Ecologists build pyramids again

Researchers are abandoning recent attempts to chart the flow of energy through the ecosystem. The older approach—Charles Elton's "pyramid of number"—makes much more sense

Steve Cousins

ECOLOGY is a science from which much is expected. It provides the foundations for our understanding of agriculture, forestry and fisheries and is called upon to predict the effects of everything from pollutants to the construction of dams. To answer these practical problems, ecologists throughout the world embarked in 1964 on one of the largest programmes of collaborative science ever undertaken: the International Biological Programme (IBP). It aimed to determine the productivity of all the major ecosystems, from the Arctic to the tropics, on land and in water. The IBP was to span a decade, from 1964-1974. It took its theoretical base from the work of a young American, Raymond Lindeman, who worked at Yale University and died at the age of 27.

Lindeman advanced the notion that ecosystems could be seen as being composed of "trophic" (or feeding) levels arranged as a hierarchy—starting with plants (level 1), then herbivores (level 2) and carnivores (level 3) and so on. Researchers could study ecosystems, he suggested, by mapping the flow of food—in the form of dead or living organisms—between these trophic levels. These flows of food could be expressed in units of energy. Yet instead of generating a more thorough understanding of the way ecosystems work, the IBP primarily showed that Lindeman's ideas did not fit the real world. Ecologists could not find the trophic levels they were expecting.

The reaction of ecological researchers at the time to what was really an astonishing embarrassment was, with a few exceptions, quite low key. Rather than reappraise their methods of looking at ecosystems, ecologists voted with their feet: they stopped studying large ecosystems. New research centred on the minutiae of predation or simple interactions between parasites and hosts, situations where trophic levels could apparently still be found. Yet some ecologists, such as fisheries researchers, had to continue to study large complex ecosystems. Their research shows that the notion of trophic levels fails largely because it is the size of an organism that profoundly influences what it does in an ecosystem. Such a conclusion is strikingly ironic: it was also the conclusion that Charles Elton of the University of Oxford reached from his study of ecosystems in the 1920s.

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Two of the giants of the early days of ecological science: Charles Elton (top right) and Raymond Lindeman (above). Their scientific fortunes are now reversed

In the early part of this century, ecology had not yet become a respectable part of zoology. Its study was confined to natural history societies outside universities. The zoologists of the day were preoccupied with comparative anatomy, physiology and taxonomy, while the natural history societies collected specimens from the length and breadth of Britain. Elton offered a scientific explanation of the distribution and abundance of these creatures. He analysed the abundance of creatures in terms of a "pyramid of number". He saw that an ecosystem is populated by a very large number of small organisms and a progressively smaller number of larger organisms (Figure 1). Within this pyramid, large animals eat smaller animals, which in turn eat animals smaller than themselves. In this way "food-chains" are created.

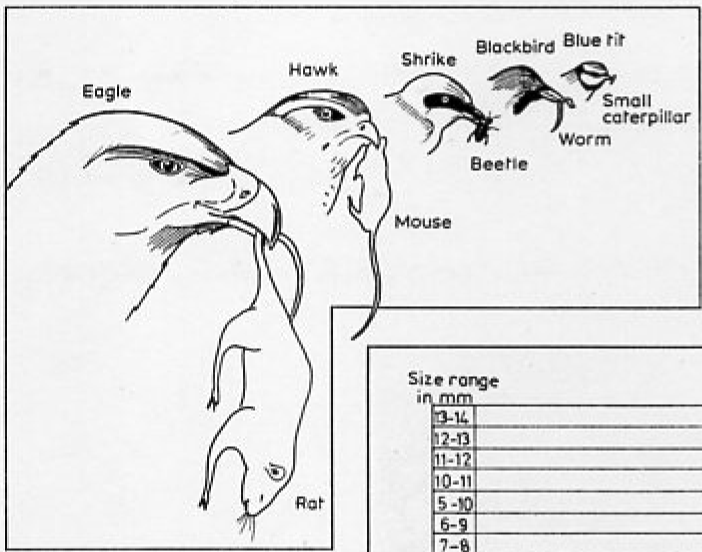
Birth of a new science

When Charles Elton was still an undergraduate at Oxford, he served on Oxford University's expedition to Spitzbergen in 1921, having been encouraged to join the expedition by Julian Huxley. On the expedition Elton collaborated with a botanist to survey a simple ecosystem—simple, that is, in comparison to ecosystems in the vicinity of Oxford. Because relatively few animals and plants live in arctic areas, Elton could list the species inhabiting the local ecosystem and identify the feeding relationships between them (Figure 2). This study was a good example of what Elton himself called "scientific natural history"—his definition for the new science of ecology.

Elton thoroughly developed the description of the animal community as a pyramid of number. First, he observed that creatures need energy to exist—obtained either by eating plants that derived energy from sunlight, or by eating animals or other material that had ultimately been derived from plants. But he also noted that animals fed on each other in a particular way. Although the animals doing the eating were larger than their prey, the prey were never so small that it took a long time for the feeding organism to collect, nor were they so large that the prey were difficult to catch and overpower.

Thus Elton concluded that there is a limited range of food size for each predator. This conclusion foreshadowed the development of optimal foraging theory, one of the most successful chapters in post-IBP research. However, the size of the creature also determined how fast it could reproduce. Small creatures reproduce much faster than large creatures, so the "surplus" offspring of small creatures effectively powers the food chain.

Thus the size of animals influences the way an ecosystem operates. Size determines both the way the predator and prey interact and their reproductive rate. But Elton realised that not all aspects of the food cycle depended on size. He noted that animals of all different sizes fed upon plants, from aphids to deer or perhaps bacteria to elephants. The pyramid of number was a pyramid of number of animals and not a pyramid of animals and plants.



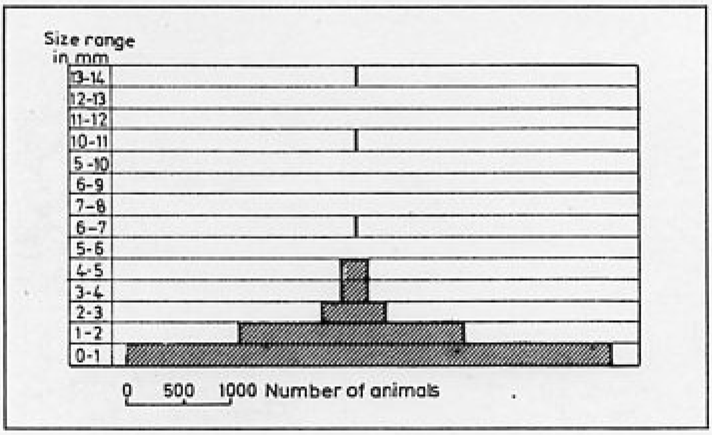


Figure 1 *The size of an item of food affects who can eat it. The Eltonian approach (right) takes size into account to create a pyramid of number—here, the number of animals on the floor of a forest in Panama*

Lindeman's description of the feeding relationship of an ecosystem in terms of trophic levels came to almost totally supersede Elton's approach using the pyramid of number (Figure 3). The concept of the trophic level was elegant in its simplicity. Furthermore, the attraction of measuring the contents of the levels and transfers between levels in energy units proved overwhelming. No one wanted to go around counting organisms of different sizes now that energetics and the second law of thermodynamics had entered ecology.

Lindeman spent five years studying the ecology of a small lake, as a PhD student at the University of Minnesota. He was assisted throughout much of his fieldwork by his wife, Eleanor, who was herself an expert on the identification of diatoms. After completing his thesis, he went to Yale where he developed, with Evylyn Hutchinson, a modified version of the final chapter of his thesis which became the now-famous 1942 paper. While at Yale, Lindeman suffered a relapse of a liver disease, and shortly after an exploratory operation he died. His paper was published postumously.

In Lindeman's model all plant life constitutes trophic level 1. The herbivores that feed on the plants form trophic level 2, while the carnivores that eat the herbivores constitute trophic level 3 and their carnivores are trophic level 4, and so on to trophic level 5. Levels 6 and above are generally thought to be rare and not important. In the idealised case, ecologists could find the weight (biomass) and hence the energy content of plants and of animals in each of the trophic levels. Similarly, they could determine the flow of energy between trophic levels by measuring the mass of biological material that crosses from one level to the next.

Based on the limited number of studies which Lindeman had at his disposal in 1941, he hypothesised that the amount of biomass supported by one gram of food entering a trophic level increased at successive trophic levels. He speculated further that this progressive improvement in the efficiency of using food increased as ecosystems evolved, that is during ecological succession.

Seduced by trophic levels

The elegance of the technique and the power of the hypothesis made the trophic level a natural choice for the International Biological Programme. Indeed, the IBP probably came into being because ecologists felt that they now had a technique that needed to be applied worldwide. However, all was not well with the model. In Lindeman's definition of trophic level, energy from one level passes to the next—it cannot jump a level—but in his diagram of the trophic levels in a lake "swimming predators" at trophic level 4 are feeding on phytoplankton (trophic level 1), zooplankton (trophic level 2) and plankton predators, which are the only 'correct' food at trophic level 3. Dead material and bacteria that feed upon it are also shown as providing food to levels 1, 2 and 3.

Difficulties of two types are apparent here. First, how can we allocate organisms to a trophic level when they feed on both animals and plants, or when carnivores feed from different levels? Secondly, because the trophic level model is based on the number of feeding levels away from the green plant, how are we to deal with dead material? Dead plants, undigested food in dung, and carcasses of dead animals are important sources of food which have been produced at a particular trophic level when they were alive; but where should they be put when dead and decaying? On land this is a particularly important problem because up to 80 per cent of the energy fixed by plants decays.

These problems appeared during IBP, but not initially because ecologists agreed that the problem of dead material would be solved by treating all detritus as "starting again" in the trophic level way of things: it would become trophic level 1, and the ecosystem would be split into a herbivore pathway, based on the plant as trophic level 1, and a detritus pathway, also trophic level 1.

When ecologists reported the conclusions of the IBP research in 1974, the limitations of the trophic-level method were clear. The occasion was the first international congress of ecology, organised by the International Association of Ecology (INTECOL) in The Hague, Netherlands. Yet the grandeur of the occasion did not allow ecologists to avoid the problem of actually identifying the trophic levels in order to determine their properties. As Lindeman had observed, the trophic levels of green plant and herbivore were relatively easy to identify and measure, but carnivores (levels 3 and above) were not. The people charged with breaking this news

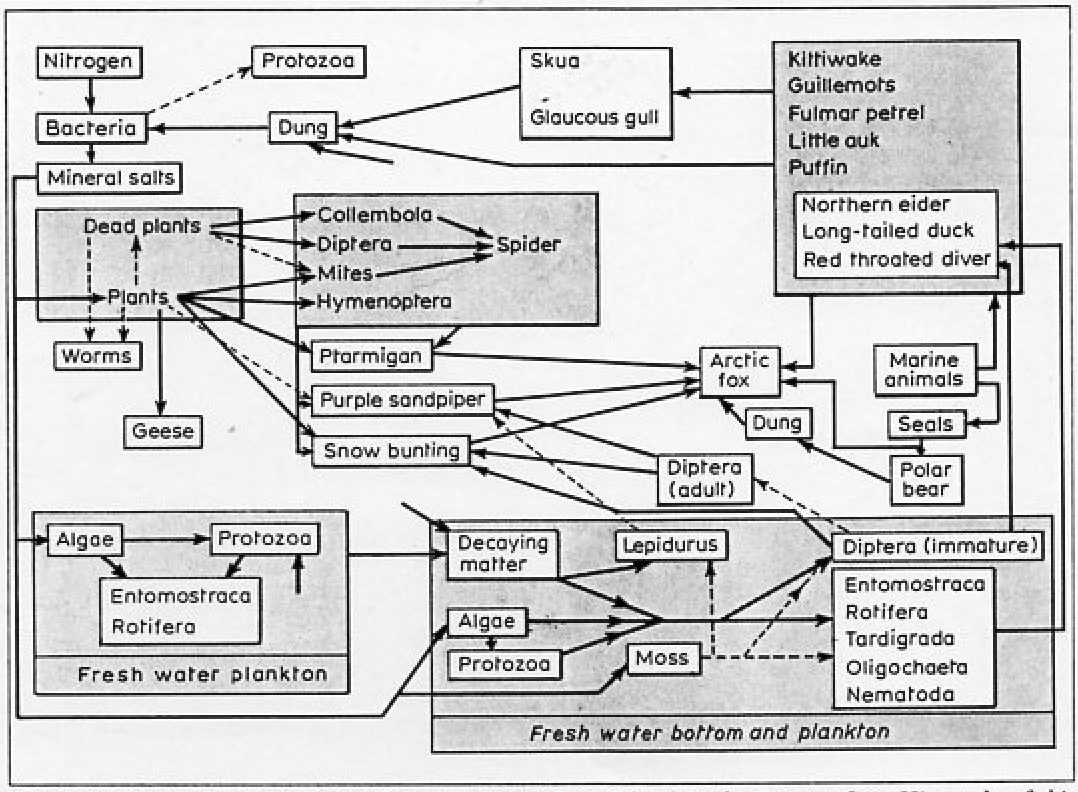


Figure 2 *Elton's diagram shows who eats who on Bear Island in the Barents Sea. His study of this relatively simple ecosystem was a good example of "scientific natural history"—Elton's definition of the new science of ecology*

were Bill Heal of the Institute of Terrestrial Ecology at Grange-over-Sands in Cumbria and Steve MacLean of the University of Alaska Institute for Arctic Biology. They presented a joint paper that summarised and compared the results of the analyses of trophic levels from all the IBP projects. Only the productivity of plants was left out of their remit. However, Heal and MacLean reported that "currently there are few measurements of . . . production for trophic levels, as opposed to species, from which patterns of variation can be examined". Instead, they developed a "modified" model that identified the flow of energy between broad groups of creatures such as vertebrates, invertebrates and microorganisms.

By the end of the IBP, researchers could measure relatively accurately the energy inputs into any organism. The problem came in allocating the creature to a trophic level. By definition, each creature is placed at a trophic level one above its food. But this strategy simply restates the problem: at what trophic level is the food? If the food species is itself a carnivore, we must then know the feeding history of all the organisms that the carnivore has eaten, before we can place it in a trophic level. No wonder trying to place carnivores in their trophic levels was difficult.

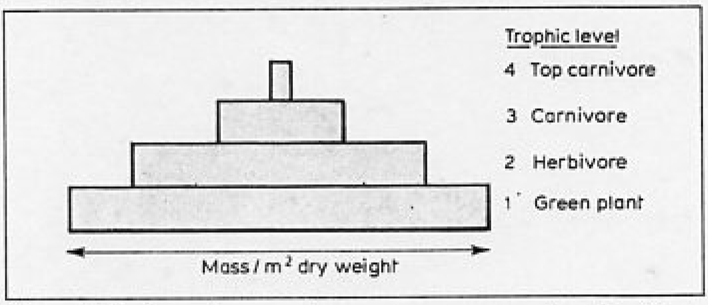


Figure 3 *Lindeman's approach to ecosystem trys to slot animals into trophic (feeding) levels*

At The Hague there was much debate about whether the concept of trophic levels had any place in a *science* of ecology. Frank Rigler, then the president of INTECOL, launched a blistering attack. Trophic levels had no physical reality and therefore could not have properties, he said. Trophic levels are mere mental constructions, truisms that could not be falsified by scientific endeavour. This heated debate was not resolved at the time. Yet progress was achieved quite quickly, however. In 1977, a group of marine biologists, led by Trevor Platt at the Bedford Institute of Oceanography, Nova Scotia, recreated many features of the model that Elton had invented in 1927. They observed that in the open ocean larger creatures fed on smaller creatures which all ultimately extracted energy from the phytoplankton. There was no need to posit trophic levels because although A fed on B—because A was bigger than B—A′, which was slightly larger than A, fed on B′, which was slightly larger than B and so on. In a continuum of feeding relationships, biomass or energy was transferred from the smallest to the largest. The researchers developed equations for the flow of biomass through a continuum or "spectrum" of marine organisms of different sizes. Whereas marine ecologists struggled to identify trophic levels at sea, they could measure the size of animals relatively easily by towing automatic particle-counting equipment behind research vessels.

On land, counting animals of different sizes is more difficult and requires a variety of techniques—nets, traps, observation and so on. A further problem arises: unlike marine ecosystems, where plants (mostly phytoplankton) can be treated as particles of different sizes, land plants cannot be as simply described. This problem was tackled the year after Platt published his paper and the findings given at the second international congress of ecology, held in Jerusalem in 1978. There I presented a description of the continuum of feeding relationships which could also apply to ecosystems on land. This model is based on animal size and a classification of plant parts—seeds, young leaves, mature leaves, wood and leaf drip or root mucilage (Figure 4).

Meanwhile, at McGill University in Montreal, Robert Peters, formerly a student of Frank Rigler, developed Rigler's concern that ecological phenomena should be observable and hypotheses about them testable. His interest also centred on the importance of body size and he assembled some 1050 equations linking the mass of individuals of different types—fish, bird, insects—with factors important to their ecology. These equations constitute, Peters says, "by far the greatest body of quantitative general theories in biology". Much of his data came out of the IBP activity, and it quantified for the first time the processes which Elton had seen as important determinants of the pyramid of number. The rate of production, the quantity of food required daily, the size of food required, the speed of locomotion, defaecation rates, requirements for water, all could be predicted from data about body weight. These data are given in his book *The*

Ecological Implications of Body Size (Cambridge University Press 1983).

Our work at the Open University and the work of Peters and Platt and his colleagues present alternatives to the trophic level model. They have their roots in Elton's pioneering research.

The trophic-level model considers that change has occurred only when something eats something else. It does not recognise other changes in state, such as the growth of animals. Yet such changes can profoundly affect a food web. Plants present another problem to the Lindeman approach. It has always amazed me how botanists can be enthusiastic about a theory that demotes the green plant to a single compartment, "level 1", and cannot distinguish between parts of plants or between phytoplankton, grass and even trees. Yet the plant completely jumbles up the categories of carnivory. A hawk, for instance, appears at each trophic level because plants supply food to a wide range of herbivores of different sizes (Figure 4). Trophic level 3 contains a bit of a hawk, a bit more of a small bird, a substantial proportion of each carnivorous mite and beetle and so on.

This haphazard "unit", trophic level 3, has been created by the scaling that treating the plant as a single unit imposes on the analysis of the interactions of a food web. And there is another problem. The concept of trophic levels also treats all feeding interactions as being exactly the same; that is, a transfer of energy from one trophic level to the next. In Elton's model, feeding interactions can occur over different distances in the pyramid of number; that is, within size classes and between adjacent or more distant size classes.

The last criticism of Lindeman's model is more abstract but of fundamental importance. Before they can allocate animals to trophic levels, ecologists have to determine the feeding history of all the organisms in the ecosystem, which would, of course, involve a colossal amount of field work. Yet a knowledge of the biomass at each trophic level will tell us very little about the next day's feeding relationships. We would have described the history of energy flow and not the present state of resources in the system. Energy does not retain its history. The following example may clarify this point. Imagine two glasses of warm water both at the same temperature, but one glass of water had been heated and

1: Feed the birds, test an ecological theory

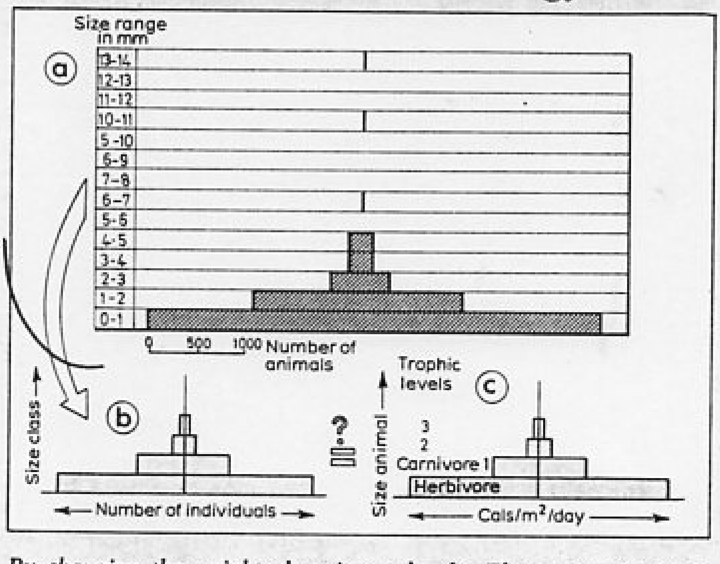
WHEN you next have bread to feed the birds, try an experiment. Cut the bread into fairly large pieces and scatter it over an area where you can watch what happens. Preferably half should be scattered over a concrete path and the other half over short grass. Then note which birds come to feed and where. You do not have to know the species; just note their sizes. Repeat this experiment the next day with moderately finely chopped bread. On the final day, scatter very finely chopped crumbs so they are "lost" in the grass and form a fine layer on the concrete. Which, if any, birds feed now and which birds stayed longest feeding? What eats the bread if the birds do not?

If you use one white slice for each test and scatter the bread on a defined area you know that the quantity of energy added is the same on each day and is at the same trophic level. However, the effect on the ecosystem is (we expect) quite different. Thus to know the effect of adding energy to the system we need to know the quantity (one slice) and the quality (particle size) of the material added in order to predict the outcome with respect to the relative fortunes of the creatures in that ecosystem.

Energy resources in the ecosystem require a description of both the quantity and quality of that resource. Elton's model *is* appropriately based with both a quantity (number of individuals) and quality (particle or body size). In contrast, the Lindeman model contains only a description of a measure of quantity (biomass); hence it is fatally flawed and consequently non-predictive. Unlike body size, an individual's trophic level does not describe the quality or availability of energy, not least because the same individual (such as a hawk or a human) can exist at several trophic levels. □

2: How the textbooks on ecology cheat

MANY textbooks devoted to ecology imply that the model of trophic levels is a logical extension and improvement of Elton's pyramid of number. These textbooks achieve the transformation of Elton's to Lindeman's model by a sleight of hand. First, the pyramid of number is shown, then it is shown again but compressed into a few broader size-classes which then look, as if by magic, just the same as the trophic-level model (Figure). In both cases the green plant and detritus compartments are suspiciously absent. In Elton's model the green plant is eaten by herbivores in each of the size classes, whereby in Lindeman's model, level 2 is exclusively composed of herbivores but these come from each of the weight classes of the pyramid of number. Similarly, carnivores of trophic level 3 will be of a wide variety of sizes and come from each of the size classes.



By changing the weight class intervals, the Elton pyramid (a) is transformed (b) to look much like the trophic level model (c). But note that the compartments representing green plants and detritus are suspiciously absent in the textbook diagram. Plants present a problem to the Lindeman approach

Textbooks have also got around the problem of "ominivory". Organisms that feed at several trophic levels have the biomass of that organism allocated proportionately to one level above each of the levels from which it derives its food.

The Lindeman and Elton models *can* be rearranged so that they relate to each other (Figure 4 overleaf). Here the hawk is a single individual feeding at five different trophic levels because it eats small birds, some of which are seed-eaters (trophic level 2) while others eat insects which are themselves from various trophic levels. From Figure 4 we see that trophic level 3 contains part of the hawk, small birds, carnivorous insects and other organisms of a variety of sizes. In the trophic-level model this ragbag of organisms and parts of organisms is expected to have definable properties, particularly with respect to "food-chain dynamics", that is, how the system changes in time. Even here body size wins out because the greatest change with time is caused by the exponential growth of animal populations which is itself very much affected by body size. Small species reproduce faster than large and as Charles Elton observed in 1927 this was the mechanism that ensured there would be small organisms for the large ones to eat. □

* A description of the trophic continuum model, presented at the second International Ecological Congress in Jerusalem, is published as S. H. Cousins (1980) "A trophic continuum derived from plant structure, animal size and a detritus cascade" in the *Journal of Thoretical Biology*, vol 82, p 607-618.

cooled twice, and the other six times. They have different histories, but the properties of the water are dependent on its present temperature, not its history. Thus we have theoretical grounds for thinking that historical models of energy flow, such as trophic levels, could not work even if it *were* possible to slot organisms accurately in trophic levels.

Of all the research papers produced in ecology, Lindeman's paper of 1942 is probably the most famous. It is regularly quoted as having provided the foundation to the study of the flow of energy through food chains. Because of Lindeman's early death we will never know how he might have gone on to develop the concepts and hypotheses he proposed. Yet the use to which his paper has been put is different to the path that Lindeman set out upon. His 1942 paper was about the mechanisms of ecological succession—the driving force behind the replacement of one species by another in an ecosystem. He used the trophic-level analysis as a technique with which to analyse this problem.

Lindeman attributed the concept of the trophic level to the Swiss, Thienemann, and its mathematical description to his mentor at Yale, Evylyn Hutchinson. Thus it is to Hutchinson that we might expect to look for the development of the concept. Here again lies one of the great ironies of this story. Although Hutchinson retained a belief in the concept of the trophic level certainly as far as 1978, his own research was much concerned with the properties of animal size. In the late 1950s, he published a paper, jointly with Robert MacArthur, proposing a theory of the distribution of animals of different sizes in an ecosystem. His other achievements were in noting the importance of the size of feeding apparatus—a bird's beak, for instance—in its feeding opportunities, and he compared the sizes of feeding apparatus used by species in a community. Finally, he was intrigued by the change in diet of an organism, say a fish, as it grew from tiny fry to full adult. Here was the best example of how ecosystems were populated by species which could not fit into discrete trophic levels.

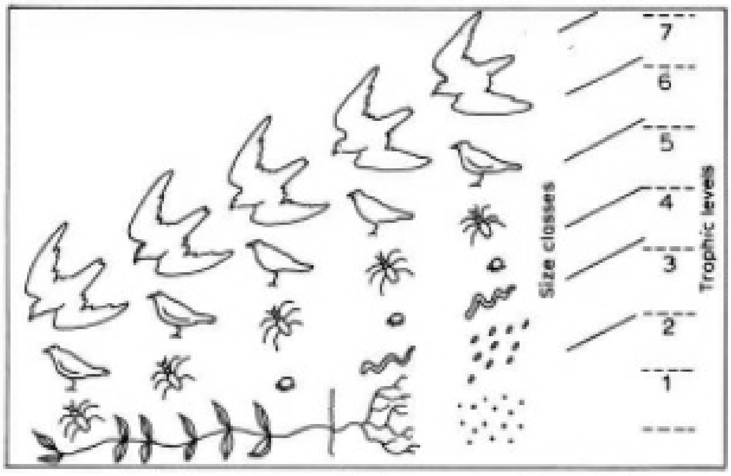


Figure 4 *The Lindeman and Elton models, rearranged so that they relate to one another: a hawk feeds at five trophic levels*

Ecology does not quite have to go back 60 years to start again with Elton's work. But there is much rethinking to be done. The trophic level concept is not just wrong at the edges; it is erroneous in fundamental ways that create many difficulties for ecological science. Marine biologists have begun making Eltonian pyramids again, and so have a very few terrestrial biologists. It is time more joined in. □

Dr Steve Cousins is a researcher in the Energy Research Group of the Open University and a member of the UNESCO Scientific Committee on Oceanographic Research (SCOR) working group on ecosystem theory.