

number of patterns are manifest in aspects of energy flow and nutrient cycling. *SEE ECOLOGICAL SUCCESSION.*

**Functional organization.** Living organisms are characterized not only by spatial and temporal structure but by an apparent purpose or activity. In short, they are "doing something," and this activity has been termed teleonomy. In humans, for example, various physiological functions are continuously under way until death intervenes. Communities have functions analogous to physiology.

In the first place, the various species within a community have different trophic relationships with one another. One species may eat another, or be eaten by another. A species may be a decomposer, living on dead tissue of one or more other species. Some species are omnivores, eating many kinds of food; others are more specialized, eating only plants or only animals, or even just one other species. These trophic relationships certainly unite the species in a community into a common endeavor, the transmission of energy through the community. This energy flow is patently analogous to an organism's mobilization and transmission of energy from the food it eats. *SEE ECOLOGICAL ENERGETICS.*

One aspect of energy flow is a candidate for an emergent property: the topology of the food web. Examination of this topology for a number of webs suggests that they are highly constrained in structure. For example, the maximum number of trophic levels in a web rarely exceeds five. One reason may be that the total amount of energy that has not already been degraded by the time the energy has passed through three or four levels may not be enough to sustain a viable population of a species that would feed at still higher levels. An alternative explanation is that the population dynamics of a web with so many levels would probably confer mathematical instability on the web, so that one or more species would be eliminated. Other properties of food webs that have been discerned include a low number of omnivore species (those feeding on more than one level), and a tendency for the number of predator species and the number of prey species to be in the ratio of 4:3. No explanation is forthcoming for the latter observation. The former is held to reflect mathematical instability that arises from the presence of omnivores in a web. Other workers contend that neither pattern will be maintained when much more comprehensive data are available on what paths calories actually follow as they flow through a community. If these patterns do not turn out to be artifacts of incomplete knowledge, they would appear to be emergent properties reflecting a high degree of organization. *SEE FOOD WEB; POPULATION DYNAMICS.*

Just as energy flows through the communities, so do nutrients move. A calorie of energy does not move in the abstract from organism to organism; rather, the calorie is bound up in a molecule that moves when one organism eats (or decomposes) another. Or the calorie may be respired away as a result of the metabolism of the organism that ingests it. A calorie of energy, once respired by some member of the community, is no longer available to the community. But the molecule associated with that calorie, or a new molecule produced from it, is still present and can go through the food web again. Thus nutrients can cycle within a community, while energy flow, once the energy is transformed to heat, is one-way. Nutrient cycling is analogous to circulation in an organism, and

combines with energy flow to support the superorganism metaphor. Different nutrients cycle at different rates, and for several nutrients the cycle within the community is linked to cycles in other communities. Nutrients exist in abiotic entities, as well as biotic organisms, so nutrient cycling is as much an ecosystem trait as a community one. A number of properties of nutrient cycling (such as rate, turnover times, and sizes of different pools or compartments) have been measured. Whether any of these are emergent as opposed to collective properties has yet to be determined.

**Productivity.** By virtue of differing rates of photosynthesis by the dominant plants, different communities have different primary productivities. Tropical forests are generally most productive, while extreme environments such as desert or alpine conditions harbor rather unproductive communities. Agricultural communities are intermediate. Algal communities in estuaries are the most productive marine communities, while open ocean communities are usually far less productive. The efficiency with which various animals ingest and assimilate the plants and the structure of the trophic web determine the secondary productivity (production of organic matter by animals) of a community. Marine secondary productivity generally exceeds that of terrestrial communities. *SEE AGROECOSYSTEMS; BIOLOGICAL PRODUCTIVITY.*

**Reproduction.** A final property that any organism must have is the ability to reproduce itself. Communities may be seen as possessing this property, though the sense in which they do so does not support the superorganism metaphor. A climax community reproduces itself through time simply by virtue of the reproduction of its constituent species, and may also be seen as reproducing itself in space by virtue of the propagules that its species transmit to less mature communities. For example, when a climax forest abuts a cutover field, if no disturbance ensues, the field undergoes succession and eventually becomes a replica of the adjacent forest. Both temporally and spatially, then, community reproduction is a collective rather than an emergent property, deriving directly from the reproductive activities of the component species. *SEE ALTITUDINAL VEGETATION ZONES; BOG; CHAPARRAL; DESERT; ECOLOGY; GRASSLAND ECOSYSTEM; MANGROVE SWAMP; MAQUIS; MUSKEG; PARAMO; PUNA; WORLD VEGETATION ZONE.*

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## Ecological energetics

The 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 or organisms within eco-

neighboring soils. Thus they support plant species that are very different from those found in nearby nonserpentine areas, and these different plant species support animal species partially different from those of adjacent areas. Here two different communities are sharply bounded from each other.

Usually, however, communities grade into one another more gradually, through a broad intermediate region (an ecotone) that includes elements of both of the adjacent communities, and sometimes other species as well that are not found in either adjacent community. One has little difficulty telling when one is in the center of either of the adjacent communities A and B, but exactly when one passes from A to B is not easily discerned. The reason is that, though each species in a community is adapted to its physical environment and to some extent to other species in the community, the adaptations to the physical environment are usually not identical, and most of the adaptations to one another are not obligatory.

The environment created by the dominant species, by their effects on temperature, light, humidity, and other physical factors, and by their biotic effects, such as allelopathy and competition, may entrain some other species so that these other species' spatial boundaries coincide with those of the dominants. The mangrove skipper, *Phocides pygmalion*, can feed only on red mangrove, *Rhizophora mangle*, so whatever aspects of the physical environment limit the mangrove (especially temperature), the skipper will also be limited to the same sites. However, many other species that feed on the mangrove (for example, the io moth, *Automeris io*) also feed on other plants, and their spatial boundaries do not coincide with that of the mangrove. Nor do most of the species in a community share identical physical requirements. Black mangrove (*Avicennia germinans*) co-occurs with red mangrove in most sites, and the two are normal constituents of a community often termed mangrove swamp. But *Avicennia* can tolerate much colder weather than can *Rhizophora*, and so it is found much farther north in the Northern Hemisphere. Eventually it too ceases, and the mangrove community is replaced in more northerly areas by salt marsh communities. In some intermediate regions, salt marsh grasses and black mangrove are found together. There is no clear boundary between the two communities.

This continuous intergradation of most communities argues against the superorganism concept, but there are aspects of the spatial arrangement within communities that suggest that the component species are far from independent, and indicate, if not complete holism, at least that some community properties are not easily predicted from exhaustive knowledge of the component species. One example is stratification, the vertical arrangement of canopy layers in most forests. Individuals of the different species do not have heights that are independently and continuously distributed from the ground to the top of the tallest tree. Instead, there are a few rather distinct strata, with each species at maturity characteristically occupying one of these. Tropical forests from all parts of the world, even though they may have completely different species compositions, usually contain five fairly clear strata: a topmost layer composed of the tallest tree species, two lower layers of smaller trees, a shrub layer, and a ground layer. There are doubtless good physical reasons why the diffusion of light can explain this characteristic structure given a knowledge

of evolution and plant physiology (though no completely compelling explanation has yet surfaced), so it may be that this is an elaborate collective property rather than an emergent one. In either case, there is clearly a high degree of multispecies organization in this spatial arrangement. *SEE PHYSIOLOGICAL ECOLOGY (PLANT)*.

In addition to vertical arrangement, horizontal locations of individuals of different species are usually not random. Usually, individuals of a given species are clumped; they are found on average closer to one another than one would have predicted. Probably the major reason for this is response to habitat heterogeneity: conspecific individuals tend to favor more similar habitats than do heterospecific individuals. Individuals of different species may also be nonrandomly arranged with respect to one another. Competitive interactions may cause two species typically to be found in different microsites, while mutualistic interactions or preference for a similar physical habitat may cause two species to be associated spatially. *SEE ECOLOGICAL INTERACTIONS*.

**Succession.** More or less distinct communities tend to follow one another in rather stylized order. As with recognition of spatial boundaries, recognition of temporal boundaries of adjacent communities within a sere is partly a function of the expectations that an observer brings to the endeavor. Those who view communities as superorganisms are inclined to see sharp temporal and spatial boundaries, and the perception that one community does not gradually become another community over an extended period of time confirms the impression that communities are highly organized entities, not random collections of species that happen to share physical requirements. In this superorganismic view, ecological succession of communities in a sere is analogous to the life cycle of an organism, and follows a quite deterministic course. That secondary succession following a disturbance often leads to a community resembling the original one is the analog in the superorganism to wound repair in an organism. The driving force for succession, in this conception, is that the community or its dominant species modify the environment so that these dominant species are no longer favored, and when the dominant species are replaced, the bulk of the community, complexly linked to the dominant species and to one another, disappears as well, to be replaced by the next community in the sere.

This superorganismic conception of succession has been replaced by an individualistic succession. Data on which species are present at different times during a succession show that there is not abrupt wholesale extinction of most members of a community and concurrent simultaneous colonization by most species of the next community. Rather, most species within a community colonize at different times, and as the community is replaced most species drop out at different times. Thus, though one can usually state with assurance that the extant community is of type A or type B, there are extended periods when it is difficult to assign the assemblage of species at a site to any recognizable community.

That succession is primarily an individualistic process does not mean that there are not characteristic changes in community properties as most successions proceed. Species richness usually increases through most of the succession, for example, and stratification becomes more highly organized and well defined. A

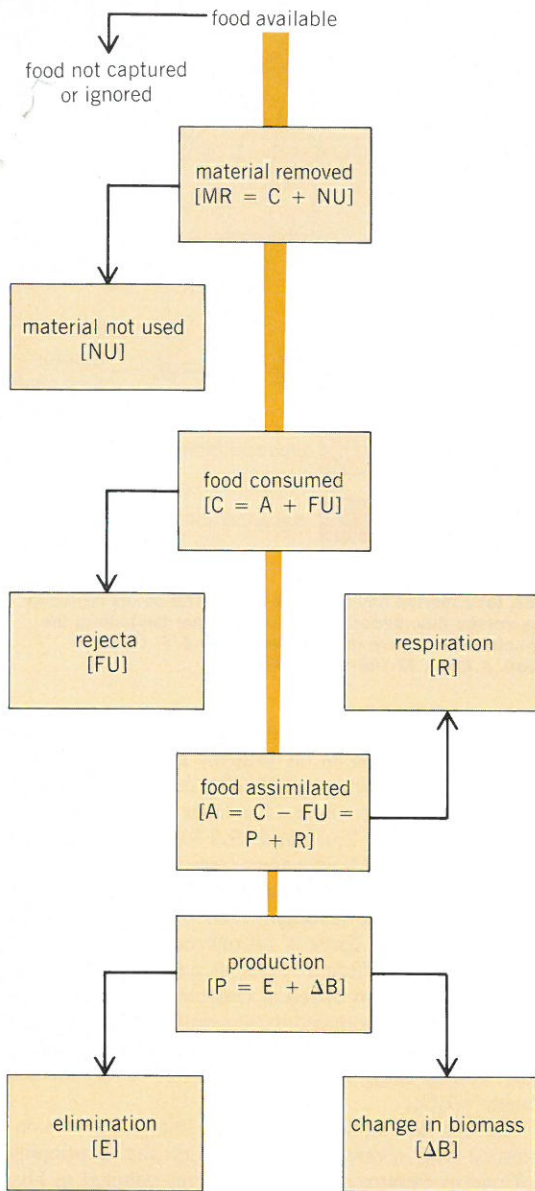


Fig. 1. Diagrammatic representation of energy flow through an ecological unit; abbreviations are explained in the text.

logical 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.

tems. SEE 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.

**Pathways.** Energy flows through the consumer food chain (from plants to herbivores to carnivores)

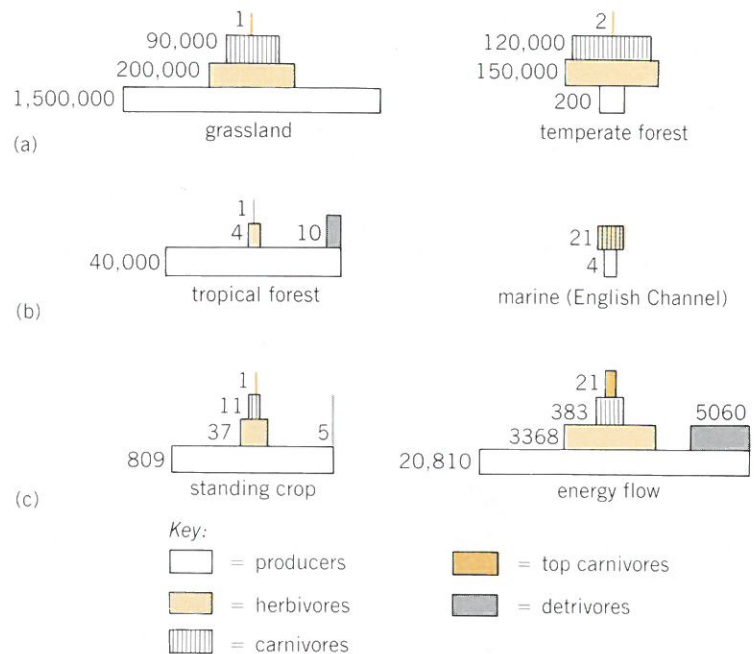


Fig. 2. Trophic levels of a number of ecosystems represented in different units. (a) As numbers of individuals per 1000 m<sup>2</sup> of grassland and temperate forest community in summer; microorganisms and soil animals excluded. (b) The standing crop or biomass (grams dry weight per meter squared) 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)

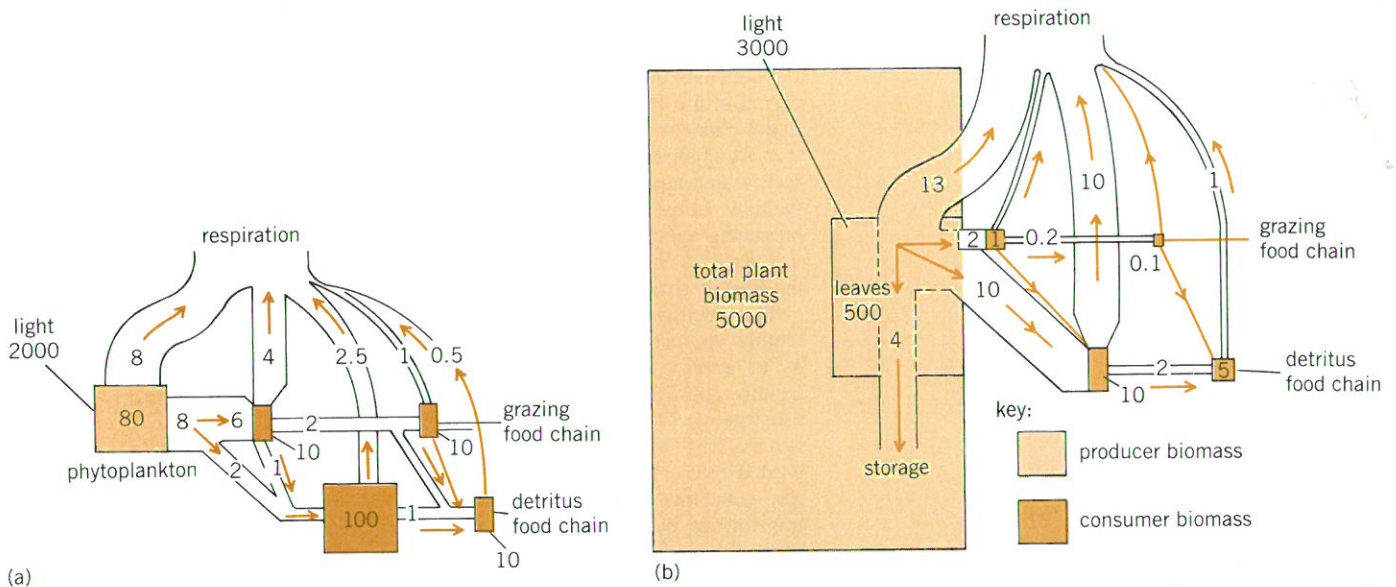


Fig. 3. Models of energy flow through two contrasting ecosystems, (a) a marine bay and (b) a forest. The boxes represent the biomass in kilocalories per meter and the flow lines show the energy flux (kilocalories per meter per day) along the various pathways. The boxes and the flux lines are scaled to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

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).

**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

**Production efficiency of populations of various classes of animals living in the wild\***

Animal group	Production efficiency (P/A), %
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, *J. Anim. Ecol.*, 48:427-454, 1979.

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 organism 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.

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 BIOMASS; ECOLOGICAL COMMUNITIES; ECOSYSTEM.*

W. F. Humphreys

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## Ecological interactions

Relationships between members of different species belonging to a particular ecological community. Ecologists generally classify interactions according to the effect that members of one species have on the population growth rate of a second species. If an increase in one species' population increases the growth rate of a second species' population, the effect is positive or beneficial (denoted by +). If an increase in one species' population decreases the growth rate of a second species' population, the effect is negative or harmful (denoted by -). If neither occurs, the effect is neutral (denoted by 0). Effects may be indirect, in

which case they involve one or more additional species in the community. For example, earthworms increase plant growth and thereby provide more food for caterpillars. Alternatively, effects may be direct; for example, injuries or death may result from territorial fighting between members of different species. *SEE ECOLOGICAL COMMUNITIES.*

An ecological interaction between two species A and B can be denoted by a pair of signs, each member of which may be +, -, or 0. One sign denotes the effect of A on B, and the other denotes the effect of B on A. In this designation, direct effects are usually used; but in the case of competition for food, indirect effects involving the food species are also frequently considered. Effects between species that are more indirect than the latter are not discussed here.

Pairwise combinations of signs give six possible types of interactions. The interaction (+, +), in which each species benefits the other, is mutualism. Some authorities still use the term symbiosis to describe the (+, +) interaction, but this term is now generally defined as any kind of nonneutral interaction among species, positive or negative. The interaction (-, -), in which each species harms the other, is called competition. The interaction (+, -), in which one species benefits and the other is harmed, is called predation. [Parasitism, also (+, -), in which the benefitted species is much smaller than the harmed species and usually derives food or shelter from it, is sometimes distinguished from other types of predation.] The interaction (+, 0), in which one species benefits and the other is unaffected, is called commensalism. The interaction (-, 0), in which one species is harmed and the other is unaffected, is called amensalism. Finally, the interaction (0, 0), in which neither species is affected, is called neutralism. One may argue that species in the same ecological community always have some effect, however small, on each other, so that these last three types of interactions cannot really occur. One may counterargue that if the effect is small enough, it can be ignored, so that it is still useful to think in terms of interactions with zero effect. Nonetheless, examples of amensalism are virtually unreported, and examples of commensalism are relatively rare. Of the first three interactions, ecologists have concentrated much more on competition and predation than on mutualism, possibly because of mutualism's lesser importance. However, as illustrated below, numerous examples of mutualism do exist.

**Competition.** Interspecific competition occurs when two species negatively affect one another. Two principal kinds of competition are recognized. Exploitative competition between species occurs when individuals of one species, by consuming some resource, usually food, deprive individuals of another species of that resource and thereby lower the second species' population growth rate. Interference competition is more direct; it occurs when individuals of one species directly harm individuals of a second species. The degree to which such an effect is harmful can be quite varied. Organisms may kill other organisms by producing toxins or by fighting; fighting may also produce injuries. More subtle types of interference competition occur when individuals interact with one another in such a way as to use energy that might have been used for the production of offspring, or take up time that might have been used to gather additional energy for the production of offspring.

**Frequency: interference versus exploitative.** The relative frequencies of these two types of competition vary among different kinds of organisms. Interference seems most common among organisms that compete for space. For example, a myriad of fouling organisms settle on bare space in marine habitats such as rock, coral surfaces, and the bottoms of boats; examples are barnacles, sponges, tunicates, and various algae. Such organisms compete by secretion of toxins and by physical overgrowth and overcrowding. Among vertebrates, competition for space between individuals of different species is rarer, though it is common in coral reef fishes and is known in birds and lizards. In these vertebrates, the mechanism of competition is fighting or more subtle modes of aggression. In all cases, individuals of the competing species require much the same resource: the fouling organisms require space on which to settle and gather food or light, and the vertebrates eat much the same types of food in the same habitats. Such common requirements explain the adaptive significance of interference mechanisms; were it not for the consequent acquisition of resources necessary for the production of offspring, the time and energy spent in interference would not be worthwhile.

Interspecific exploitative competition is probably at least as widespread in nature as interference competition, owing to the reason just stated: where interference behavior occurs, the adaptive rationale is to secure resources that would otherwise be depleted by members of another species. However, because the mechanisms are more indirect, it is more difficult to observe in its entirety. In contrast to interference behavior such as fighting, which is directly observable, to show exploitative competition one must observe resource depletion by members of one species and then demonstrate that those resources would probably have been used by members of the other species. For both types of competition, one must also demonstrate that the interference or resource depletion adversely affects population growth rate. The difficulty of doing so without elaborate experiments implies that most evidence for competition is inferential. For example, it is frequently assumed that if two species live in the same area and use much the same resources, they are in competition; indeed, the intensity of such competition is frequently measured by the degree of overlap in resource types, such as foods. If this assumption is usually true, the implication is that exploitative competition is very common, since species frequently overlap in resource use. However, such competition may not be very intense, since the overlap is frequently small. Indeed, a low overlap in resource use is frequently taken as evidence of past competition, and may be the result of evolutionary changes developing from selection to avoid competition.

**Adaptations of competitors.** Species similar in many ways frequently differ in certain structures or behaviors that allow them to exploit most efficiently different types of foods or other resources. For example, three species of ground-inhabiting finches occur in the same community on the Galapagos Islands. As was first noted by Darwin, these species differ greatly in the sizes of their beaks, and several ecologists have recently demonstrated that the species take different sizes of seeds. The Galapagos finches represent a group that has evolved from a common ancestral species in virtual isolation, and it is thought that the adaptive significance of different-sized beaks is to

avoid interspecific exploitative competition.

**Use of resources.** How species differ in their use of resources is called resource partitioning, and numerous studies have demonstrated a variety of such differences. Most frequently, animals differ in the habitats in which they feed. For example, certain lizard species differ in the places in vegetation in which they forage; some inhabit leaves, others twigs, others trunks, and others foliage near the ground. Differences in food type (such as size or hardness) are almost as common, as in the Galapagos finches. Least common are differences in the time of resource use, though insect or lizard species frequently differ in daily activity time.

**Experimental demonstrations.** In part because of their greater difficulty, experimental demonstrations of ongoing competition are much rarer than inferences from observations of the sort just discussed. Such demonstrations are perhaps most common for plants and have led to the conclusion that plant height is usually the most important characteristic correlated with competitive success. This is because plants compete most frequently for light, and taller individuals can shade other individuals, making it difficult for the latter to photosynthesize and ultimately leading to their deaths. Among animals, competition has been most frequently demonstrated in species that compete for space. A classical study showed that the depth zonation of two species of barnacles in an intertidal habitat results from a combination of competition and physiological limitation. Larvae of the higher species could settle and grow at the depth occupied by the lower species, but under natural conditions were prevented from doing so: the lower species grew against the other and slowly "bulldozed" it off the rock. The lower species, which is the superior competitor, does not take over the entire habitat, however, since it cannot survive the desiccation to which the higher species is exposed. Another well-studied example involves two starfish species co-occurring over much of the northwestern American coast. These species are carnivorous and are of greatly different sizes. Apparently, they coexist largely by taking different-sized foods, though interference also occurs: one pinches the other with numerous structures called pedicellariae. The resource overlap is significant enough, however, so that experiments have shown substantial ongoing competition: when the larger species population is artificially depressed, the other increases; when it is increased, the other decreases. Although competition experiments have usually been performed with closely related species, an interesting exception involves rodents and ants from southwestern American deserts. Using huge enclosures, ecologists have recently demonstrated that members of these two groups compete for seeds.

**Population dynamics.** By definition, when two species of competitors meet, they negatively affect one another's population growth rate. The ultimate outcome of this process, in terms of the survival or extinction of the species in the area of competition, is varied. The outcome may, but need not, depend on the population sizes of the species when they first come together. Three cases are distinguished: (1) One or the other species always wins. (2) The species coexist, but their equilibrium population sizes are below those found in the absence of competition. (3) One or the other species wins, depending on the initial population sizes—roughly, the more abundant a species