightarrow \text{stores} \rightarrow \text{maintenance} \rightarrow \text{growth} \rightarrow \text{reproduction} \rightarrow \text{locomotion}
7.3 Cousins and Smith (1982)
BIOGEOGRAPHICAL VARIATION IN SEED SIZE OF A FLORA

Seed size data for the flora around SHEFFIELD has been published by Grime et al (J.Ecol. 69:1017-1060, 1981). These data allow a preliminary estimate of the distribution of seed size in the UK flora.

MAP 1

This map shows the UK distribution of the 81 annual forb species found around Sheffield by Grime et al. It indicates, perhaps not surprisingly, that the number of species declines most steeply in a northerly direction and away from the coast, ie species density declines with higher latitude and altitude.

MAP 2

Have annual forbs (from the Sheffield area) with larger or smaller seeds survived at higher altitudes and latitudes?

Map 2 shows the forbs with smaller seeds to have 'perished' and the larger seeded species have survived. This is to us an unexpected result given other work showing seed size to decrease with altitude (Baker, H.J., Ecology, 53:997-1010, 1972).

Number of species

45 - 54

55 - 63

64 - 72

73 - 81
<table>
<thead>
<tr>
<th>Median seed weight g</th>
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<tr>
<td>0.290 - 0.322</td>
</tr>
<tr>
<td>0.323 - 0.355</td>
</tr>
<tr>
<td>0.356 - 0.387</td>
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<tr>
<td>0.388 - 0.420</td>
</tr>
</tbody>
</table>

SHEFFIELD [S]
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11. SPECIES SIZE DISTRIBUTIONS OF BIRDS AND SNAILS IN AN URBAN AREA

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SUMMARY

Urban ecosystems are hypothesized to present a gradient of declining 'green' patch size towards the urban centre. Small bird species are predicted to survive in urban centres for that reason. Analysis of a London bird atlas shows that average species size per 100 km² does decline towards central London. No such relationship is found for land snails and it is suggested that water relations may determine the snails' survival. Trophic structure based on the size of feeder and food 'packet' size is affected by any factor influencing organism size. Human food wastage creates a subsidy of large food 'packets' favouring some larger bird species.

INTRODUCTION

We can suppose that for most species the environment in cities becomes more dissected by human activities and artifacts as one passes from the outskirts to the centre. So although we may not know the dimensions of the patches or 'habitat islands' perceived by different species, we can conclude that for most species (but not all) the 'habitat islands' will become smaller and more isolated towards the city centre. A simple inequality of this type can be a powerful tool with which to analyse the complex problem of ecosystem patchiness.

Schoener (1968) has shown for birds that the territory or area inhabited by a species is positively correlated with its body size. So if we predict that on average green patch size decreases with urbanization, then for birds we should expect the size of species to decline on average also.

Whereas for bird species recolonization of suitable habitats is a relatively simple process, for snails it appears a major problem. Once extinction occurs locally, recolonization may take a long time. Thus for this group of relatively immobile species fecundity might be expected to play an important role in lessening the chances of extinction. Small species have shorter generation times and high rates of reproduction (Fenchel 1974), so small species might be
favoured at the city centre. However, large species move more quickly than small ones and would recolonize more rapidly although the rate of colonization must also be a function of species abundance. I shall examine the hypothesis that it is not the speed of recolonization but the reproductive effort that ensures survival in habitat patches perceived by snails. These patches might be expected to become smaller and more isolated near the city centre. So again I predict that smaller species will be favoured in central urban areas.

**BIRD SPECIES SIZE IN LONDON**

Data are taken from Montier (1977). Species breeding records were collected for each 2 x 2 km grid square and then aggregated to presence or absence of breeding species in each of 24 10 x 10 km contiguous grid squares covering the whole of London. A 25th grid square is included at the centre of the city, also of area 100 km². It overlaps the four central contiguous squares. The accuracy of these data relies on the evenness of observation over London. Montier confirms that there may have been some under-collection of data in North-east London although it should also be noted that the failure of ornithologists to visit an area may mean that it is genuinely species-poor. Figure 11.1 shows both the location of the study area and gives an index of observer effort. Units of the index are absence of breeding records per 2 km square for the ubiquitous species Starling, *Sturnus vulgaris* (Linne), Blackbird, *Turdus merula* (Linne) and Song thrush, *T. philomelos* (Brehm). Data from square 4 (Fig. 11.1) were omitted from further analysis due to the low level of observer effort identified by this method.

Of all the bird species found breeding in London, only land birds are considered here. Different groups of land birds, such as resident species or migrants, are also compared. The single species distributions from Montier (1977) were used to produce composite maps showing the number of species present per 10 km square or some attribute of that collection such as average species weight. Note that average species weight applies to the mean of the weights of a collection of species, and does not reflect the abundance of those species other than their presence or absence. Weight data are from Cousins (1976). Figures 11.2–11.6 were obtained using the SYMAP programme (Dudnik 1972). SYMAP is an interpolative contour mapping programme and the values of the contours are given on each map. Habitat data used here are derived from the records of the London Natural History Society (Sandford 1972, 1975, 1977, 1979) for rainfall, built environment, soils and sulphur dioxide pollution, respectively. All correlations given are Spearman's rank coefficients.

London conforms to the general model of an urban environment, set up by Erz (1966), of concentric rings of habitat; the outermost ring is semi-natural...
with a predominance of vegetation leading through dwelling areas to the city
centre itself with high-rise close standing buildings and little plant life. Figure
11.2 shows the roughly concentric distribution of an index of London’s built
environment. For this index Sandford’s (1975) land-use classification of each
2 km square was adopted and scored 1.5 for ‘settlements without gardens’, 1.0
for ‘settlements with gardens’, and 0.0 if settlements were not the predominant
land use. These values were summed for each 10 km square.

The concentric distribution of land bird species density, Figure 11.3, can
be seen clearly. The maximum species density of 77 breeding species per 10 km
square in outer London was compared to 43 species in the central 10 km
square. Species density was negatively correlated with the built environment
index at $-0.90$ significant at $P = 0.001$. 

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*Fig. 11.1.* The study zone of $24\, 10 \times 10$ km grid squares and central rectangle is
shown within a radius of $32.5$ km (20 miles) of St Paul’s Cathedral marked by cross. In
Figures 11.2–11.6 data are interpolated to the hatched lines. The river Thames is shown.
Figures in brackets are an index of observer effort and indicate the number of absent
records of three common breeding bird species in $25.4$ km$^2$ plots of each $100$ km$^2$. 

*Species size distributions of urban birds and snails*
The large parks situated to the west of central London raise the species density of that area, thus 60 and 64 species are recorded as breeding compared with 43, 49 and 53 species in the central and east central regions. The corresponding values for the built environment index are 27.5, 28.5, 35, 30 and 28.5.

The distribution of species size (Fig. 11.4) is correlated with the built environment index at \( -0.66 \) and \( -0.63 \) for average species weight, and median species weight, respectively, with both significant at \( P=0.001 \). Median species weight is fairly stable at 20–22 g but with 22 g at the outskirts and 20 g at the centre. Average species weight ranges from 122 g on the outskirts to 90 g at the centre.
Given the well-known heat island effect of urban areas (Chandler 1965) it is interesting to investigate the species size distributions of resident and migratory birds, separately. Kendeigh et al (1977) have calculated the relative energy costs of migration or overwintering for birds of different weights and show that small birds profit more by migration than do large birds. Overall, migrants and residents show the same basic features as their composite distributions, although the decline in species density from 21 to 10 migrant species is steeper than that for resident species from 56 to 33. Similarly, the decline in mean species weight is steeper for migrants at 43 g to 18 g compared to 150 g to 113 g for residents. The species density of residents was correlated with the built environment index at $-0.90$, $P = 0.001$ compared to migrants at

**Fig. 11.3.** Land bird species density/100 km$^2$. Contours 1–4 (light to dark), 43–51 species, 52–60 species, 61–68 species, 69–77 species.
Average species weight of residents was correlated with the built environment index at $-0.60, P=0.001$ compared to migrants at $-0.47, P=0.011$. Median species weight was significantly correlated with the built environment index at $-0.66, P=0.001$ for resident species but was not significant for migrant species.

**SNAIL SPECIES SIZE IN LONDON**

The size of snail species was estimated from the scale drawings in Cameron and Redfern (1976) by taking the external shell dimensions and approximating the
Species size distributions of urban birds and snails

shells to cones or cylinders. Species density and size distribution maps were constructed in the same way as for land birds.

The presence or absence of land snail species in each of the 24 contiguous 10 km grid squares of London was taken from Kerney (1976). An analysis of the number of species in each square showed the species size (volume) distributions were skewed to the left (Kurtosis values —0.68 to —1.9) except for square 3 (Fig. 11.1) which skewed to the right (Kurtosis value 2.6). Data from that square was omitted from Figures 11.5 and 11.6 and the correlations, assuming there to have been under collection that area.

The species density of London's land snails decreases rapidly towards the city centre (see Fig. 11.5). Data extremes are 42 species at the city edge in the North-West and South, and nine species in the North-east square of centralLondon.

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**Fig. 11.5.** Land snail species density/100 km². Contours 1–4 (light to dark) 9–17 species, 18–25 species, 26–33 species, 34–42 species.
London. Data are not available for the 25th grid square but only as part of the four central squares. The steepness of the decline in species density suggests that the analysis of snail distributions at a smaller scale than 10 km square would reveal quite large areas virtually without snail species. Perhaps there has been some under-recording where only nine species were found, although the large parks in the western areas of central London may have enabled more species to survive, accounting for the 19 to 28 species found there.

Boycott (1934) identified three main factors influencing snail distributions. These are human influence, the moisture conditions of the habitat and calcareous soils. Of these, calcareous soils can be considered a factor independent of urbanization. Urban environments are typically drier than...
Species size distributions of urban birds and snails

their surroundings. Soils are often compacted which aids water run-off. Chandler (1965) notes the improvement in drainage in urban areas but also points to some added precipitation due to the particle burden of the urban atmosphere; relative humidity is markedly lower in the city centre, a factor he ascribes to the heat island effect.

Correlating the species density distributions with various environmental factors supports Boycott’s conclusions. Species density is negatively correlated with the built environment index at $-0.49 (P<0.01)$, it is positively correlated with rainfall at $0.55 (P<0.01)$, positively correlated with calcareous soils at $0.45 (P<0.05)$ and negatively correlated with atmospheric sulphur dioxide levels at $-0.77 (P<0.01)$.

The prediction that smaller species would be selected in central urban areas has been refuted by the data. Average species size was not significantly correlated with the built environment index. However, one very large species, *Helix pomatia*, has a disproportionate effect on the data. If this calciphile species is omitted from the correlation then species size is positively correlated with the built environment index at $0.53, P<0.01$. The distribution of average species size is shown in Figure 11.6. Similarly, there was a positive correlation of species size (omitting *H. pomatia*) with SO$_2$ levels at $0.58, P<0.01$. Median species size is significantly correlated with rainfall at $-0.34, P<0.01$ but not with the built environment index.

DISCUSSION

Both birds and snails show a decline in species density with increasing urbanization. For snails, the effects of urbanization appear greatly intensified by slow speed and poor powers of dispersal. In birds, smaller species tend to survive towards the city centre, unlike snails where the effect of species size is less clear. Earlier it was observed that desiccation of the environment was part of the phenomenon of urbanization (in temperate zones at least). Because snails depend upon the production of mucous as a surface on which to move, they are much affected by the moisture conditions of their habitat. Calow (1976) has pointed to the surface to volume relationship in which water content is proportional to the snail’s volume while water loss is a function of its surface area. Because of the declining ratio of surface to volume with increasing size, large snails can be at an advantage under dry conditions. The preceding section may provide at least part of the explanation of snail species size distributions in urban areas.

Certain authors (Platt & Denman 1977; Cousins 1980) have argued that energy flows in ecosystems can be efficiently modelled by analysing food flows between size classes of animals. The size of an organism determines its food demand and the size of species it may eat. Each organism consumes ‘packets’
of food and is itself a ‘packet’ of food to other organisms. There are features of examining ecosystems in this way which have particular application to urban systems. Firstly, any cause of body size selection, be it the size of ‘habitat islands’, moisture conditions, reproductive strategy or heat island effect, will have implications for feeding interactions between species. Secondly, the waste food, resulting from human activity in towns, occurs at relatively large ‘packet’ sizes which is suitable for large species. This may offer an explanation of the paradox that whilst bird species are on average smaller in towns, the characteristic urban species, Feral Pigeon *Columba livia* (Gmelin), Starling, Herring Gull *Larus argentatus* (Pontoppidan) are quite large. Examples of large ‘packet’ food supplies are grain spills, offal, food at rubbish dumps, household waste food and waste from take-away foodshops. It may also be worth noting that although the House Sparrow *Passer domesticus* (Linne) feeds on smaller food particles it, together with the above three ‘urban’ species, is a gregarious feeder that does not defend a feeding territory. These species can be compared to the majority of species in the study area which defend a feeding territory (Williamson 1967) and which may be more dependent on there being suitably large areas of habitat for their survival in towns (Schoener 1968).

In conclusion, the gradients of environment in urban areas and in particular the distribution of vegetated and non-vegetated space offers opportunities for research in the spatial ecology of single species or communities. Since so many functional attributes of an organism are associated with its size, the examination of the spatial distribution of organism size can help assess the importance of spatial phenomena in ecology.

REFERENCES


Species size distributions of urban birds and snails


Biologists are attracted by the use of diversity indices to condense species abundance distributions into one or perhaps two statistics which appear to characterise properties of the group or "community" sampled. Various authors (Tramer 1969, Goodman 1975, Huribert 1971) have questioned the ecological significance of these indices. Here I examine the assumption that certain diversity indices are independent of sample size and, more importantly, the assumption that diversity measures should be independent of sample size in order to provide valid measures of community properties.

Williams (1964) has amply documented the empirical observation that as the number of individuals (N) identified in a sample increase so does the number of species identified (S). There are upper limits to this relationship but these need not concern us here. Since the number of species in a sample is fundamental to the calculation of a diversity index, the index must be either independent of sample size or circumscribed by reference to the size of the sample.

The Shannon index (Pieilou 1975) has been partitioned to give two measures of diversity: J, a measure of the evenness of distribution of individuals into species; and log2S a measure of species richness. H' is perceived as a composite index determined by species richness and species evenness, such that

\[ H' = J \log_2 S \]  

(1)
Fig. 1. The relationship between $H'$ and $\log_2 S$; calculated on the data of Common Birds Census 1973 for the farmland

Fig. 2. The relationship between evenness index ($J$) and number of species ($S$)
The indices $H'$ and $J$ are widely used without reference to sample size. However, since $S$ is known to increase with sample size, it follows from equation (1) that $H'$ and $J$ cannot both be constants, as would be required if $H'$ and $J$ were both independent of sample size. Figure 1 shows the relationship between $H'$ and $\log_2 S$ for the farmland census plots of the 1973 Common Birds Census made by the British Trust for Ornithology. The census plots are distributed throughout the United Kingdom, although most plots are found in central and southern England. For details of the method see (Williamson and Homes 1964). The slope of the graph gives the value of average $J$, which equals 0.85 for the farmland plots studied. This is similar to Tramer's (1969) graph of $H'$ against $\log_2 S$ for bird communities of different vegetational types at various latitudes, for which average $J$ is 0.87. He concluded that since $J$ varied only from 0.718 in tundra to 0.921 in rain forest it could be treated as a constant. Diversity could then be described by $S$ alone without the trouble of calculating $H'$. One might reach the same conclusion from the farm data, except that we know $S$ to be dependent on the sample size as well as on ecological causes.

In order to test how sample size affects the parameters of equation (1) the 1973 census data was re-extracted from the base maps. Each map was divided into approximately 10 ha sectors and the numbers of species and individuals in each sector were recorded. These sub-samples were added together at random to simulate increasing sample size. Further details are given in the appendix.

The evenness measure $J$ proved to be highly dependent on sample size. On plot 209, $J$ had correlation coefficients of $-0.74$ and $-0.72$ with the number of species and number of individuals respectively. On plot 305 (Fig. 2) the correlations were stronger at $-0.89$ and $-0.88$. 

Fig. 3. The effect of sample size $(N)$ on $\log_2 S$ and $H'$
for $S$ and $N$ respectively. When $S$ is less than about 10 species, $J$ varies widely due to chance variation in making the sample.

In Figure 3 the graphs of $\log_{10} S$ and $H'$ against $\log_{10} N$ show that indices are affected by the size of sample $N$. $H'$ is more obviously asymptotic than $\log_{10} S$. $H'$ is progressively less sensitive to sample size but it does remain so throughout the range of sample sizes encountered in the Common Birds Census. As an initial conclusion we may say that neither of the parameters in equation 1 can be assumed to be independent of sample size.

There have been several attempts to modify $H$ and $J$ to make them independent of sample size. Pielou (1975) discussed increasing the sample size until $S$ reaches an upper limit, the corresponding values of $H$ and $J$ being taken as representative of the community sampled. Such an approach would be particularly difficult on farmland where the overall habitat is a mosaic of fields, meadows, hedges, streams, woods etc. Pielou acknowledges that it is intrinsically impossible to estimate the upper limit to $S$. If the purpose of the diversity index is to monitor change in the farming environment through a census of bird populations, it makes little sense to attempt to enlarge the sample until $H'$ has reached a value which is truly independent of sample size. Such a measure would lack the very sensitivity to population change that is required. As Fager (1972) has observed, diversity indices represent a tremendous loss of information since the identities of the species, their abundance and location are all lost in a single value. The enlargement of the sample to include all habitats on the farm, with the aim of making the diversity index independent of sample size, will only increase the loss of information and the lack of sensitivity.

Returning to look briefly at the evenness measures of diversity, a general approach to attaining independence of sample size has taken the form

$$\frac{\text{observed index value} - \text{minimum index value}}{\text{maximum value} - \text{minimum value}}$$

The maximum value of an index when used to measure evenness of distribution is obtained when each species has exactly the same number of individuals, $N/S$. The minimum value, i.e. the most uneven distribution, is given when each species has only one individual except for a single species which has all the other individuals, $N-(S-1)$. For $H'$ a measure of evenness, $V$, which is independent of sample size is given by

$$V = \frac{H_{\text{obs}} - H_{\text{min}}}{H_{\text{max}} - H_{\text{min}}}$$

One other measure Fager's (1972) ("Number of Moves") has been used in this paper. The basis of this is overtly non-biological. It is simply a count of the "Number of Moves" required to transform an observed distribution into a perfectly even one. The species are ranked so that the most abundant species has rank 1, the next most abundant rank 2 etc. Then since the even condition is one where $N/S$ individuals are present in each species, individuals are "moved" from the most abundant species to species with less than $N/S$ individuals. Each time an individual moves from one rank to another the value of $NM$ is increased by one. A value of $NM$ which is nationally independent of sample size is obtained from

$$NM = \frac{NM_{\text{obs}} - NM_{\text{min}}}{NM_{\text{max}} - NM_{\text{min}}}$$
One fundamental problem with measures of diversity which are truly independent of sample size is that the measures are unaltered by large increases or large decreases in the bird population. For example, using Williams (1964) $\alpha$ which is determined simply from the parameters $S$ and $N$, the value of $\alpha$ is equal to 16 for each of the following pairs of $(S, N)$ values: (33, 100); (46, 200); (51, 300). Therefore habitat changes which halved the bird population from 200 to 100 individuals would go unrecorded by the diversity index $\alpha$, provided that 13 species were also lost. If less than 13 species were lost then $\alpha$ would record an increase in diversity.

COMMUNITY MEASURES PER UNIT AREA

Rather than attempting to construct indices which are independent of sample size, I believe it may be easier and biologically more realistic to concentrate on measuring community diversity.

Fig. 4. Species density as the number of species holding territory at any 25 m$^2$; total number of species ($S$) equals 45. total number of territories ($N$) = 185
Fig. 5. Species density as the number of species holding territory at any 25 m²; total number of species ($S$) = 22, total number of territories ($N$) = 51.

Table 1

The comparison of several indices and measurements among particular farmland bird communities

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<th>209</th>
<th>315</th>
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<td>482</td>
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<td>97</td>
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<td>9</td>
<td>9</td>
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<td>$S_{20ha}$</td>
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<tr>
<td>$NM$ - edge</td>
<td>0.279</td>
<td>0.370</td>
<td>0.281</td>
<td>0.280</td>
<td>0.393</td>
<td>0.294</td>
<td>0.306</td>
<td>0.307</td>
</tr>
<tr>
<td>$V$ (evenness measure)</td>
<td>0.832</td>
<td>0.805</td>
<td>0.775</td>
<td>0.800</td>
<td>0.775</td>
<td>0.722</td>
<td>0.772</td>
<td>0.756</td>
</tr>
<tr>
<td>$V$ - edge</td>
<td>0.822</td>
<td>0.805</td>
<td>0.757</td>
<td>0.743</td>
<td>0.831</td>
<td>0.715</td>
<td>0.775</td>
<td>0.777</td>
</tr>
</tbody>
</table>
attributes on an area basis. Area is a fundamental unit in ecology since the energy supply from sunlight is available per unit area. The numbers of individuals and species in an area determine the size and variety of pathways through which that energy is dissipated. Similarly the number of species present in a small area determines the contemporary level of interaction between species.

I have used two area-based approaches. The first was to map the number of species present in each 25 m x 25 m square on plots 368 and 205. This was done by counting the number of territories which were present in each square. The maps of overlapping territories are shown in Figure 4. For the Dorset dairy farm (368) areas of low species density include all fields. Moderate species density (4–7 species) is found along the hedgerows. Species densities of 8 or higher are associated with standard trees being present in the hedgerows. The large area of high species density at the foot of the figure is due to a 1.6 ha wood and a disused railway line running obliquely from the foot of the figure up to the left. Plot 205 in Figure 5 is on an arable farm where internal hedgerows have been removed. The remaining areas of moderate species density are found at the boundary hedges at the top left and bottom right of the figure and also at a pond at bottom centre.

The second approach was to calculate species richness on the basis of the number of species found on 10, 20 and 40 ha areas. The calculation of this definition of species density has been made by drawing curves of the number of species (log$_2$S) against sample size (log$_{10}$N). From these curves the values of S can be found corresponding to the mean number of individuals occurring on 10, 20 and 40 ha. The results are given in Table 1 and are adjusted for edge effects. This adjustment is needed because boundary habitat features can be responsible for as much as 50% of the total numbers of birds found on some census areas. This is the case for plot 205 where 24 of the 51 territories were considered to be at the edge.

The table illustrates how the comparison of farms by the measurement of species density gives a very different picture to the comparison using $H'$. Plot 205 has 1/3 the bird density of plot 259, and far fewer species, yet it exhibits higher "diversity", as measured by $H'$. The measurement of species richness is relatively simple — one counts the number of species. For species evenness, one is attempting to measure the inverse of species dominance: It is not clear that any of the evenness indices do this in a meaningful way. The indices have to be invested with meaning by comparison between samples, with the hope that particular ranges of index values are correlated with other properties which are directly measurable.

Lastly, how should one equate species richness with species evenness? It was stated that $H'$ is a product of evenness and richness, but Hurlbert (1971) has noted that there is no empirical basis for the manner in which evenness should be combined with richness. Since from Table 1 it seems that the nonbiologically based index $NM$ shows no better or worse performance than the other evenness indices, it would at least appear to have the advantage that it cannot be combined with species richness attributes. Using S per unit area and $NM$, the concepts of species richness and evenness can remain distinct.

The adjustment for edge effect resulted in marked changes in evenness for farms 315 and 072 only. Edge effect adjustments are important when measuring bird or species density.

CONCLUSION

I began by describing two options necessitated by the observation that the number of species in a sample increase with the size of sample. Either diversity measures must be independent of
sample size, or they must be circumscribed by the size of the sample. To date diversity indices have been designed to be independent of sample size although for certain indices this aim has not been fully achieved. Sample size independence is convenient for the observer since, within broad limits, the index will not be affected by the amount of time spent in the field and the boundaries of the observation area need not be precise. However, the convenience of the observer is gained at great cost. The very sample size independence means that the index is designed not to detect changes in bird density. Hence the use of such indices to monitor environmental change is very limited. If instead of sample size independence, species richness is circumscribed by sample size in the form of species density, then changes in bird populations can be monitored directly. Fine-grained variation in species richness can be demonstrated easily. Also the species density approach does not lead to the presumption that there is a “community structure” which is measurable. Indeed, without the diversity “fog” things may become much clearer “down on the farm”.

APPENDIX

SUBSAMPLE SELECTION AND EDGE TERRITORY COMPENSATION

The Common Birds Census species maps for the farm land plots were divided into sectors, which were then reaggregated, in the following manner.

1. The number of sectors required was chosen by dividing the farm area (in hectares) by 10.
2. For approximately square or round plots the sectors radiated out from a central point; for narrow or irregularly shaped areas the sectors radiated out from two or more points. Sector edges were not placed along linear habitats.
3. The number of territories and the identity of each species was recorded for each sector. A territory was taken as being inside a given sector if it had more registrations in that sector than in any other sector.
4. Where the sector edge was also the plot edge, the number of territories on the plot edge was halved for each species. Edge territories were defined as those which were likely to be recorded on the adjacent plot if it were also being censused. Thus an edge territory is one which has 3 or more registrations on the plot edge, or which has 2 on the edge and only 1 internal, or where the size of territory which includes the edge is small compared to those territories internal to the plot. The key arbiter in doubtful cases was the test, “would the territory be likely to be recorded on the adjacent plot”?
5. Aggregating the sectors was done by using a random number generator subject to the condition that each sector could not be included more than once in an aggregation. For each plot an increasing number of sectors was aggregated until the whole plot was reconstituted.

I would like to thank Tim Reed, Leo Batten, Janet Wingfield and Mike O’Carroll for their help with this project.

STRESZCZENIE

Author na podstawie spostrzeżenia, że liczba gatunków wzrasta w miarę zwiększania badanej próbki, udowadnia, iż nie istnieją wskaźniki różnorodności zespołu (diversity) niezależne od wielkości próbki. Wydaje się łatwiejsze i biologicznie bardziej uzasadnione skoncentrowanie się na pomiarach cech zespołu zwierzęcego odnoszonych do wielkości badanej powierzchni od prób konstrowania nowych wskaźników niezależnych lub mniej zależnych od wielkości próbki. Obszar (powierzchnia) jest bowiem podstawową jednostką w ekologii, gdyż ilość energii słonecznej obliczana jest również na jednostkę powierzchni.

Zaleca się zatem, zamiast wskaźnika Shannona i tym podobnych, stosowanie obliczenia zagęszczenia gatunków. Na przykładzie materiałów z liczeń ptaków na farmach angielskich dokonano obliczenia zagęszczenia gatunków i przedstawiono na mapkach (fig. 4–5). Możliwość uniknięcia zniekształcającego wpływu wielkości próbki (powierzchni) autor widzi w stosowaniu podziału badanych obszarów na
drobniejsze jednostki o jednakowej wielkości, np. na 10 ha. Te części powierzchni oprócz zapewnienia porównywalności gęstości populacji i zagęszczenia gatunkowego zwiększyłyby również materiał (liczbę prób) umożliwiając statystyczne opracowanie danych.

Autor opowiada się za odrębnym wyrażaniem dwóch komponentów zróżnicowania gatunkowego zespołu, tj. bogactwa (liczby) gatunków (richness) i równomierności ich udziału ilościowego (evenness). Bogactwo gatunków autor zaleca badać za pomocą obliczeń zagęszczenia gatunków (liczba gatunków na jednostkę powierzchni), a równomierność udziału ilościowego ptaków wskaźnikiem F a g e r a (1972), tzw. \( NM \), podanym w obecnej pracy.

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W i l l i a m s o n  K. and H o m e s  R. C. 1964 — Methods and preliminary results of the Common Birds Census 1962–1963 — Bird Study 11: 240–256.
A Trophic Continuum derived from Plant Structure, Animal Size and a Detritus Cascade

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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 detritovore 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.
“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.
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

<table>
<thead>
<tr>
<th>Autotroph states</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Root mucilage and leaf drip</td>
</tr>
<tr>
<td>2 Woody tissue</td>
</tr>
<tr>
<td>3 Mature tissue: mature leaves</td>
</tr>
<tr>
<td>4 Young tissue: twigs, leaves, small roots</td>
</tr>
<tr>
<td>5 Growth sites: shoots, root tips, cork cambium</td>
</tr>
<tr>
<td>6 Storage organs: seeds and propagules</td>
</tr>
</tbody>
</table>

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.
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.

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, \( P_h \). 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 detrivore 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.

<p>| Table 2 |</p>
<table>
<thead>
<tr>
<th>Detritus states</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
</tr>
<tr>
<td>2</td>
</tr>
<tr>
<td>3</td>
</tr>
<tr>
<td>4</td>
</tr>
</tbody>
</table>

(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.
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/detritovore 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 detritovores 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 may 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”.

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On some Relationships between Energy and Diversity Models of Ecosystems

STEVEN COUSINS

Introduction

Energy modellers and diversity modellers adopt radically different approaches to the study of community ecology. Whole system energy models such as that recommended for use in the International Biological Program (PETRUSEWICZ & MACFADYEN, 1970) depend on partitioning the ecosystem into a few discrete compartments, trophic levels, and measuring the biomass at, and energy flows between, compartments. This method ignores species identity within each level and the complexity of species interactions between levels. However, it would also be difficult if not impossible to provide a meaningful diversity index of a trophic level since each level will include species from many classes from protozoa to vertebrata.

Species diversity modellers stress the importance of complexity of interaction between species as a fundamental variable of interest yet their unit, the taxon, includes species which are, according to trophic level descriptions, as unrelated as herbivores, carnivores and detritivores.

Both schools of thought use their models to approach the question of the stability of ecosystems, the diversity-stability relationship being one field of endeavour, and stability as a function of the number of trophic levels (PIMM & LAWTON, 1977) another.

Energy models

The opportunity to suggest that there is a much closer relationship between the analysis of energy flow and the study of species diversity comes from a reassessment of how we model energy flow. Earlier this century the study of trophic interactions, later to become ecosystem energetics, was centred on examining the abundance of organisms of different size classes. These were represented as a pyramid of number or Elton's pyramid in which the ecosystem was populated by a few large and a progressively larger number of smaller organisms. HARDY (1924) described how the herring's food web interactions change with changing size (age) of the fish. In 1927 ELTON wrote: "Size has a remarkably great influence on the organisation of animal communities. We have already seen how animals form food chains in which the species become progressively larger in size, or in the case of parasites, smaller in size. A little consideration will show that size is the main reason underlying the existence of these food chains and that it explains many phenomena connected with the food cycle (web)."

A lower limit on the size of food taken may be considered (SCHOENER, 1971) to arise from the costs in time and energy of the search, capture and chemical reassortment of the prey. An upper limit can be defined by the inability of the would-be predator to pursue and subdue the prey item — again neatly summarized by ELTON as "Spiders do not catch elephants in their webs nor do water scorpions prey on geese".

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In short, scattered packets of energy are harvested by larger organisms at an energy cost of collection and processing. The balance of that energy transaction has been collected into a larger packet – the ingesting organism itself – which is then available for ingestion by still larger organisms.

This process of energy concentration also occurs in the green plant, but it is not determined by ingestion. This is the fundamental point of departure from Lindeman's (1942) trophic level model. Energy can change its packet size or its concentration, i.e. change its state in trophic space in ways other than ingestion although this is the principal method in the interactions between animals. In plants this is achieved by translocation and chemical transformation creating a variety of states from low energy density foods such as leaf drip up to high energy density seeds and reproductive units shown as $A_m$ to $A_n$ in Figure 1. Detritus may also be conceived of as a variety of energy densities or packets which are in a general state of disintegration by the process of weathering, and dismembering by detritovores $D_n$ to $D_m$. Thus detritus too can change state without being ingested. Animal size classes, $H_3$ greater than $H_2$ etc, are shown in the central row of Figure 1. A minimum of connecting flows are shown in Figure 1: double arrow heads indicate a feeding flow, single arrow heads a non-feeding flow; no respiratory flows are shown. The abundance of organisms in each $H$ state gives Elton's pyramid, although biomass in energy flux can replace abundance as a measure.

The variety of energy states in the green plant have different entropies and cannot be summed to give a reference point for the interactions of heterotrophs. This is, however, the whole basis of the Lindeman model. Similarly the variety of detritus states cannot be summed in order to scale heterotroph interactions. Heterotrophs may, however, be studied using body size classes as a descriptor of trophic state. For clarification consider the following example.

A slice of bread eaten by humans sustains human action; if the bread is divided into eight pieces and scattered over an ecosystem, say a field, then the likelihood of the bread becoming human food is diminished and the chance of it being ingested by birds and small mammals increases; if it is split into a thousand pieces and distributed, the likelihood of
ingestion by birds and mammals decreases and ingestion by collembola, beetles and worms is greater; if it is pulped in water and sprayed thinly over the system only bacteria and fungi are the likely feeders. At any point in this process the sum of energy or the material inputs to the system is constant. Yet the entropy, the quantity of disorder that the food represents, is different in each case.

Elsewhere I have developed the argument (Cousins, in press) that a change in the size of energy packets represents a change in entropy and that Elton's model of the trophic pyramid therefore derives from the second law of thermodynamics as well as the first. In contrast Lindeman's model ignores energy states other than the change from food substrate to respiratory products and as such ignores significant second law descriptions of ecosystems.

Diversity

The taxonomic group is the fundamental class studied by diversity modellers. Taxonomic groups are made up of members which generally have similar size. Thompson (1916) discussed the importance of size relative to taxonomic classes. Thompson's law of form states that if an organism changes size it must also change shape, with large changes in size requiring major changes in the structure of the organism, e.g. there are limits to the size of insects because of tracheal respiration and the possession of an exo- rather than an endoskeleton.

Taxonomic groups are limited in the size range of their member species and therefore limited in their position in trophic space. If we consider the group represented by all breeding bird species in the British Isles then variation in species size is just over three orders of magnitude, from the Goldcrest (5.5 g) to the Mute Swan (11 kg). The distribution of breeding bird species density as a measure of species richness is shown for each order of magnitude in Figures 2-4. Figure 5 shows the overall species density with four 50 x 50 km sample broken down into the species density of 8 size classes.

The maps were produced from those in Sharrock (1976) by registering the presence of each species in 10 by 10 km areas covering the whole of the British Isles. Grid squares which contained more than 5% open water were excluded, and coastal species density values were obtained using contiguous sample areas along the coast, each sample having the same area as the inland sites. Species density values were interpolated by the SYMAP program using five class intervals between the maximum and minimum species density values in each map. There are just four observations that I wish to make from the figures.

(1) There is a change in the species density of each size class on a north-south axis. Larger numbers of smaller species are found in the south while large species are more numerous in the north. The distribution of the small species is more significant because much of the size differences observed in the larger (greater than 465 g) birds can be attributed to the coastal species. Intermediately sized species show maximum abundance south of the maximum size class peak. The overall species density (Figure 5) does not show any decrease in species richness with northerly latitude, yet the change in species size distribution suggests that the species diversity is differently distributed within the trophic pyramid. Where diversity is distributed within the trophic pyramid may have implications for any diversity-stability relationship.
Figure 2. Breeding bird species densities for species weighing up to 45 g.

Figure 3. Breeding bird species density for species weighing 45-465 g.

Figure 4. Breeding bird species density for species weighing more than 465 g.

Figure 5. Breeding bird species density for all species, with detailed species size distributions for four 10 x 10 km squares.
(2) The effect of inclusion of a new habitat in the sampling frame is shown by the high species density values of the coastal sites. Much species density work uses a square grid which is only partially filled at coastal sites unlike the present study. The effects of coastal bird diversity is particularly evident in Ireland. This raises the general point that if species richness is generated by a change in habitat and as such represents the discontinuity of subsystems, then species richness may be a measure of disfunction or the heterogeneity of the environment, and there may be no inherent reason for species richness to generate stability.

(3) Why should aquatic birds be so much larger than their land counterparts and what effect does this have on the trophic structure?

(4) Why should there be a gap in species abundance in the 45–105 g class? This gap is also evident in Eltonian pyramids of woodland birds.

Conclusion

Taxonomic groups occupy limited positions in trophic space which may be further delineated by considering particular size classes of the taxon. This is a much closer energy-diversity relationship than was apparent from trophic level concepts. A case has been made that the plant and detritus respectively cannot be used to scale trophic space and therefore that the LINDEMANN trophic level model does not hold. The species diversity of different size classes has implications for diversity-stability theory but with the constraint that species richness may be a measure of disfunction within an environment.

References


Resource Exploitation Patterns and the Structure of a Forest Bird Community

RICHARD T. HOLMES

Introduction

This report is concerned with how food resources are exploited by bird species breeding in a northern hardwoods forest in the northeastern United States. The similarities and differences in foraging patterns among 22 syntopic species, with special emphasis on sexual differences, are examined with the use of multivariate statistical techniques. We have shown in a previous paper (HOLMES et al., 1978) that these methods can help to define objectively the guild structure of a bird community and can identify similar species that may be potential competitors. The factors influencing the observed patterns of resource exploitation and therefore the structure of the bird community are discussed.

Study area and methods

The study was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, USA. The forest consists of an uneven aged, well stocked stand of northern hardwoods, with the canopy height averaging about 25-30 m. The dominant trees are American Beech (Fagus grandifolia), Sugar Maple (Acer saccharum), and Yellow Birch (Betula lutea). Detailed descriptions of the Hubbard Brook forest, its climate and vegetation, and bird communities, can be obtained from LIKENS & BORMANN (1972) and HOLMES & STURGES (1975).

Foraging behaviors of bird species breeding in the Hubbard Brook forest were quantified during June and July in 1974, 1975, and 1976. Each time a bird was seen performing a foraging maneuver, the following information was recorded: its species and whenever possible its sex, the time of day, type of foraging maneuver (hover, glean, hawk, probe-drill), the substrate (leaf, twig, bark, ground, etc.) and plant species to which it was directed, the height, and if in a tree, whether it was in the region proximal to the main axis of the tree bole or distal, along the outer halves of branches. The various combinations of these categories resulted in 27 ‘foraging characters’ (Table 1). The rationale for including these particular categories is discussed by HOLMES et al. (1978).

Even though many individuals on the study area were individually color-banded, it was not always possible to distinguish sexes, particularly for the ground foraging species such as thrushes. For those species for which sample sizes exceeded at least 50 foraging maneuvers for males and for females, the sexes were separated and treated as separate ‘species’ in the analysis. For others, the data for the sexes are combined and represent species-typical foraging patterns. A total of 7732 foraging maneuvers and their associated data were used in this analysis. Sample sizes per ‘species’ ranged from 58 to 687, averaging 221.4.

Multivariate statistical analyses were performed on the data matrix consisting of 35 rows (22 taxonomic species, 13 with males and females considered separately) by 27 columns

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widespread such intertaxa interactions may be, but by constraining our studies of bird communities over the past decades with such a strong taxonomic bias, we may well have produced a perception of community organization that bears a closer resemblance to science fiction than science fact. MacArthur's definition of a community as any set of organisms living near each other and about which it is interesting to talk may have provided a comfortable rationale for avian community studies, but it has little inherent biological meaning. We rarely know (or seem to care) whether there are any sorts of natural boundaries about the communities we study, whether there are any discontinuities in biological processes that might act to define a functionally interrelated assemblage of organisms in which we might really expect patterns of organization to have some adaptive significance.

What, then, must we do? I submit that we must turn our attention to more intensive, long-term studies of defined local populations and environments, in relation to defined (and measured) resource bases. If assemblages of organisms are not just haphazard they must result from the operation of biotic processes, and these are expressed through individuals and populations. Only by first looking there, and then by attempting to tease apart the real from the spurious processes with manipulative field experiments, may we determine whether bird communities are biologically real, and if so whether there are "rules" governing their structure.