

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".

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 LINDEMANS (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 detritivores 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 arrowheads indicate a feeding flow, single arrowheads 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.

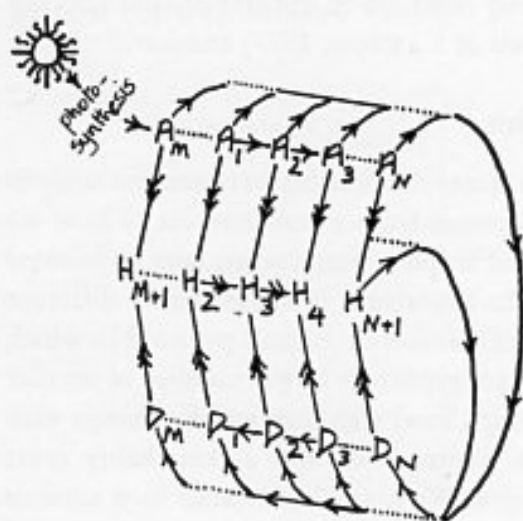


FIGURE 1. A trophic continuum. For explanation, see the text.

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.

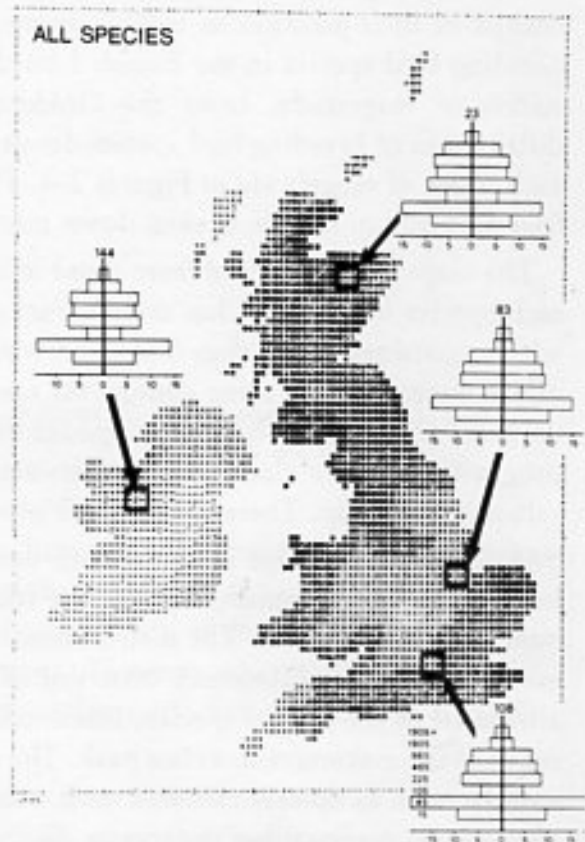


FIGURE 5. Breeding bird species density for all species, with detailed species size distributions for four 10 x 10 km squares.

(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 LINDEMAN 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

- COUSINS, S. H. (in press): A trophic continuum derived from plant structure, animal size and a detritus cascade.
- ELTON, C. S. (1927): *Animal ecology*. London. Sidgwick and Jackson.
- HARDY, A. C. (1924): *Fish Invest. Lond., Ser. II, 7, No. 3*.
- LINDEMAN, R. L. (1942): *Ecology* 23, 399–418.
- PIMM, S. L., & J. H. LAWTON (1977): *Nature* 268, 329–331.
- PETRUSEWICZ, K., & A. MACFADYEN (1970): *Productivity of terrestrial animals*. Oxford. Blackwell Scientific Publications.
- SCHOENER, T. W. (1971): *Ann. Rev. Ecol. Syst.* 2, 369–404.
- SHARROCK, J. T. R. (1976): *The atlas of breeding birds in Britain and Ireland*. Tring. British Trust for Ornithology/Irish Wildbird Conservancy.
- THOMPSON, D'A. (1916): *On growth and form*. Cambridge. Cambridge Univ. Press.