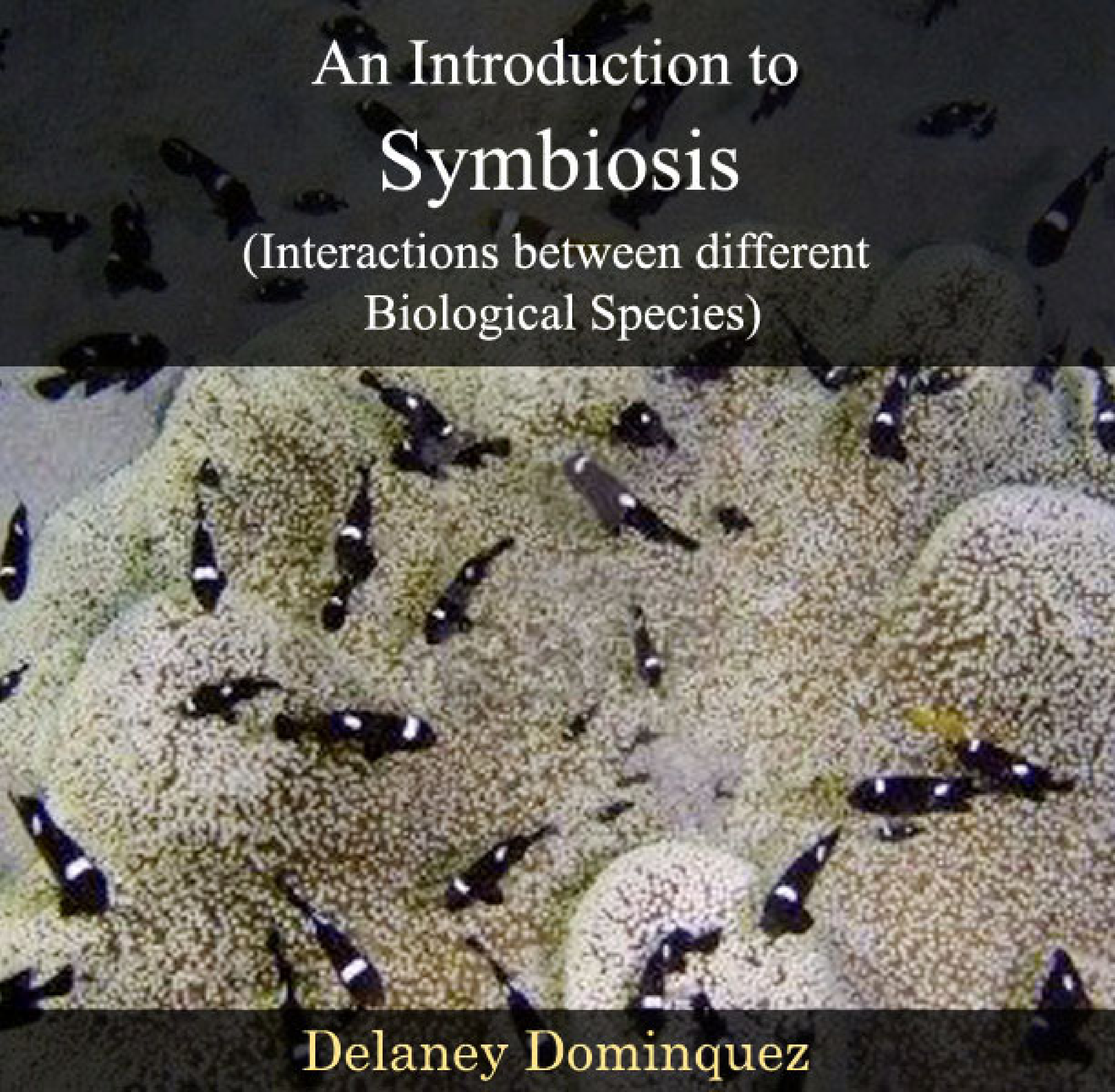

An Introduction to Symbiosis

(Interactions between different Biological Species)

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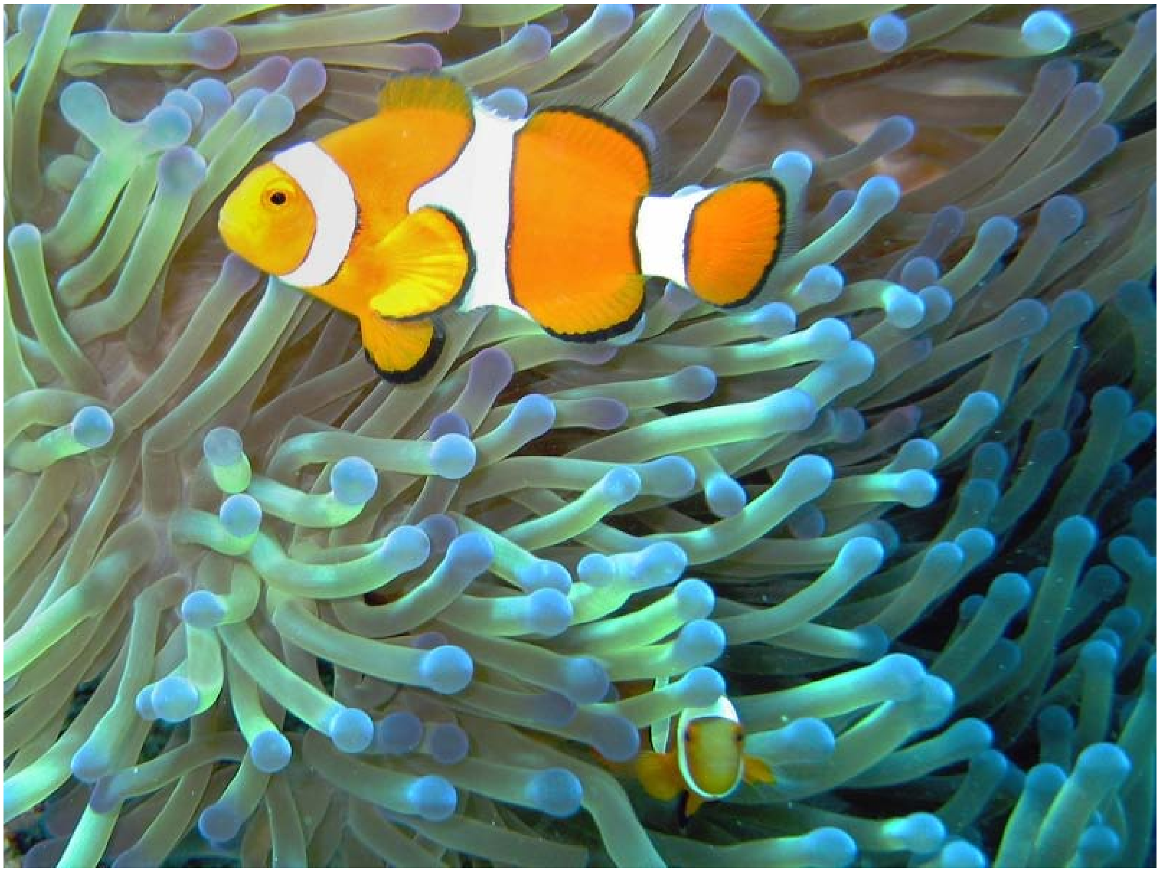
Introduction to Symbiosis



In a symbiotic commensalism, the clownfish feeds on small invertebrates which otherwise potentially could harm the sea anemone and the fecal matter from the clownfish provides nutrients to the sea anemone.

Symbiosis (from the Greek: σύν *syin* "with"; and βίωσις *biosis* "living") is close and often long-term interactions between different biological species. In 1877 Bennett used the word symbiosis (which previously had been used of people living together in community) to describe the mutualistic relationship in lichens. In 1879 by the German mycologist Heinrich Anton de Bary, defined it as "the living together of unlike organisms." The definition of symbiosis is in flux and the term has been applied to a wide range of biological interactions. The symbiotic relationship may be categorized as mutualistic, commensal, or parasitic in nature. Some symbiotic relationships are obligate, meaning that both symbionts entirely depend on each other for survival. For example, many lichens consist of fungal and photosynthetic symbionts that cannot live on their own. Others are facultative, meaning that they can but do not have to live with the other organism.

Symbiotic relationships include those associations in which one organism lives on another (ectosymbiosis, such as mistletoe), or where one partner lives inside the other (endosymbiosis, such as lactobacilli and other bacteria in humans or zooxanthelles in corals). Symbiotic relationships may be either obligate, i.e., necessary for the survival of at least one of the organisms involved, or facultative, where the relationship is beneficial but not essential for survival of the organisms.

Physical interaction

Alder tree root nodule

Endosymbiosis is any symbiotic relationship in which one symbiont lives within the tissues of the other, either in the intracellular space or extracellularly. Examples are rhizobia, nitrogen-fixing bacteria that live in root nodules on legume roots; actinomycete nitrogen-fixing bacteria called *Frankia*, which live in alder tree root nodules; single-celled algae inside reef-building corals; and bacterial endosymbionts that provide essential nutrients to about 10%–15% of insects.

Ectosymbiosis, also referred to as *exosymbiosis*, is any symbiotic relationship in which the symbiont lives on the body surface of the host, including the inner surface of the digestive tract or the ducts of exocrine glands. Examples of this include ectoparasites such as lice, commensal ectosymbionts such as the barnacles that attach themselves to the jaw of baleen whales and mutualist ectosymbionts such as cleaner fish.

Amensalism

Amensalism is the type of symbiotic relationship that exists where one species is inhibited or completely obliterated and one is unaffected. This type of symbiosis is relatively uncommon in rudimentary reference texts, but is omnipresent in the natural world. An example is a sapling growing under the shadow of a mature tree. The mature tree can begin to rob the sapling of necessary sunlight and, if the mature tree is very large, it can take up rainwater and deplete soil nutrients. Throughout the process the mature tree is unaffected. Indeed, if the sapling dies, the mature tree gains nutrients from the decaying sapling. Note that these nutrients become available because of the sapling's decomposition, rather than from the living sapling.

Symbiosis and evolution

Leafhoppers protected by an army of meat ants

While historically, symbiosis has received less attention than other interactions such as predation or competition, it is increasingly recognised as an important selective force behind evolution, with many species having a long history of interdependent co-evolution. In fact, the evolution of all eukaryotes (plants, animals, fungi and protists) is believed under the endosymbiotic theory to have resulted from a symbiosis between various sorts of bacteria.

Vascular Plants

Up to 80% of vascular plants worldwide form symbiotic relationships with fungi, for example, in arbuscular mycorrhiza.

Symbiogenesis

The biologist Lynn Margulis, famous for her work on endosymbiosis, contends that symbiosis is a major driving force behind evolution. She considers Darwin's notion of evolution, driven by competition, as incomplete and claims that evolution is strongly based on co-operation, interaction and mutual dependence among organisms. According to Margulis and Dorion Sagan, "Life did not take over the globe by combat, but by networking."

Co-evolution

Symbiosis played a major role in the co-evolution of flowering plants and the animals that pollinate them. Many plants that are pollinated by insects, bats, or birds have highly specialized flowers modified to promote pollination by a specific pollinator that is also correspondingly adapted. The first flowering plants in the fossil record had relatively simple flowers. Adaptive speciation quickly gave rise to many diverse groups of plants and, at the same time, corresponding speciation occurred in certain insect groups. Some groups of plants developed nectar and large sticky pollen, while insects evolved more specialized morphologies to access and collect these rich food sources. In some taxa of plants and insects the relationship has become dependent, where the plant species can only be pollinated by one species of insect.

Chapter- 2

Predation

Indian Python swallowing a full grown Chital deer at Mudumalai National Park

A juvenile Red-tailed Hawk eating a California Vole

Meat ants feeding on a cicada; some species can prey on individuals of far greater size, particularly when working cooperatively

In ecology, **predation** describes a biological interaction where a **predator** (an organism that is hunting) feeds on its **prey** (the organism that is attacked). Predators may or may not kill their prey prior to feeding on them, but the act of predation always results in the death of its prey and the eventual absorption of the prey's tissue through consumption. The other main category of consumption is detritivory, the consumption of dead organic material (detritus). It can at times be difficult to separate the two feeding behaviors, for example where parasitic species prey on a host organism and then lay their eggs on it for their offspring to feed on its decaying corpse. The key characteristic of predation however is the predator's direct impact on the prey population. On the other hand, detritivores simply eat what is available and have no direct impact on the "donor" organism(s).

Selective pressures imposed on one another has led to an evolutionary arms race between prey and predator, resulting in various antipredator adaptations.

The unifying theme in all classifications of predation is the predator lowering the fitness of its prey, or put another way, it reduces its prey's chances of survival, reproduction, or both. Ways of classifying predation surveyed here include grouping by trophic level or diet, by specialization and by the nature of the predator's interaction with prey.

Functional classification

Classification of predators by the extent to which they feed on and interact with their prey is one way ecologists may wish to categorize the different types of predation. Instead of focusing on what they eat, this system classifies predators by the way in which they eat and the general nature of the interaction between predator and prey species. Two factors are considered here: How close the predator and prey are physically (in the latter two cases the term *prey* may be replaced with *host*). Additionally, whether or not the prey are directly killed by the predator is considered, with true predation and parasitoidism involving certain death.

True predation

Lion and cub eating a Cape Buffalo

A true predator can commonly be known as one which kills and eats another organism. Whereas other types of predator all harm their prey in some way, this form certainly kills them. Predators may hunt actively for prey, or sit and wait for prey to approach within striking distance, as in ambush predators. Some predators kill large prey and dismember or chew it prior to eating it, such as a jaguar; others may eat their (usually much smaller) prey whole, as does a bottlenose dolphin swallowing a fish, or a snake or duck or stork swallowing a frog. Some predation entails venom which subdues a prey creature before the predator ingests the prey by killing, which the box jellyfish does, or disabling it, found in the behavior of the cone shell. In some cases the venom, as in rattlesnakes and some spiders, contributes to the digestion of the prey item even before the predator begins eating. In other cases, the prey organism may die in the mouth or digestive system of the predator. Baleen whales, for example, eat millions of microscopic plankton at once, the prey being broken down well after entering the whale. Seed predation and egg predation are other forms of true predation, as seeds and eggs represent potential organisms. Predators of this classification need not eat prey entirely, for example some predators cannot digest bones, while others can. Some may eat only part of an organism, as in grazing (see below), but still consistently cause its direct death.Some of the prominent examples of true predators are lion, tiger,etc.

Grazing

Grazing organisms may also kill their prey species, but this is seldom the case. While some herbivores like zooplankton live on unicellular phytoplankton and have no choice but to kill their prey, many only eat a small part of the plant. Grazing livestock may pull some grass out at the roots, but most is simply grazed upon, allowing the plant to regrow once again. Kelp is frequently grazed in subtidal kelp forests, but regrows at the base of the blade continuously to cope with browsing pressure. Animals may also be 'grazed' upon; female mosquitos land on hosts briefly to gain sufficient proteins for the development of their offspring. Starfish may be grazed on, being capable of regenerating lost arms.

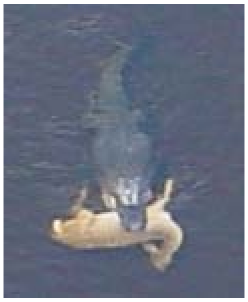
Parasitism

Parasites can at times be difficult to distinguish from grazers. Their feeding behavior is similar in many ways, however they are noted for their close association with their host species. While a grazing species such as an elephant may travel many kilometers in a single day, grazing on many plants in the process, parasites form very close associations with their hosts, usually having only one or at most a few in their lifetime. This close living arrangement may be described by the term symbiosis, 'living together,' but unlike mutualism the association significantly reduces the fitness of the host. Parasitic organisms range from the macroscopic mistletoe, a parasitic plant, to microscopic internal parasites such as cholera. Some species however have more loose associations with their hosts. Lepidoptera (butterfly and moth) larvae may feed parasitically on only a single plant, or they may graze on several nearby plants. It is therefore wise to treat this classification system as a continuum rather than four isolated forms.

Parasitoidism

Parasitoids are organisms living in or on their host and feeding directly upon it, eventually leading to its death. They are much like parasites in their close symbiotic relationship with their host or hosts. Like the previous two classifications parasitoid predators do not kill their hosts instantly. However, unlike parasites, they are very similar to true predators in that the fate of their prey is quite inevitably death. A well known example of a parasitoids are the ichneumon wasps, solitary insects living a free life as an adult, then laying eggs on or in another species such as a caterpillar. Its larva(e) feed on the growing host causing it little harm at first, but soon devouring the internal organs until finally destroying the nervous system resulting in prey death. By this stage the young wasp(s) are developed sufficiently to move to the next stage in their life cycle. Though limited mainly to the insect order Hymenoptera, Diptera and Coleoptera parasitoids make up as much as 10% of all insect species.

Degree of specialization



An opportunistic Alligator swims with a deer

Among predators there is a large degree of specialization. Many predators specialize in hunting only one species of prey. Others are more opportunistic and will kill and eat almost anything (examples: humans, leopards and dogs). The specialists are usually particularly well suited to capturing their preferred prey. The prey in turn, are often equally suited to escape that predator. This is called an evolutionary arms race and tends to keep the populations of both species in equilibrium. Some predators specialize in certain classes of prey, not just single species. Almost all will switch to other prey (with varying degrees of success) when the preferred target is extremely scarce and they may also resort to scavenging or a herbivorous diet if possible.

Trophic level

Mantis eating a bee

Predators are often another organism's prey and likewise prey are often predators. Though blue jays prey on insects, they may in turn be prey for cats and snakes, which, in the latter's case, may themselves be the prey of hawks. One way of classifying predators is by trophic level. Organisms which feed on autotrophs, the producers of the trophic pyramid, are known as herbivores or *primary consumers*; those that feed on heterotrophs such as animals are known as *secondary consumers*. Secondary consumers are a type of carnivore, but there are also tertiary consumers eating these carnivores, quartary consumers eating them and so forth. Because only a fraction of energy is passed on to the next level, this hierarchy of predation must end somewhere and very seldom goes higher than five or six levels and may go only as high as three trophic levels (for example, a lion that preys upon large herbivores such as wildebeest which in turn eat grasses). A predator at the top of any food chain (that is, one that is preyed upon by no organism) is called an apex predator; examples include the orca, sperm whale, anaconda, Komodo dragon, tiger, lion, bald eagle and Nile crocodile -- and even omnivorous humans and grizzly bears. An apex predator in one environment may not retain this position as a top predator if introduced to another habitat, such as a dog among alligators or a snapping turtle among jaguars; a predatory species introduced into an area where it faces no predators, such as a domestic cat or a dog in some insular environments, can become an apex predator by default.

Many organisms (of which humans are prime examples) eat from multiple levels of the food chain and thus make this classification problematic. A carnivore may eat both secondary and tertiary consumers and its prey may itself be difficult to classify for similar reasons. Organisms showing both carnivory and herbivory are known as omnivores. Even herbivores such as the giant panda may supplement their diet with meat. Scavenging of carrion provides a significant part of the diet of some of the most fearsome predators. Carnivorous plants would be very difficult to fit into this classification, producing their own food but also digesting anything that they may trap. Organisms which eat detritivores or parasites would also be difficult to classify by such a scheme.

Predation as competition

An alternative view offered by Richard Dawkins is of predation as a form of competition: the genes of both the predator and prey are competing for the body (or 'survival machine') of the prey organism. This is best understood in the context of the gene centered view of evolution.

Ecological role

Predators may increase the biodiversity of communities by preventing a single species from becoming dominant. Such predators are known as keystone species and may have a profound influence on the balance of organisms in a particular ecosystem. Introduction or removal of this predator, or changes in its population density, can have drastic cascading effects on the equilibrium of many other populations in the ecosystem. For example, grazers of a grassland may prevent a single dominant species from taking over.

The elimination of wolves from Yellowstone National Park had profound impacts on the trophic pyramid. Without predation, herbivores began to over-graze many woody brow species, affecting the area's plant populations. Additionally, wolves often kept animals from grazing in riparian areas, which protected beavers from having their food sources encroached upon. The removal of wolves had a direct effect on beaver populations, as their habitat became territory for grazing. Furthermore, predation keeps hydrological features such as creeks and streams in normal working order. Increased browsing on willows lenr and conifers along Blacktail Creek due to a lack of predation resulted in channel incision because those species helped slow the water down and hold the soil in place.

Adaptations and behavior

The act of predation can be broken down into a maximum of four stages: Detection of prey, attack, capture and finally consumption. The relationship between predator and prey is one which is typically beneficial to the predator and detrimental to the prey species. Sometimes, however, predation has indirect benefits to the prey species, though the individuals preyed upon themselves do not benefit. This means that, at each applicable stage, predator and prey species are in an evolutionary arms race to maximize their respective abilities to obtain food or avoid being eaten. This interaction has resulted in a vast array of adaptations in both groups.

Camouflage of the dead leaf mantis makes it less visible to both its predators and prey

One adaptation helping both predators and prey avoid detection is camouflage, a form of crypsis where species have an appearance which helps them blend into the background. Camouflage consists of not only color, but also shape and pattern. The background upon which the organism is seen can be both its environment (e.g. the praying mantis to the right resembling dead leaves) or other organisms (e.g. zebras' stripes blend in with each other in a herd, making it difficult for lions to focus on a single target). The more convincing camouflage is, the more likely it is that the organism will go unseen.

Mimicry in *Automeris io*

Mimicry is a related phenomenon where an organism has a similar appearance to another species. One such example is the drone fly, which looks a lot like a bee, yet is completely harmless as it cannot sting at all. Another example of batesian mimicry is the io moth, (*Automeris io*), which has markings on its wings which resemble an owl's eyes. When an insectivorous predator disturbs the moth, it reveals its hind wings, temporarily startling the predator and giving it time to escape. Predators may also use mimicry to lure their prey, however. Female fireflies of the genus *Photuris*, for example, copy the light signals of other species, thereby attracting male fireflies which are then captured and eaten.

Predator

A South China Tiger as the predator feeding on the blesbuck, the prey

Great blue heron with prey

Lizard with prey

While successful **predation** results in a gain of energy, hunting invariably involves energetic costs as well. When hunger is not an issue, most predators will generally not seek to attack prey since the costs outweight the benefits. For instance, a large predatory fish like a shark that is well fed in an aquarium will typically ignore the smaller fish swimming around it (while the prey fish take advantage of the fact that the apex predator is apparently uninterested). Surplus killing represents a deviation from this type of behaviour. The treatment of consumption in terms of cost-benefit analysis is known as optimal foraging theory and has been quite successful in the study of animal behavior. Costs and benefits are generally considered in energy gain per unit time, though other factors are also important, such as essential nutrients that have no caloric value but are necessary for survival and health.

Social Predation offers the possibility of predators to kill creatures larger than those that members of the species could overpower singly. Lions, hyenas, wolves, dholes, African wild dogs and piranhas can kill large herbivores that single animals of the same species could never dispatch. Social predation allows some animals to organize hunts of creatures that would easily escape a single predator; thus chimpanzees can prey upon colobus monkeys and harris hawks can cut off all possible escapes for a doomed rabbit. Extreme specialization of roles is evident in some hunting that requires co-operation between predators of very different species: humans with the aid of falcons or dogs, or fishing with cormorants or dogs. Social predation is often very complex behavior and not all social creatures (for example, domestic cats) perform it. Even without complex intelligence but instinct alone, some ant species can destroy much-larger creatures.

Size-selective predation involves predators preferring prey of a certain size. Large prey may prove troublesome for a predator, while small prey might prove hard to find and in any case provide less of a reward. This has led to a correlation between the size of predators and their prey. Size may also act as a refuge for large prey, for example adult elephants are generally safe from predation by lions, but juveniles are vulnerable.

It has been observed that well-fed predator animals in a lax captivity (for instance, pet or farm animals) will usually differentiate between putative prey animals who are familiar co-inhabitants in the same human area from wild ones outside the area. This interaction can range from peaceful coexistence to close companionship; motivation to ignore the predatory instinct may result from mutual advantage or fear of reprisal from human masters who have made clear that harming co-inhabitants will not be tolerated. Pet cats and pet mice, for example, may live together in the same human residence without incident as companions. Pet cats and pet dogs under human mastership often depend on each other for warmth, companionship and even protection, particularly in rural areas.

Antipredator adaptations

Antipredator adaptations have evolved in prey populations due to the selective pressures of predation over long periods of time.

Aggression

Predatory animals often use their usual methods of attacking prey to inflict or to threaten grievous injury to their own predators. The electric eel uses the same electrical current to kill prey and to defend itself against animals (anacondas, caimans, jaguars, egrets, cougars, giant otters, humans and dogs) that ordinarily prey upon fish similar to an electric eel in size; the electric eel thus remains an apex predator in a predator-rich environment. Many non-predatory prey animals, such as a zebra, can give a strong kick that can maim or kill, while others charge with tusks or horns.

Mobbing behavior

Mobbing behavior occurs when members of a species drive away their predator by cooperatively attacking or harassing it. Most frequently seen in birds, mobbing is also seen in other social animals. For example, nesting gull colonies are widely seen to attack intruders, including humans. Costs of mobbing behavior include the risk of engaging with predators, as well as energy expended in the process, but it can aid the survival of members of a species.

While mobbing has evolved independently in many species, it tends to be present only in those whose young are frequently preyed on, especially birds. It may complement cryptic behavior in the offspring themselves, such as camouflage and hiding. Mobbing calls may be made prior to or during engagement in harassment.

Mobbing can be an interspecies activity: it is common for birds to respond to mobbing calls of a different species. Many birds will show up at the sight of mobbing and watch and call, but not participate. It should also be noted that some species can be on both ends of a mobbing attack. Crows are frequently mobbed by smaller songbirds as they prey on eggs and young from these birds' nests, but these same crows will cooperate with smaller birds to drive away hawks or larger mammalian predators. On occasion, birds will mob animals that pose no threat.

Advertising unprofitability

Thomson's Gazelles exhibit stotting behavior

A Thomson's Gazelle seeing a predator approach may start to run away, but then slow down and *stot*. Stotting is jumping into the air with the legs straight and stiff and the white rear fully visible. Stotting is maladaptive for outrunning predators; evidence suggests that stotting signals an unprofitable chase. For example, cheetahs abandon more hunts when the gazelle stots and in the event they do give chase, they are far less likely to make a kill.

Aposematism, where organisms are brightly colored as a warning to predators, is the antithesis of camouflage. Some organisms pose a threat to their predators—for example they may be poisonous, or able to harm them physically. Aposematic coloring involves bright, easily recognizable and unique colors and patterns. Upon being harmed (e.g. stung) by their prey, the appearance in such an organism will be remembered as something to avoid.

Terrain Fear Factor

The "terrain fear factor" is an idea which assesses the risks associated with predator/prey encounters. This idea suggests that prey will change their usual habits to adjust to the terrain and its effect on the species' predation. For example, a species may forage in a terrain with a lower predation risk as opposed to one with high predation risk.

Population dynamics

It is fairly clear that predators tend to lower the survival and fecundity of their prey, but on a higher level of organization, populations of predator and prey species also interact. It is obvious that predators depend on prey for survival and this is reflected in predator populations being affected by changes in prey populations. It is not so obvious, however, that predators affect prey populations. Eating a prey organism may simply make room for another if the prey population is approaching its carrying capacity.

The population dynamics of predator-prey interactions can be modelled using the Lotka–Volterra equations. These provide a mathematical model for the cycling of predator and prey populations.

Predators tend to select young, weak and ill individuals.

Evolution of predation

Predation appears to have become a major selection pressure shortly before the Cambrian period—around 550 million years ago—as evidenced by the almost simultaneous development of calcification in animals and algae and predation-avoiding burrowing. However, predators had been grazing on micro-organisms since at least 1,000 million years ago.

Humans and predation

As predators

Humans are omnivorous and use tools to exploit their environments; from snares, clubs, spears, fishing gear, firearms to boats and motor vehicles. Humans even use other predatory species, (such as dogs, cormorants and falcons) in hunting and fishing; some people even enlist such non-predatory beasts, like horses, camels and elephants in getting approaches to prey.

Humans have reshaped huge expanses of the world as ranges and farms for the raising of livestock, poultry and fish to be eaten as meat. However, it can be debated whether or not harvesting livestock fits strictly in the definition of predation.

Human raising and eating of livestock is part of agriculture and involves the feeding of and caring for animals, followed by their being slaughtered with an appropriate tool, cutting up and cooking. In many cultures, animals are hunted or farmed by specialists (such as ranchers or fishermen), brought to a marketplace and sold in pieces to the people who actually consume the meat.

As prey

A lone naked human is at a physical disadvantage to other comparable apex predators in areas such as speed, bone density, weight and physical strength. Humans also lack innate weaponry such as claws. Without crafted weapons, society, or cleverness, a lone human can easily be defeated by fit predatory animals, such as wild dogs, big cats and bears. There are even recorded instances of lone humans being preyed upon by large carnivores.

However humans are not solitary creatures; they are social animals with highly developed social behaviors. Further humans and their ancestors (such as *Homo erectus*) have been using stone tools and weapons for well over a million years. Anatomically modern humans have been apex predators since they first evolved and many species of carnivorous megafauna actively avoid interacting with humans; the primary environmental competitor for a human is other humans. Cannibalism has occurred in various places, among various cultures and for various reasons. At least a few people, such as the Donner party, are said to have resorted to it in desperation.

In conservation

Predators are an important consideration in matters relating to conservation. Introduced predators may prove too much for populations which have not coevolved with them, leading to possible extinction. This will depend largely on how well the prey species can adapt to the new species and or not the predator can turn to alternative food sources when prey populations fall to minimal levels. If a predator can use an alternative prey instead, it may shift its diet towards that species, while still eating the last remaining prey organisms. On the other hand the prey species may be able to survive if the predator has no alternative prey—in this case its population will necessarily crash following the decline in prey, allowing some small proportion of prey to survive. Introduction of an alternative prey may well lead to the extinction of prey, as this constraint is removed.

Predators are often the species endangered themselves, especially apex predators who are often in competition with humans. Competition for prey from other species could prove the end of a predator—if their ecological niche overlaps completely with that of another the competitive exclusion principle requires only one can survive. Loss of prey species may lead to coextinction of their predator. In addition, because predators are found in higher trophic levels, they are less abundant and much more vulnerable to extinction.

Biological pest control

Predators may be put to use in conservation efforts to control introduced species. Although the aim in this situation is to remove the introduced species entirely, keeping its abundance down is often the only possibility. Predators from its natural range may be introduced to control populations, though in some cases this has little effect and may even cause unforeseen problems. Besides their use in conservation biology, predators are also important for controlling pests in agriculture. Natural predators are an environmentally friendly and sustainable way of reducing damage to crops and are one alternative to the use of chemical agents such as pesticides.

Chapter- 3

Endosymbiont

An **endosymbiont** is any organism that lives within the body or cells of another organism, i.e. forming an **endosymbiosis** (Greek: ἔνδον *endon* "within", σύν *syn* "together" and βίωσις *biosis* "living"). Examples are nitrogen-fixing bacteria (called rhizobia) which live in root nodules on legume roots, single-celled algae inside reef-building corals and bacterial endosymbionts that provide essential nutrients to about 10%–15% of insects. Many instances of endosymbiosis are obligate- that is, either the endosymbiont or the host cannot survive without the other, such as the gutless marine worms of the genus *Riftia*, which get nutrition from their endosymbiotic bacteria. The most common examples of obligate endosymbiosis are mitochondria and chloroplasts. Some human parasites, e.g.: *Wucherichia bancrofti* and *Mansonella perstans* thrive in their hosts because of an obligate endosymbiosis with *Wolbachi spp.*. They can both be eliminated from their host by treatments that target this bacterium. However, not all endosymbioses are obligate. Also, some endosymbioses can be harmful to either of the organisms involved.

It is generally agreed that certain organelles of the eukaryotic cell, especially mitochondria and plastids such as chloroplasts, originated as bacterial endosymbionts. This theory is called the endosymbiotic theory and was first articulated by the Russian botanist Konstantin Mereschkowski in 1905.

Endosymbiosis theory and mitochondria and chloroplasts

The endosymbiosis theory attempts to explain the origins of organelles such as mitochondria and chloroplasts in eukaryotic cells. The theory proposes that chloroplasts and mitochondria evolved from certain types of bacteria that prokaryotic cells engulfed through endophagocytosis. These cells and the bacteria trapped inside them entered a symbiotic relationship, a close association between different types of organisms over an extended time. However, more specifically, the relationship was endosymbiotic, meaning that one of the organisms (the bacteria) lived within the other (the prokaryotic cells).

According to endosymbiosis theory, an anaerobic cell probably ingested an aerobic bacterium but failed to digest it. The aerobic bacterium flourished within the cell because the cell's cytoplasm was abundant in half-digested food molecules. The bacterium digested these molecules with oxygen and gained great amounts of energy. Because the bacterium had so much energy, it probably leaked some of it as Adenosine triphosphate into the cell's cytoplasm. This benefited the anaerobic cell because it enabled it to digest food aerobically. Eventually, the aerobic bacterium could no longer live independently from the cell and it therefore became a mitochondrion. The origin of the chloroplast is very similar to that of the mitochondrion. A cell must have captured a photosynthetic cyanobacterium and failed to digest it. The cyanobacterium thrived in the cell and eventually evolved into the first chloroplast. Other eukaryotic organelles may have also evolved through endosymbiosis; it has been proposed that cilia, flagella, centrioles and microtubules may have originated from a symbiosis between a Spirochaete bacterium and an early eukaryotic cell, but this is not widely accepted among biologists.

There are several examples of evidence that support endosymbiosis theory. Mitochondria and chloroplasts contain their own small supply of DNA, which may be remnants of the genome the organelles had when they were independent aerobic bacteria. The single most convincing evidence of the descent of organelles from bacteria is the position of mitochondria and plastid DNA sequences in phylogenetic trees of bacteria. Mitochondria have sequences that clearly indicate origin from a group of bacteria called the alpha-Proteobacteria. Plastids have DNA sequences that indicate origin from the cyanobacteria (blue-green algae). In addition, there are organisms alive today, called living intermediates, that are in a similar endosymbiotic condition to the prokaryotic cells and the aerobic bacteria. Living intermediates show that the evolution proposed by the endosymbiont theory is possible. For example, the giant amoeba *Pelomyxa* lacks mitochondria but has aerobic bacteria that carry out a similar role. A variety of corals, clams, snails and one species of *Paramecium* permanently host algae in their cells. Many of the insect endosymbionts have been shown to have ancient associations with their hosts, involving strictly vertical inheritance. In addition, these insect symbionts have similar patterns of genome evolution to those found in true organelles: genome reduction, rapid rates of gene evolution and bias in nucleotide base composition favoring adenine and thymine, at the expense of guanine and cytosine.

Further evidence of endosymbiosis are the prokaryotic ribosomes found within chloroplasts and mitochondria as well as the double-membrane enclosing them. It used to be widely assumed that the inner membrane is the original membrane of the once independent prokaryote, while the outer one is the food vacuole (phagosomal membrane) it was enclosed in initially. However, this view neglects the fact that i) both modern cyanobacteria and alpha-proteobacteria are Gram negative bacteria, which are surrounded by double membranes; ii) the outer membranes of the endosymbiotic organelles (chloroplasts and mitochondria) are very similar to those of these bacteria in their lipid and protein compositions. Accumulating biochemical data strongly suggest that the double membrane enclosing chloroplasts and mitochondria derived from those of the ancestral bacteria and the phagosomal membrane disappeared during organelle evolution. Triple or quadruple membranes are found among certain algae, probably resulting from repeated endosymbiosis (although little else was retained of the engulfed cell).

These modern organisms with endosymbiotic relationships with aerobic bacteria have verified the endosymbiotic theory, which explains the origin of mitochondria and chloroplasts from bacteria. Researchers in molecular and evolutionary biology no longer question this theory, although some of the details, such as the mechanisms for loss of genes from organelles to host nuclear genomes, are still being worked out.

Bacterial endosymbionts in marine invertebrates

Extracellular endosymbionts are also represented in all four extant classes of Echinodermata (Crinoidea, Ophiuroidea, Echinoidea and Holothuroidea). Little is known of the nature of the association (mode of infection, transmission, metabolic requirements, etc.) but phylogenetic analysis indicates that these symbionts belong to the alpha group of the class Proteobacteria, relating them to *Rhizobium* and *Thiobacillus*. Other studies indicate that these subcuticular bacteria may be both abundant within their hosts and widely distributed among the Echinoderms in general.

Some marine oligochaeta (e.g. Olavius or Inanidrillus) have obligate extracellular endosymbionts that fill the entire body of their host. These marine worms are nutritionally dependent on their symbiotic chemoautotrophic bacteria lacking any digestive or excretory system (no gut, mouth or nephridia).

Symbiodinium *dinoflagellate endosymbionts in marine metazoa and protists*

Dinoflagellate endosymbionts of the genus *Symbiodinium*, commonly known as zooxanthellae, are found in corals, mollusks (esp. giant clams, the *Tridacna*), sponges and foraminifera. These endosymbionts drive the amazing formation of coral reefs by capturing sunlight and providing their hosts with energy for carbonate deposition.

Previously thought to be a single species, molecular phylogenetic evidence over the past couple decades has shown there to be great diversity in *Symbiodinium*. In some cases there is specificity between host and *Symbiodinium* clade. More often, however, there is an ecological distribution of *Symbiodinium*, the symbionts switching between hosts with apparent ease. When reefs become environmentally stressed, this distribution of symbionts is related to the observed pattern of coral bleaching and recovery. Thus the distribution of *Symbiodinium* on coral reefs and its role in coral bleaching presents one of the most complex and interesting current problems in reef ecology.

Endosymbionts in protists

Mixotricha paradoxa is a protozoan that lacks mitochondria, however, spherical bacteria live inside the cell and serve the function of the mitochondria. *Mixotricha* also has three other species of symbionts that live on the surface of the cell.

Paramecium bursaria, a species of ciliate, has a mutualistic symbiotic relationship with green alga called Zoochlorella. The algae live inside the cell, in the cytoplasm.

Bacterial endosymbionts in insects

Scientists classify insect endosymbionts in two broad categories, 'Primary' and 'Secondary'. Primary endosymbionts (sometimes referred to as P-endosymbionts) have been associated with their insect hosts for many millions of years (from 10 to several hundred million years in some cases), they form obligate associations (see below) and display cospeciation with their insect hosts. Secondary endosymbionts exhibit a more recently developed association, are sometimes horizontally transferred between hosts, live in the hemolymph of the insects (not specialized bacteriocytes, see below) and are not obligate.

Among primary endosymbionts of insects, the best studied are the pea aphid (*Acyrthosiphon pisum*) and its endosymbiont *Buchnera sp.* APS, the tsetse fly *Glossina morsitans morsitans* and its endosymbiont *Wigglesworthia glossinidia brevipalpis* and the endosymbiotic protists in lower termites. As with endosymbiosis in other insects, the symbiosis is obligate in that neither the bacteria nor the insect is viable without the other. Scientists have been unable to cultivate the bacteria in lab conditions outside of the insect. With special nutritionally-enhanced diets, the insects can survive, but are unhealthy and at best survive only a few generations.

In some insect groups, these endosymbionts live in specialized insect cells called bacteriocytes (also called *mycetocytes*) and are maternally-transmitted, i.e. the mother transmits her endosymbionts to her offspring. In some cases, the bacteria are transmitted in the egg, as in *Buchnera*; in others like *Wigglesworthia*, they are transmitted via milk to the developing insect embryo. In termites, the endosymbionts reside within the hindguts and are transmitted through trophallaxis among colony members.

The primary endosymbionts are thought to help the host either by providing nutrients that the host cannot obtain itself, or by metabolizing insect waste products into safer forms. For example, the putative primary role of *Buchnera* is to synthesize essential amino acids that the aphid cannot acquire from its natural diet of plant sap. Similarly, the primary role of *Wigglesworthia* is probably to synthesize vitamins that the tsetse fly does not get from the blood that it eats. In lower termites, the endosymbiotic protists play a major role in the digestion of lignocellulosic materials which constitutes a bulk of the termites' diet.

Bacteria benefit from the reduced exposure to predators and competition from other bacterial species, the ample supply of nutrients and relative environmental stability inside the host.

Genome sequencing reveals that obligate bacterial endosymbionts of insects have among the smallest of known bacterial genomes and have lost many genes that are commonly found in closely related bacteria. Several theories have been put forth to explain the loss of genes. Presumably some of these genes are not needed in the environment of the host insect cell. A complementary theory suggests that the relatively small numbers of bacteria inside each insect decrease the efficiency of natural selection in 'purging' deleterious mutations and small mutations from the population, resulting in a loss of genes over many millions of years. Research in which a parallel phylogeny of bacteria and insects was inferred supports the belief that the primary endosymbionts are transferred only vertically (i.e. from the mother) and not horizontally (i.e. by escaping the host and entering a new host).

Attacking obligate bacterial endosymbionts may present a way to control their insect hosts, many of which are pests or carriers of human disease. For example aphids are crop pests and the tsetse fly carries the organism *Trypanosoma brucei* that causes African sleeping sickness. Other motivations for their study is to understand symbiosis and to understand how bacteria with severely depleted genomes are able to survive, thus improving our knowledge of genetics and molecular biology.

Less is known about secondary endosymbionts. The pea aphid (*Acyrthosiphon pisum*) is known to contain at least three secondary endosymbionts, *Hamiltonella defensa*, *Regiella insecticola* and *Serratia symbiotica*. *H. defensa* aids in defending the insect from parasitoids. *Sodalis glossinidius* is a secondary endosymbiont tsetse flies that lives inter- and intracellularly in various host tissues, including the midgut and hemolymph. Phylogenetic studies have not indicated a correlation between evolution of *Sodalis* and tsetse. Unlike tsetse's P-symbiont *Wigglesworthia*, though, *Sodalis* has been cultured *in vitro*.

Viral endosymbionts and endogenous retrovirus

During pregnancy in viviparous mammals, endogenous retrovirii (ERVs) are activated and produced in high quantities during the implantation of the embryo. On one hand they act as immunodepressors and protect the embryo from the immune system of the mother and on the other hand viral fusion proteins cause the formation of the placental syncytium in order to limit the exchange of migratory cells between the developing embryo and the body of the mother, where an epithelium won't do because certain blood cells are specialized to be able to insert themselves between adjacent epithelial cells. The ERV is a virus similar to HIV (the virus causing AIDS in humans). The immunodepressive action was the initial normal behavior of the virus, similar to HIV. The fusion proteins was a way to spread the infection to other cells by simply merging them with the infected one (similar to HIV). It is believed that the ancestors of modern vivipary mammals evolved after an accidental infection of an ancestor with this virus, that permitted the fetus to survive the immune system of the mother.

Example:

Rhizobia

Soybean root nodules, each containing billions of *Bradyrhizobium* bacteria

Rhizobia are soil bacteria that fix nitrogen (diazotrophy) after becoming established inside root nodules of legumes (Fabaceae). Rhizobia require a plant host; they cannot independently fix nitrogen. Morphologically, they are generally gram negative, motile, non-sporulating rods.

History

The first species of rhizobia, *R. leguminosarum*, was identified in 1889 and all further species were initially placed in the *Rhizobium* genus. However, more advanced methods of analysis have revised this classification and now there are many in other genera. Most research has been done on crop and forage legumes such as clover, alfalfa, beans and soy; recently, more work is occurring on North American legumes.

The word *rhizobia* comes from the Ancient Greek ῥίζα, "rhíza," meaning "root," and βίος, "bios," meaning "life." The word *rhizobium* is still sometimes used as the singular form of *rhizobia*.

Taxonomy

Rhizobia are a paraphyletic group which fall into two classes of the proteobacteria—the alpha- and beta-proteobacteria. As shown below, most belong to the order Rhizobiales but several rhizobia occur in distinct bacterial orders of the proteobacteria.

α-proteobacteria

Rhizobiales
Bradyrhizobiaceae
Bradyrhizobium
B. canariense
B. elkanii
B. japonicum
B. liaoningense
B. yuanmingense
Brucellaceae
Ochrobactrum
O. cytisi
O. lupini
Hyphomicrobiaceae
Azorhizobium
A. caulinodans
A. doebereinerae
Devosia
D. neptuniae
Methylobacteriaceae
Methylobacterium
M. nodulans
Phyllobacteriaceae
Mesorhizobium
M. albiziae
M. amorphae
M. chacoense
M. ciceri
M. huakuii
M. loti
M. mediterraneum
M. plurifarium
M. septentrionale
M. temperatum
M. tianshanense
Phyllobacterium
P. ifriqiyense
P. leguminum
P. trifolii

Rhizobiaceae
Rhizobium
R. cellulosilyticum
R. daejeonense
R. etli
R. galegae
R. gallicum
R. giardinii
R. hainanense
R. huautlense
R. indigoferae
R. leguminosarum
R. loessense
R. lupini
R. lusitanum
R. mongolense
R. miluonense
R. sullae
R. tropici
R. undicola
R. yanglingense
Sinorhizobium (*Ensifer*)
S. abri
S. adhaerens
S. americanum
S. arboris
S. fredii
S. indiaense
S. kostiense
S. kummerowiae
S. medicae
S. meliloti
S. mexicanus
S. morelense
S. saheli
S. terangae
S. xinjiangense

β-proteobacteria

Burkholderiales
Burkholderiaceae
Burkholderia
B. caribensis
B. dolosa
B. mimosarum
B. phymatum
B. tuberum
Cupriavidus
C. taiwanensis
Oxalobacteraceae
Herbaspirillum
H. lusitanum

These groups include a variety of non-symbiotic bacteria. For instance, the plant pathogen *Agrobacterium* is a closer relative of *Rhizobium* than the *Bradyrhizobium* that nodulate soybean (and may not really be a separate genus). The genes responsible for the symbiosis with plants, however, may be more closely related than the organisms themselves, acquired by horizontal transfer (via bacterial conjugation) rather than vertical gene transfer (from a common ancestor).

Importance in agriculture

Although much of the nitrogen is removed when protein-rich grain or hay is harvested, significant amounts can remain in the soil for future crops. This is especially important when nitrogen fertilizer is not used, as in organic rotation schemes or some less-industrialized countries. Nitrogen is the most commonly deficient nutrient in many soils around the world and it is the most commonly supplied plant nutrient. Supply of nitrogen through fertilizers has severe environmental concerns.

Symbiosis

Rhizobia are unique because they live in a symbiotic relationship with legumes. Common crop and forage legumes are peas, beans, clover and soy.

Infection and signal exchange

The symbiotic relationship implies a signal exchange between both partners that leads to mutual recognition and development of symbiotic structures. Rhizobia live in the soil where they are able to sense flavonoids secreted by the root of their host legume plant. Flavonoids trigger the secretion of Nod factors, which in turn are recognized by the host plant and can lead to root hair deformation and several cellular responses such as ion fluxes. The best known infection mechanism is called intracellular infection, in this case the rhizobia enter through a deformed root hair in a similar way to endocytosis, forming an intracellular tube called the infection thread. A second mechanism is called "crack entry", in this case no root hair deformation is observed and the bacteria penetrate between cells, through cracks produced by lateral root emergence. Later on bacteria become intracellular and an infection thread is formed like in intracellular infections.

The infection triggers cell division in the cortex of the root where a new organ, the nodule appears as a result of successive processes.

Nodule formation and functioning

Infection threads grow to the nodule, infect its central tissue and release the rhizobia in these cells where they differentiate morphologically into **bacteroids** and fix nitrogen from the atmosphere into a plant usable form, ammonium (NH_4^+), utilizing the enzyme nitrogenase. In return the plant supplies the bacteria with carbohydrates, proteins and sufficient oxygen so as not to interfere with the fixation process. Leghaemoglobins, plant proteins similar to human hemoglobins help to provide oxygen for respiration while keeping the free oxygen concentration low enough not to inhibit nitrogenase activity. Recently, it was discovered that a *Bradyrhizobium* strain forms nodules in *Aeschynomene* without producing Nod factors, suggesting the existence of alternative communication signals other than Nod factors.

The legume–rhizobium symbiosis is a classic example of mutualism—rhizobia supply ammonia or amino acids to the plant and in return receive organic acids (principally as the dicarboxylic acids malate and succinate) as a carbon and energy source—but its evolutionary persistence is actually somewhat surprising. Because several unrelated strains infect each individual plant, any one strain could redirect resources from nitrogen fixation to its own reproduction without killing the host plant upon which they all depend. But this form of cheating should be equally tempting for all strains, a classic tragedy of the commons. There are two competing hypotheses for the mechanism that maintains legume-rhizobium symbiosis (though both may occur in nature). The **sanctions hypothesis** suggests that plants police cheating rhizobia. Sanctions could take the form of reduced nodule growth, early nodule death, decreased carbon supply to nodules, or reduced oxygen supply to nodules that fix less nitrogen. The **partner choice hypothesis** proposes that the plant uses pre-nodulation signals from the rhizobia to decide whether to allow nodulation and chooses only non-cheating rhizobia. There is evidence for sanctions in soybean plants, which reduce rhizobium reproduction (perhaps by limiting oxygen supply) in nodules that fix less nitrogen. Similarly, wild lupine plants allocate less resources to nodules containing less-beneficial rhizobia, limiting rhizobial reproduction inside. This is consistent with the definition of sanctions just given, although called "partner choice" by the authors. However, other studies have found no evidence of plant sanctions and instead support the partner choice hypothesis.

Other diazotrophs

Many other species of bacteria are able to fix nitrogen (diazotrophs), but few are able to associate intimately with plants and colonize specific structures like Legume nodules. Bacteria that do associate with plants include the actinobacteria *Frankia*, which form symbiotic root nodules in actinorhizal plants and several cyanobacteria (*Nostoc*) associated with aquatic ferns, *Cycas* and *Gunneras*. Free-living diazotrophs are often found in the rhizosphere and in the intercellular spaces of several plants including rice and sugarcane, but in this case the lack of a specialized structure results in poor nutrient transfer efficiency compared to legume or actinorhizal nodules.

Chapter- 4

Commensalism

The cattle egret, *Bubulcus ibis*, is a classic example of commensalism. It forages in fields among cattle and horses, feeding on insects stirred up by the grazing animals. The egret benefits from this relationship, while the livestocks are typically unaffected by it.

In ecology, **commensalism** is a class of relationship between two organisms where one organism benefits but the other is neutral (there is no harm or benefit). There are three other types of association: mutualism (where both organisms benefit), competition (where both organisms are harmed) and parasitism (one organism benefits and the other one is harmed).

Commensalism derives from the English word *commensal*, meaning "sharing of food" in human social interaction, which in turn derives from the Latin *cum mensa*, meaning "sharing a table". Originally, the term was used to describe the use of waste food by second animals, like the carcass eaters that follow hunting animals, but wait until they have finished their meal.

Examples of commensal relationships

Commensalism is harder to demonstrate than parasitism and mutualism, for it is easier to show a single instance whereby the host is affected, than it is to prove or disprove that possibility. Often, a detailed investigation will show that the host indeed has become affected by the relationship.

Cattle egrets and livestock

An example of commensalism: cattle egrets foraging in fields among cattle or other livestock. As cattle, horses and other livestock graze on the field, they cause movements that stir up various insects. As the insects are stirred up, the cattle egrets following the livestock catch and feed upon them. The egrets benefit from this relationship because the livestock have helped them find their meals, while the livestock are typically unaffected by it.

Tigers and golden jackals

In India, lone golden jackals expelled from their pack have been known to form commensal relationships with tigers. These solitary jackals, known as *kol-bahl*, will attach themselves to a particular tiger, trailing it at a safe distance in order to feed on the big cat's kills. A *kol-bahl* will even alert a tiger to a kill with a loud *pheal* (thereby straying into mutualism). Tigers have been known to tolerate these jackals: one report describes how a jackal confidently walked in and out between three tigers walking together a few feet away from each other. Tigers will however kill jackals on occasion: the now extinct tigers of the Amu Darya region were known to eat jackals frequently.

Other examples

Another example of commensalism: birds following army ant raids on a forest floor. As the army ant colony travels on the forest floor, they stir up various flying insect species. As the insects flee from the army ants, the birds following the ants catch the fleeing insects. In this way, the army ants and the birds are in a commensal relationship because the birds benefit while the army ants are unaffected.

Orchids and mosses are plants that can have a commensal relationship with trees. The plants grow on the trunks or branches of trees. They get the light they need as well as nutrients that run down along the tree. As long as these plants do not grow too heavy, the tree is not affected.

Barnacles

Barnacles, a type of arthropod in the subphylum Crustacea

Barnacles are highly sedentary crustaceans that must attach themselves permanently to a hard substrate, such as rocks, shells, whales, or anything else on which they can gain a foothold. When they attach to the shell of a scallop, for instance, barnacles benefit by having a place to stay, leaving the scallop presumably unaffected.

Arguments

Whether the relationship between humans and some types of our gut flora is commensal or mutualistic is still unanswered.

Some biologists argue that any close interaction between two organisms is unlikely to be completely neutral for either party and that relationships identified as commensal are likely mutualistic or parasitic in a subtle way that has not been detected. For example, epiphytes are "nutritional pirates" that may intercept substantial amounts of mineral nutrients that would otherwise go to the host plant. Large numbers of epiphytes can also cause tree limbs to break or shade the host plant and reduce its rate of photosynthesis. Similarly, the phoretic mites may hinder their host by making flight more difficult, which may affect its aerial hunting ability or cause it to expend extra energy while carrying these passengers.

Types

Phoretic mites on a fly (*Pseudolynchia canariensis*)

Like all ecological interactions, commensalisms vary in strength and duration from intimate, long-lived symbioses to brief, weak interactions through intermediaries.

Phoresy

One animal attaching to another for transportation only. This concerns mainly arthropods, examples of which are mites on insects (such as beetles, flies, or bees), pseudoscorpions on mammals or beetles and millipedes on birds. Phoresy can be either obligate or facultative (induced by environmental conditions).

Inquilinism

Using a second organism for housing. Examples are epiphytic plants (such as many orchids) that grow on trees, or birds that live in holes in trees.

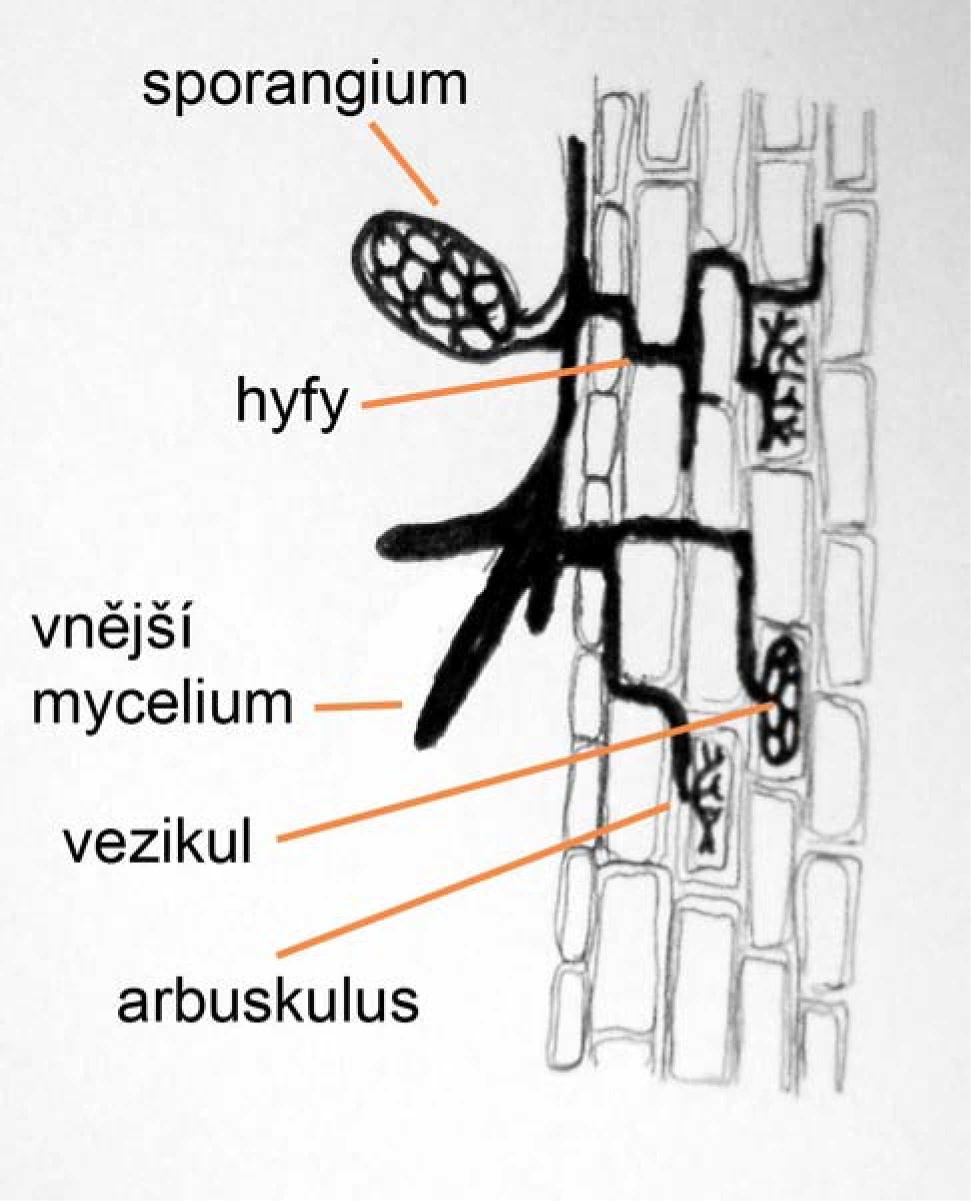
Metabiosis

A more indirect dependency, in which one organism creates or prepares a suitable environment for a second. Examples include maggots, which feast and develop on corpses and hermit crabs, which use gastropod shells to protect their bodies.

Chapter- 5

Mutualism

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



Arbuscular mycorrhiza

Mutualism is the way two organisms biologically interact where each individual derives a fitness benefit (i.e. increased survivorship). Similar interactions within a species are known as co-operation. It 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 and symbiosis are sometimes used as if they are synonymous, but this is strictly incorrect: symbiosis is a broad category, defined to include relationships which are mutualistic, parasitic or commensal. Mutualism is only one *type*.

A well known example of mutualism is the relationship between ungulates (such as cows) 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. However mutualism has historically received less attention than other interactions such as predation and parasitism.

Measuring the exact fitness benefit to the individuals is not always straightforward, particularly when the individuals can receive benefits from a range 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 versus 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).

Types of relationships

Mutualistic transversals can be thought of as a form of "biological barter" in which species trade resources (for example carbohydrates or inorganic compounds) or services such as gamete, offspring dispersal, or protection from predators.

Resource-resource relationships

Resource-resource interactions, in which one type of resource is traded for a different resource, are probably the most common form of mutualism; for example 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 which fix nitrogen for leguminous plants (family Fabaceae) in return for energy-containing carbohydrates.

Service-resource relationships

The Red-billed Oxpecker eats ticks on the impala's coat

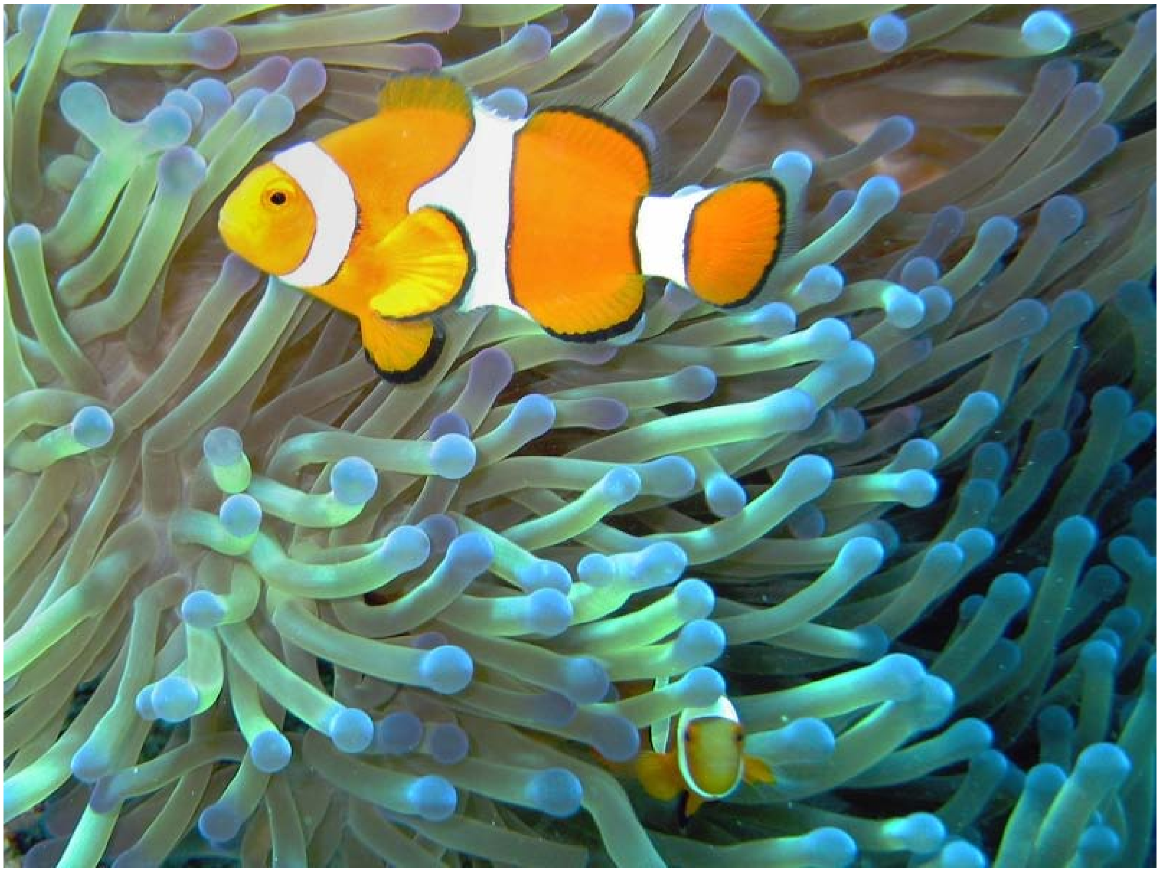
Service-resource relationships are also common.

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 ladybird beetles.

Phagophiles feed (resource) on ectoparasites, thereby providing anti-pest service.

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, overabundance of seeds) for animals that disperse the seeds (service).

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. One example is the relationship between sea anemones and anemonefish 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. 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 which 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".

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, provisioning 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 greedy 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.

Humans and mutualism

Dogs and sheep were among the first animals to be domesticated

Humans also engage in mutualisms with other species, including their gut flora (without which they would not be able to digest food efficiently) and domesticated animals such as horses, which provide transportation in return for food and shelter. In traditional agriculture, many plants will function mutualistically as companion plants, providing each other with shelter, soil fertility and the repelling of pests. For example, beans may grow up cornstalks as a trellis, while fixing nitrogen in the soil for the corn, as exploited in the Three Sisters gardening technique.

Mathematical theory

In 1989, David Hamilton Wright developed a mathematical explanation for mutualism using the Lotka–Volterra equation. Wright modified the Lotka-Volterra equations by adding a new term, $\beta M/K$, to represent a mutualistic relationship.

The mutalistic relationship is quantified by:

$dN/dt = r_1 N(1 – N/K1 + \beta_{12} M/K_1)$

$dM/dt = r_2 M (1 – M/K2 + \beta_{21} N/K_2)$

where,

- N and M = the population density
- 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 essentially 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. 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

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

$ax/(1 + axT_H)$.

where,

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

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

$dN/dt = N\,[r(1-cN) + \beta M(X+M)]$

where,

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

Rearranged: $dN/dt = N[r(1-cN) + baM/(1+aT_HM)]$

These two graphs show the isoclines of mutualistic relationships. Presence of the mutualist has a positive effect on the recipient population at low densities of mutualists but at high densities, saturation takes place and further increases in mutualist populations have little effect. Arrows indicate the stability or instability of equilibrium points.

Graph A illustrates a facultative mutualism in which both species derive benefits from each other, but do not depend on the existence of the other for survival.

Graph B demonstrates an obligate mutualism in which both species are interdependent on each other in a way that one species cannot survive without the other. Once the population of one species drops below the first equilibrium point, both populations will go extinct.

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.

Chapter- 6

Host-Parasite Coevolution

Host-parasite coevolution is a special case of coevolution, which is defined as the reciprocal adaptive genetic change of two antagonists (e.g. different species or genes) through reciprocal selective pressures. In the particular case of host-parasite coevolution the antagonists are different species of host and parasite.

Introduction

Hosts and parasites exert reciprocal selective pressures on each other, which may lead to rapid reciprocal adaptation. For organisms with short generation times host-parasite coevolution can be observed in comparatively small time periods, making it possible to study evolutionary change in real-time under both field and laboratory conditions. These interactions may thus serve as a counter-example to the common notion that evolution can only be detected across extended time scales.

The high dynamics associated with these interactions are summarized in the Red Queen hypothesis. It states that "it takes all the running you can do to keep in the same place", i.e. both host and parasite have to change continuously to keep up with each other's adaptations.

Relevance

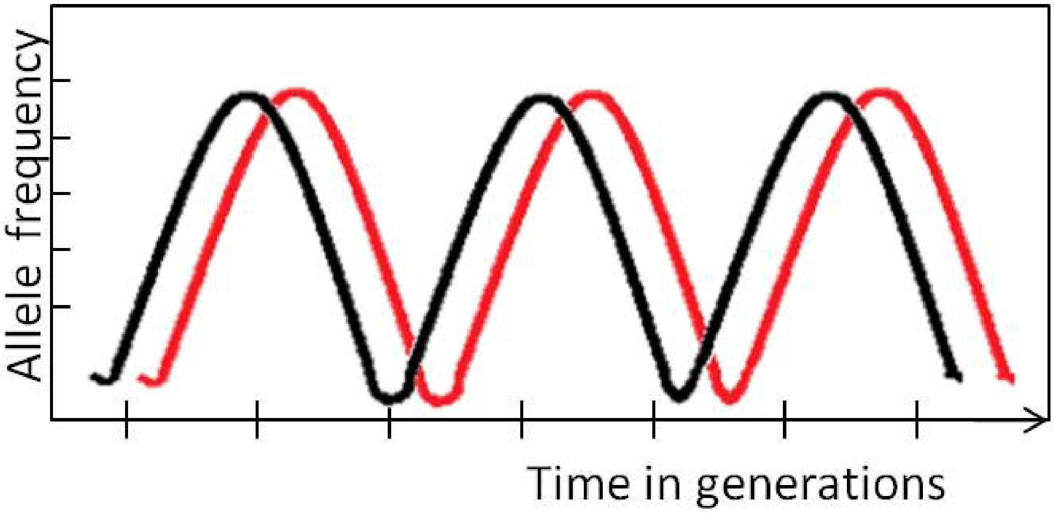
Host-parasite coevolution is a ubiquitous phenomenon of potential importance to all living organisms, including humans. Many medically relevant diseases (e.g. malaria, AIDS and influenza) are caused by coevolving parasites. Therefore detailed understanding of the coevolutionary adaptations between parasite ‘attack strategy’ and host immune system may result in the development of novel medications and vaccines and thus help save human life.

Furthermore these interactions are of major concern in agriculture. Coevolving parasites are responsible for crop failure and especially in industrial agriculture, pesticides are indispensable. Livestock is similarly affected by numerous coevolving parasites. Therefore a clearer understanding of host-parasite coevolution will point to new possibilities for organic farming and reduce the application of ecologically harmful chemicals.

Selection Dynamics

Host-parasite coevolution is characterized by reciprocal genetic change and thus changes in allele frequencies within populations. These changes may be determined by three main types of selection dynamics.

Negative frequency dependent selection



Negative frequency dependent selection in the coevolution of hosts and parasites; black curve: host; red curve: parasite

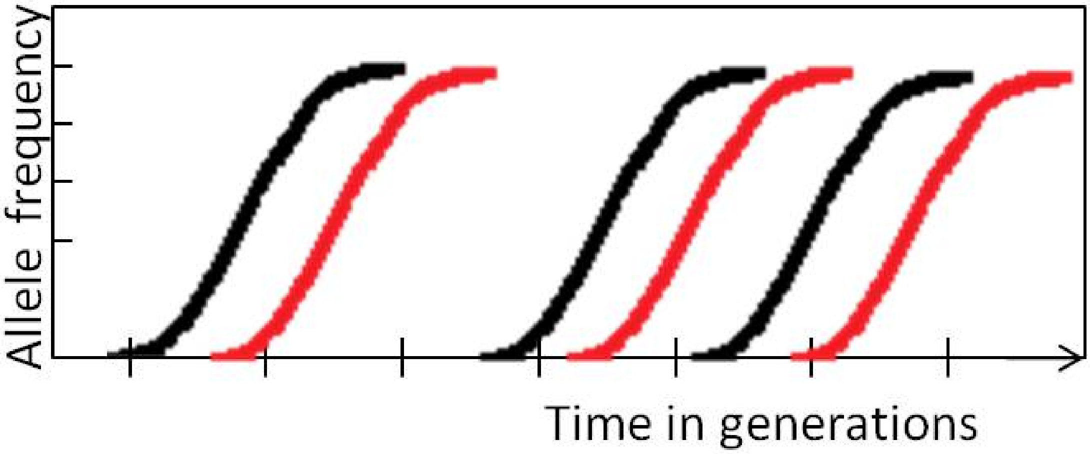
An allele is subject to negative frequency dependent selection if a rare allelic variant has a selective advantage. For example, the parasite should adapt to the most common host genotype, because it can then infect a large number of hosts. In turn, a rare host genotype may then be favored by selection, its frequency will increase and eventually it becomes common. Subsequently the parasite should adapt to the former infrequent genotype.

Coevolution determined by negative frequency dependent selection is rapid, potentially occurring across few generations. It maintains high genetic diversity by favoring uncommon alleles. This selection mode is expected for multicellular hosts, because adaptations can occur without the need for novel advantageous mutations, which are less likely to be frequent in these hosts because of relatively small population sizes and relatively long generation times.

Overdominant selection

Overdominance occurs if the heterozygote phenotype has a fitness advantage over both homozygotes ("heterozygote advantage" or "heterosis"). One example is sickle cell anemia. It is due to a mutation in the hemoglobin gene leading to sickle shape formation of red blood cells, causing clotting of blood vessels, restricted blood flow and reduced oxygen transport. At the same time, the mutation confers resistance to malaria, caused by Plasmodium parasites, which are passed off in red blood cells after transmission to humans by mosquitoes. Hence, homozygote and heterozygote genotypes for the sickle-cell disease allele show malaria resistance, while the homozygote suffers from severe disease phenotype. The alternative homozygote, which does not carry the sickle cell disease allele, is susceptible to Plasmodium. As a consequence, the heterozygote genotype is selectively favored in areas with a high incidence of malaria.

Directional selection



Directional selection: recurrent selective sweeps in the coevolution of hosts and parasites; black curve: host; red curve: parasite

If an allele provides a fitness benefit, its frequency will increase within a population - selection is directional or positive. Selective sweeps are one form of directional selection, where the increase in frequency will eventually lead to the fixation of the advantageous allele. The process is considered to be slower in comparison to negative frequency dependent selection. It may produce an "arms race", consisting of the repeated origin and fixation of new parasite virulence and host defence traits.

This mode of selection is likely to occur in interactions between unicellular organisms and viruses due to large population sizes, short generation times, often haploid genomes and horizontal gene transfer, which increase the probability of beneficial mutations arising and spreading through populations.

Current challenges

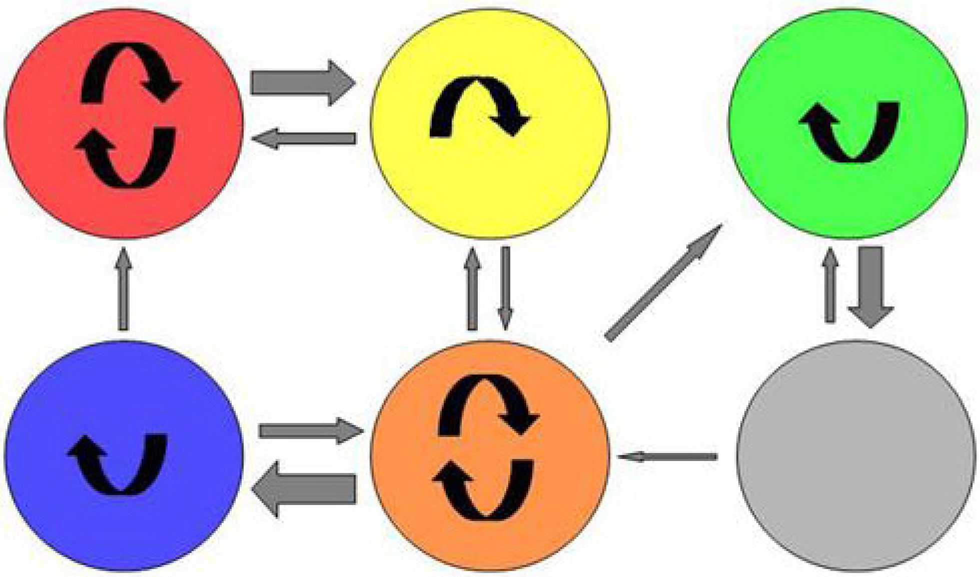
The relative importance of these different selective dynamics for host-parasite coevolution is still under debate. One problem is that the unambiguous identification of the underlying dynamics is not straightforward. For example, if the plot of allele frequency changes indicates a selective sweep, then it is possible that the curve represents a small part of the fluctuating cycles expected for negative frequency dependent selection and that the time scale of the analysis is too short to allow clear discrimination of the alternatives.

In addition the modes of selection can differ between the various loci involved in host-parasite interactions. Therefore the various loci may be subject to different selection dynamics.

Geographic Mosaic Theory of Coevolution

The Geographic Mosaic Theory of Coevolution by John N. Thompson hypothesizes that there is spatially divergent coevolutionary selection, producing genetic differentiation across populations.

The model assumes that there are three crucial elements that jointly fuel ongoing coevolutionary change:



Hypothetical example of a Geographic Mosaic of Coevolution between two species: The coloured circles stand for biological communities; the arrows within the circles show interactions within local communities and represent selection on one or both (or none) species (truly reciprocal selection = hotspot). Selection among communities is generated from disparities in biotic or abiotic habitat quality. The arrows between the communities indicate gene flow (thicker arrows = more gene flow).

1) **There is a selection mosaic among populations**. Natural selection on interspecific interactions differs among populations. Thus genotype-by-genotype-by-environment (G x G x E) interactions affect fitness of the antagonists. In other words, the specific environmental conditions determine how any genotype of one species influences the fitness of another species (biotic and abiotic components).

2) **There are coevolutionary hotspots**. Coevolutionary hotspots are communities in which selection on the interaction is truly reciprocal. These hotspots are intermixed with so-called coldspots in which only one or neither species adapts to the antagonist.

3) **There is a geographic mixing of traits**. Between the communities/regions there is a continuous "mixing" of traits by gene flow, random genetic drift, population extinction, or mutations. This remixing determines the exact dynamics of the Geographic Mosaic by shifting the spatial distributions of potentially coevolving alleles and traits.

In summary, the theory claims that species interactions commonly coevolve as complex geographic mosaics of populations, formed by differences in local selection and gene flow. It ties together the processes operating over space and time to determine the outcome of coevolutionary interactions and furthermore provides a reference framework for future (especially field) research on this topic.

Costs of adaptation

Ressources are generally limited. Therefore, investment in one trait (e.g. virulence or immunity) limits investment in other life-history traits (e.g. reproductive rate). Moreoever, genes often have pleiotropic effects. Thus, a change in a pleiotropic immunity or virulence gene may automatically affect other traits. There is thus a trade-off between benefits and costs of the adaptive changes that then may prevent the host population to become fully resistant or the parasite population to express very high pathogenicity.

One example for costs related to gene pleiotropy was found for coevolving *Escherichia coli* and bacteriophages.

To inject their genetic material, phages need to bind to a specific bacterial cell surface receptor. The bacterium may prevent injection by altering the relevant binding site, e.g. in response to point mutations or deletion of the receptor. However, these receptors have important functions in bacterial metabolism. Their loss would thus decrease fitness (i.e. growth rate). As a consequence, there is a trade-off between the advantages and disadvantages of a mutated receptor, leading to polymorphisms at this locus within bacterial populations coevolving with phages.

Studying host-parasite coevolution

Field studies across space and/or time

Field studies across space at a single time point may be useful to study coevolution for host systems with long generation times, for which temporal changes cannot be easily assessed within the often restricted timeline of research projects. Such spatial studies rely on the concept of local adaptation: Due to chance effects and varying environmental conditions host and parasite are likely to coevolve along different trajectories in different locations. The comparison of locations may reveal various stages of the coevolutionary cycle. A major challenge is to distinguish patterns of local adaptation caused by reciprocal coevolutionary change versus directional selection to any other environmental factor.

Long term field studies of populations from one or more sites represent the ideal approach to analyse the dynamics and consequences of coevolution, because they allow the direct detection of reciprocal genetic change. A particular challenge is to relate the temporal dynamics to variation in environmental factors (i.e. G x G x E effects). Long term studies including several locations may also help to understand the dynamics of the geographic mosaic of coevolution.

Experiments under controlled lab conditions

Laboratory-based evolution experiments may represent a highly efficient approach to dissect the importance of particular selective factors and to characterize in detail the dynamics and consequences of coevolution. Most importantly, they allow to minimize confounding environmental influences and to test single factors, which can be varied between treatments. Therefore, this approach may allow distinction of cause and effect. Such evolution experiments require host systems with short generation times like bacteria or invertebrates. A particular challenge is to relate the results from the artificial laboratory environment to the complexity encountered in nature.

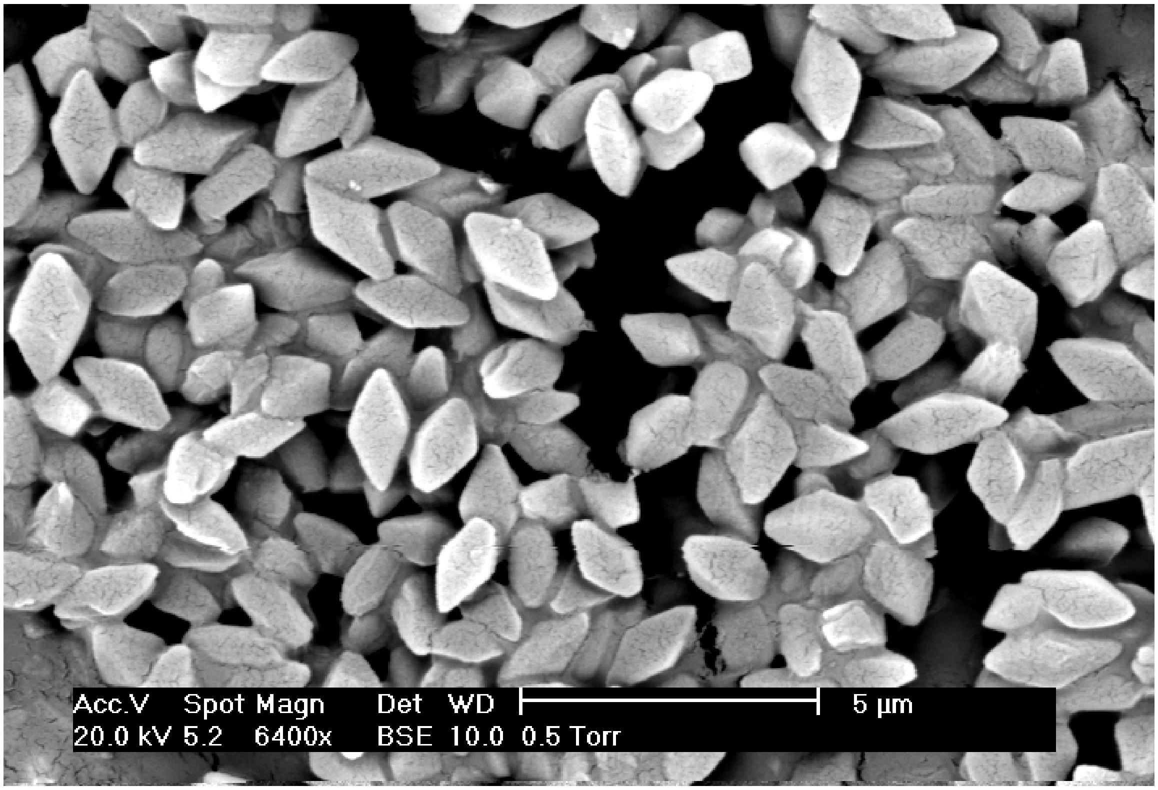
Potamopyrgus antipodarum and its trematode

Potamopyrgus antipodarum

The New Zealand freshwater snail *Potamopyrgus antipodarum* and its different trematode parasites represent a rather special model system. Populations of *P. antipodarum* consist of asexual clones and sexual individuals and therefore can be used to study the evolution and advantages of sexual reproduction.

Long term laboratory experiments and field studies revealed that there is a high correlation between the presence of parasites and the frequency of sexual individuals within the different populations. This result is consistent with the Red Queen hypothesis that sexual reproduction is favoured during host-parasite coevolution. At the same time, the persistance of sex may also rely on other factors, for example Muller's ratchet and/or the avoidance of the accummulation of deleterious mutations (deterministic mutation model).

Caenorhabditis elegans and *Bacillus thuringiensis*



Bacillus thuringiensis

Caenorhabditis elegans

The nematode *Caenorhabditis elegans* and the bacterium *Bacillus thuringiensis* were only recently established as a model system for studying host-parasite coevolution. Laboratory evolution experiments provided evidence for many of the basic predictions of these coevolutionary interactions, including reciprocal genetic change and increases in the rate of evolution and genetic diversity.

The widespread use of *C. elegans* in different branches of biology makes it a good choice for evolutionary research. On the one hand evolutionary studies may help to close the gaps in knowledge still persistent for *C. elegans* biology. On the other hand the information already available on this species may help to work out the molecular mechanisms underlying evolutionary change.

Daphnia and its parasites

Daphnia magna

The crustacean Daphnia and its numerous parasites have become one of the main model systems for studying coevolution. One valuable characteristic of this system is that the reproduction of the host can be asexual as well as sexual (inducing by changes in the external environment), so that conditions for sexual reproduction can be stimulated in the laboratory.

Coevolution was especially studied between *Daphnia magna* and the bacterium *Pasteuria ramosa*. For example, Decaestecker et al. reconstructed the evolution of the populations across decades, by reanimating resting stages of both species from laminated pond sediments and exposed hosts from each layer to parasites from the past, the same and the future layers. The study demonstrated that parasites were on average most infective on their contemporary hosts. in consistency with negative frequency dependent selection

Tribolium castaneum and *Nosema whitei*

Tribolium castaneum

As many other arthropods *Tribolium castaneum*, the red flour beetle, is a host for the microsporidia *Nosema whitei*.

Nosema whitei kills its host for transmission, thus the host's lifespan is important for the parasite's success. In turn, parasite fitness most likely depends on a trade-off between transmission (spore load) and virulence: A higher virulence would increase the potential for the production of more offspring, but a higher spore load would affect the host's lifespan and therefore the transmission rate. This trade-off is supported by coevolutionary experiments, which revealed the decrease of virulence, a constant transmission potential and an increase in the host's lifespan over a period of time. Further experiments demonstrated a higher recombination rate in the host during coevolutionary interactions, which may be selectively advantageous because it should increase diversity of host genotypes.

Plantago and its parasites

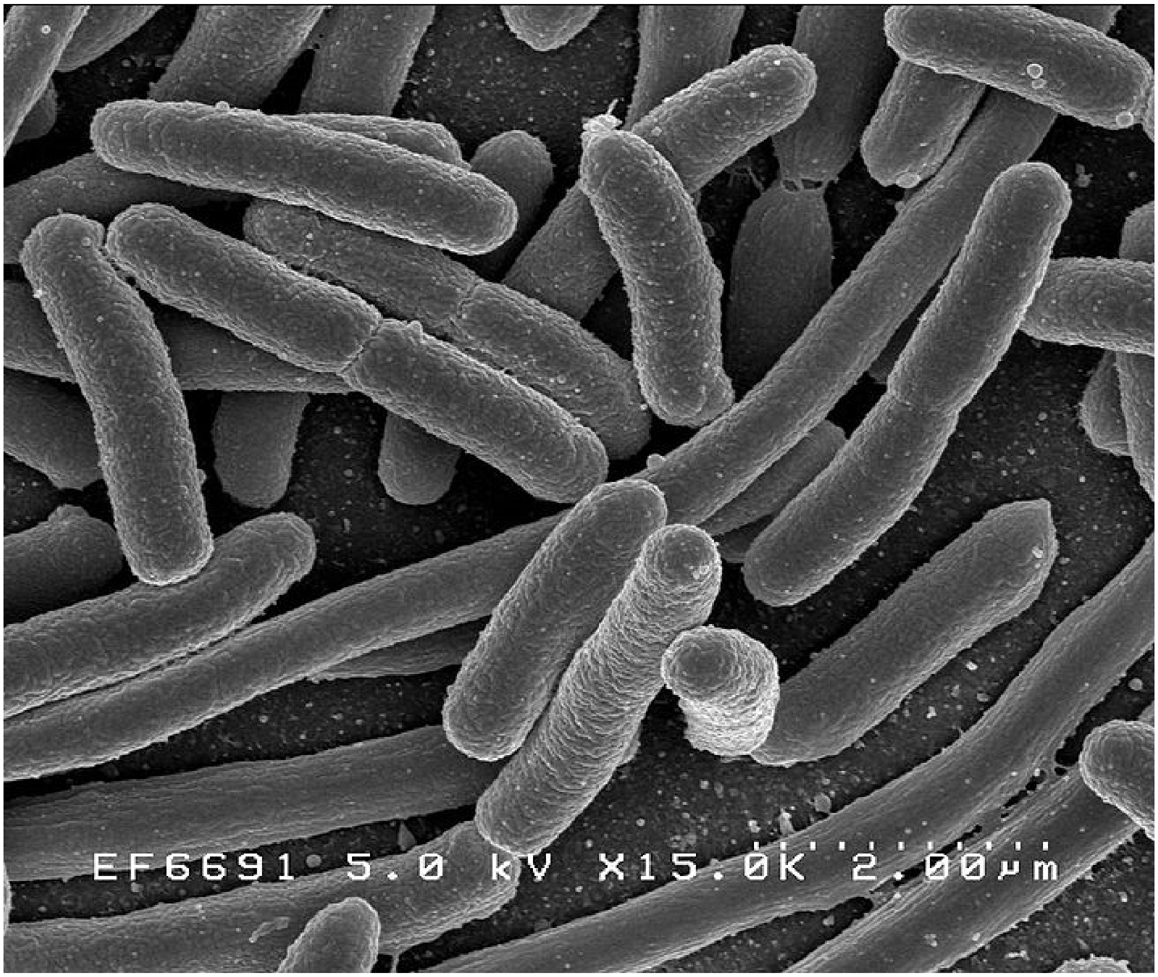
Plantago lanceolata

Host-parasite coevolution is studied in a diversity of plant systems. One example is *Plantago lanceolata* and its parasite *Podosphaera plantaginis*, which has been intensively studied on the Aland islands in south-western Finland. *P. plantaginis* is a powdery mildew obtaining nutrients from its host, a perennial herb, by sending feeding roots into the plant.

There are more than 3000 host populations known in this region, where both populations can evolve freely, in absence of human-imposed selection, in a very heterogeneous landscape. Both antagonists can reproduce asexually or sexually. This system was used to demonstrate spatially divergent coevolutionary dynamics across two metapopulations and it provided support for the predictions of the Mosaic Theory of Coevolution.

Bacteria and their parasites

Biological communities are often complex, they are influenced by diverse factors and therefore, they are very difficult to study. A possible solution is to focus on simple community systems under controlled laboratory conditions, for example microbial communities consisting of *Escherichia coli* or *Pseudomonas fluorescens* and their bacteriophages.



Escherichia coli

E. coli, a Gram-negative proteobacterium, is a common model in biological research, for which comprehensive data on various aspects of its life-history is available. It has been used extensively for evolution experiments, including those related to coevolution with phages. These studies revealed - among others - that coevolutionary adaptation may be influenced by pleiotropic effects of the involved genes. In particular, binding of the bacteriophage to *E. coli* surface receptor is the crucial step in the virus infection cycle. A mutation in the receptor's binding site may cause resistance. Such mutations often show pleiotropic effects and may cause a cost of resistance. In the presence of phages, such pleiotropy may lead to polymorphisms in the bacterial population and thus enhance biodiversity in the community. Another model system consists of the plant- and animal-colonizing bacterium *Pseudomonas* and its bacteriophages. This system provided new insights into the dynamics of coevolutionary change. It demonstrated that coevolution may proceed via recurrent selective sweeps, favouring generalists for both antagonists. Furthermore, coevolution with phages may promote allopatric diversity, potentially enhancing biodiversity and possibly speciation. Host-parasite coevolution may also affect the underlying genetics, for example by favouring increased mutation rates in the host.

Chapter- 7

Myco-Heterotrophy and Zooxanthella

Myco-heterotrophy

Monotropa uniflora, an obligate myco-heterotroph known to parasitize fungi belonging to the Russulaceae.

Myco-heterotrophy is a symbiotic relationship between certain kinds of plants and fungi, in which the plant gets all or part of its food from parasitism upon fungi rather than from photosynthesis. A **myco-heterotroph** is the parasitic plant partner in this relationship. Myco-heterotrophy is considered a kind of cheating relationship and myco-heterotrophs are sometimes informally referred to as "**mycorrhizal cheaters**". This relationship is sometimes referred to as **mycotrophy**, though this term is also used for plants that engage in mutualistic mycorrhizal relationships.

Relationship between myco-heterotrophs and host fungi

Myco-heterotrophic roots of *Monotropa uniflora* with *Russula brevipes* mycelium

Full (or obligate) myco-heterotrophy exists when a non-photosynthetic plant (a plant largely lacking in chlorophyll or otherwise lacking a functional photosystem) gets all of its food from the fungi that it parasitizes. Partial (or facultative) myco-heterotrophy exists when a plant is capable of photosynthesis, but parasitizes fungi as a supplementary food supply. There are also plants, such as some orchid species, that are non-photosynthetic and obligately myco-heterotrophic for part of their life cycle and photosynthetic and facultatively myco-heterotrophic or non-myco-heterotrophic for the rest of their life cycle. Not all non-photosynthetic or "achlorophyllous" plants are myco-heterotrophic – some non-photosynthetic plants like dodder directly parasitize the vascular tissue of other plants.

In the past, non-photosynthetic plants were mistakenly thought to get food by breaking down organic matter in a manner similar to saprotrophic fungi. Such plants were therefore called "saprophytes". It is now known that no plant is physiologically capable of direct breakdown of organic matter and that in order to get food, non-photosynthetic plants must engage in parasitism, either through myco-heterotrophy or direct parasitism of other plants.

The interface between the plant and fungal partners in this association is between the roots of the plant and the mycelium of the fungus. Myco-heterotrophy therefore closely resembles mycorrhiza (and indeed is thought to have evolved from mycorrhiza), except that in myco-heterotrophy, the flow of carbon is from the fungus to the plant, rather than vice versa.

Most myco-heterotrophs can therefore be seen as ultimately being epiparasites, since they take energy from fungi that in turn get their energy from vascular plants. Indeed, much myco-heterotrophy takes place in the context of a common mycorrhizal network, in which plants use mycorrhizal fungi to exchange carbon and nutrients with other plants. In these systems, myco-heterotrophs play the role of "mycorrhizal cheaters", taking carbon from the common network, with no known reward.

In congruence with older reports, it has been recently shown that some myco-heterotrophic orchids can be supported by saprotrophic fungi, exploiting litter- or wood-decaying fungi. In addition, several green plants (evolutionarily close to myco-heterotrophic species) have been shown to engage in partial myco-heterotrophy, that is, they are able to take carbon from mycorrhizal fungi, in addition to their photosynthetic intake.

Species diversity of myco-heterotrophs and host fungi

Myco-heterotrophs are found among a number of plant groups. All monotropes and non-photosynthetic orchids are full myco-heterotrophs, as is the non-photosynthetic liverwort *Cryptothallus*. Partial myco-heterotrophy is common in the Gentian family, with a few genera such as *Voyria* being fully myco-heterotrophic, in photosynthetic orchids and a number of other plant groups. Some ferns and clubmosses have myco-heterotrophic gametophyte stages. The fungi that are parasitized by myco-heterotrophs are typically fungi with large energy reserves to draw on, usually mycorrhizal fungi, though there is some evidence that they may also parasitize parasitic fungi that form extensive mycelial networks, such as *Armillaria*.

Zooxanthellae

Symbiodinium **Fossil range: Inferred as Eocene–Recent**	
Scientific classification	
Domain:	Eukaryota
Kingdom:	Chromalveolata
Superphylum:	Alveolata

Phylum: Dinoflagellata
Class: Dinophyceae
Order: Suessiales
Family: Blastodiniaceae
Genus: **Symbiodinium**

Zooxanthellae are flagellate protozoa that are golden-brown intracellular endosymbionts of various marine animals and protozoa, especially anthozoans such as the scleractinian corals and the tropical sea anemone, *Aiptasia*.

Zooxanthellae live in other protozoa (foraminiferans and radiolarians) and in some invertebrates. Most are autotrophs and provide the host with energy in the form of translocated reduced carbon compounds, such as glucose, glycerol and amino acids, which are the products of photosynthesis. Zooxanthellae can provide up to 90% of a coral's energy requirements. In return, the coral provides the zooxanthellae with protection, shelter, nutrients (mostly waste material containing nitrogen and phosphorus) and a constant supply of carbon dioxide required for photosynthesis. Available nutrients, incident light and expulsion of excess cells limits their population.

Hermatypic (reef-building) corals largely depend on zooxanthellae, which limits that coral's growth to the photic zone. The symbiotic relationship enables corals' success as reef-building organisms in tropical waters. However, under high environmental stress, corals die after losing their zooxanthellae either by expulsion or digestion resulting in coral bleaching.

Relationship

The coral-zooxanthella relationship has traditionally been considered mutualistic -- that is, both partners benefit from the arrangement. However, whilst the benefit for the coral is clear in terms of its enhanced growth and calcification rate, the benefit for the algae has been called into question.

Benefits cited for the algae include protection from predation and enhanced provision with chemicals such as carbon dioxide and ammonium. However, a number of conditions are thought to be necessary in order to maintain a symbiotic relationship; on a very simple level, the symbiont's optimal reproductive strategy must be to remain in the host. It is not clear that these conditions are met in the coral-zooxanthella instance; reproduction of the zooxanthella is retarded by almost two orders of magnitude when it dwells inside a coral.

The relationship may be better thought of as a parasitic relationship, with the coral parasitic upon its enslaved algae. The coral ensnares the algae by secreting a chemical attractant, before ingesting algal calls and incorporating the most appropriate into its cells. They are then surrounded by a 'symbiosome' membrane and confined within the host cell, separated from its cytoplasm. The host cell then emits chemical signals that prevent the zooxanthella from reproducing.

The presence of the alga results in the production of excess oxygen, which must be removed from the cell quickly in order to avoid destructive oxidation. The corals have mechanisms whereby they can kill over-oxygenated cells if necessary.

Coral bleaching

Normal coral (left) and bleached coral (right)

Coral bleaching occurs when zooxanthellae densities within coral tissue become low or the concentration of photosynthetic pigments within each zooxanthella decline. Color loss also comes from reduced concentrations of pigments produced by the cnidarian itself. The result is a ghostly white calcareous skeleton. The coral will then die unless conditions improve enough to allow the zooxanthellae to return.

Zooxanthellae directly or indirectly experience the stress that their containing corals undergo. Exposure to air during low tides and damage from solar radiation in shallow water environments are two of the ecological stressors coral and zooxanthellae face. Temperature changes now provide the most stress to the zooxanthellae-coral relationship. A 1-2 degree Celsius temperature rise for 5–10 weeks and a 3-5 degree decline for 5–10 days have produced a coral bleaching event. Such temperature changes induce cell adhesion dysfunction which detaches zooxanthellae from their cnidarian endodermal cells.

Geological history

Whilst there are genetic differences between the zooxanthellae of different species of coral, there is not agreement as to whether these are significant enough to denote different species.

Some see several different species of zooxanthellae within the *Symbiodinium* monophylum. *Symbiodinium* is related to *Gymnodinium simplex*, *Gymnodinium beii* and *Polarella glacialis*.

The scleractinian-zooxanthella relationship evolved multiple times independently in the mid-Triassic, 245 million years ago and probably enabled the corals to build carbonate skeletons in the adverse Triassic seas (which had caused the tabulate and rugose corals to become extinct). However, genetic evidence suggests that *Symbiodinium* did not begin to diversify until the early-to-middle Eocene, just 50 million years ago.

Life cycle

The genus, *Symbiodinium*, was defined by Hugo Freudenthal in 1970, after his identification of the life cycle of zooxanthella from *Cassiopea*. At that time he proved that symbodinia had a motile stage which resembled a "gymnodinioid" dinoflagellate. Being both symbiotic and a dinoflagellate, he named the genus *Symbiodinium* and the species epithet *microadriaticium*, after its resemblance to a similar free-living species.

Dr. Freudenthal demonstrated that zooxanthellae go through a vegetative stage, a cyst stage and a motile stage as part of their life cycle. Note that both hermatypic (zooxanthellae containing) and ahermatypic corals may be reef-building.

Coral acquisition

Polyps can acquire Zooxanthellae by direct ingestion. However, their hosts do not digest them. In other cases, zooxanthellae may be transmitted by coral eggs and planulae.

Zooxanthellae reproduce asexually by budding (one individual splitting into multiple descendants).

Other animal relationships

Other organisms which can host zooxanthellae include jellyfish, clams, foraminifera, sea slugs i.e. nudibranchs such as *Pteraeolidia ianthina* and also ciliates and radiolaria.

Chapter- 8

Parasitism

Brood parasitism is a common form of parasitism

Parasitism is a type of symbiotic relationship between organisms of different species where one organism, the **parasite**, benefits at the expense of the other, the host. Traditionally **parasite** referred to organisms with lifestages that went beyond one host (e.g. Taenia solium), which are now called macroparasites (typically protozoa and helminths). Parasites can now also refer to microparasites, which are typically smaller, such as viruses and bacteria and can be directly transmitted between hosts of one species. Parasites are generally much smaller than their host, show a high degree of specialization for their mode of life and reproduce at a faster rate than their hosts. Classic examples of parasitism include interactions between vertebrate hosts and diverse animals such as tapeworms, flukes, the *Plasmodium* species and fleas. Parasitism is differentiated from parasitoidism, a relationship in which the host is normally killed by the parasite and which occurs in some species of moth, butterfly, ant, fly and other insects.

The harm and benefit in parasitic interactions concern the biological fitness of the organisms involved. Parasites reduce host fitness in many ways, ranging from general or specialized pathology (such as castration), impairment of secondary sex characteristics, to the modification of host behaviour. Parasites increase their fitness by exploiting hosts for resources necessary for the parasite's survival: (i.e. food, water, heat, habitat and dispersal).

Although the concept of parasitism applies unambiguously to many cases in nature, it is best considered part of a continuum of types of interactions between species, rather than an exclusive category. Particular interactions between species may satisfy some but not all parts of the definition. In many cases, it is difficult to demonstrate that the host is harmed. In others, there may be no apparent specialization on the part of the parasite, or the interaction between the organisms may be short-lived. In medicine, only eukaryotic organisms are considered parasites, with the exclusion of bacteria and viruses. Some branches of biology, however, regard members of these groups as parasitic.

Etymology

First attested in English 1539, the word *parasite* comes from the Medieval French *parasite*, from the Latin *parasitus*, the romanization of the Greek "παράσιτος" (*parasitos*), "one who eats at the table of another" and that from "παρά" (*para*), "beside, by" + "σῖτος" (*sitos*), "wheat". Coined in English 1611, the word *parasitism* comes from the Greek "παρά" (*para*) + "σιτισμός" (*sitismos*) "feeding, fattening".

Types of parasitism

Parasites are classified based on their interactions with their hosts and on their life cycles.

Parasites that live on the surface of the host are called **ectoparasites** (e.g. some mites) and those that live inside the host are called **endoparasites** (including all parasitic worms). Endoparasites can exist in one of two forms: intercellular (inhabiting spaces in the host’s body) or intracellular (inhabiting cells in the host’s body). Intracellular parasites, such as bacteria or viruses, tend to rely on a third organism which is generally known as the carrier or vector. The vector does the job of transmitting them to the host. An example of this interaction is the transmission of malaria, caused by a protozoan of the genus *Plasmodium*, to humans by the bite of an anopheline mosquito.

An *epiparasite* is one that feeds on another parasite. This relationship is also sometimes referred to as *hyperparasitism* which may be exemplified by a protozoan (the hyperparasite) living in the digestive tract of a flea living on a dog.

Social parasites take advantage of interactions between members of social organisms such as ants or termites. In *kleptoparasitism*, parasites appropriate food gathered by the host. An example is the brood parasitism practiced by many species of cuckoo and cowbird, which do not build nests of their own but rather deposit their eggs in nests of other species and abandon them there. The host behaves as a "babysitter" as they raise the young as their own. If the host removes the cuckoo's eggs, some cuckoos will return and attack the nest to compel host birds to remain subject to this parasitism. The cowbird's parasitism does not necessarily harm its host's brood; however, the cuckoo may remove one or more host eggs to avoid detection and furthermore the young cuckoo may heave the host's eggs and nestlings from the nest.

Parasitism can take the form of isolated *cheating* or *exploitation* among more generalized mutualistic interactions. For example, broad classes of plants and fungi exchange carbon and nutrients in common mutualistic mycorrhizal relationships; however, some plant species known as myco-heterotrophs "cheat" by taking carbon from a fungus rather than donating it.

Parasitoids are organisms whose larval development occurs inside or on the surface of another organism, resulting in the death of the host. This means that the interaction between the parasitoid and the host is fundamentally different from that of a true parasite and shares some of the characteristics of predation.

An adelpho-parasite is a parasite in which the host species is closely related to the parasite, often being a member of the same family or genus. An example of this is the citrus blackfly parasitoid, *Encarsia perplexa*, unmated females of which may lay haploid eggs in the fully developed larvae of their own species. These result in the production of male offspring. The marine worm *Bonellia viridis* has a similar reproductive strategy, although the larvae are planktonic.

Evolutionary aspects

Biotrophic parasitism is a common mode of life that has arisen independently many times in the course of evolution. Depending on the definition used, as many as half of all animals have at least one parasitic phase in their life cycles and it is also frequent in plants and fungi. Moreover, almost all free-living animals are host to one or more parasite taxa.

Restoration of a *Tyrannosaurus* with parasite infections. A 2009 study showed that holes in the skulls of several specimens might have been caused by *Trichomonas*-like parasites

Parasites evolve in response to defense mechanisms of their hosts. Examples of host defenses include the toxins produced by plants to deter parasitic fungi and bacteria, the complex vertebrate immune system, which can target parasites through contact with bodily fluids and behavioral defenses. An example of the latter is the avoidance by sheep of open pastures during spring, when roundworm eggs accumulated over the previous year hatch en masse. As a result of these and other host defenses, some parasites evolve adaptations that are specific to a particular host taxon and specialize to the point where they infect only a single species. Such narrow host specificity can be costly over evolutionary time, however, if the host species becomes extinct. Thus, many parasites are capable of infecting a variety of host species that are more or less closely related, with varying success.

Host defenses also evolve in response to attacks by parasites. Theoretically, parasites may have an advantage in this evolutionary arms race because of their more rapid generation time. Hosts reproduce less quickly than parasites and therefore have fewer chances to adapt than their parasites do over a given span of time.

In some cases, a parasite species may coevolve with its host taxa. In theory, long-term coevolution should lead to a relatively stable relationship tending to commensalism or mutualism, in that it is in the evolutionary interest of the parasite that its host thrives. A parasite may evolve to become less harmful for its host or a host may evolve to cope with the unavoidable presence of a parasite to the point that the parasite's absence causes the host harm. For example, although animals infected with parasitic worms are often clearly harmed and therefore parasitized, such infections may also reduce the prevalence and effects of autoimmune disorders in animal hosts, including humans.

The presumption of a shared evolutionary history between parasites and hosts can sometimes elucidate how host taxa are related. For instance, there has been dispute about whether flamingos are more closely related to the storks and their allies, or to ducks, geese and their relatives. The fact that flamingos share parasites with ducks and geese is evidence these groups may be more closely related to each other than either is to storks.

Parasitism is part of one explanation for the evolution of secondary sex characteristics seen in breeding males throughout the animal world, such as the plumage of male peacocks and manes of male lions. According to this theory, female hosts select males for breeding based on such characteristics because they indicate resistance to parasites and other disease.

Co-speciation

In rare cases, a parasite may even undergo co-speciation with its host. One particularly remarkable example of co-speciation exists between the simian foamy virus (SFV) and its primate hosts. In one study, the phylogenies of SFV polymerase and the mitochondrial cytochrome oxidase subunit II from African and Asian primates were compared. Surprisingly, the phylogenetic trees were very congruent in branching order and divergence times. Thus, the simian foamy viruses may have co-speciated with Old World primates for at least 30 million years.

Ecology

Quantitative ecology

When considering the distribution of a single parasite species, one finds that they exhibit an aggregated distribution among host individuals, which means that most hosts harbour few parasites, while a few hosts carry the vast majority of parasite individuals. This poses considerable problems for students of parasite ecology: the use of parametric statistics should be avoided. Log-transformation of data before the application of parametric test, or the use of non-parametric statistics is recommended by several authors. However, these give rise to further problems. Therefore, modern day quantitative parasitology is based on more advanced biostatistical methods.

Diversity ecology

Hosts represent discrete habitat patches that can be occupied by parasites. A hierarchical set of terminology has come into use to describe parasite assemblages at different host scales.

Infrapopulation	All the parasites of one species in a single individual host.
Infracommunity	All the parasites of all species in a single individual host.
Component community	All the parasites of all species in a host population.
Compound community	All the parasites of all species in all host species in an ecosystem.

Metapopulation

A **metapopulation** consists of a group of spatially separated populations of the same species which interact at some level. The term metapopulation was coined by Richard Levins in 1970 to describe a model of population dynamics of insect pests in agricultural fields, but the idea has been most broadly applied to species in naturally or artificially fragmented habitats. In Levins' own words, it consists of "a population of populations".

A metapopulation is generally considered to consist of several distinct populations together with areas of suitable habitat which are currently unoccupied. In classical metapopulation theory, each population cycles in relative independence of the other populations and eventually goes extinct as a consequence of demographic stochasticity (fluctuations in population size due to random demographic events); the smaller the population, the more prone it is to extinction.

Although individual populations have finite life-spans, the metapopulation as a whole is often stable because immigrants from one population (which may, for example, be experiencing a population boom) are likely to re-colonize habitat which has been left open by the extinction of another population. They may also emigrate to a small population and rescue that population from extinction (called the *rescue effect*).

The development of metapopulation theory, in conjunction with the development of source-sink dynamics, emphasised the importance of connectivity between seemingly isolated populations. Although no single population may be able to guarantee the long-term survival of a given species, the combined effect of many populations may be able to do this.

Metapopulation theory was first developed for terrestrial ecosystems and subsequently applied to the marine realm. In fisheries science, the term "sub-population" is equivalent to the metapopulation science term "local population". Most marine examples are provided by relatively sedentary species occupying discrete patches of habitat, with both local recruitment and recruitment from other local populations in the larger metapopulation. Kritzer & Sale have argued against strict application of the metapopulation definitional criteria that extinction risks to local populations must be non-negligible.

An important contributor to metapopulation theory is the Finnish biologist, Ilkka Hanski, of the University of Helsinki.

Predation and Oscillations

The first experiments with predation and spatial heterogeneity were conducted by G.F. Gause in the 1930's, based on the Lotka-Volterra equation, which was formulated in the mid-1920s, but no further application had been conducted. The Lotka-Volterra equation suggested that the relationship between predators and their prey would result in population oscillations over time based on the initial densities of predator and prey. Gause's early experiments to prove the predicted oscillations of this theory failed because the predator-prey interactions were not influenced by immigration. However, once immigration was introduced, the population cycles accurately depicted the oscillations predicted by the Lotka-Volterra equation, with the peaks in prey abundance shifted slightly to the left of the peaks of the predator densities. Huffaker's experiments expanded on those of Gause by examining how both the factors of migration and spatial heterogeneity lead to predator-prey oscillations.

Huffaker's experiments on predator-prey interactions (1958)

In order to study predation and population oscillations, Huffaker used mite species, one being the predator and the other being the prey. He set up a controlled experiment using oranges, which the prey fed on, as the spatially structured habitat in which the predator and prey would interact. At first, Huffaker experienced difficulties similar to those of Gause in creating a stable predator-prey interaction. By using oranges only, the prey species quickly went extinct followed consequently with predator extinction. However, he discovered that by modifying the spatial structure of the habitat, he could manipulate the population dynamics and allow the overall survival rate for both species to increase. He did this by altering the distance between the prey and oranges (their food), establishing barriers to predator movement and creating corridors for the prey to disperse. These changes resulted in increased habitat patches and in turn provided more areas for the prey to seek temporary protection. When the prey would go extinct locally at one habitat patch, they were able to reestablish by migrating to new patches before being attacked by predators. This habitat spatial structure of patches allowed for coexistence between the predator and prey species and promoted a stable population oscillation model. Although the term metapopulation had not yet been coined, the environmental factors of spatial heterogeneity and habitat patchiness would later describe the conditions of a metapopulation relating to how groups of spatially separated populations of species interact with one another. Huffaker's experiment is significant because it showed how metapopulations can directly affect the predator-prey interactions and in turn influence population dynamics.

The Levins model

Levins' original model applied to a metapopulation distributed over many patches of suitable habitat with significantly less interaction between patches than within a patch. Population dynamics within a patch were simplified to the point where only presence and absence were considered. Each patch in his model is either populated or not.

Let N be the fraction of patches occupied at a given time. During a time dt, each occupied patch can become unoccupied with an extinction probability edt. Additionally, $1 - N$ of the patches are unoccupied. Assuming a constant rate c of propagule generation from each of the N occupied patches, during a time dt, each unoccupied patch can become occupied with a colonization probability $cNdt$. Accordingly, the time rate of change of occupied patches, dN/dt, is

$$\frac{dN}{dt} = cN(1-N) - eN.$$

This equation is mathematically equivalent to the logistic model, with a carrying capacity K given by

$$K = 1 - \frac{e}{c}$$

and growth rate r

$$r = c - e.$$

At equilibrium, therefore, some fraction of the species's habitat will always be unoccupied.

Stochasticity and Metapopulations

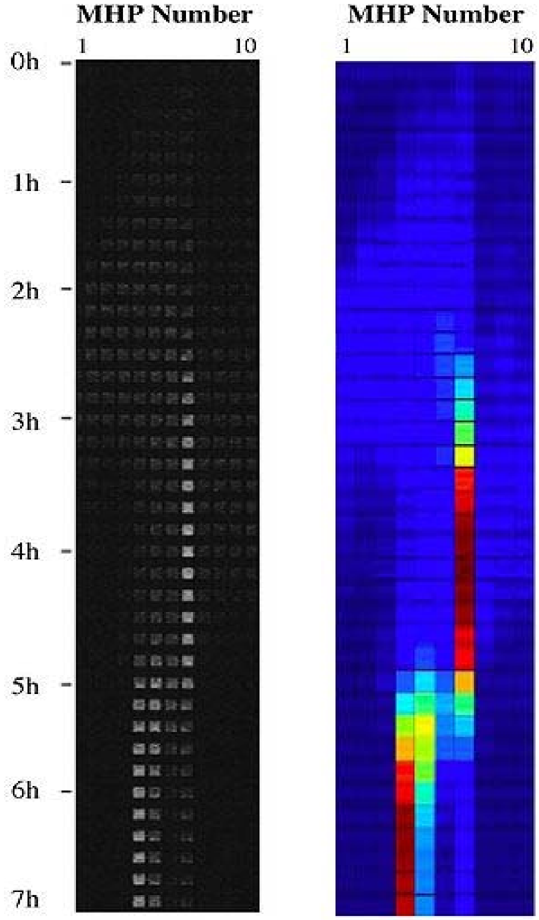
Huffaker's studies of spatial structure and species interactions are an example of early experimentation in metapopulation dynamics. Since the experiments of Huffaker and Levins, models have been created which integrate stochastic factors. These models have proven that the combination of environmental variability (stochascity) and relatively small migration rates cause indefinite or unpredictable persistence. However, Huffaker's experiment almost guaranteed infinite persistence because of the controlled immigration variable.

Stochastic patch occupancy models (SPOMs)

One major drawback of the Levins model is that it is deterministic, whereas the fundamental metapopulation processes are stochastic. Metapopulations are particularly useful when discussing species in disturbed habitats and the viability of their populations, i.e., how likely they are to become extinct in a given time interval. The Levins model cannot address this issue. A simple way to extend the Levins' model to incorporate space and stochastic considerations is by using the contact process (mathematics). Simple modifications to this model can also incorporate for patch dynamics. At a given percolation threshold, habitat fragmentation effects take place in these configuration predicting more drastic extinction thresholds.

For conservation biology purposes, metapopulation models must include (a) the finite nature of metapopulations (how many patches are suitable for habitat) and (b) the probabilistic nature of extinction and colonisation. Also, note that in order to apply these models, the extinctions and colonisations of the patches must be asynchronous.

Micro Habitat Patches (MHPs) and bacterial metapopulations



E. coli metapopulation on-chip

By combining nanotechnology with landscape ecology, a habitat landscape can be nanofabricated on-chip by building a collection of nanofabricated bacterial habitats and connecting them by corridors in different topological arrangements and with nano-scale channels providing them with the local ecosystem service of habitat renewal. These landscapes of MHPs can be used as physical implementations of an adaptive landscape: by generating a spatial mosaic of patches of opportunity distributed in space and time. The patchy nature of these fluidic landscapes allows for the study of adapting bacterial cells in a metapopulation system operating on-chip within a synthetic ecosystem. The metapopulation biology and evolutionary ecology of these bacterial systems, in these synthetic ecosystems, can be addressed using experimental biophysics.

Life history evolution

Metapopulation models have been used to explain life-history evolution, such as the ecological stability of amphibian metamorphosis in small vernal ponds. Alternative ecological strategies have evolved. For example, some salamanders forgo metamorphosis and sexually mature as aquatic neotenes. The seasonal duration of wetlands and the migratory range of the species determines which ponds are connected and if they form a metapopulation. The duration of the life history stages of amphibians relative to the duration of the vernal pool before it dries up regulates the ecological development of metapopulations connecting aquatic patches to terrestrial patches.

The diversity ecology of parasites differs markedly from that of free-living organisms. For free-living organisms, diversity ecology features many strong conceptual frameworks including Robert MacArthur and E. O. Wilson's theory of island biogeography, Jared Diamond's assembly rules and, more recently, null models such as Stephen Hubbell's unified neutral theory of biodiversity and biogeography. Frameworks are not so well-developed for parasites and in many ways they do not fit the free-living models. For example, island biogeography is predicated on fixed spatial relationships between habitat patches ("sinks"), usually with reference to a mainland ("source"). Parasites inhabit hosts, which represent mobile habitat patches with dynamic spatial relationships. There is no true "mainland" other than the sum of hosts (host population), so parasite component communities in host populations are metacommunities.

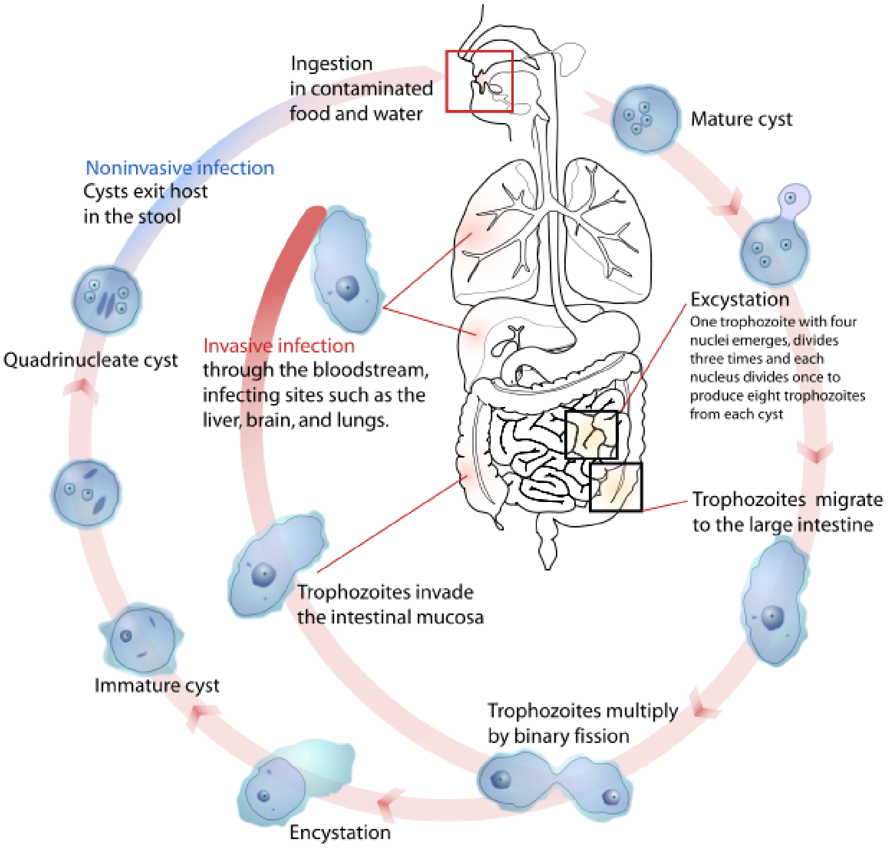
Nonetheless, different types of parasite assemblages have been recognised in host individuals and populations and many of the patterns observed for free-living organisms are also pervasive among parasite assemblages. The most prominent of these is the interactive-isolationist continuum. This proposes that parasite assemblages occur along a cline from interactive communities, where niches are saturated and interspecific competition is high, to isolationist communities, where there are many vacant niches and interspecific interaction is not as important as stochastic factors in providing structure to the community. Whether this is so, or whether community patterns simply reflect the sum of underlying species distributions (no real "structure" to the community), has not yet been established.

Adaptation

Parasites infect hosts that exist within their same geographical area (sympatric) more effectively. This phenomenon supports the "Red Queen hypothesis - which states that interactions between species (such as host and parasites) lead to constant natural selection for adaptation and counter adaptation." The parasites track the locally common host phenotypes, therefore the parasites are less infective to allopatric (from different geographical region) hosts.

Experiments published in 2000 discuss the analysis of two different snail populations from two different sources- Lake Ianthe and Lake Poerua in New Zealand. The populations were exposed to two pure parasites (digenetic trematode) taken from the same lakes. In the experiment, the snails were infected by their sympatric parasites, allopatric parasites and mixed sources of parasites. The results suggest that the parasites were more highly effective in infecting their sympatric snails than their allopatric snails. Though the allopatric snails were still infected by the parasites, the infectivity was much less when compared to the sympatric snails. Hence, the parasites were found to have adapted to infecting local populations of snails.

Transmission



Life cycle of *Entamoeba histolytica*, an anaerobic parasitic protozoan.

Parasites inhabit living organisms and therefore face problems that free-living organisms do not. Hosts, the only habitats in which parasites can survive, actively try to avoid, repel and destroy parasites. Parasites employ numerous strategies for getting from one host to another, a process sometimes referred to as parasite *transmission* or *colonization*.

Some endoparasites infect their host by penetrating its external surface, while others must be ingested. Once inside the host, adult endoparasites need to shed offspring into the external environment in order to infect other hosts. Many adult endoparasites reside in the host's gastrointestinal tract, where offspring can be shed along with host excreta. Adult stages of tapeworms, thorny-headed worms and most flukes use this method.

Among protozoan endoparasites, such as the malarial parasites and trypanosomes, infective stages in the host's blood are transported to new hosts by biting-insects, or vectors.

Larval stages of endoparasites often infect sites in the host other than the blood or gastrointestinal tract. In many such cases, larval endoparasites require their host to be consumed by the next host in the parasite's life cycle in order to survive and reproduce. Alternatively, larval endoparasites may shed free-living transmission stages that migrate through the host's tissue into the external environment, where they actively search for or await ingestion by other hosts. The foregoing strategies are used, variously, by larval stages of tapeworms, thorny-headed worms, flukes and parasitic roundworms.

Some ectoparasites, such as monogenean worms, rely on direct contact between hosts. Ectoparasitic arthropods may rely on host-host contact (e.g. many lice), shed eggs that survive off the host (e.g. fleas), or wait in the external environment for an encounter with a host (e.g. ticks). Some aquatic leeches locate hosts by sensing movement and only attach when certain temperature and chemical cues are present.

Some parasites modify host behaviour to make transmission to other hosts more likely. For example, in California salt marshes the fluke *Euhaplorchis californiensis* reduces the ability of its killifish host to avoid predators. This parasite matures in egrets, which are more likely to feed on infected killifish than on uninfected fish. Another example is the protozoan *Toxoplasma gondii*, a parasite that matures in cats but can be carried by many other mammals. Uninfected rats avoid cat odours, but rats infected with *T. gondii* are drawn to this scent, a change which may increase transmission to feline hosts.

Roles in ecosystems

Modifying the behaviour of infected hosts to make transmission to other hosts more likely is one way parasites can affect the structure of ecosystems. For example, in the case of *Euhaplorchis californiensis* (discussed above) it is plausible that the abundance of local predator and prey species would be different if this parasite were absent from the system.

Although parasites are often omitted in depictions of food webs, they usually occupy the top position. Parasites can function like keystone species, reducing the dominance of superior competitors and allowing competing species to co-exist.

Many parasites require multiple hosts of different species to complete their life cycles and rely on predator-prey or other stable ecological interactions to get from one host to another. In this sense, the parasites in an ecosystem reflect the "health" of that system.

Chapter- 9

Mutualisms and Conservation

Conservation is the maintenance of biological diversity. Conservation can focus on preserving diversity at genetic, species, community or whole ecosystem levels. We will examine conservation at the species level, because mutualisms involve interactions between species. The ultimate goal of conservation at this level is to prevent the extinction of species. However, species conservation has the broader aim of maintaining the abundance and distribution of all species, not only those threatened with extinction (van Dyke 2008). Determining the value of conserving particular species can be done through the use of evolutionary significant units, which essentially attempt to prioritise the conservation of the species which are rarest, fastest declining and most distinct genotypically and phenotypically (Moritz 1994, Fraser and Bernatchez 2001).

Mutualisms can be defined as “interspecific interactions in which each of two partner species receives a net benefit” (Bronstein et al. 2004). Here net benefit is defined as, a short-term increase in inclusive fitness (IF). Incorporating the concept of genetic relatedness (through IF) is essential because many mutualisms involve the eusocial insects, where the majority of individuals are not reproductively active. The short-term component is chosen because it is operationally useful, even though the role of long-term adaptation is not considered (de Mazancourt et al. 2005). This definition of mutualism should be suffice, although it neglects discussion of the many subtitles of IF theory applied to mutualisms and the difficulties of examining short-term compared to long-term benefits, which are discussed in Foster and Wenselneers (2006) and de Mazancourt et al. (2005) respectively. Mutualisms can be broadly divided into two categories. Firstly, obligate mutualism, where two mutualistic partners are completely interdependent for survival and reproduction. Secondly, facultative mutualism, where two mutualistic partners both benefit from the mutualism, but can theoretically survive in each others’ absence.

Mutualisms are remarkably common, in fact all organisms are believed to be involved in a mutualism at some point during their lives (Bronstein et al. 2004). This is particularly likely to be true for the definition of mutualism adopted here, where herbivory can paradoxically be mutualistic, for example in a situation where a plant overcompensates by producing more biomass when grazed on. Therefore, any species identified as particularly important to conserve will probably have mutualistic partners.

Mutualism Coextinction

A mutualism coextinction event is where a species goes extinct upon the loss of its mutualist (Koh et al. 2004). Models have attempted to predict when the breakdown of a mutualism leads to coextinction, because in this situation protecting the mutualism will be particularly important for conservation. These models are multi-dimensional, so examine complex networks of interactions, rather than just pairs of interacting species. This means that these models incorporate modelling the breakdown of obligate mutualisms (which lead directly to coextinction), but also the breakdown of facultative mutualisms (which can lead indirectly to coextinction). Koh et al. (2004) use a “nomographic model of affiliate extinctions”, which estimates the probability that the extinction of a species leads to the extinction of its mutualist, for a given estimate of the specificity of the mutualism. By applying the model to actual species, Koh et al. (2004) estimate that 200 coextinctions have occurred since records of species extinction began in the past few centuries and 6300 coextinctions are at risk of occurring in the near future. However, these estimates are not exclusively for mutualism coextinctions (e.g. parasitic coextinctions are incorporated), but mutualism coextinctions make up a significant proportion of the number quoted. Additionally the model predicts that these coextinctions can start extinction cascades, where many other species in the surrounding ecosystem go extinct. Other recent models largely agree with this one, predicting that mutualism coextinction is a very significant cause of species loss and that it can lead to extinction cascades (Dunn et al. 2009).

Surprisingly, given the model predictions, there are very few recorded examples of global mutualism coextinctions actually occurring (Bronstein et al. 2004, Dunn et al. 2009) and many examples often quoted are unconvincing on examination. For example, a well documented case of animal-plant coextinction and an extinction cascade involves a butterfly (Maculinea arion) to ant (Myrmica sableti) interaction. M. arion larvae provide honeydew for the M. sableti workers, which raise the caterpillars in their nest. When the Myxoma virus was introduced to control rabbit populations in the UK, the subsequent increase in grassland caused a decrease in soil temperatures at ground level. This caused reductions in the M. sableti populations, which led to the extinction of the M. arion populations (Dunn 2005). However, this is actually a relatively weak example, because it was a local (rather than a global) extinction and the nature of the interaction is often not viewed as mutualisitic, because it has been long known that the M. sableti caterpillars eat M. sableti larvae (Elmes and Thomas 1992).

So, why are there very few documented examples of mutualism coextinctions? There are various possible reasons. Perhaps global mutualism coextinctions are genuinely uncommon and the model predictions are inaccurate. The models may overestimate the specificity of the mutalisms, because species may only associate with alternative species when their ‘normal’ mutualist is rare or absent. For example, oligolectic bees visit a small number of flowers for pollen. However, these bees do not generally have strongly specialised anatomy, morphology or physiology. Therefore, in the absence of these usual flowers, many oligolectic bee species are able switch to collecting pollen from flower species they would never normally associate with (Wcislo and Cane 1996). Even some fig wasps, often considered to be in completely obligate relationships, have maintained low population densities when introduced to new areas without their natural mutualist fig tree species (McKey 1989). The models may also underestimate the robustness of the mutualisms. For example, fig trees and fig wasps are coadapted so that the wasps can find the trees from a long distances away (Bronstein et al. 1994).

Alternatively, there may simply be many global mutualism coextinctions that have occurred which we are not yet aware of. This explanation is not unlikely, because mutualisms have generally been understudied as interactions (Bronstein 1994, Richardson et al. 2000). There is additionally the difficulty of defining when a species becomes globally extinct, compared to just extremely rare or maintained exclusively through captive breeding programs. Of course, these stated explanations are not mutually exclusive. However, more research is required to rectify the model predictions of many mutualism coextinctions, with the lack of empirical evidence for such events. Only then can we discover if conserving mutualisms is likely to prevent many global species extinction.

Mutualism 'Codeclines'

Even if global mutualism coextinctions are genuinely rare, conserving mutualisms may still be important for conservation. As mentioned previously, conservation is not just about preventing extinctions, but also about preventing species decline. Unlike with coextinctions, there are numerous recorded examples of where the decline or extinction of a species has led to the decline of its mutualist ('codeclines'). A documented example of a pollination mutualism breakdown leading to population declines is the Indian Rubber Tree (Ficus elastica) to its pollinator wasp (Pleistodontes clavigar) interaction. Habitat fragmentation has led to the F. elastica declining to very low population levels. However, F. Elastic can propagate clonally, so has remained extant. Meanwhile, P.clavigar is virtually extinct globally, because the mutualist relationship is probably obligate for P.clavigar (Mawsdley et al. 1998). An example of a seed dispersal mutualism breakdown causing population declines comes from two endemic species on Menorca Island. A frugiverous lizard (Podarcis lilfordi) is a seed disperser of a shrub (Daphne rodriguezii). When P. Lilfordi became extinct on Menorca, due to the introduction of carnivorous mammals, D. rodriguezii numbers declined significantly to endangered levels. This D. rodriguezii decline could be attributed to the local extinction of P. Lilfordi, due the lack of seedling recruitment on Menorca compared to other nearby islands, where P. Lilfordi remained extant and D. rodriguezii populations larger (Traveset and Riera 2005).

However, in some cases it has been shown that declines of one partner in a mutualism do not lead to significant declines in the other. For example, a Hawaiian vine (Freycinetia arborea) was pollinated in the nineteenth century by four species of birds. These bird species are all now either locally endangered or extinct. Despite this, F. Arborea continues to survive in reasonable abundance, but is now mainly pollinated by the recently introduced white-eye (Zosterops japonica) (Cox and Elmqvist 2000). In this case, conservation of the mutualism was not required to maintain the F. Arborea population. There are probably no published estimates of how frequently declines of one species do not result in declines of that species' mutualist, due to a 'replacement' mutualist. However, judging by the few examples in the literature where this replacement has been reported to have happened, it seems to be a relatively rare occurrence.

Alien Species in Mutualisms

The Hawaiian vine example also illustrates that alien species can be involved in animal-plant mutualisms. In fact, alien species are often dependent on mutualisms to establish themselves in new habitats (particularly on islands) and especially those alien species requiring animal mediated pollination (Richardson et al. 2000). These alien species will, by definition, be beneficial to the short-term inclusive fitness of the species they form a mutualism with. However, the alien species will impact negatively with other species in the ecosystem, for example through competition for resources (including competition for mutualist partners) (Kaiser-Bunbury et al. 2009). In fact, these negative impacts could theoretically cascade through the ecosystem and lead to the alien species having an indirect long-term negative impact on its mutualist. This means that mutualisms involving alien species may important in conservation. However, the action taken by a conservation organisation could be either to conserve or disrupt the mutualism.

In some situations, a conservation organisation will want to conserve the mutualism involving the alien species. For example, many of the Hawaiian Islands have lost the vast majority of their native seed dispersers and introduced bird species now act as very major seed dispersers of native species. In fact, these exotic species appear to actually facilitate the re-growth of native forests in some areas (Foster and Robinson 2007). In these situations, conserving the native mutualism may become less important than conserving the new one. Alien species involved in mutualisms may actually be desirable for conservationists to protect in a more general way. Alien species are particularly likely to generate highly generalised and asymmetric mutualisms, which help stabilise communities, making them less vulnerable to decline and extinctions (Aizen et al. 2008).

In other situations, conservation will be facilitated by disrupting mutualisms involving alien species. For example alien bumblebees (Bombus terrestris) have displaced many native pollinators and pollinated some unwanted weed species, across the globe (Hingston et al. 2002). These mutualisms could lead to a decline in both animal and plant species of particular value to conservation. The empirical evidence would suggest that in the majority of cases a conservation organisation should try and disrupt the mutualisms involving the alien species (Kaiser-Bunbury et al. 2009).