



TROPHIC LEVELS

Peter Yodzis
University of Guelph

- I. Food Chains and Trophic Levels
 - II. The Utility of Trophic Levels
 - III. Food Webs and Trophic Levels
-

significance of trophic levels both as categories of description universally applicable to all ecosystems and as expressions of ecosystem bioenergetics.

GLOSSARY

- basal species** A species that eats no other species.
- ecological transfer efficiency** The ratio of energy ingested by a population's predators to energy ingested by the population.
- food chain** A sequential relationship of the form x_1 is eaten by x_2 which is eaten by x_3 which is eaten by \dots which is eaten by x_n .
- food web** A specification of which species eat which in an ecosystem.
- trophic level of a species** $1 +$ a weighted average of the lengths of all food chains linking that species to basal species. Different weightings may be appropriate for addressing different questions.
-

THE TROPHIC LEVEL OF A SPECIES in an ecosystem is a measure of the length of food chains linking that species to basal species (autotrophs + detritus). This article will present the several different ways in which this concept can be construed, will indicate the appropriate context for each definition, and will discuss the

I. FOOD CHAINS AND TROPHIC LEVELS

Trophic ecology has to do with feeding relations—for instance, weasels eat mice, mice eat herbs—and is among the most basic organizing principles underlying biodiversity in natural ecosystems. One of the earliest attempts to identify ecosystem structure was based on trophic ecology, as follows. Some species in nature (mostly plants) do not eat anything; instead they utilize solar energy through photosynthesis and are called *primary producers* or *autotrophs*. Other species eat autotrophs and are called *herbivores* (Fig. 1). *Carnivores* eat herbivores, *secondary carnivores* eat carnivores, *tertiary carnivores* eat secondary carnivores, and so on (Fig. 1). These are, of course, highly aggregated entities: each of the categories just mentioned contains many species in any given ecosystem.

A *food chain* is a sequential relationship of the form x_1 is eaten by x_2 which is eaten by x_3 which is eaten by \dots which is eaten by x_n , where the entities x_i might be individual species, or they might be aggregations such as those just defined.

Early trophic ecology (approximately the 1930s

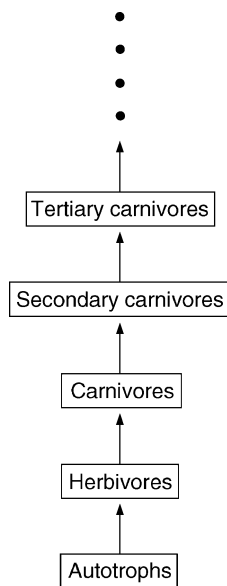


FIGURE 1 The IBP conception of an ecosystem as a linear sequence of trophic levels.

through 1970s) viewed an ecosystem as a single food chain involving the aggregated entities just defined, as depicted in Fig. 1. In this view of an ecosystem, autotrophs constitute “trophic level” 1, carnivores constitute “trophic level” 2, secondary carnivores are “trophic level” 3, and so on. [I am using “scare quotes” for the term “trophic level” because there are difficulties with this particular definition, which I will discuss in Section III.] The International Biological Program (IBP) of 1964–1974 was very much organized around this concept of ecosystem structure.

The concepts of food chain and trophic level are very closely related. Thus, in the formulation sketched in Fig. 1, species in the n th trophic level are linked to primary production (autotrophs) through a food chain of length $n - 1$.

There is another food chain that is very important in a great many ecosystems, namely, the one that is based on detritus. Detritus is certainly eaten by a wide variety of organisms, but it is not itself a living organism, so it cannot exactly be said to “eat” anything. However, biomass does move from living organisms into detritus as they decay after dying. If one is concerned to follow the recycling of specific nutrients, one needs to keep track of this entire dynamic. For purely trophic studies it is generally adequate (and far simpler) to treat detritus as though it were another organism that, like an autotroph, does not eat anything. Then autotrophs and detritus together are called *basal species*, and the detriti-

vores are lumped together with the herbivores in trophic level number 1.

II. THE UTILITY OF TROPHIC LEVELS

The trophic level concept has been exceptionally durable: it has been one of the basic concepts of ecology for six decades and is one of the few ecological concepts contained in the vocabulary of most educated people. The reason for this distinguished place in the scheme of things is that the concept is both simple and useful. Furthermore, it is universal: it applies to all ecosystems.

Because of this universality, trophic levels enable us to compare the role of vastly different species in vastly different systems. For instance, we can discuss and understand a lake and the surrounding forest with a common language: the forest has its vegetation and its leaf litter; the lake has its phytoplankton and its dissolved organic matter (basal species). The forest has herbivorous insects, birds, and mammals; the lake has zooplankton (herbivores). And so on. We can use the same language to compare these two systems with any other ecosystem anywhere in the world.

This categorical and conceptual role can be made more quantitative and detailed, revealing important similarities and important differences among systems, by adopting a *bioenergetic* viewpoint, as follows.

Biological organisms contain caloric energy, which is transferred to organisms in the next step up a food chain: herbivores gain energy from consuming basal species, carnivores gain energy by consuming herbivores, and so forth. Each organism, or set of organisms such as a trophic level, *produces* energy at a certain rate. This is the maximum rate at which the next trophic level up the food chain could in principle ingest energy.

The rate of energy production by a trophic level must necessarily be less than the rate of energy ingestion by that trophic level. First, not all energy ingested by an organism is available to be metabolized by that organism. Some of it will be lost to excretion. The ratio of metabolizable energy to ingested energy is called *assimilation efficiency* and is typically about 0.45 for herbivores and 0.85 for carnivores. Of the metabolizable energy, some is lost to respiration, being used up by the organism to carry out its various activities and also simply to live, and the remainder is available for the production of new tissue, which can in principle be consumed by the next trophic level. The ratio of energy production to metabolizable energy is called *production efficiency* and ranges from about 0.1 to 0.4 for invertebrate ectotherms to about 0.01–0.03 for endotherms.

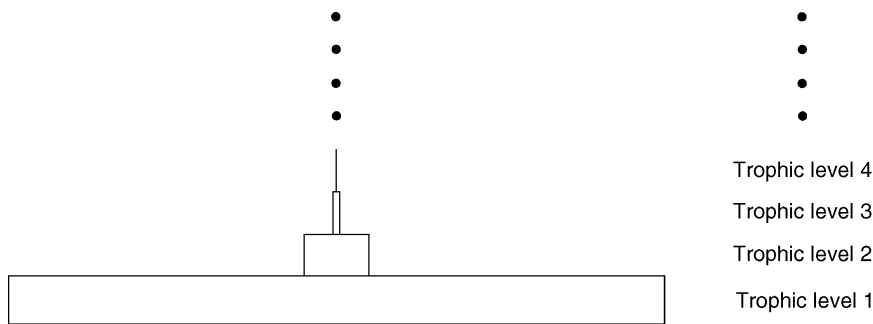


FIGURE 2 The pyramid of production in an ecosystem. The width of each layer is proportional to the rate of production of biomass in the corresponding trophic level. Because energy is dissipated in each transfer from one trophic level to the next, production decreases at an approximately geometric rate as trophic level increases.

Furthermore, not all of the energy produced at a trophic level will actually be ingested by the next higher trophic level: much of it will be missed and end up as detritus. There is no generally agreed term for this form of energy loss, nor is there a great deal of quantitative data for it.

The *ecological transfer efficiency* of a trophic level is the ratio of (energy ingested from that trophic level by the next highest trophic level) to (energy ingested by that trophic level). It is the product of the three efficiencies explicated in the preceding paragraph. Ecological transfer efficiency ranges from 0.001 or smaller (depending upon losses to detritus) up to a maximum of about 0.5.

It quickly becomes apparent that energy is dissipated quite rapidly as we ascend a food chain. Suppose, for example, that each ecological transfer efficiency in a food chain is 0.1, which is rather high. Then of the energy produced by basal species (primary production), one-tenth is produced by herbivores. One-tenth of that, or one-hundredth of primary production, is produced by carnivores. One-tenth of that, or one-thousandth of primary production, is produced by secondary carnivores, and so on up the food chain. Less and less energy is available to higher trophic levels as we move up a food chain. One can visualize this phenomenon as a “pyramid of production” for a food chain (Fig. 2).

This geometrically decreasing production as we move up a food chain, hence the rapidly decreasing available energy flow for the next higher trophic level, has been offered as one possible explanation for the apparently limited number of trophic levels in natural systems. Eventually, as we move up a food chain, the small fraction of primary production available to a putative next highest trophic level simply will not be enough to support a viable biological population.

The pyramid of production is an inescapable conse-

quence of the dissipative processes, sketched above, that lead to ecological transfer efficiencies less than 1. There are a couple of similar “pyramids” that, while not universal in this way, are fairly typical of trophic levels. They follow from the circumstance that, for the most part, predators tend to be larger than their prey. For a predator to be larger (hence also faster and stronger) than its prey greatly facilitates the capture and consumption of prey.

Thus, as we move to higher trophic levels, we will, generally speaking, see larger animals. And yet, moving to higher trophic levels, these larger animals need to live on smaller energy production from the next trophic level down. As a result, there will usually be fewer animals at higher trophic levels. This “pyramid of numbers” is frequently, though not necessarily always, observed.

An obvious exception to the pyramid of numbers emerges if we treat parasites and parasitoids as “predators”; they are almost always smaller than their “prey.” Even though parasitism is tremendously widespread in nature, these are not really trophic relationships, and so most trophic studies do not include parasites or parasitoids.

What about total biomass [= (number of animals) \times (weight of each animal)] at each trophic level? The number of animals tends to decrease as trophic level increases, while the weight of each animal tends to increase. The result is equivocal. Particularly in aquatic systems, where very small organisms at low trophic levels have very rapid rates of biomass turnover and can be grazed to quite low levels, one frequently (but not always) sees “inverted pyramids” of biomass, with more biomass at higher trophic levels. But terrestrial systems typically (though by no means always) display pyramids of biomass, with less biomass at higher trophic levels.

There are exceptions to this scheme, but they prove the rule; that is, they make sense in terms of the ideas underlying the scheme. For instance, some of the very largest animals, such as elephants and big ungulates, are herbivores. These animals are so large that they could not possibly range far enough to live by eating, say, lions. The only way to get a high enough energy density to support such large animals is by feeding directly on plants.

Just as energy propagates upward through food chains, so may chemical substances contained in organisms. This becomes particularly interesting when toxic contaminants are present. If those toxic substances are absorbed and/or ingested by animals at some trophic level, then, depending upon the rate at which they are excreted, there may be residues in the tissue consumed by higher trophic levels. Under some circumstances, the concentration of toxins may increase as trophic level increases, which is called *biomagnification*.

III. FOOD WEBS AND TROPIC LEVELS

The conception of an ecosystem as a linear chain of “trophic levels” (Fig. 1) is a useful starting point, but if we examine trophic relations with a higher degree of taxonomic resolution—that is, not lumping so many biological species together as we did in motivating Fig. 1—we find quite a different trophic structure. A *food web* is a specification of which species eat which in an ecosystem. For instance, Fig. 3 is a food web for Wytham Wood, a forest near Oxford in England. An arrow from one kind of organism to another indicates that the organisms at the head of the arrow eat the organisms at the other end.

One can detect something like “trophic levels” here (partly because of the way I chose to draw the picture), but there is certainly not a simple flow of energy through a linear sequence of levels as in Fig. 1; this picture is more “webby.” For instance, we might put weasels at “trophic level” 5, because they eat titmice, which eat spiders, which eat insects, which eat herbs. But weasels also eat voles and mice, which eat herbs: this would put weasels at “trophic level” 3.

We do not want to throw away the trophic level concept altogether—it is too useful for that—but in the light of more refined data such as Fig. 3, we need to refine our concept of trophic level. In fact, there are a number of different ways that we may define the term “trophic level,” and it seems imprudent to insist that any one definition is “The Right” one. Rather, different

trophic level concepts may be appropriate for different purposes.

The constant theme linking all trophic level concepts together is the idea that trophic level has to do with the lengths of food chains linking a species to basal species. We just have to bear in mind that a species will generally be linked to basals through several food chains, which might be of different lengths. For instance, there are 13 food chains that link weasels to basal species in the Wytham Wood food web of Fig. 3. Three of these have length 2, 9 of them have length 3, and 1 of them has length 4. The relative importance assigned to these 13 food chains distinguishes several different definitions of “trophic level.” Five commonly used definitions are listed here; following discussion of these, a sixth, in a considerably different spirit, will be addressed:

1. $1 +$ the length of the shortest food chain linking a species to some basal species.
2. $1 +$ the length of the longest food chain linking a species to some basal species.
3. $1 +$ the mean length of food chains linking a species to some basal species.
4. $1 +$ the weighted mean length of food chains linking a species to some basal species, where the weighting reflects energy flow through each food chain.
5. $\lambda + (\delta X_{\text{organism}} - \delta X_{\text{reference level}})/E$, where E is the average enrichment of a heavy isotope and $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$. Here X denotes the heavy isotope (for instance, ^{13}C , ^{15}N , or ^{34}S) and R denotes the heavy/light ratio (for instance, $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, or $^{34}\text{S}/^{32}\text{S}$). The trophic level of the reference level organisms is λ : this might be basal species ($\lambda = 1$), or perhaps herbivores ($\lambda = 2$).

Definition 5 requires explanation. Certain heavy isotopes are enriched relative to the light isotope in biochemical reactions. As a result, the ratio of heavy to light isotope in an organism’s tissue may bear a systematic relation to the ratio in that organism’s diet. For instance, the ratio $^{15}\text{N}/^{14}\text{N}$ appears to be enriched by $E = 3.4\text{‰}$ ($\pm 1\text{‰}$) in a wide variety of organisms. Therefore, if we know the isotope ratio for organisms at some reference trophic level, we can use Definition 5 to calculate a trophic level from measurements of the isotope ratio in other organisms. The resulting numbers, which are a weighted average over all food chains from the reference level to the organisms in question, are probably fairly close to what we would get from Definition 4. This method requires far less effort than a direct calculation

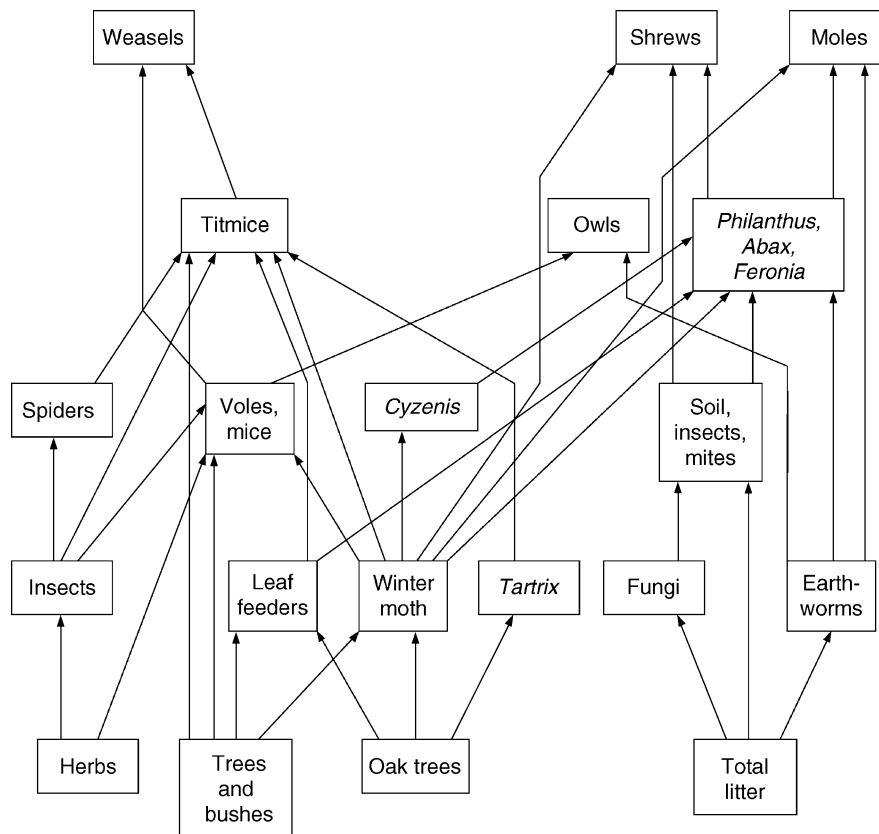


FIGURE 3 A food web for Wytham Wood, England (based on data in Varley, 1970).

of Definition 4 would; for instance, there is no need to measure dietary proportions. It does require careful calibration of isotope ratios at the reference level, including allowance for possible differences among species at that level. In practice, use of the $^{13}\text{C}/^{12}\text{C}$ ratio has not been fruitful, in part because so little ^{13}C is enriched at each trophic transfer, but as of this writing, the $^{15}\text{N}/^{14}\text{N}$ ratio appears to hold promise as a tool for trophic studies.

Table I shows, for each nonbasal species in the Wytham Wood food web, the frequency distribution of food chains linking that species to basals and the consequent trophic level according to Definitions 1–3. (Definitions 4 and 5 require more data than are available for the Wytham Wood food web.) For instance, depending upon the relative importance attached to the 13 food chains linking weasels to basal species, we may put weasels at trophic level 3 (shortest chain; Definition 1), 5 (longest chain; Definition 2), or 3.8 (mean length; Definition 3).

Generally speaking, one would like to use something like Definition 4, even though it means replacing the

notion of discrete trophic levels with a trophic continuum. However, calculating trophic level in this way requires a tremendous amount of data. Definition 5 may be a good surrogate, but it still requires data beyond the food web itself. One is tempted to regard Definition 3 as a reasonably good substitute, but if we are thinking energetically, then because of the dissipation of energy as we move up a food chain, the shorter chains may well be more important energetically than the longer ones, so the equal weighting of Definition 3 may be deceptive. Definition 2 is what one has in mind implicitly when one draws tidy pictures such as Fig. 3, but the existence of very long food chains can be deceptive. Animals that have a food chain to basals with 8, 9, or even 10 links exist, but they invariably also have chains no longer than 3 links, and these shorter chains are likely more important energetically. However, very long food chains may be particularly significant if one is concerned with biomagnification of toxin concentrations.

Another viewpoint, which ought to produce a sixth trophic level definition if it could be articulated pre-

TABLE I
Food Chains and Trophic Levels in the Wytham Wood Food
Web of Fig. 3

| Species | Number of chains to basal species of length | | | | Trophic level using | | |
|--|---|---|---|---|---------------------|------------------|----------------|
| | 1 | 2 | 3 | 4 | Shortest chain | Longest chain | Mean length |
| Insects | 1 | 0 | 0 | 0 | 2 | 2 | 2.0 |
| Winter moth | 2 | 0 | 0 | 0 | 2 | 2 | 2.0 |
| <i>Tartrix</i> | 1 | 0 | 0 | 0 | 2 | 2 | 2.0 |
| Leaf feeders | 2 | 0 | 0 | 0 | 2 | 2 | 2.0 |
| Earthworms | 1 | 0 | 0 | 0 | 2 | 2 | 2.0 |
| Fungi | 1 | 0 | 0 | 0 | 2 | 2 | 2.0 |
| Voles, mice | 2 | 3 | 0 | 0 | 2 | 3 | 2.6 |
| Spiders | 0 | 1 | 0 | 0 | 3 | 3 | 3.0 |
| Titmice | 1 | 6 | 1 | 0 | 2 | 4 | 2.9 |
| <i>Cyzenis</i> | 0 | 2 | 0 | 0 | 3 | 3 | 3.0 |
| <i>Philanthus</i> , <i>Abax</i> , <i>Feronia</i> | 0 | 6 | 3 | 0 | 3 | 4 | 3.3 |
| Soil insects, mites | 1 | 1 | 0 | 0 | 2 | 3 | 2.5 |
| Owls | 0 | 3 | 3 | 0 | 3 | 4 | 3.5 |
| Weasels | 0 | 3 | 9 | 1 | 3 | 5 | 3.8 |
| Shrews | 0 | 3 | 7 | 3 | 3 | 5 | 4.0 |
| Moles | 0 | 3 | 6 | 3 | 3 | 5 | 4.0 |

cisely enough, emphasizes the *top-down* aspect of trophic relationships. This viewpoint, which has been put forward by S. Fretwell and L. Oksanen, counts a predator as one trophic level higher than its prey only if it

significantly controls the biomass or dynamics of the prey species. Oksanen suggests that on this basis the distinction among carnivores, secondary carnivores, tertiary carnivores, and so on largely evaporates, leaving only three true trophic levels: basal species, herbivores, and carnivores—except in pelagic systems, where, due to the very small size of the primary producers and the consequent small size of zooplankton, planktivory and piscivory emerge as truly distinct trophic roles, permitting four trophic levels. This notion that there are actually only a few trophic levels despite the existence of some very long food chains is consonant with the implications of energetics noted in the preceding paragraph.

Thus, the term “trophic level” needs to be used with caution, and if we are to speak quantitatively of trophic levels, we need to specify exactly which definition we are using and to choose a definition that sheds the most light on the particular issues of concern.

See Also the Following Articles

ECOTOXICOLOGY • ENERGY FLOW AND ECOSYSTEMS •
FOOD WEBS • PREDATORS, ECOLOGICAL ROLE OF •
SPECIES INTERACTIONS

Bibliography

- Polis, G. A., and Winemiller, K. O. (1996). *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York.
- Rundel, P. W., Ehleringer, J. R., and Nagy, K. A. (Eds.) (1989). *Stable Isotopes in Ecological Research*. Springer-Verlag, New York.
- Varley, G. C. (1970). The concept of energy applied to a woodland community. In *Animal Populations in Relation to Their Food Resources* (A. Watson, Ed.). Blackwell Sci., Oxford.
- Yodzis, P. (1989). *Introduction to Theoretical Ecology*. Harper-Collins, New York.