

» Environmental Science: » Ecology - general



## Ecological energetics

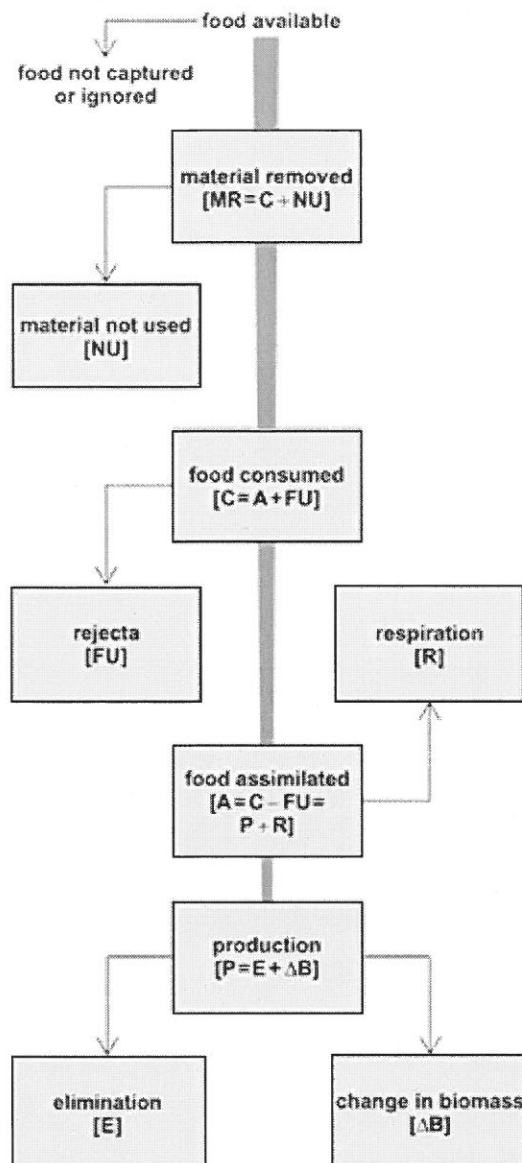
**T**he study of the flow of energy within an ecological system from the time the energy enters the living system until it is ultimately degraded to heat and irretrievably lost from the system. It is also referred to as production ecology, because ecologists use the word production to describe the process of energy input and storage in ecosystems.

Ecological energetics provides information on the energetic interdependence of organisms within ecological systems and the efficiency of energy transfer within and between organisms and trophic levels. Nearly all energy enters the biota by green plants' transformation of light energy into chemical energy through photosynthesis; this is referred to as primary production. This accumulation of potential energy is used by plants, and by the animals which eat them, for growth, reproduction, and the work necessary to sustain life. The energy put into growth and reproduction is termed secondary production. As energy passes along the food chain to higher trophic levels (from plants to herbivores to carnivores), the potential energy is used to do work and in the process is degraded to heat. The laws of thermodynamics require the light energy fixed by plants to equal the energy degraded to heat, assuming the system is closed with respect to matter. An energy budget quantifies the energy pools, the directions of energy flow, and the rates of energy transformations within ecological systems. See also: [Biological productivity](#); [Food web](#); [Photosynthesis](#)

The peak of studies in ecological energetics occurred in the 1960s and early 1970s largely because a major concern of the International Biological Program was an appraisal of the biological productivity of terrestrial and aquatic communities in relation to human welfare. Initially considered to have the potential of becoming a unifying language in ecology—an ecological Rosetta Stone—the subject has yielded little in the way of general theory.

The essentials of ecological energetics can be most readily appreciated by considering the schema ([Fig. 1](#)) of energy flowing through an individual; it is equally applicable to populations, communities, and ecosystems. Of the food energy available, only part is harvested (MR) in the process of foraging. Some is wasted (NU), for example, by messy eaters, and the rest consumed (C). Part of the consumed food is transformed but is not utilized by the body, leaving as fecal material (F) or as nitrogenous waste (U), the by-product of protein metabolism. The remaining energy is assimilated (A) into the body, part of which is used to sustain the life functions and to do work—this is manifest as oxygen consumption. The remainder of the assimilated energy is used to produce new tissue, either as growth of the individual or as development of offspring. Hence production is also the potential energy (proteins, fats, and carbohydrates) on which other organisms feed. Production (P) leads to an increase in biomass (B) or is eliminated (E) through death, migration, predation, or the shedding of, for example, hair, skin, and antlers.

**Fig. 1** Diagrammatic representation of energy flow through an ecological unit; abbreviations are explained in the text.

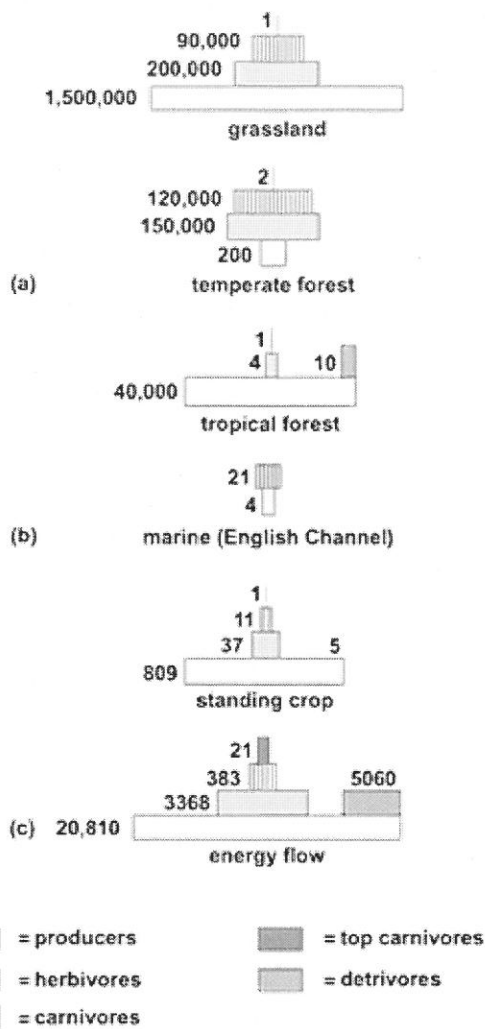


### Pathways

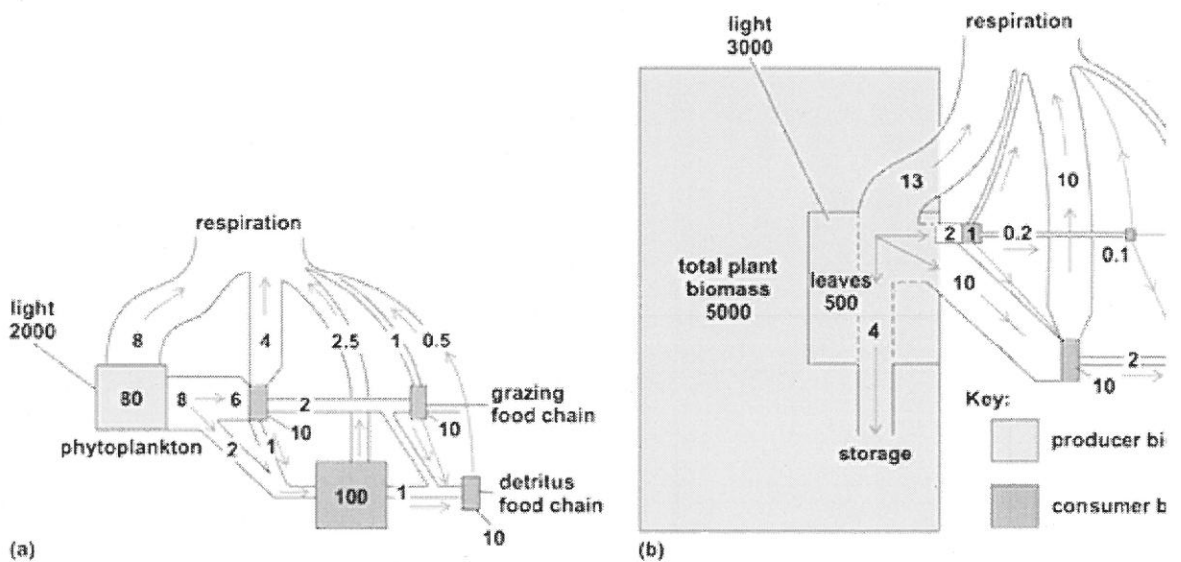
Energy flows through the consumer food chain (from plants to herbivores to carnivores) or through the detritus food chain. The latter is fueled by the waste products of the consumer food chain, such as feces, shed skin, cadavers, and nitrogenous waste. Most detritus is consumed by microorganisms such as bacteria and fungi, although this food chain includes conspicuous carrion feeders like beetles and vultures. In terrestrial systems, more than 90% of all primary production may be consumed by detritus feeders. In aquatic systems, where the plants do not require tough supporting tissues, harvesting by herbivores may be efficient with little of the primary production passing to the detritivores.

Pyramids of biomass are used to depict the amount of living material, or its energetic equivalent, present at one time in the different trophic levels (Fig. 2). Although the energy flow cannot increase at higher trophic levels, pyramids of biomass may be inverted, especially in aquatic systems. This occurs because the index  $P/B$  is inversely related to the size of the organisms. Hence a small biomass may support a high level of production if the biomass is composed of small individuals (Fig. 3).

**Fig. 2** Trophic levels of a number of ecosystems represented in different units. (a) As numbers of individuals per 1000 m<sup>2</sup> of grassland and temperate forest community in summer; microorganisms and soil animals excluded. (b) The standing crop or biomass (grams dry weight per meter squared) of terrestrial (Panamanian tropical rainforest) and marine (English Channel) communities; note the inversion of the marine pyramid. (c) The aquatic community of Silver Springs, Florida, represented as standing crop (kilocalorie per meter) and energy flow (kilocalories per meter per year). (After E. P. Odum, *Fundamentals of Ecology*, 3d ed., W. B. Saunders, 1971)



**Fig. 3** Models of energy flow through two contrasting ecosystems: (a) a marine bay and (b) a forest. The boxes represent the biomass in kilocalories per meter and the flow lines show the energy flux (kilocalories per meter per day) along the various pathways. The boxes and the flux lines are scaled to indicate their relative magnitudes. (After E. P. Odum, *Relationships between structure and function in the ecosystem*, *Jap. J. Ecol.*, 12:108-118, 1962)



**Units**

Traditionally the calorie, a unit of heat energy, has been used, but this has been largely replaced by the joule. Confusion is possible, especially in the field of nutrition, because with an initial capital, Calorie may denote kilocalories. Biomass or standing crop is expressed as potential energy per unit

area, but the other compartments in Fig. 1, for example *P* and *R*, are expressed in terms of energy flux or rates. The efficiency values such as  $P/A$  are dimensionless, but the ratio  $P/B$  is a rate—the inverse of the turnover time.

**Measurement of energy flow**

For illustrative purposes some general methods for assessing biological productivity are described here in the context of energy flow through a population. Production is measured from individual growth rates and the reproductive rate of the population to determine the turnover time. The energy equivalent of food consumed, feces, and production can be determined by measuring the heat evolved on burning a sample in an oxygen bomb calorimeter, or by chemical analysis —determining the amount of carbon or of protein, carbohydrate, and lipid and applying empirically determined caloric equivalents to the values. The latter three contain, respectively, 16.3, 23.7, and 39.2 kilojoules per gram of dry weight. Maintenance costs are usually measured indirectly as respiration (normally the oxygen consumed) in the laboratory and extrapolated to the field conditions. Error is introduced by the fact that animals have different levels of activity in the field and are subject to different temperatures, and so uncertainty has surrounded these extrapolations. Oxygen consumption has been measured in animals living in the wild by using the turnover rates of doubly labeled water ( $D_2O$ ).

**Levels of inquiry**

Ecological energetics is concerned with several levels of inquiry: the partitioning of energy between the compartments denoted in Fig. 1 ; the pathways traced by the energy as it passes through the trophic levels; and the efficiency of energy transfer between trophic levels. The ratio of energy flux through one compartment in Fig. 1 to any previous compartment is referred to as an efficiency. Numerous efficiencies can be calculated both within and between trophic levels. The most common are the assimilation efficiency ( $A/C$ ), namely the proportion of energy assimilated by the body from the food consumed, and the production efficiency ( $P/A$ ), which denotes the proportion of energy assimilated which ends up as new tissue. These various efficiencies combine to limit the energy available to the higher trophic levels. The ratio of food consumed or ingested at one trophic level to that ingested by the next lower level is termed ecological efficiency. A value of 10% for this efficiency is often cited; consideration of the  $A/C$  and  $P/A$  efficiencies of most organisms shows that it could seldom exceed 15-20%. However, the effect of heat losses at each trophic level in limiting the length of food chains in nature remains controversial.

**Factors affecting efficiency**

Respiration rate of organisms is scaled as the three-quarters power of body weight. Hence larger organisms have proportionately slower rates of respiration. This scaling factor seems to affect many rate processes in the body so that size does not influence those efficiencies which are the focus of ecological energetics. However, different types of organisms of the same size have different metabolic rates. For example, warm-blooded animals have much higher weight-specific respiration rates than cold-blooded ones. Analysis of energy budgets derived for wild-living animals shows that a number of taxonomic and trophic groups can be distinguished according to characteristic production efficiencies (see table). Production efficiency appears to be related to the general level of metabolic activity—animals with high rates of metabolism generally having low production efficiency.

<b>Production efficiency of populations of various classes of animals living in the wild*</b>	
<b>Animal group</b>	<b>Production efficiency (P/A), %</b>
Shrews	0.9
Birds	1.3
Other mammals	3.1
Fish, ants, and termites	9.8
Invertebrates other than insects	25.0
Herbivores	20.8
Carnivores	27.6
Detrivores	36.2
Insects except ants and termites	40.7

Herbivores	38.8
Detrivores	47.0
Carnivores	55.6
*After W. F. Humphreys, Production and respiration in animal populations, <i>J. Anim. Ecol.</i> , 48:427-454, 1979.	

Due to the loss of usable energy with each transformation, in an area more energy can be diverted into production by plants than by consumer populations. For humans this means that utilizing plants for food directly is energetically much more efficient than converting them to eggs or meat. See also: [Biomass](#); [Ecological communities](#); [Ecosystem](#)

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**For Further Study**

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