Mutualism (biology)

Hummingbird hawkmoth drinking from Dianthus*. Pollination is a classic example of mutualism.*

Mutualism is the way two organisms of different species exist in a relationship in which each individual benefits from the activity of the other. Similar interactions within a species are known as co-operation. Mutualism can be contrasted with interspecific competition, in which each species experiences *reduced* fitness, and exploitation, or parasitism, in which one species benefits at the *expense* of the other. Mutualism is a type of symbiosis. Symbiosis is a broad category, defined to include relationships that are mutualistic, parasitic, or commensal. Mutualism is only one *type*.

A well-known example of mutualism is the relationship between ungulates (such as Bovines) and bacteria within their intestines. The ungulates benefit from the cellulase produced by the bacteria, which facilitates digestion; the bacteria benefit from having a stable supply of nutrients in the host environment.

Mutualism plays a key part in ecology. For example, mutualistic interactions are vital for terrestrial ecosystem function as more than 48% of land plants rely on mycorrhizal relationships with fungi to provide them with inorganic compounds and trace elements. In addition, mutualism is thought to have driven the evolution of much of the biological diversity we see, such as flower forms (important for pollination mutualisms) and co-evolution between groups of species.[1] However mutualism has historically received less attention than other interactions such as predation and parasitism.[2][3]

Measuring the exact fitness benefit to the individuals in a mutualistic relationship is not always straightforward, particularly when the individuals can receive benefits from a variety of species, for example most plant-pollinator mutualisms. It is therefore common to categorise mutualisms according to the closeness of the association, using terms such as obligate and facultative. Defining "closeness," however, is also problematic. It can refer to mutual dependency (the species cannot live without one another) or the biological intimacy of the relationship in relation to physical closeness (*e.g.*, one species living within the tissues of the other species).[4]

The term "mutualism" was introduced by Pierre-Joseph van Beneden in 1876.[5]

1 Types of relationships

Mutualistic transversals can be thought of as a form of "biological barter"[4] in mycorrhizal associations between plant roots and fungi, with the plant providing carbohydrates to the fungus in return for primarily phosphate but also nitrogenous compounds. Other examples include rhizobia bacteria that fix nitrogen for leguminous plants (family Fabaceae) in return for energy-containing carbohydrates.[6]

1.1 Service-resource relationships

The red-billed oxpecker eats ticks on the impala's coat

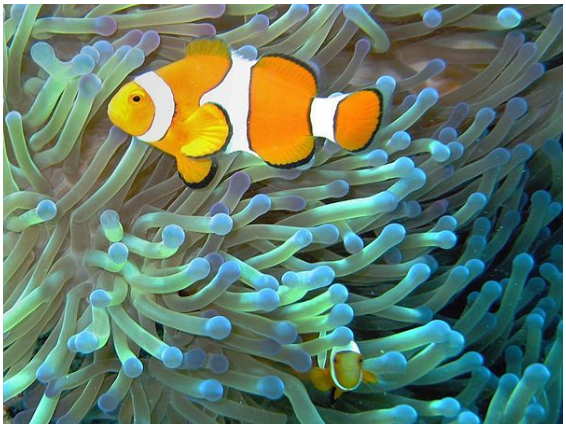
Service-resource relationships are also common.

Pollination in which nectar or pollen (food resources) are traded for pollen dispersal (a service) or ant protection of aphids, where the aphids trade sugar-rich honeydew (a by-product of their mode of feeding on plant sap) in return for defense against predators such as ladybugs.

Phagophiles feed (resource) on ectoparasites, thereby providing anti-pest service, as in cleaning symbiosis. Elacatinus and Gobiosoma, genus of gobies, also feed on ectoparasites of their clients while cleaning them.[7]

Zoochory is an example where animals disperse the seeds of plants. This is similar to pollination in that the plant produces food resources (for example, fleshy fruit, over-abundance of seeds) for animals that disperse the seeds (service).

1.2 Service-service relationships



An example of mutual symbiosis is the relationship between Ocellaris clownfish that dwell among the tentacles of Ritteri sea anemones.

Strict service-service interactions are very rare, for reasons that are far from clear.[4] One example is the relationship between sea anemones and anemone fish in the family Pomacentridae: the anemones provide the fish with protection from predators (which cannot tolerate the stings of the anemone's tentacles) and the fish defend the anemones against butterflyfish (family Chaetodontidae), which eat anemones. However, in common with many mutualisms, there is more than one aspect to it: in the anemonefish-anemone mutualism, waste ammonia from the fish feed the symbiotic algae that are found in the anemone's tentacles.[8][9] Therefore what appears to be a service-service mutualism in fact has a service-resource component. A second example is that of the relationship between some ants in the genus *Pseudomyrmex* and trees in the genus *Acacia*, such as the whistling thorn and bullhorn acacia. The ants nest inside the plant's thorns. In exchange for shelter, the ants protect acacias from attack by herbivores (which they frequently eat, introducing a resource component to this service-service relationship) and competition from other plants by trimming back vegetation that would shade the acacia. In addition, another service-resource component is present, as the ants regularly feed on lipid-rich food-bodies called Beltian bodies that are on the *Acacia* plant.

In the neotropics, the ant, *Myrmelachista schumanni* makes its nest in special cavities in *Duroia hirsute*. Plants in the vicinity that belong to other species are killed with formic acid. This selective gardening can be so aggressive that small areas of the rainforest are dominated by *Duroia hirsute*. These peculiar patches are known by local people as "devil's gardens".[10]

In some of these relationships, the cost of the ant's protection can be quite expensive. *Cordia* sp. trees in the Amazonian rainforest have a kind of partnership with *Allomerus* sp. ants, which make their nests in modified leaves. To increase the amount of living space available, the ants will destroy the tree's flower buds. The flowers die and leaves develop instead, providing the ants with more dwellings. Another type of *Allomerus* sp. ant lives with the *Hirtella* sp. tree in the same forests, but in this relationship the tree has turned the tables on the ants. When the tree is ready to produce flowers, the ant abodes on certain branches begin to wither and shrink, forcing the occupants to flee, leaving the tree's flowers to develop free from ant attack.[10]

The term "species group" can be used to describe the manner in which individual organisms group together. In this non-taxonomic context one can refer to "same-species groups" and "mixed-species groups." While same-species groups are the norm, examples of mixed-species groups abound. For example, zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) can remain in association during periods of long distance migration across the Serengeti as a strategy for thwarting predators. *Cercopithecus mitis* and *Cercopithecus ascanius*, species of monkey in the Kakamega Forest of Kenya, can stay in close proximity and travel along exactly the same routes through the forest for periods of up to 12 hours. These mixed-species groups cannot be explained by the coincidence of sharing the same habitat. Rather, they are created by the active behavioural choice of at least one of the species in question.[11]

2 Humans and mutualism

Humans also engage in mutualisms with other species, including their gut flora without which they would not be able to digest food efficiently.[12] Apparently, head lice infestations might have been beneficial for humans by fostering an immune response that helps to reduce the threat of body louse borne lethal diseases.[13]

Some relationships between humans and domesticated animals and plants are to different degrees mutualistic. Agricultural varieties of maize are unable to reproduce without human intervention because the leafy sheath does not fall open, and the seedhead (the "corn on the cob") does not shatter to scatter the seeds naturally.[14]

Dogs and sheep were among the first animals to be domesticated.

In traditional agriculture, some plants have mutualist as companion plants, providing each other with shelter, soil fertility and/or natural pest control. For example, beans may grow up cornstalks as a trellis, while fixing nitrogen in the soil for the corn, a phenomenon that is used in Three Sisters farming.[15]

Boran people of Ethiopia and Kenya traditionally use a whistle to call the honey guide bird, though the practice is declining. If the bird is hungry and within earshot, it guides them to a bees' nest. In exchange the Borans leave some food from the nest for the bird.[16]

A population of bottlenose dolphins in Laguna, Brazil coordinates, via body language, with local net-using fishermen in order for both to catch schools of mullet.[17]

Pat Shipman, a retired professor of anthropology has argued for the theory that a key advantage that Homo Sapiens had over Neanderthals in competing for similar habitats was the former's mutualism with dogs.[18]

3 Mathematical modeling

One of the simplest frameworks for modeling species interactions is the Lotka–Volterra equations. In this model, the change in population density of the two mutualists is quantified as:

$$\frac{dN}{dt} = r_1 N \left(1 - \frac{N}{K_1} + \beta_{12}\frac{M}{K_1}\right)$$

$$\frac{dM}{dt} = r_2 M \left(1 - \frac{M}{K_2} + \beta_{21}\frac{N}{K_2}\right)$$

where

- N and M = the population densities.
- r = intrinsic growth rate of the population.
- K = carrying capacity of its local environmental setting.
- β = coefficient converting encounters with one species to new units of the other.

Mutualism is in essence the logistic growth equation + mutualistic interaction. The mutualistic interaction term represents the increase in population growth of species one as a result of the presence of greater numbers of species two, and vice versa. As the mutualistic term is always positive, it may lead to unrealistic unbounded growth as it happens with the simple model.[19] So, it is important to include a saturation mechanism to avoid the problem.

In 1989, David Hamilton Wright modified the Lotka–Volterra equations by adding a new term, $\beta M/K$, to represent a mutualistic relationship.[20] Wright also considered the concept of saturation, which means that with higher densities, there are decreasing benefits of further increases of the mutualist population. Without saturation, species' densities would increase indefinitely. Because that isn't possible due to environmental constraints and carrying capacity, a model that includes saturation would be more accurate. Wright's mathematical theory is based on the premise of a simple two-species mutualism model in which the benefits of mutualism become saturated due to limits posed by handling time. Wright defines handling time as the time needed to process a food item, from the initial interaction to the start of a search for new food items and assumes that processing of food and searching for food are mutually exclusive. Mutualists that display foraging behavior are exposed to the restrictions on handling time. Mutualism can be associated with symbiosis.

3.1 Type II functional response

In 1959, C. S. Holling performed his classic disc experiment that assumed the following: that (1), the number of food items captured is proportional to the allotted searching time; and (2), that there is a variable of handling time that exists separately from the notion of search time. He then developed an equation for the Type

II functional response, which showed that the feeding rate is equivalent to

$$\frac{ax}{1 + axT_H}$$

where,

- a = the instantaneous discovery rate
- x = food item density
- TH = handling time

The equation that incorporates Type II functional response and mutualism is:

$$\frac{dN}{dt} = N[r(1 - cN) + \beta M(X + M)]$$

where

- N and M = densities of the two mutualists
- r = intrinsic rate of increase of N
- c = coefficient measuring negative intraspecific interaction
- X = 1/a TH
- β = b/TH
- a = instantaneous discovery rate
- b = coefficient converting encounters with M to new units of N

Rearranged:

$$\frac{dN}{dt} = N\left[r(1 - cN) + \frac{baM}{1 + aT_H M}\right]$$

The model presented above is most effectively applied to free-living species that encounter a number of individuals of the mutualist part in the course of their existences. Of note, as Wright points out, is that models of biological mutualism tend to be similar qualitatively, in that the featured isoclines generally have a positive decreasing slope, and by and large similar isocline diagrams. Mutualistic interactions are best visualized as positively sloped isoclines, which can be explained by the fact that the saturation of benefits accorded to mutualism or restrictions posed by outside factors contribute to a decreasing slope.

4 The structure of mutualistic networks

Mutualistic networks made up out of the interaction between plants and pollinators were found to have a similar structure in very different ecosystems on different continents, consisting of entirely different species.[21] The structure of these mutualistic networks may have large consequences for the way in which pollinator communities respond to increasingly harsh conditions.

Mathematical models, examining the consequences of this network structure for the stability of pollinator communities suggest that the specific way in which plant-pollinator networks are organized minimizes competition between pollinators[22] and may even lead to strong indirect facilitation between pollinators when conditions are harsh.[23] This makes that pollinator species together can survive under harsh conditions. But it also means that pollinator species collapse simultaneously when conditions pass a critical point. This simultaneous collapse occurs, because pollinator species depend on each other when surviving under difficult conditions.[23]

Such a community-wide collapse, involving many pollinator species, can occur suddenly when increasingly harsh conditions pass a critical point and recovery from such a collapse might not be easy. The improvement in conditions needed for pollinators to recover, could be substantially larger than the improvement needed to return to conditions at which the pollinator community collapsed.[23]

5 See also

- Arbuscular mycorrhiza
- Co-adaptation
- Co-evolution
- Ecological facilitation
- Frugivory
- Greater Honeyguide - has an interesting mutualism with humans
- Interspecific communication
- List of symbiotic relationships
- Müllerian mimicry
- Mutualisms and Conservation
- *Mutual Aid: A Factor of Evolution*
- Symbiogenesis

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