

Food Webs: From the Lindeman Paradigm to a Taxonomic General Theory of Ecology

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Introduction

Food web studies hold a special place within the discipline of ecology. Fretwell (1987) has made this explicit by the rhetorical title of his paper "Food chain dynamics: The central theory of ecology?" A central, or, general theory of ecology would require that the key components of the science could be derived solely from the study of food chains or food webs. The concept of ecosystem is of particular importance to a general theory of ecology and it is shown how the ecosystem can be defined from the food web. The statement (McNaughton et al., 1989) that "Ecosystems are structurally organized as food webs" identifies the approach taken here, which is quite distinct from the Tansley-Lindeman concept that ecosystems are physical-chemical-biological systems. A general theory of ecology should also exhibit a clear relationship to the theory of evolution and to the domains of other sciences. The spatial scale derived from foraging areas within a food web is used to define intrinsic spatial scale in ecology and from this to define the domain of ecology as distinct from other sciences. The requirement that any general theory of ecology should be consistent with the theory of evolution is met both in the definition of the ecosystem as a reproductive lineage (Hull, 1974) and by the rejection of trophic level categories in favor of taxonomic categories from which to derive the properties of food webs (Cousins, 1985, 1988).

The search for general theories in ecology persists (Allen and Hoekstra, 1991) despite

the unpopularity of the approach (McIntosh, 1987). At this time, progress in science is anticipated from local theories which are not required to be mutually coherent. "Let a thousand flowers bloom," appears to be the motto of current science. However I believe that progress has come in food web studies where mutual coherence has been sought, e.g., by linking food webs to other ecological phenomena: to nutrient cycling (DeAngelis, 1992), spatial scale (Kitching, 1987; Cousins, 1990; Pahl-Wostl, 1993; Holt, this volume), predator life cycles, (see Sir Alistair Hardy in Colinvaux (1973), and Winemiller (this volume)) and many other combinations. Perhaps seen in this light of the successful but piecemeal integration of broad ecological processes into food web studies, Fretwell's objective of food webs providing ecology with its core theory appears less controversial.

To achieve a coherent theory of food webs, and therefore of ecology, is still a major goal. In my view, it is necessary to step back to the origins of the food web approach (Elton, 1927; Lindeman, 1942) and to reassemble the parts in a different way.

Lindeman's Contribution

The idea that trophic relationships occupy a central place in ecological theory is certainly supported by Lindeman's writings. In his 1942 paper he develops Tansley's concept of ecosystem (Tansley, 1935) into the now widely used definition of a unit with no intrinsic

sic scale that contains both biotic and abiotic parts. The evolution of ecosystem states (succession) through the mechanism of increasingly efficient trophic transfers is the core hypothesis and the meaning of the 1942 paper's title. The state variables to be measured were not species populations but the biomass contents of trophic levels. Nutrient cycling is a feature of Lindeman's trophic network. In reviewing Elton (1927) he discussed the importance of body size and the number of links commonly found in food chains. Finally, he adopted the measurement of energy content of food and feeder and suggested that general theories of thermodynamics could be applied to ecology.

The context that Lindeman set still forms the framework with which food web ecology grapples. Where should system boundaries be placed? What is an ecosystem? Do such systems evolve? What is the relevance of the species to ecosystems? How is nutrient cycling incorporated in food webs? How do we balance food chain dynamics with energy flow measures and thermodynamics? Lindeman's framework has become so much a part of our education and assumptions that we often cease to look at it critically.

Critique

Food webs are representations of ecological systems which are determined by two issues: the definition of the categories of the web and the nature of the interactions between them. These are mutually dependent, so that the selection of stocks (categories) determines flows (interactions) or *vice versa*. If a coherent theory of food webs is to develop it will come from the analysis of which categories to draw or which interactions to measure. At this stage, it is appropriate to examine the assumptions implicit in certain category constructions and so open the way for other ways of viewing the system.

We can first examine the framework that trophic level analysis has bequeathed to food web studies. I have critiqued the trophic level concept elsewhere (Cousins, 1980, 1987). Here I draw attention to one particular aspect—the (vertical) scaling of trophic space

that the trophic level imposes. I then examine and propose alternative scaling methods.

In a three-trophic-level chain (the categories are biomasses that have undergone the same number of trophic transfers) the food web has three nodes and two arcs (Figure 23.1a). Plant photosynthesis, herbivory, and carnivory are often taken as approximations to the interactions of three integer levels in Figure 23.1a). However those flows are exact interactions between taxonomic categories. Thus if we replace the trophic level categories by taxonomic kingdoms (1 *Plantae*, 2 *Animalia*) then we have the combinations of plants, animals eating plants, animals eating animals (Figure 23.1b).

In Figure 23.1c flows are used to determine categories (1 plants, 2 animals that only eat plants, 3 animals that eat animals) still provides a taxonomic classification. If we now wish to calculate the trophic level position of the categories in this web, it is obviously 1 for the plant, 2 for the herbivore, and some value greater than 3 for the carnivore category. Why this is the case can be seen by comparison of Figure 23.1c with Figure 23.1a. The precise value of any of these categories is dependent on the scaling that was set by treating the green plant as unity and adding one for each trophic transfer of any kind.

The quality of green plants as food varies greatly both among species (diatoms, trees) and among plant parts (seeds, leaves, wood). Thus the term *herbivory* is applied to very different mechanical and chemical interactions depending on the plant, or plant part eaten. Why then are we content to scale trophic space with a metric, the green plant, which is itself highly variable? A ruler which utilized centimeters of varied and arbitrary length would not be a very useful device to understand the action of force and distance even if some information, and certainly lots of data, were produced as a result of using it.

An alternative metric can be constructed from the thermodynamic principles that Lindeman sought to apply in ecology. Taking Elton's (1927) approach and considering the distribution of animals as particles of different sizes (the pyramid of number), we may consider the ecosystem to be populated by

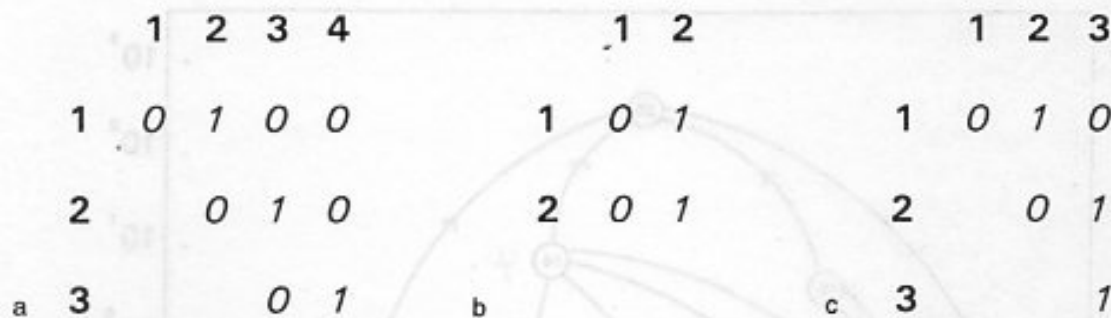


Figure 23.1. Food web for one system (a) with stocks as trophic levels 1–4, (b) with stocks as taxonomic kingdoms, Plantae 1, Animalia, 2, (c) with stocks determined by taxonomically defined flows as herbivory and carnivory.

statistically unlikely occurrences of local, high-energy-dense states which are the organisms themselves. The creation of these energy-dense states can be described by calculable changes in entropy (Cousins, 1988). A new scaling arises when we consider biological processes as concentrators which create local organizations, or concentration, by capturing solar-derived energy and reradiating only part of it as heat. If, as Morowitz (1968) declares, most animal biomass is made of similar material, then the concentration achieved is the size of the particle and trophic space is scaled by particle size. A similar approach was developed by Odum in his Crafoord Lecture (Odum 1988) and see also Patten (1992), Gaedke (1993), and Platt (1985).

Figure 23.2 shows a food web which has been scaled by the body masses of the identified web components of a swamp in South Florida (see Cohen 1989, Cohen et al. 1990, and Jonsson and Ebenman (1994). The web is a sink web to the alligator node (25), the top predator of the water body. Similar webs can be constructed for the terrestrial top predator in the area, the bobcat, and the areal top predators, the raptors. Dependent on the size of predator and the size of food, very different degrees of concentration occur for each trophic transfer as, for example, the link 1 → 10 (phytoplankton and periphyton to crayfish) compared to the link 7 → 12 (insect larvae to mosquito fish). A more systematic data structure is required if the food web is to accurately represent the process of biomass concentration.

Odum (1988) identifies low energy quality with dispersed energy sources and sees trophic interactions as concentrators which cre-

ate smaller quantities of high-quality protoplasm, with "large flows of low-quality energy being converged and transformed into smaller and smaller volumes of higher and higher-quality types of energy. . . . Thus it is incorrect to use energy as a measure of work where more than one type of energy is concerned." Cousins (1988) similarly states that energy quality needs to be taken into account in any energy description of ecosystems which is consistent with the second law of thermodynamics; two biomasses are not equivalent if they exist at different body masses.

The key difference between these two approaches is the adherence to trophic level transfers as the metric for scaling trophic space in Odum's case and direct measurement of concentration here. Odum's view implies that large size and higher trophic level are effectively the same. However each trophic level has members of all sizes (bacteria to elephants can form level 2), and at a particular body size all trophic levels can be found. So even at a simplistic level, if concentration is the core process, then a direct measure of concentration is preferred.

It is important to note that in an ecosystem description structured by biological concentration processes, some plant parts will be at a considerably higher state, as defined by the density of available energy, than some animal states similarly defined; the seed at a higher state than the bacterium, the seed and the herbivorous insect at the same state and both eaten by the finch. When we view the green plant from this perspective, we do not see the plant as being at the base of the food chain but at the side, since different parts

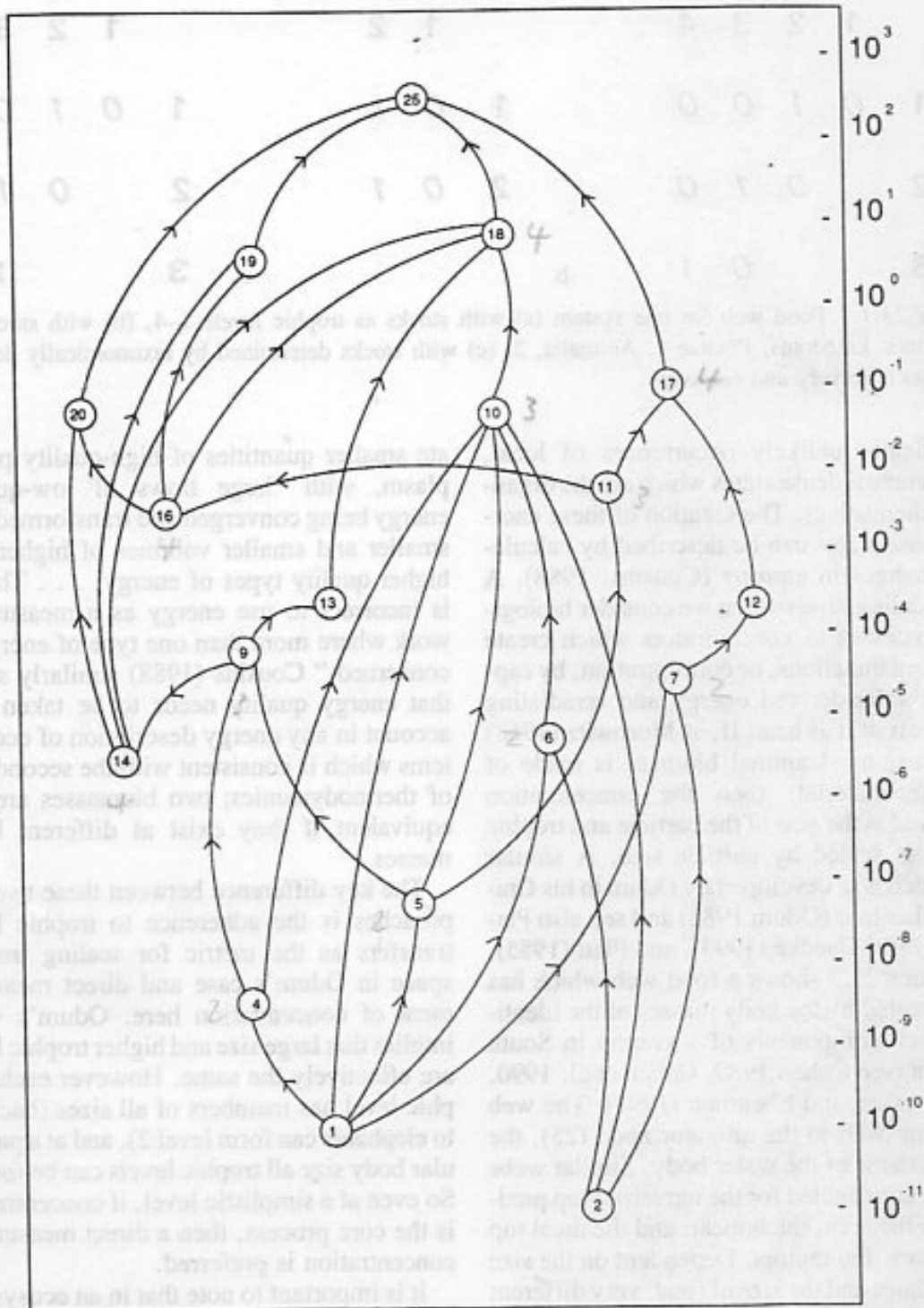


Figure 23.2. The sink web of the alligator for web 47 (Cohen 1988) with interactions scaled by body weight in kg. Node identities and masses (Johnsson and Ebenman 1994), 1 phytoplankton 1×10^{-10} kg, periphyton, 2 detritus 1×10^{-11} kg, 4 copepods 5×10^{-9} kg, 5 cladocerans 5×10^{-8} kg, 6 amphipods 7×10^{-6} kg, 7 insect larvae 4×10^{-5} kg, 9 plecopterans 5×10^{-5} kg, odenates 5×10^{-4} kg, hemipterans 4×10^{-5} kg, 10 crayfish 5×10^{-2} kg, 11 cyprodontids 5×10^{-3} kg, 12 mosquitofish 8×10^{-4} kg, 13 coleopterans 2×10^{-4} kg, 14 dipterans 3×10^{-6} kg, 16 centrachids 3×10^{-3} kg, 17 snakes 0.1 kg, turtles, 0.2 kg, 18 bowfin 8 kg, 19 gar 3 kg, 20 pickerel 5×10^{-2} kg, 25 alligators 300 kg.

are differently concentrated from seeds and storage organs to dispersed leaf drip. Thus plants and animals overlap on a food web space dimensioned by available energy represented by body size in animals and different plant parts.

A further concept sees plant energy availability as a function of the intimate mixture of inert or defense compounds with digestible plant parts (Cousins, 1980), thereby making the digestible parts less available. In Figure 23.3, the green plant is represented as biomass m at different resource value states where the resource value is defined as the assimilated fraction v , determined by an ingesting herbivore. To make v unique for a given ecosystem, it is further defined as the maximal value of assimilation achieved by the local herbivores. The particular categories identified in Figure 23.3 are important functionally and have interesting temporal behavior (Parkin and Cousins, 1981). The plant biomass distribution $m(v)$ is analogous to the animal number distribution $n(w)$, which describes energy availability by the number of organisms at different weights w . Demment and Van Soest (1989) propose a measure of plant energy availability in terms of plant fiber content.

One of the most important aspects of this change in food web paradigm is that the process of concentration occurs by methods other than by eating. Thus plant and animal growth, decay, defecation, are processes that need to be included formally in a coherent model. For every trophic transfer web, Figure 23.4b, there is a material transfer web, Figure 23.4a. This symbolic representation the particular web (Giles et al., 1986) is of special interest because pike (*Esox lucius*) is a top predator that is also cannibalistic. Thus, a three-species full ecosystem can be created by feeding pike fry on herbivorous zooplank-

ters, and then energy is passed by growth and predation all the way to the largest individual pike which are the top predators. In the material web, the pike show growth, create feces, and ultimately decay if not predated; feces and carcasses decay. A set of equations has been proposed (Parkin and Cousins, 1981; Cousins, 1985) for each of the processes in the predation and materials matrices applying to organisms of all sizes. Predation was determined by a body size-dependent foraging strategy (Pullium, 1974; Charnov, 1976) and applied with parameters specific to different taxonomic classes.

Taxonomy

Snaydon (1973) was perhaps the first to explore, somewhat briefly, the idea that higher taxonomic classes are functional classes in ecology. "There is still a surprising similarity between taxonomic groupings and ecological behavior; plants, animals, fungi are broadly equivalent to producer, consumer, and decomposer levels in ecosystems. Within each of these groups there are also broadly equivalent taxonomic and ecological groupings; for example the taxonomic grouping into algae, bryophytes, and angiosperms broadly correspond to ecological differences and the major taxonomic groupings within the algae broadly correspond to ecological differences." I believe that much of the intrinsic appeal of Lindeman's trophic levels lay in the ease of observing interactions between taxonomic kingdoms (Figure 23.1c), and that problems of observation are enormous once this was no longer possible (i.e., at levels > 3) (Heal and McClean, 1975).

I have described the importance of body size as a measure of biomass concentration and therefore of energy availability of prey

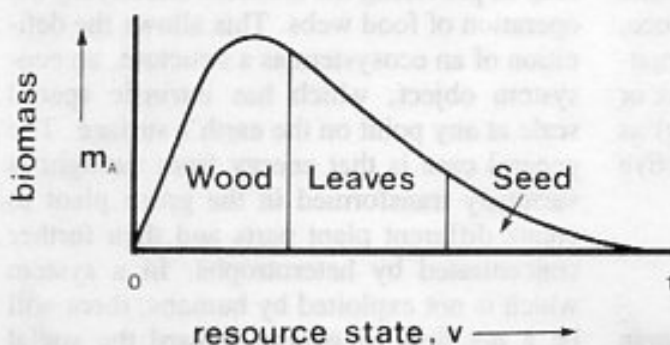


Figure 23.3. The terrestrial plant biomass distribution for resource states defined by assimilation fraction v achieved by the herbivore.

Materials Matrix (Carbon)

	1	2	3	4	5
1 Carcass	1				
2 Feces	1	0			
3 Phytoplankton	1	0	1		
4 Zooplankton	1	1	0	1	
5 Pike	1	1	0	0	1

Predation Matrix

	1	2	3	4	5
1 Carcass	0	0	0	1	0
2 Feces	0	0	1	0	0
3 Phytoplankton			0	1	0
4 Zooplankton				0	1
5 Pike					1

Figure 23.4. A carbon currency web for trophic and material flows affecting resource concentration.

to a potential predator. However this is only one side of the predator-prey relationship and to predict the likelihood of predator-prey encounters and their outcome, characteristics of the predator need to be defined. Body size and higher taxonomy are both important here—an organism's demand for food is influenced by body size-dependent metabolic rates which are taxonomically distinct for unicells, multicellular poikilotherms, and multicellular homiotherms (Hemmingsen, 1960). To meet this food demand the organism has to capture the food in some way, and the processes of foraging and capture are also dependent on the structure of its body, the body plan. This is a mechanistic approach in which evolved structures, which have been taxonomically classified, are seen as setting limits or creating opportunities for trophic interactions; chloroplasts, fins, gills, exoskeletons, wings, sonar, and so on. Thus, although body size is an important ecological parameter (Peters, 1983), allometric relationships hold more precisely within taxonomic groups. In predicting the spatial and, hence, trophic interactions of a 10-g particle, it matters greatly whether it is a bird, a mollusk or a fish. The body plan (higher taxonomy) as well as body size is important for predictive ecology.

Ecosystem Objects

The definition of ecosystem that Lindeman (1942) developed from Tansley (1935) is

problematic in at least two ways. If ecosystems include organisms and their environment, this is difficult in the sense that systems are normally defined by an excluded environment at the system boundary. The second problem is similar: Lindeman sees ecosystems as having physical-chemical-biological interactions; being made up of biotic and abiotic; and being present at any scale on earth. By these definitions, ecosystems are everything, yet a definition which includes everything tells you nothing. Although systems may be defined at any spatial scale (Holling 1992), are they all ecosystems? The class of self-organizing systems (Nicholis and Prigogine, 1977; Allen, 1985) includes living organisms and their interactions. Unlike the subjective view of system definition, Allen and Starr (1982), if we know the system attractors of self-organizing systems this allows the identification of structures that those attractors create.

The process of biomass concentration is seen as providing the attractor underlying the operation of food webs. This allows the definition of an ecosystem as a structure, an ecosystem object, which has intrinsic spatial scale at any point on the earth's surface. The general case is that energy from sunlight is variously transformed in the green plant to create different plant parts and then further concentrated by heterotrophs. In a system which is not exploited by humans, there will be a net flow of energy toward the social group of the top predator defined as the indi-

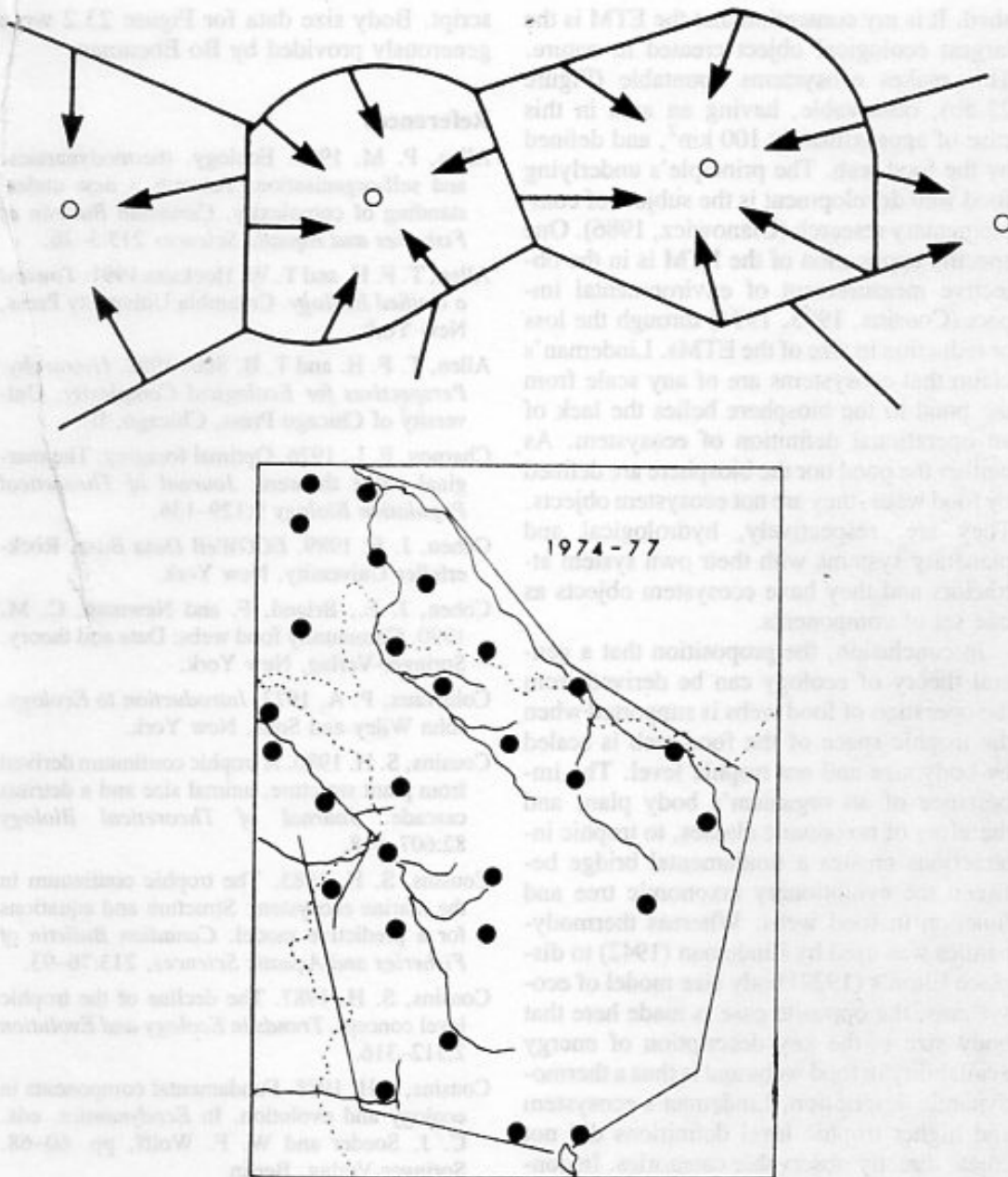


Figure 23.5. The Ecosystem Trophic Module (ETM) shown (a) as a photon shed created by the territorial boundaries of the top predator social group where the arrows represent the net direction of energy flow for the food web to the territory center; and (b) as an empirical distribution, or field, of ETMs identified by centers of prides of lion (•) on the Serengeti (Hanby and Bygott, 1979).

viduals of the largest species that can predate (not parasitize) the largest prey species. The group size may be one individual, but larger social groups allow for both cooperative hunting and for the structure to persist longer than lifetimes of component members.

Little of the energy incident on the top predator's territory will reach the predator itself but its direction of net flow will depend on which side of the top predator territorial

boundary it falls (Figure 23.5a). This ecological unit which includes all organisms found within the territorial boundary has been named the Ecosystem Trophic Module (ETM) (Cousins, 1988, 1990). More recently Power (personal communication) has viewed the ETM as a photon shed, a basin of attraction for the movement of chemically fixed energy originating in solar radiation, analogous to the movement of water on a water-

shed. It is my contention that the ETM is the largest ecological object created in nature. This makes ecosystems countable (Figure 23.5b), observable, having an area in this case of approximately 100 km², and defined by the food web. The principle's underlying food web development is the subject of complementary research (Ulanowicz, 1986). One specific application of the ETM is in the objective measurement of environmental impact (Cousins, 1993, 1994) through the loss or reduction in size of the ETMs. Lindeman's claim that ecosystems are of any scale from the pond to the biosphere belies the lack of an operational definition of ecosystem. As neither the pond nor the biosphere are defined by food webs, they are not ecosystem objects. They are, respectively, hydrological and planetary systems with their own system attractors and they have ecosystem objects as one set of components.

In conclusion, the proposition that a general theory of ecology can be derived from the operation of food webs is supported when the trophic space of the food web is scaled by body size and not trophic level. The importance of an organism's body plan, and therefore of taxonomic classes, to trophic interactions creates a fundamental bridge between the evolutionary taxonomic tree and function in food webs. Whereas thermodynamics was used by Lindeman (1942) to displace Elton's (1927) body size model of ecosystems, the opposite case is made here that body size is the key description of energy availability in food webs and is thus a thermodynamic description. Lindeman's ecosystem and higher trophic level definitions did not create directly observable categories. In contrast, organism mass, body plan, and top predator territory form an observable basis from which to create a coherent ecology structured on the food web. Defining the ecosystem from the food web gives ecology an intrinsic scale and differentiates ecology from other sciences.

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