

Mutualistic Symbioses

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Abstract

Mutualistic symbioses are symbioses that are beneficial to both (or all) symbiotic partners; they are intricate, complex and variable in their interactions. Widely distributed both geographically and taxonomically, they play an important ecological and evolutionary role in the biosphere.

Defining Mutualistic Symbiosis

In theory, mutualistic symbiosis is a simple-to-understand phenomenon: a symbiotic association that is beneficial to both (or all) symbiotic partners. In reality, however, mutualistic symbioses are more complex, more diverse and more variable than their simple definition suggests. Some of the diversity arises from the fact that several symbioses dubbed, 'mutualistic' may not really be mutually beneficial symbioses. In several such symbiotic 'mutualisms', for instance, the benefits of symbiosis to one partner have been demonstrated clearly, while the effects of symbiosis on the other species partner are unknown or a matter of debate. In other symbiotic 'mutualisms', benefits to symbionts and hosts have been hypothesized, but have received little direct investigation. Complicating still further the question of symbiont effects in these incompletely understood symbioses is the fact that long-term evolutionary benefits or selective advantage in nature can be difficult to demonstrate in short-term, laboratory-based experiments. See also: Interspecific interaction; Endosymbionts; Natural selection: introduction;

Even in those symbioses in which all symbiotic partners are known clearly to benefit from symbiotic association, the dynamics of such mutualistic symbioses can be quite complex. There can be a significant cost to mutualistic symbiosis, in addition to its benefits; interactions between species partners are intricate, diverse and often difficult to assay; and the cost–benefit balance among partners of mutualistic symbioses can vary with environmental conditions.

Lynn Margulis has defined symbiosis as a 'parasexual phenomenon' – as a kind of interspecies 'marriage', in which the lives of two or more species are intertwined, in protracted intimate association. From this perspective, mutualistic symbiosis can be described as an interspecies 'marriage' of mutual benefit to the species partners in question. Taking the metaphor further, the complexity of human marriages can be used to illustrate the complexity of interspecific mutualistic symbioses. Human marriages are intraspecific, mutualistic intimate associations – or at least associations

with aspirations to mutualism! As most humans know from experience, even the most stable and happy (or ‚mutually beneficial’) human marriages can be quite complex relationships. They have costs as well as benefits; the diversity and intricacy of their multiple interactions and interdependencies often defy easy analysis, and their internal dynamic can be influenced – sometimes profoundly – by external conditions. So it is also with interspecific, mutualistic symbioses. Focusing on endosymbiotic mutualisms, this article reviews the ecological importance of mutualistic symbioses, as well as the complexity of their metabolic and cellular interactions and of their physiological and evolutionary dynamics. See also: Margulis, Lynn; Mutualism among free-living species; The Ubiquity of Mutualistic Symbioses

[The distribution of mutualistic symbioses](#)

Mutualistic symbioses are everywhere. Geographically, they are widely distributed, occurring throughout terrestrial and aquatic ecosystems, all latitudes, and all altitudes. Taxonomically, they are also widely distributed: symbiotic mutualists include representatives of animals, plants, fungi, protists, eubacteria and archaea. Moreover, growing interest in mutualism and symbiosis among biologists, coupled with advances in investigative methods, continues to stimulate the discovery of new mutualistic symbioses.

The abundance and frequency of these associations in particular habitats and particular taxonomic groups are a measure of the key roles that symbiotic mutualisms play in many ecosystems, and suggest the possibility that mutualistic symbiosis has also played a role in the evolution and radiation of several taxa. See also: Diversity of life;

Moreover, most symbioses known or suspected to be mutualisms are ‚chronic’ symbioses: in many mutualistic symbioses 100% of host populations or 100% of both hosts and symbionts are found in symbiotic association in nature. Thus, with their frequently universal presence among particular hosts, mutualistic symbionts can also be a pervasive influence on host biology at the population level, in addition to their effects on individual hosts. The tendency of mutualisms toward 100% infection distinguishes mutualistic symbiosis from parasitism, which rarely affects 100% of host populations, and suggests that the microevolutionary population dynamics of mutualistic and parasitic symbioses may differ in significant ways. See also: Parasitism; Microevolution and Macroevolution: introduction;

Some particularly conspicuous symbioses illustrate the ecological importance of symbiotic mutualisms.

[Mutualistic symbioses in plant and fungal hosts](#)

Lichens are mutualistic symbioses between fungi (there are more than 13 000 species of lichen fungi, representing 20% of all fungi species) and photosynthetic microbes (mostly green algae and cyanobacteria). Lichens are visible colonizers of rocks, tree trunks and other exposed surfaces in

many different ecosystems, including forests, deserts, alpine areas and the upper reaches of rocky intertidal zones. In some areas, especially in polar regions, lichens are of particularly great ecological importance: more than 90% of terrestrial photosynthetic organisms in the Antarctic are lichens, which also form the dominant vegetation in parts of the Arctic tundra. See also: Lichens; Fungi and the history of mycology; Fungi: ecological importance and impact on humans; Arctic ecosystems;

Terrestrial plants are characteristically associated with a number of microbial symbionts, forming widespread, mutualistic symbioses of ecological and agricultural importance. Nitrogen-fixing bacteria (*Rhizobium*) are found in root nodules of many legumes; more than a hundred species of trees and shrubs from eight plant families, including species of *Alnus*, *Casuarina* and *Ceanothus*, contain nitrogen-fixing actinomycete symbionts in nodulated roots. These nitrogen-fixing symbionts enhance the growth of host plants in nitrogen-limited soils by supplying metabolically usable nitrogen directly to their hosts, and indeed many such plants are key species in low-nitrogen habitats. Symbiotic nitrogen fixation is at the very least a very significant component of biological nitrogen fixation worldwide, and may even equal or exceed rates of nitrogen fixation by free-living bacteria in oceans and terrestrial soils. See also: Nitrogen fixation; Coevolution: plant–microorganism; Global nitrogen, phosphorus and sulfur cycles; Root nodules (*Rhizobium*, legumes);

In addition to their importance in natural ecosystems, nitrogen-fixing legumes also play a major role in agricultural production. Cultivated legumes, including soybeans, alfalfa, clover, peas and other species, not only serve as food sources for humans and livestock, but also contribute significantly to global levels of fixed nitrogen. Among cultivated legumes alone, yearly levels of nitrogen fixation have been estimated at about 40 tonnes per year, about half the yearly global industrial production of nitrogen fertilizer. See also: Agricultural production;

The roots of all but a few vascular plant families form mycorrhizae (‘fungus roots’) with various fungal taxa. Ectomycorrhizae, which form hyphal sheaths around the roots of host plants, are characteristic of trees such as oaks, beeches, eucalypts and many gymnosperms. Most of the 6000 species of ectomycorrhizal fungi are basidiomycetes and ascomycetes; the ‘fairy ring’ mushrooms around forest trees, for instance, are the reproductive stages of ectomycorrhizal basidiomycetes. Specialized ‘arbutoid’ and ‘monotropoid’ ectomycorrhizae form, among photosynthetic species and achlorophyllous parasitic species respectively, in the heath family (Ericaceae). In contrast to the external sheaths characteristic of ectomycorrhizal fungi, most of the biomass of arbuscular mycorrhizal fungi is found within root cells of the plant hosts. Arbuscular mycorrhizal fungi, especially species of the zygomycete genus *Glomus*, are very widely distributed among terrestrial plants from all latitudes, including not only angiosperms, but also mosses, ferns and gymnosperms. The roots of orchids and some members of the Ericaceae also form intracellular mycorrhizae, but with morphologies that differ from arbuscular mycorrhizae and with fungal symbionts other than

zygomycetes. In short, the vast majority of terrestrial plant species today are mycorrhizal. The prevalence of mycorrhizal associations among plants has led to the hypothesis that terrestrial plants evolved in symbiosis with root fungi; and indeed, arbuscular mycorrhizae have been described from Devonian plant fossils. Today, the benefits of mycorrhizae to nutrient uptake in host plants, especially in low-phosphorus soils, are widely recognized; for that reason, mycorrhizae play increasingly significant roles in horticultural, agricultural and forestry practices and in land reclamation. See also: Mycorrhiza; Roots: contribution to the rhizosphere; Roots and root systems; Soil resource conservation;

Recently, a third microbial–plant symbiosis has received research attention. Fungal ‘endophytes’ have been found in the above-ground tissues of various plant families, especially in grasses and woody plants. Although the best studied endophytes are ascomycetous fungi (especially the genus *Neotyphodium/Epichloe*), other fungal taxa also form endophytic associations in plants. There is evidence for mutualism among some endophyte–plant symbioses: in at least some cases, endophyte infections have been found to deter herbivory and pathogen infections in grasses. However, continuing research suggests that endophyte–plant symbioses are diverse and complex in their effects; thus, the mutualistic effects of endophytes on host grasses may be just one of many dimensions, and many effects, of these associations. See also: Ascomycota;

[Mutualistic symbioses in animal and protozoan hosts](#)

As mutualistic symbioses pervade terrestrial plant communities, so are they common among the animals that eat those plants. Gut symbioses are especially strongly associated with diets restricted to lower-nutrient plant parts: herbivore specialists on leaves, wood, xylem and phloem fluids and similar nutrient-limited diets are often assisted by microbial symbionts. Typically, these symbionts contribute digestive enzymes (notably, cellulase) or supplemental nutrients to their hosts. The guts of ruminants, leaf-eating *Colobus* monkeys, herbivorous marsupials (koalas, wombats, kangaroos), herbivorous iguanas, surgeonfish, phloem-ingesting aphids, wood-digesting termites, weevils and others are all hosts to complex microbial communities. Since these microbes make possible the herbivorous habits of their hosts, these symbioses are of obvious ecological impact. They are also of great importance to agriculture, as many important livestock species, including cows, sheep, goats, camels, horses and rabbits, are dependent on symbiotic gut microbes for utilization of plant diets. See also: Herbivory; Cellulose: biogenesis and degradation; Animal nutritional requirements;

Gut symbionts certainly have an impact on the biology of individual hosts as well: in addition to the novel metabolic repertoire which they provide to their hosts, they make up a large portion of their host’s biomass. In termites, for instance, gut bacteria and protozoa account for 33–50% of termite biomass; similarly, an individual grain weevil (*Sitophilus oryzae*) contains 10 million bacterial cells in its gut, approximately equal to the number of host weevil cells. The rumen of cows and other ruminant

mammals contains a diverse and dense microflora, comprising about 200 species of prokaryotes (both eubacteria and archaea) and at least 20 protistan (mostly protozoan) species, in concentrations of 10^{10} prokaryotic cells and 10^6 protozoan cells per millilitre; a single 50–100 L rumen of a large adult ruminant thus harbours a staggering number of microbes: 500–1000 trillion bacterial cells and 50–100 billion protozoa per animal. See also: Rumen: microorganisms; Bacterial ecology; Ecology of invertebrate nutrition; Protozoan symbioses;

Reef-building corals are symbioses of scleractinian corals (colonial, calcium-clad relatives of sea anemones) and dinoflagellates (yellow-brown, photosynthetic algal protists). Corals, especially those in shallowest waters, are highly dependent on their photosynthetic symbionts for organic food (provided as organic photosynthetic products released by the dinoflagellates to their hosts); they also require dinoflagellates for construction of their hard, calcareous skeletons. With the assistance of their symbionts, corals build reefs of geographical and navigational scale, forming the basis of tropical marine ecosystems of unusually high productivity and species diversity. The dependence of corals on dinoflagellate symbionts is further reflected in the devastating effect of 'coral bleaching' – the expulsion of dinoflagellate symbionts from corals in certain environmental circumstances – on coral productivity and coral health. The tight interdependence of dinoflagellate symbiosis and reef-building in corals has led some palaeontologists to suggest that photosynthetic dinoflagellates may always have been key to tropical reefs, even when the dominant reef-building animals have been taxa other than scleractinian corals. See also: Dinoflagellates; Cnidaria (coelenterates); Biotic response to climatic change;

In addition to algal symbiosis among reef-building corals, mutualistic microbial symbioses have been detected in many other ocean habitats. Among various animals inhabiting deep-sea regions near hydrothermal vents, several contain symbiotic chemosynthetic prokaryotic microbes, especially sulfur-oxidizing bacteria and methanogens. One of the most notable such hosts are vestimentiferan pogonophorans, gutless, mouthless tubeworms (currently classified as highly modified annelids), whose autotrophic sulfur-oxidizing symbionts are key to the survival and growth of these animals in their bizarre but ecologically important deep-sea habitat. See also: Hydrothermal vent communities;

Especially common in intermediate ocean depths, but also found in some shallow seas, bioluminescent squid and fish are a common, and always striking, sight. In several instances, the bioluminescence of these squid and fish is not endogenous to the animals, but instead arises from bioluminescent bacterial symbionts contained in specialized light organs of their hosts. Mutualistic (or at least apparently benign) symbioses are present in a diverse array of other marine organisms as well, including foraminifera and radiolarians (dinoflagellate symbionts), Placozoa (bacteria), sponges (cyanobacteria and heterotrophic bacteria), jellyfish and sea anemones (dinoflagellate symbionts), flatworms (algal symbionts), oligochaetes and clams (chemosynthetic bacteria), shipworms (nitrogen-fixing and cellulose-digesting bacteria), and didemnid

(cyanobacteria) and molgulid tunicates (protists and bacteria). Green algal symbionts are found in some freshwater animals, including some sponges, and green hydra (*Chlorohydra*). See also: Bioluminescence; Shallow seas ecosystems; Porifera (sponges); Platyhelminthes (flatworms); Urochordata (tunicates);

The influence of mutualistic endosymbiosis on evolution of host taxa

The above examples provide abundant evidence of the extraordinarily wide geographic and taxonomic distribution of mutualistic symbioses in the biosphere. Further, mutualistic symbiosis is thought to have played a key role in the radiation of several host taxa – notably, aphids, molgulid tunicates and vestimentifera, among others – in which all species members contain benign microbial symbionts. In some of these cases (molgulids and aphids), the microbial endosymbionts are obligately symbiotic and apparently live exclusively with (and are arguably coevolved with) their host taxa. Beyond the examples of these contemporary symbioses, it is now widely accepted that two eukaryotic organelles – chloroplasts and mitochondria – evolved from bacterial symbionts sometime in eukaryote evolution. Taking the probable symbiotic origins of these organelles into consideration, one could say that nearly every eukaryote bears the profound imprint of a symbiotic history. See also: Endosymbionts; Eukaryotes and multicells: origin; Mitochondria: origin; Plant chloroplasts and other plastids;

Metabolic and Other Chemical Interactions in Mutualistic Endosymbioses

In endosymbiosis, host cells and endosymbionts coexist in close proximity. Not surprisingly, this physical juxtaposition is accompanied by extensive metabolic interactions, with effects on the development, nutrition and energy budget of both hosts and endosymbionts. In many mutualistic symbioses, the metabolic contributions of symbionts and hosts tend to complement each other. The nutritional complementarity provided by each symbiont can benefit the other symbiont(s) by replacing a metabolic 'deficiency' of the other symbiont. Occasionally, this complementarity has a stronger, synergistic effect on the partnership, resulting in a symbiotic association that produces novel metabolic products, or thrives in nutritional or environmental conditions that would be impossible for each of the species partners alone. See also: Ecology of invertebrate nutrition; Ecology of vertebrate nutrition;

Autotroph–heterotroph endosymbiosis

Associations between autotrophic and heterotrophic organisms are among the best-known and most intensely studied mutualistic symbioses. At first glance, associations between photosynthetic autotrophs (cyanobacteria, algae or plants) and heterotrophs (protozoans, animals or fungi) seem to encompass an overwhelming diversity of habitats, taxa and morphologies: reef-building corals, sponges, sea anemones, freshwater hydras, flatworms, giant clams, didemnid tunicates and marine and freshwater protozoans with cyanobacterial or algal symbionts; lichens; legumes, alders and other plants with nitrogen-fixing bacteria; and a wide variety of terrestrial plants (including legumes) with root fungi may not seem to have much in common, taxonomically or ecologically. But a closer look

does elicit some metabolic commonalities. See also: Cyanobacteria; Algae: phylogeny and evolution; Algal symbioses;

For instance, in lichens, reef corals and mycorrhizal plants, photosynthate flows from the photosynthetic partner to the heterotroph. The photosynthetic partner, in turn, receives nitrogen and/or phosphorus nutrients from heterotrophic symbionts. This tight cycling of carbon, energy and nutrients enables some of these symbiotic associations to persist in environmentally stressful, oligotrophic (nutrient-poor) habitats, allowing mycorrhizal plants to grow in low-phosphorus soils, coral reefs to flourish as atolls in tropical open oceans (where nitrogen levels are close to zero) and lichens to survive life on alpine rocks. See also: Photosynthesis: ecology; Photosynthesis;

The synergistic effects of these symbioses are evident at several levels. Coral animals themselves are carnivores, but symbiotic corals in shallow waters become net photosynthesizers, which contribute significantly to the primary productivity of reef ecosystems. Typically, one would expect to find terrestrial fungi and algae in damp, somewhat sheltered habitats. But the algal–fungal partnerships we know as lichens thrive in drier, more exposed habitats than either partner could survive alone. The synergy of lichen symbiosis is also reflected chemically in lichen acids produced only in symbiosis; in the plant-like morphology of many lichens, which led botanists to consider them as single organisms until the second half of the nineteenth century; and the development of a workable (although not phylogenetically based) taxonomy for identification of these ‘superorganisms’ in the field. See also: Evolution of ecosystems: marine; Shallow seas ecosystems;

A second class of autotroph–heterotroph symbioses, discovered in the last two decades, includes heterotrophic marine invertebrate animals with endosymbiotic chemosynthetic (usually sulfur-oxidizing or methanogenic) prokaryotes. These symbioses were first found in deep-sea, sulfur-rich hydrothermal vents, in large, gutless vestimentiferan pogonophoran worms. Since then, parallel symbioses have been found in other sulfur-rich habitats (offshore sewage outfalls, benthic regions near coastal saw mills, sulfur-rich salt marshes) and in other marine invertebrates, often also with reduced or absent guts, including lucinid and thyasirid clams, oligochaetes and perviate pogonophorans. Animal hosts with reduced guts are clearly dependent on their chemosynthetic symbionts for much of the organic carbon and energy they need to lead their heterotrophic lives. In turn, sulfur-oxidizing endosymbionts (as a particular example) acquire, through physiological and behavioural activities of their hosts, the improbable mix of oxygen, carbon dioxide and reduced sulfur necessary for autotrophic sulfur oxidation. The ecological effects of such symbioses are reminiscent of those of photosynthetic–heterotrophic marine symbioses. Just as reef-building corals in open oceans create oases of high productivity amidst low-nutrient tropical waters, so do hydrothermal vent communities, fuelled in part by chemosynthetic–heterotroph symbioses, serve as underwater ‘islands’ of high productivity amidst the sparsely populated communities of the abyssal ocean plains. See also: Methanogenesis; Hydrothermal vent communities; Marine communities;

The effects of mutualistic endosymbiosis on nutrient and catabolite metabolism of animal hosts

The microbial communities populating herbivore guts also complement and supplement the metabolic capabilities of their animal hosts. Plant diets are nutritionally difficult in several ways. First, various plant compounds, especially cellulose and lignin, are notably resistant to digestion: relatively few animals possess endogenous cellulases, and thus are benefited by the presence of cellulose-digesting microbes. Second, many specialized plant diets, such as wood and phloem, are very low in nitrogen. Thus, in addition to cellulose-digesting microbes, various wood-eating termites contain in their midgut nitrogen-fixing bacteria (which provide metabolically usable nitrogen to their termite hosts), or bacteria which enzymatically recycle the termite's own uric acid 'waste', returning nitrogenous metabolites to termite tissues (thus maximizing conservation of nitrogen in the termites). Similarly, in low-nitrogen conditions, rumen microbes in camels recycle their host's 'waste' urea, making its metabolites available to both the symbionts and the camel host; and bacterial symbionts of aphids and grain weevils produce B vitamins and sterols. See also: Herbivory; Cellulose: biogenesis and degradation; Basidiomycota; Ecology of invertebrate nutrition;

The taxonomic diversity typical of gut microbial communities is accompanied by metabolic diversity among those microbes, a circumstance well-suited to addressing the multiple nutritional challenges of plant diets for their animal hosts. Rumen microbes, for instance, have enzymes that digest cellulose, hemicellulose, xylan, starch, pectin, complex sugars, protein and lipids; they detoxify various plant compounds (and also toxify a few); they utilize peptides, oxalate, lactate, glycerol, sugars, formate, pyruvate and acetyl-CoA as nutrient sources, and produce at least five volatile fatty acids, lactate, hydrogen gas, ethanol, ammonia, carbon dioxide and methane as fermentation and degradation products. In addition to protein, they can utilize many forms of nonprotein nitrogen, including urea, potentially reducing the dietary requirements of many ruminants for high-protein diets. See also: Rumen: microorganisms; Animal nutritional requirements;

The benefits to microbes of symbiotic life in animal guts have not been studied so extensively as those to the host, but usually are asserted to be the provision of a 'stable', food-rich, anaerobic habitat for the microbes in question. Certainly, most gut mutualists are obligate anaerobes, and indeed most are obligately symbiotic. But whether an animal gut's 'stability' is part of the benefit to the endosymbionts, or whether indeed an animal gut can be considered a stable habitat at all, is an open question.

Other animals on nutritionally narrow diets also benefit from nutrient supplementation of microbial symbionts. Various invertebrate animals – including leeches, tsetse flies, sucking lice, bed bugs and several mite species – owe their ability to dine on a diet of vertebrate blood to the B vitamins and other nutritional supplements provided by their microbial

symbionts. Like termites, cockroaches may also recycle uric acid, synthesized and stored in their fat body, with the help of bacteria resident in fat body cells. Since uric acid stores are depleted when food is unavailable, these symbiotic bacteria may enable cockroaches to survive periods of starvation by making available nitrogen- and carbon-rich metabolites in such conditions. In several other symbioses, endosymbionts are known or suspected to metabolize urate produced by their animal hosts, but the potential benefits of this activity to the host are not as obvious. In the marine acoel flatworm *Convoluta roscoffensis*, uric acid deposits disappear when the worms acquire algal symbionts. In molgulid tunicates, the protistan symbiont *Nephromyces* (including its own intracellular bacterial symbionts), living among urate deposits of its host, has very high urate oxidase activity, while its animal host has none. The potential benefits of symbiont-induced metabolism of uric acid are relatively obvious in nitrogen-starved termites and food-starved cockroaches. But both *Convoluta* and molgulids live in high-nutrient habitats, where neither nitrogen *per se* (for the 'autotrophic' algal-infected *Convoluta*), nor food in general (for molgulids) seems conspicuously limiting. These latter two symbioses are among the several examples which suggest that the metabolic benefits of mutualistic symbioses are not limited merely to provision of nitrogen, phosphorus or organic carbon, nor merely to survival in low-nutrient habitats, nor even to nutrition in general. Mutualistic symbioses can have other metabolic and ecological dimensions as well. See also: Uric acid metabolism;

Other effects of metabolic interactions in mutualistic symbioses

In some mutualistic symbioses, chemical interactions between host and symbiont affect aspects of host biology other than host nutrition. For instance (as discussed above), symbiotic fungal endophytes may deter herbivory on some host grasses. Epibiotic bacteria on marine crustacean embryos apparently prevent infection of host embryos by pathogenic fungi; similarly, an additional benefit of mycorrhizal infection may be increased resistance of host plants to infection by fungal pathogens. See also: Plant defences against herbivore and insect attack; Fungal pathogens of nonhuman animals;

Symbioses between marine animals and luminescent bacteria are an especially dramatic example of the non-nutritional dimensions of mutualistic endosymbioses. In both fish and squid, bacteria are contained in specialized organs whose morphologies are astonishingly well suited to their twin functions of symbiont acquisition and culture and controlled light production. In some cases (as in sepiolid squid), some steps in the development of the symbiotic light organs are induced by the symbionts; and there are cases among both fish and squid in which the coevolution of the symbiosis is clearly closely tied to the evolution of the light organ that houses the symbionts. The adaptive significance of symbiont-provided luminescence is not always completely understood; but in at least several cases, the steady glow of bacterial bioluminescence provides animal hosts with ventral camouflage against brightly lit upper waters. In other cases, symbiont-assisted luminescence may serve functions of species

recognition, predator deterrence or prey attraction. See also: Bioluminescence;
Complexity and Variability in the Dynamics of Mutualistic Symbioses

More often than not, the beneficial effects of mutualism are better understood in one symbiont than the other. Since our understanding of these symbioses is so incomplete, it is certain that we have an overly simple conception of the evolutionary and ecological dynamics not only of particular symbioses, but of the phenomenon of mutualistic symbiosis in general.

Are endosymbionts benefited by mutualistic symbiosis?

Lichens serve to illustrate the extent and depth of the problem. Visible to casual observers of nature, and studied by biologists for almost 150 years, lichen symbioses nevertheless remain poorly understood, especially in terms of the coevolutionary dynamics of lichen symbionts. Strong ecological evidence points to lichens as mutualisms: lichen symbioses can live in environments where free-living algae and fungi cannot, and free-living counterparts of lichen fungi and lichen algae have been seen only very rarely. Both of these observations strongly suggest that, in nature, symbiosis is beneficial to, and perhaps even obligate for, both algal and fungal species partners in the lichen symbiosis. Generally, the consensus remains that lichen symbioses are mutualisms. However, some cell biologists studying lichens noted the presence of haustorial projections in lichen fungi, abutting algal cells; since haustoria are characteristic also of pathogenic fungi, these biologists suggested that lichen fungi might also be acting as pathogens, parasitizing their algal partners. This apparent contradiction illustrates not only deficiencies in our database, but the general difficulties of extrapolating the evolutionary and ecological consequences of biochemical and cellular phenomena observed in laboratory conditions. See also: Lichens; Algal symbioses;

Observations of dinoflagellate symbionts in reef-building corals, and of rhizobial bacteria in legume roots, raise particular questions about the effects of 'mutualism' on some endosymbionts. The dinoflagellate symbionts of corals can be raised easily in the laboratory; in these 'free-living' (albeit artificial) conditions, the cell division rate of these algae is greater than inside the host. In culture, the symbionts reacquire their cell wall and their flagella, all of which are lost when they take up residence in the cells of their coral host. Further, dinoflagellates in symbiosis 'leak' up to 95% of their photosynthate to their coral host, while in free-living culture, the dinoflagellates manage to keep most of their photosynthate for their own use. Thus, for the 'benefits' of symbiotic life, the dinoflagellate symbionts of corals give up their cell wall and their flagella, sacrifice most of their photosynthetic products, and reduce their reproductive rate. Rhizobia pose even more of a paradox: while rhizobia do reproduce when 'free-living' in the soil, once they have infected the root cells of their leguminous host and begun to fix nitrogen, they no longer reproduce at all. For rhizobia and for the dinoflagellate symbionts of corals, it is appropriate to ask the question: do these endosymbionts really benefit from their 'mutualistic' symbiosis, or are they merely artfully

exploited prisoners of their hosts, and generally better off without their hosts? See also: Dinoflagellates; Root nodules (Rhizobium, legumes);

Are hosts benefited by mutualistic symbiosis?

In addition, the benefits of mutualistic symbiosis to hosts are also not always clear. The sea anemone *Anthopleura elegantissima*, well known from the Pacific coast of North America, usually contains photosynthetic dinoflagellate symbionts that are known to provide to the host about 40% of their needs for organic carbon. Not surprisingly, individuals of symbiont-containing *A. elegantissima* show higher individual growth rates than their aposymbiotic counterparts. But at the same time, rates of fission of individuals – a kind of asexual reproduction seemingly related to individual body growth – are unaffected by the presence or absence of symbionts.

Similarly, molgulid tunicates contain microbes that are clearly obligate symbionts, and the universal presence of these symbionts among molgulids in nature suggests that the symbiosis is also beneficial, perhaps even obligate, for molgulids as well. But census of survivorship and reproduction among symbiotic and aposymbiotic molgulids in the laboratory produces results which, while suggesting generally that symbiosis enhances molgulid reproduction, are also notably variable, especially with variation in aquarium size, seawater characteristics and other growing conditions.

The costs of mutualism

Some of the paradoxes of laboratory experiments can be partly explained by remembering that there is a cost to mutualistic symbiosis, and that in certain experimental (or even natural) conditions, that cost may outweigh benefits to the extent that the whole evolutionary balance of the symbiosis is thereby altered. Agricultural scientists have learned this lesson with mycorrhizae, noting that some mycorrhizal fungi can be pathogens when paired with some plant hosts, and that the balance of arbuscular mycorrhizal symbioses can be changed by varying phosphorus levels in the soil. Although arbuscular mycorrhizae generally enhance host plant growth in low-phosphorus soils, they can depress plant growth (thus 'parasitizing' the plant) in higher phosphorus levels. In very high phosphorus soils, mycorrhizal associations do not form at all. A similar phenomenon has been observed in *Chlorohydra*, the green alga-infected 'green hydra' found in some freshwater habitats. When grown in the laboratory under light, and in the absence of organic food, green hydra survive and grow, in contrast to aposymbiotic hydra, which do not survive without external organic food. In such conditions, the green algae benefit *Chlorohydra* by providing their hosts with organic carbon. However, when *Chlorohydra* were grown in light, but with organic food, there was no difference in growth rate between symbiotic and aposymbiotic individuals; when grown in the dark, and with organic food, the growth rate of symbiont-free *Chlorohydra* surpassed that of their symbiotic counterparts. Investigations of fungal endophytes suggest that the prevalence of *Epichloe* on plant hosts, and its effect on plant hosts, can vary with mode

of symbiont transmission and taxon of plant host. These experiments demonstrate that there is an energetic cost to maintaining even mutualistic endosymbionts, that 'mutualistic' symbionts are not mutualistic with all species partners and that symbiotic mutualisms can have at least temporary parasitic effects in certain environmental conditions. See also: Mycorrhiza; Green algae;

In sum, we know that mutualistic symbioses play important ecological and evolutionary roles in the biosphere. Despite numerous studies of and growing general interest in these symbioses, however, we still know very little about the evolutionary and ecological dynamics of these important associations. What we do know suggests that mutualistic symbioses are intricate, complex and variable in their interactions. In nature, there can be a very fine line between parasitism and mutualism: a symbiosis with mutually beneficial effects seems often an association in relatively fragile balance, a balance that can be shifted by changing biotic and physical conditions in the environment.

See also: Parasitism; Mutualism among free-living species; Interspecific interaction; Microbial symbioses;

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