

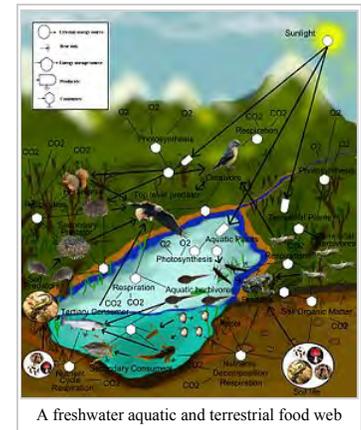
## Food web

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A **food web** (or **food cycle**) is the natural interconnection of food chains and a graphical representation (usually an image) of what-eats-what in an ecological community. Another name for **food web** is a consumer-resource system. Ecologists can broadly lump all life forms into one of two categories called trophic levels: 1) the autotrophs, and 2) the heterotrophs. To maintain their bodies, grow, develop, and to reproduce, autotrophs produce organic matter from inorganic substances, including both minerals and gases such as carbon dioxide. These chemical reactions require energy, which mainly comes from the sun and largely by photosynthesis, although a very small amount comes from hydrothermal vents and hot springs. A gradient exists between trophic levels running from complete autotrophs that obtain their sole source of carbon from the atmosphere, to mixotrophs (such as carnivorous plants) that are autotrophic organisms that partially obtain organic matter from sources other than the atmosphere, and complete heterotrophs that must feed to obtain organic matter. The linkages in a food web illustrate the feeding pathways, such as where heterotrophs obtain organic matter by feeding on autotrophs and other heterotrophs. The food web is a simplified illustration of the various methods of feeding that links an ecosystem into a unified system of exchange. There are different kinds of feeding relations that can be roughly divided into herbivory, carnivory, scavenging and parasitism. Some of the organic matter eaten by heterotrophs, such as sugars, provides energy. Autotrophs and heterotrophs come in all sizes, from microscopic to many tonnes - from cyanobacteria to giant redwoods, and from viruses and bdellovibrio to blue whales.

Charles Elton pioneered the concept of food cycles, food chains, and food size in his classical 1927 book "Animal Ecology"; Elton's 'food cycle' was replaced by 'food web' in a subsequent ecological text. Elton organized species into functional groups, which was the basis for Raymond Lindeman's classic and landmark paper in 1942 on trophic dynamics. Lindeman emphasized the important role of decomposer organisms in a trophic system of classification. The notion of a food web has a historical foothold in the writings of Charles Darwin and his terminology, including an "entangled bank", "web of life", "web of complex relations", and in reference to the decomposition actions of earthworms he talked about "the continued movement of the particles of earth". Even earlier, in 1768 John Bruckner described nature as "one continued web of life".

Food webs are limited representations of real ecosystems as they necessarily aggregate many species into trophic species, which are functional groups of species that have the same predators and prey in a food web. Ecologists use these simplifications in quantitative (or mathematical) models of trophic or consumer-resource systems dynamics. Using these models they can measure and test for generalized patterns in the structure of real food web networks. Ecologists have identified non-random properties in the topographic structure of food webs. Published examples that are used in meta analysis are of variable quality with omissions. However, the number of empirical studies on community webs is on the rise and the mathematical treatment of food webs using network theory had identified patterns that are common to all. Scaling laws, for example, predict a relationship between the topology of food web predator-prey linkages and levels of species richness.



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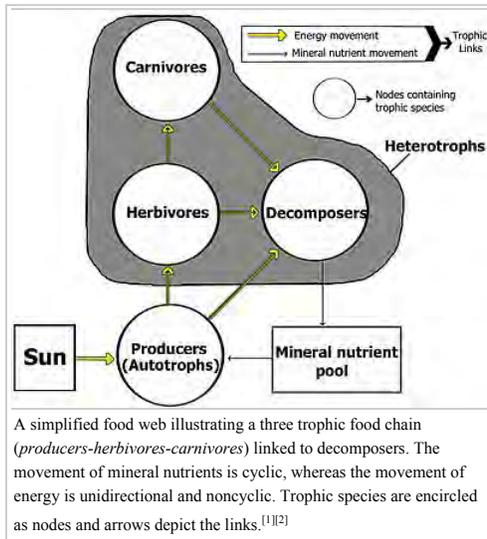
### Taxonomy of a food web

Links in food webs map the feeding connections (who eats whom) in an ecological community. *Food cycle* is an obsolete term that is synonymous with food web. Ecologists can broadly group all life forms into one of two trophic layers, the autotrophs and the heterotrophs. Autotrophs produce more biomass energy, either chemically without the sun's energy or by capturing the sun's energy in photosynthesis, than they use during metabolic respiration. Heterotrophs consume rather than produce biomass energy as they metabolize, grow, and add to levels of secondary production. A food web depicts a collection of polyphagous heterotrophic consumers that network and cycle the flow of energy and nutrients from a productive base of self-feeding autotrophs.<sup>[3][4][5]</sup>

The base or basal species in a food web are those species without prey and can include autotrophs or saprophytic detritivores (i.e., the community of decomposers in soil, biofilms, and periphyton). Feeding connections in the web are called trophic links. The number of trophic links per consumer is a measure of food web connectance. Food chains are nested within the trophic links of food webs. Food chains are linear (noncyclic) feeding pathways that trace monophagous consumers from a base species up to the top consumer, which is usually a larger predatory carnivore.<sup>[6][7][8]</sup>

Linkages connect to nodes in a food web, which are aggregates of biological taxa called trophic species. Trophic species are functional groups that have the same predators and prey in a food web. Common examples of an aggregated node in a food web might include parasites, microbes, decomposers, saprotrophs, consumers, or predators, each containing many species in a web that can otherwise be connected to other trophic species.<sup>[9][10]</sup>

### Trophic levels



In the simplest scheme, the first trophic level (level 1) is plants, then herbivores (level 2), and then carnivores (level 3). The trophic level is equal to one more than the chain length, which is the number of links connecting to the base. The base of the food chain (primary producers or detritivores) is set at zero.<sup>[3][13]</sup> Ecologists identify feeding relations and organize species into trophic species through extensive gut content analysis of different species. The technique has been improved through the use of stable isotopes to better trace energy flow through the web.<sup>[14]</sup> It was once thought that omnivory was rare, but recent evidence suggests otherwise. This realization has made trophic classifications more complex.<sup>[15]</sup>

### Trophic dynamics

The trophic level concept was introduced in a historical landmark paper on trophic dynamics in 1942 by Raymond L. Lindeman. The basis of trophic dynamics is the transfer of energy from one part of the ecosystem to another.<sup>[13][16]</sup> The trophic dynamic concept has served as a useful quantitative heuristic, but it has several major limitations including the precision by which an organism can be allocated to a specific trophic level. Omnivores, for example, are not restricted to any single level. Nonetheless, recent research has found that discrete trophic levels do exist, but "above the herbivore trophic level, food webs are better characterized as a tangled web of omnivores."<sup>[15]612</sup>

A central question in the trophic dynamic literature is the nature of control and regulation over resources and production. Ecologists use simplified one trophic position food chain models (producer, carnivore, decomposer). Using these models, ecologists have tested various types of ecological control mechanisms. For example, herbivores generally have an abundance of vegetative resources, which meant that their populations were largely controlled or regulated by predators. This is known as the top-down hypothesis or 'green-world' hypothesis. Alternatively to the top-down hypothesis, not all plant material is edible and the nutritional quality or antiherbivore defenses of plants (structural and chemical) suggests a bottom-up form of regulation or control.<sup>[17][18][19]</sup> Recent studies have concluded that both "top-down" and "bottom-up" forces can influence community structure and the strength of the influence is environmentally context dependent.<sup>[20][21]</sup> These complex multitrophic interactions involve more than two trophic levels in a food web.<sup>[22]</sup>

Another example of a multi-trophic interaction is a trophic cascade, in which predators help to increase plant growth and prevent overgrazing by suppressing herbivores. Links in a food-web illustrate direct trophic relations among species, but there are also indirect effects that can alter the abundance, distribution, or biomass in the trophic levels. For example, predators eating herbivores indirectly influence the control and regulation of primary production in plants. Although the predators do not eat the plants directly, they regulate the population of herbivores that are directly linked to plant trophism. The net effect of direct and indirect relations is called trophic cascades. Trophic cascades are separated into species-level cascades, where only a subset of the food-web dynamic is impacted by a change in population numbers, and community-level cascades, where a change in population numbers has a dramatic effect on the entire food-web, such as the distribution of plant biomass.<sup>[23]</sup>

### Energy flow and biomass

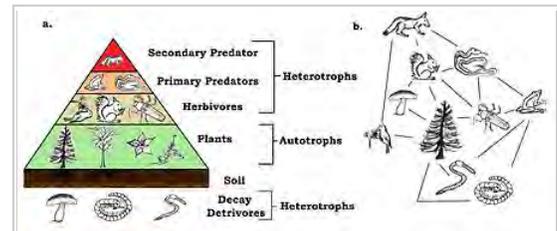
The Law of Conservation of Mass dates from Antoine Lavoisier's 1789 discovery that mass is neither created nor destroyed in chemical reactions. In other words, the mass of any one element at the beginning of a reaction will equal the mass of that element at the end of the reaction.<sup>[24]:11</sup>

Food webs depict energy flow via trophic linkages. Energy flow is directional, which contrasts against the cyclic flows of material through the food web systems.<sup>[26]</sup> Energy flow "typically includes production, consumption, assimilation, non-assimilation losses (feces), and respiration (maintenance costs)."<sup>[5]:5</sup> In a very general sense, energy flow (E) can be defined as the sum of metabolic production (P) and respiration (R), such that  $E=P+R$ .

The mass (or biomass) of something is equal to its energy content. Mass and energy are closely intertwined. However, concentration and quality of nutrients and energy is variable. Many plant fibers, for example, are indigestible to many herbivores leaving grazer community food webs more nutrient limited than detrital food webs where bacteria are able to access and release the nutrient and energy stores.<sup>[27][28]</sup> "Organisms usually extract energy in the form of carbohydrates, lipids, and proteins. These polymers have a dual role as supplies of energy as well as building blocks; the part that functions as energy supply results in the production of nutrients (and carbon dioxide, water, and heat). Excretion of nutrients is, therefore, basic to metabolism."<sup>[28]:1230-1231</sup> The units in energy flow webs are typically a measure mass or energy per m<sup>2</sup> per unit time. Different consumers are going to have different metabolic assimilation efficiencies in their diets. Each trophic level transforms energy into biomass. Energy flow diagrams illustrate the rates and efficiency of transfer from one trophic level into another and up through the hierarchy.<sup>[29][30]</sup>

Food webs have trophic levels and positions. Basal species, such as plants, form the first level and are the resource limited species that feed on no other living creature in the web. Basal species can be autotrophs or detritivores, including "decomposing organic material and its associated microorganisms which we defined as detritus, micro-inorganic material and associated microorganisms (MIP), and vascular plant material."<sup>[11]:94</sup> Most autotrophs capture the sun's energy in chlorophyll, but some autotrophs (the chemolithotrophs) obtain energy by the chemical oxidation of inorganic compounds and can grow in dark environments, such as the sulfur bacterium *Thiobacillus*, which lives in hot sulfur springs. The top level has top (or apex) predators which no other species kills directly for its food resource needs. The intermediate levels are filled with omnivores that feed on more than one trophic level and cause energy to flow through a number of food pathways starting from a basal species.<sup>[12]</sup>

Food webs are the road-maps through Darwin's famous 'entangled bank' and have a long history in ecology. Like maps of unfamiliar ground, food webs appear bewilderingly complex. They were often published to make just that point. Yet recent studies have shown that food webs from a wide range of terrestrial, freshwater, and marine communities share a remarkable list of patterns.<sup>[3]:669</sup>



A trophic pyramid (a) and a simplified community food web (b) illustrating ecological relations among creatures that are typical of a northern Boreal terrestrial ecosystem. The trophic pyramid roughly represents the biomass (usually measured as total dry-weight) at each level. Plants generally have the greatest biomass. Names of trophic categories are shown to the right of the pyramid. Some ecosystems, such as many wetlands, do not organize as a strict pyramid, because aquatic plants are not as productive as long-lived terrestrial plants such as trees. Ecological trophic pyramids are typically one of three kinds: 1) pyramid of numbers, 2) pyramid of biomass, or 3) pyramid of energy.<sup>[4]</sup>



Food webs are necessarily aggregated and only illustrate a tiny portion of the complexity of real ecosystems. For example, the number of species on the planet are likely in the general order of  $10^7$ , over 95% of these species consist of microbes and invertebrates, and relatively few have been named or classified by taxonomists.<sup>[53][54][55]</sup> It is explicitly understood that natural systems are 'sloppy' and that food web trophic positions simplify the complexity of real systems that sometimes overemphasize many rare interactions. Most studies focus on the larger influences where the bulk of energy transfer occurs.<sup>[17]</sup> "These omissions and problems are causes for concern, but on present evidence do not present insurmountable difficulties."<sup>[3]:669</sup>

There are different kinds or categories of food webs:

- **Source web** - one or more node(s), all of their predators, all the food these predators eat, and so on.
- **Sink web** - one or more node(s), all of their prey, all the food that these prey eat, and so on.
- **Community (or connectedness) web** - a group of nodes and all the connections of who eats whom.
- **Energy flow web** - quantified fluxes of energy between nodes along links between a resource and a consumer.<sup>[3][38]</sup>
- **Paleoecological web** - a web that reconstructs ecosystems from the fossil record.<sup>[56]</sup>
- **Functional web** - emphasizes the functional significance of certain connections having strong interaction strength and greater bearing on community organization, more so than energy flow pathways. Functional webs have compartments, which are sub-groups in the larger network where there are different densities and strengths of interaction.<sup>[36][57]</sup> Functional webs emphasize that "the importance of each population in maintaining the integrity of a community is reflected in its influence on the growth rates of other populations."<sup>[38]:511</sup>

Within these categories, food webs can be further organized according to the different kinds of ecosystems being investigated. For example, human food webs, agricultural food webs, detrital food webs, marine food webs, aquatic food webs, soil food webs, Arctic (or polar) food webs, terrestrial food webs, and microbial food webs. These characterizations stem from the ecosystem concept, which assumes that the phenomena under investigation (interactions and feedback loops) are sufficient to explain patterns within boundaries, such as the edge of a forest, an island, a shoreline, or some other pronounced physical characteristic.<sup>[58][59][60]</sup>

### Detrital web

In a detrital web, plant and animal matter is broken down by decomposers, e.g., bacteria and fungi, and moves to detritivores and then carnivores.<sup>[61]</sup> There are often relationships between the detrital web and the grazing web. Mushrooms produced by decomposers in the detrital web become a food source for deer, squirrels, and mice in the grazing web. Earthworms eaten by robins are detritivores consuming decaying leaves.<sup>[62]</sup>

"Detritus can be broadly defined as any form of non-living organic matter, including different types of plant tissue (e.g. leaf litter, dead wood, aquatic macrophytes, algae), animal tissue (carion), dead microbes, faeces (manure, dung, faecal pellets, guano, frass), as well as products secreted, excreted or exuded from organisms (e.g. extra-cellular polymers, nectar, root exudates and leachates, dissolved organic matter, extra-cellular matrix, mucilage). The relative importance of these forms of detritus, in terms of origin, size and chemical composition, varies across ecosystems."<sup>[46]:585</sup>

### Quantitative food webs

Ecologists collect data on trophic levels and food webs to statistically model and mathematically calculate parameters, such as those used in other kinds of network analysis (e.g., graph theory), to study emergent patterns and properties shared among ecosystems. There are different ecological dimensions that can be mapped to create more complicated food webs, including: species composition (type of species), richness (number of species), biomass (the dry weight of plants and animals), productivity (rates of conversion of energy and nutrients into growth), and stability (food webs over time). A food web diagram illustrating species composition shows how change in a single species can directly and indirectly influence many others. Microcosm studies are used to simplify food web research into semi-isolated units such as small springs, decaying logs, and laboratory experiments using organisms that reproduce quickly, such as daphnia feeding on algae grown under controlled environments in jars of water.<sup>[35][63]</sup>

While the complexity of real food webs connections are difficult to decipher, ecologists have found mathematical models on networks an invaluable tool for gaining insight into the structure, stability, and laws of food web behaviours relative to observable outcomes. "Food web theory centers around the idea of connectance."<sup>[64]:1648</sup> Quantitative formulas simplify the complexity of food web structure. The number of trophic links ( $t_L$ ), for example, is converted into a connectance value:

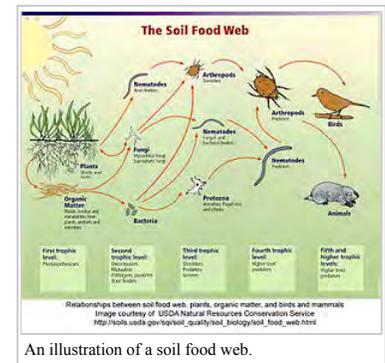
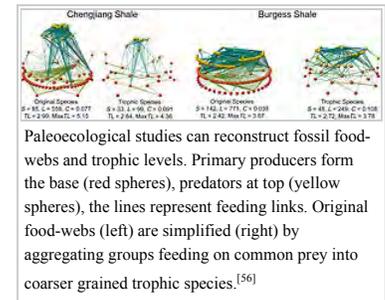
$$C = \frac{t_L}{S(S-1)/2},$$

where,  $S(S-1)/2$  is the maximum number of binary connections among  $S$  species.<sup>[64]</sup> "Connectance ( $C$ ) is the fraction of all possible links that are realized ( $L/S^2$ ) and represents a standard measure of food web complexity..."<sup>[65]:12913</sup> The distance ( $d$ ) between every species pair in a web is averaged to compute the mean distance between all nodes in a web ( $D$ )<sup>[65]</sup> and multiplied by the total number of links ( $L$ ) to obtain link-density ( $LD$ ), which is influenced by scale dependent variables such as species richness. These formulas are the basis for comparing and investigating the nature of non-random patterns in the structure of food web networks among many different types of ecosystems.<sup>[65][66]</sup>

Scaling laws, complexity, chaos, and patterned correlates are common features attributed to food web structure.<sup>[67][68]</sup>

### Complexity and stability

Food webs are complex. Complexity is a measure of an increasing number of permutations and it is also a metaphorical term that conveys the mental intractability or limits concerning unlimited algorithmic possibilities. In food web terminology, complexity is a product of the number of species and connectance.<sup>[69][70][71]</sup> Connectance is "the fraction of all possible links that are realized in a network."<sup>[72]:12917</sup> These concepts were derived and stimulated through the suggestion that complexity leads to stability in food webs, such as increasing the number of trophic levels in more species rich ecosystems. This hypothesis was challenged through mathematical models suggesting otherwise, but subsequent studies have shown that the premise holds in real systems.<sup>[69][73]</sup>





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