Review article
The Symbiotic Condition

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Abstract

Attempts to describe symbiosis by brief definitions lead to confusion. Some of the terms often used are themselves difficult to define both rigorously and sensibly (e.g., 'benefit'), or often difficult or impossible to measure experimentally (e.g., 'fitness'). Moreover, the facts about the interactions between the partners of many symbioses are too imperfectly known to use terms such as 'benefit' with any confidence.

This review attempts another approach to understanding the symbiotic condition by contrasting it with parasitism: parasites exploit their hosts, but hosts exploit symbionts. The contrast is explored by comparing parasitism and symbiosis with respect to effects on host fitness, specificity, recognition, host responses to infection, nutrient fluxes, host control over infection, transmission to next generation, and specific modifications to genomes. Further topics considered in relation to symbiosis include: assessments of the extent to which symbionts simultaneously exploit their hosts; symbionts which can exist permanently and independently from hosts; effects on different stages of host life-cycle; the role of symbiont-derived organic carbon; and difficulties in the experimental study of symbiosis.

It is concluded that the general nature of the symbiotic condition is better understood if it is regarded primarily as a situation in which a host is exploiting a symbiont. The extent to which symbionts can be considered unequivocally and simultaneously to exploit their hosts varies greatly between different types of association, so that such 'mutualistic' aspects should be assigned only minor or secondary significance in considering the general phenomenon of symbiosis.

Keywords: symbiosis, mutualism, mutual benefit, parasitism

1. Introduction

A bewildering variety of associations are being considered at this symposium. This begs the obvious question of what this diversity of associations has in common — what is the unifying theme which brings together lichenologists with coral experts, entomologists with those who study mycorrhizas?

The simple answer is that they are all considered to be examples of symbiosis. The difficult problem arises when the next question is asked, what does the term 'symbiosis' mean? This question is usually answered by one of several kinds of simple definition, but all of them lead to difficulties and confusion, so that today there is still no universally agreed definition for the term 'symbiosis'.

There are at least three reasons why the various simple definitions of symbiosis are unsatisfactory.

1. There is a permanent conflict between the De Bary definition covering all associations between dissimilar organisms, and the use of the word in everday English, where it is restricted to associations where mutual benefit is believed to occur. Although many modern writers on symbiosis advocate the use of the De Bary definition (e.g., Lewis, 1973; Ahmadjian and Paracer, 1986; Smith and Douglas, 1987), most biologists in practice seem to adopt the more restricted definition. This is illustrated, for example, by the choice of topics for this symposium and the coverage of subjects in papers published in the journal *Symbiosis*.

2. Even where the 'mutual benefit' type of definition is adopted, problems arise because 'benefit' is a very difficult concept to define in a way which is both rigorous and measurable experimentally (e.g., Douglas and Smith, 1989; Cushman and Beattie, 1991). Too often, interpretations of 'benefit' are tinged with anthropocentrism, such as the automatic assumption that increases in host size are always beneficial.

3. In a large number of associations, the facts about the interactions between the partners are too imperfectly understood to make safe and trustworthy judgements about the existence of mutual benefit.

This latter point may cause some surprise. To illustrate it, consider what many would regard as a 'typical' example of symbiosis — a heteromerous lichen — and examine what is known and what is not known about the interactions between the fungal host and its symbiont.

The following facts are known and experimentally demonstrable in lichens (e.g., see Smith, 1975):

1. Photosynthetically fixed carbon passes from symbiont to fungus as carbohydrate in laboratory experiments.

2. Lichens grow much more slowly than free-living relatives of symbionts and fungal hosts.

3. Despite very slow growth, lichens have considerable powers of nutrient absorption.

The following are some of the important facts we do *not* know about lichens.

1. The absolute amount of carbohydrate moving from symbiont to fungus, even under laboratory conditions, has never been directly measured (Smith, 1980). This is partly because, in experiments using radioactive carbon, the absolute specific activity of the ^{14}C fixed in symbiont photosynthesis has never been measured. There is very little knowledge of how carbohydrate transfer is affected by the temperature and varying moisture conditions found in natural habitats.

2. The relative proportions of carbon obtained by the fungus from symbionts and from external sources under field conditions are not known. As mentioned above, lichens display a remarkable capacity for absorbing nutrients (including organic compounds) from external solutions.

3. The importance to lichen fungi in nature of carbohydrates received from their symbionts is not understood. They could serve one or more of the following roles:

growth processes (even though these are very slow).

respiratory substrates.

maintenance of high osmotic pressures in hyphae.

cellular mechanisms for resistance to desiccation.

restoring solute losses from rewetted dry hyphae.

4. Nutrient flow from fungus to symbiont has never been demonstrated. The extent to which symbionts acquire nutrients directly from external solutions has not been clarified, although ultrastructural studies of the interface between fungus and symbiont are now beginning to indicate possible pathways for experimental investigation (Honegger, 1991).

5. The length of time for which symbionts persist in an active state in lichen thalli has never been studied.

6. The nature of the interactions at the host/symbiont interface is understood only very imperfectly.

Similar pictures of inadequate understanding of interactions between host and symbiont could be painted for a number of other types of association regarded as 'typical' examples of symbiosis. They include some, such as green hydra, which have been subject to considerable laboratory investigation (Mews and Smith, 1982). In many cases, the situation is exacerbated by the difficulty of extrapolating from what is observed in laboratory or pot experiments to what actually happens in natural environments. This is discussed later in this paper.

The lack of experimental knowledge about most of the types of association described as 'symbiotic' is such that definitions of symbiosis which lay prime emphasis on concepts of mutual benefit cannot yet be applied satisfactorily to many associations. The alternative of using the de Bary definition is fundamentally unsatisfactory because it does not take into account the fact that biologists nevertheless perceive the associations generally termed 'symbiotic' to be somehow different from those termed parasitic.

2. Understanding the Symbiotic Condition by Contrasting it With Parasitism

This paper aims to achieve a deeper understanding of the symbiotic condition, not by searching for yet another simple definition, but by exploring and analysing the contrast with parasitism. In this way, it will attempt to construct a logical and coherent framework into which the wide diversity of associations considered at this conference can fit. The framework will be one to which the term 'symbiotic' can be sensibly applied, and which will also be consistent with the very limited experimental understanding of many of these associations.

The starting point of this analysis is that associations generally termed symbiotic are usually seen as somehow contrasting with parasitism. Exploring this contrast may clarify our understanding of the nature of symbiosis.

Terminology

All associations, whether parasitic or symbiotic, are typically between a larger organism and a smaller. In the following discussion, the larger organism will be called the 'host', and the smaller either 'symbiont' or 'parasite' as appropriate (Smith and Douglas, 1987). Where necessary, symbionts and parasites collectively will be referred to as 'associates' of the host.

Exploitation of one organism by another

In parasitism, the host 'suffers' from the association, and the 'suffering' is easily demonstrated experimentally by showing that infected hosts have reduced numbers of offspring, less vigour, etc., than uninfected hosts. All would therefore agree that parasites *exploit* their hosts. In symbiosis, the host is perceived to be in the opposite category of exploiting its symbiont. However, if this is advantageous, then infection will tend to be the norm under a given set of natural conditions, so that meaningful experimental comparisons with uninfected hosts to measure the degree of advantage to the host may not be possible. Nevertheless, the contrast between symbiosis and parasitism is a contrast between hosts which exploit their associates, and hosts which are being exploited by their associates.

The question will arise of whether there are situations in which a symbiont simultaneously exploits its host as it is being exploited. Past preoccupation with 'mutualism' has already made the understanding of symbiosis both confusing and difficult. It is therefore better to defer this more complex topic until after the simple comparison between hosts which are exploited and hosts which exploit.

3. Comparisons Between Parasitism and Symbiosis

The comparison will cover the following aspects of interactions between hosts and their associates (because symbiotic associations are biotrophic, comparisons are made only with parasitic associations which are biotrophic). The essential points are summarised in Table 1.

Effects of host fitness

This is an aspect upon which most definitions of parasitism and symbiosis lay emphasis. As explained above, experimental demonstration that host fitness is reduced in parasitism is relatively easy. But in symbiosis, if host fitness is improved by infection, then infection becomes the norm and the likelihood of finding suitable uninfected hosts is usually small. The experimental demonstration of improved fitness then becomes difficult, and if the association is obligate, it is impossible.

Specificity

Nearly all biotropic parasites are highly specific, some even for subspecies rather than species of host. Presumably, such parasites become highly adapted

Table 1. A summary of comparisons between parasitism and symbiosis

Interaction	Parasitism	Symbiosis
Effect of infection on host fitness	decreased	(increased)*
Associate's specificity for host	very high/high	lower/very low
Recognition stages	one/very few	several/many
Host responses to infection	limited	often extensive
Nutrient fluxes	out of host	into host (also some out)
Host control over associate after infection established	weak	strong
Host mechanisms for transmitting associate to next generation	none	various known
Specific modifications to host genome	usually limited	often significant

* If host fitness is increased by infection with symbionts, then uninfected hosts are likely to be scarce or absent under natural conditions. Hence, experimental comparisons of the effect of symbionts on host fitness under natural conditions may often be impossible.

to overcoming one particular set of defences and existing in a particular hostile environment within a specific host type. By contrast, in those symbiotic associations where hosts acquire their biotrophic symbionts from the environment each generation, the level of specificity of symbiont for host is significantly lower (Smith and Douglas, 1987). There are obvious advantages of low specificity in terms of natural selection, ease of forming associations, etc. Even in situations where symbionts do not occur free in the natural environment and their association with the host is ecologically obligate, experimental manipulations usually demonstrate lower specificity than in biotrophic parasitism.

Recognition

The high specificity of associates for hosts in parasitic associations is often based on recognition mechanisms involving only one or a few genes, governing interactions between one or a few specific surface molecules. It is to the host's advantage to avoid recognition by the parasite, and if a parasite contacts the host, for the host to have very rapid recognition so that defences can be 'switched on'.

In symbiosis, it is to the host's advantage to be infected, and in ways that do not trigger its defence mechanisms. In some associations, absence of recognition as a parasite may well facilitate symbiont entry. Usually, surface interactions between host and symbiont are only one component of a much more complex recognition process, in which – in contrast with parasitism – the

initial contact phases are typically of low specificity, with higher specificity developing in later phases. In some cases, as in the legume/rhizobium symbioses, the host may release 'signals' which specifically attract symbionts (e.g., review by Brewin, 1991).

An apparent exception to these generalisations are the highly specific mechanisms shown in laboratory experiments to be involved in the infection by *Rhizobium* of root hairs of some legumes such as *Trifolium*. However, in considering this example, it should be borne in mind that under natural conditions, most legumes do not show such high specificity, and especially in the case of the many host species that are not infected through root hairs but through cracks in the root surface. Indeed, representatives of two different genera, *Rhizobium* and *Bradyrhizobium*, may sometimes be found in different nodules on the same root system (e.g., Sprent et al., 1987), and occasionally even within the same nodule. Sprent and Sprent (1990) comment on the paradox that such examples of low specificity can be observed in the field, yet laboratory experiments reveal the existence of highly refined recognition processes between particular host and rhizobial genomes.

If the criterion of 'successful' recognition is that a functional nodule should be formed, then many stages are involved.

Responses to infection

In parasitism, hosts need to minimise the degree to which they are exploited, and so they make biochemical or morphological (especially in plants) responses to contain, minimise or eliminate the parasite's activities. By contrast, in symbiosis, hosts need to maximise the degree to which they can exploit symbionts, so responses are generally much more complex, involving the provision of a morphological location and physiological environment that optimises the symbiont characteristics that are to be exploited.

Nutrient fluxes between host and associate

In parasitism, nutrient fluxes are almost entirely out of the host to the parasite; this may be accompanied by diversion of nutrients from other parts of the host to the site of infection. In symbiosis, the principal flux is into the host from the symbiont. There are also nearly always movements from host to symbiont, but it may be simplistic to interpret such movements as necessarily of 'mutual benefit' to the symbiont. It will be to the host's advantage to maintain the symbiont in the optimum condition for exploitation. Further, *restricting* the flow of certain nutrients to symbionts may well be a common

mechanism of host control of symbiont growth (e.g., Rees, 1986, 1989, for green hydra).

Host control over associate

Once a parasite is successfully established, hosts have only weak control over the spread of the infection. In biotrophy, there is advantage to the parasite in not destroying the host and this may be an important factor limiting spread. In symbiosis, a variety of experimental evidence shows that hosts can exert close and effective control over the location and population size of their symbionts (Smith, 1987), and there are very few examples of symbionts spreading in an uncontrolled fashion. Rather, if environmental conditions change so that symbiont exploitation is no longer advantageous compared to the uninfected state, in a number of associations host and symbiont become disassociated, and/or infection no longer occurs.

Transmission to next generation

In parasitism, it is obviously disadvantageous to the host for it to evolve mechanisms for the direct transmission of the parasite to the next generation. In many types of symbiosis, by contrast, it is frequently advantageous to the host for symbionts to be directly transmitted to the next generation, especially where the host has a degree of dependence upon symbionts. Hence, a variety of mechanisms have evolved in animal hosts for direct transmission of symbionts in sexual reproduction (Smith and Douglas, 1987) including infection of eggs (e.g., intracellular symbionts of insects; green hydra), deposition on egg capsules (e.g., *Convoluta*) and maternal behaviour to infect young offspring (e.g., ruminants).

Specific modifications to genomes

In parasitism, the extent to which host genomes are modified in respect of specific parasites is limited, and 'gene-for-gene' resistance by higher plants to certain biotrophic pathogens is one example. Hosts lose no DNA, although intracellular parasites may show substantial loss compared to free-living relatives as they become dependent on their hosts (e.g., Moulder, 1979). In symbiosis, extensive specific modifications to both host and symbiont genomes may occur, with legume/*Rhizobium* associations being especially well studied. The development of this type of symbiosis involves an extensive sequence of interactions in which gene products of the host switch on genes in the symbiont whose products then switch on other genes in the host and so on (Brewin, 1991).

If obligate mutual dependence evolves, then both host and symbiont usually lose DNA, although as Douglas (1991) has pointed out, there is no transfer of DNA from symbiont to host, unless it has become an organelle.

Some General Problems in Studying the Symbiotic Condition
Is there exploitation of hosts by symbionts?

As indicated earlier, the understanding of symbiosis has been clouded and confused by overemphasis on mutualism. Nevertheless, it is fair to ask whether there are some symbionts which unequivocally exploit their hosts. Many symbionts have very limited or no free-living phase, and are confined within the body of their hosts. Compared to free-living relatives, symbiont growth rates are often severely restricted, and there is extensive loss of nutrients to the host. It is difficult to equate this with successful 'exploitation' by symbionts.

Microbial symbionts of ruminants, although confined within the bodies of the host, do not have markedly reduced growth rates, but in this case, most of them are eventually digested by the host. The question of whether they exploit hosts is arguable.

Mycorrhizal symbionts of plant roots present a clearer case. Most of the mycelium is in the soil away from the roots, and is in competition with free-living soil microorganisms. It is reasonable to postulate successful exploitation of hosts, since substantial nutrients are gained from hosts compared to free-living relatives and competitors.

Symbionts which can have a permanent existence away from hosts

These include rhizobial and actinorhizal symbionts of plant roots, and *Vibrio* and *Photobacterium* symbionts of the light organs of fishes. Each of these types of symbionts have free-living populations in the environment, yet carry genes which are only expressed in symbiosis (such as the genes for specificity of infection and nitrogen-fixation in rhizobia.) So far, good experimental evidence is lacking as to the advantage to the free-living populations of symbionts of the costs of bearing these genes. Without marine fish or legume hosts, would the size of the free-living populations ultimately decline? These could well prove to be further examples of simultaneous exploitation of hosts by symbionts.

A possibly more complex problem is raised by those mycorrhizal symbionts of orchids such as *Rhizoctonia solani* which can be pathogens of other plants (see Harley and Smith, 1983). Such fungi seem to be completely exploited by orchid corms during their prolonged non-photosynthetic phase in the soil, and with doubtful evidence that the fungal symbionts derive appreciable fixed carbon from the mature plant once it becomes photosynthetic.

Hence, in symbiosis, while hosts always exploit symbionts, the extent to which symbions exploit hosts probably varies from one type of association to another. It is for this reason that 'mutualism', 'mutual benefit' or 'mutual exploitation' should be regarded as a secondary issue in symbiosis.

Effects on different stages of host life cycle

It is often tacitly assumed that hosts derive net advantage from their symbionts throughout their life cycle. Experimental evidence is accumulating in a number of associations that it may be only at key stages in the host life cycle that exploitation of symbionts is important. For example, *Chlorella* symbionts of green hydra shorten the time for detached buds to mature into fully grown animals (and hence also the time for animals to develop to the full their feeding capacity – essential for their existence). However, no measurable effects on other phases of the life cycle have been observed (Douglas and Smith, 1983). Again, it has been suggested that VA mycorrhizal fungi are of greater importance to their hosts at the seedling establishment phase, and sometimes also at fruiting, than at other times.

The role of symbiont-derived organic carbon

Some heterotropic hosts derive substantial organic carbon from symbionts — either from those which photosynthesise, or those which break down intractable carbon compounds. It is often assumed that the prime role of such organic carbon is for growth processes. However, it is increasingly clear that in many habitats, nitrogen and other nutrients may be more growth limiting than supplies of carbon. Analysis of interactions in symbioses such as green hydra suggest that a more important role for carbon compounds may be to 'spare' the respiration of scarce organic nitrogen compounds so that they can be wholly allocated to growth (Rees and Ellard, 1989). The role of symbiont-derived carbon in 'purchasing' nitrogen for growth has also been suggested for insects, and for marine coelenterates. Even in legumes, the host can be considered as using some of its photosynthetically fixed carbon to 'purchase' nitrogen from its rhizobial symbionts.

In other associations, bulk supplies of symbiont-derived carbon may fulfil a variety of roles other than for growth processes. Photosynthetically fixed carbon from symbionts is important in the abundant mucus production of animal hosts such as giant clams, nudibranch molluscs and *Convoluta*. In lichens, the possible role of symbiont-derived carbohydrates in the maintenance of high osmotic pressures in the host fungal mycelia has already been mentioned.

Replacing 'poor' symbionts by 'good'

It might be expected that hosts possessing symbionts which they can only poorly exploit might be able to replace them by those which bring greater advantage from exploitation, given the opportunity. This has been demonstrated for *Convoluta roscoffensis* by Provasoli et al., (1968) and Douglas (1983). Hence, it is interesting to note that when green hydra infected with 'poor' symbionts were experimentally exposed to symbionts which released much more carbohydrate, the 'good' symbionts failed to displace the 'poor' (McAuley and Smith, 1982).

Difficulties in the experimental study of symbiosis

Problems in the experimental investigation of symbiosis have been exacerbated by a number of difficulties.

1. Laboratory or pot experiments are frequently carried out under conditions so different to those in the field that extrapolation from one to the other becomes very difficult. For example, in green hydra, experiments are carried out using material grown under light, temperature and feeding regimes far different from those in the field, and with clones which are grown entirely asexually and without a period of winter dormancy for many years. Most mycorrhizal experiments are simply one plant/one fungus models in pots, yet the field situation involves complex guilds of host and symbiont. The great majority of experiments on legumes relate to associations infecting through root hairs, which helps little to understand the many associations in nature which infect differently and with lower specificity.

2. In the study of host/symbiont recognition, it has too often been assumed that the mechanisms would be highly specific and similar to those in parasitism – yet for reasons given above, there are fundamental considerations suggesting they will be different from parasitic recognition. Additionally, recognition is studied in laboratory under conditions that very rarely obtain in the field, and sometimes in systems (e.g., green hydra, *Paramecium*, certain lichens) where symbionts are directly transmitted from one host generation to the next without a recognition phase. Further — as in associations such as *Paramecium* — infection may be described as 'specific' (in the sense of an assumed specific recognition process) merely on the basis of the final outcome of an experimental resynthesis of the symbiosis, without investigating the sequence of initial

stages of infection (i.e., seeing if the early stages of contact are in fact of
only low specificity).

3. The interface between host and symbiont is of key importance, but it has
   proved extremely difficult to analyse interactions at the interface directly
   by techniques other than microscopy.

4. Many symbioses are at least 3-component, yet most experimental sys-
   tems are inevitably 2-component. Also, while it is tempting to restrict
   investigations of a type of symbiosis to the one or two associations which
   are experimentally amenable, the few cases where investigations have
   been made of a range of associations (e.g., lichens, mycorrhizas) lead to
   a much better understanding of the symbiosis. For example, despite the
   elegant molecular genetics of clover/rhizobium studies, do we have any
   idea of recognition processes in natural communities in which legumes
   are prominent, such as the monsoon rainforests of S.E. Asia?

4. Conclusions

The general nature of the symbiotic condition is better understood if it is
regarded primarily as a situation in which a host is exploiting a symbiont. The
extent to which a symbiont can be considered unequivocally and simultane-
ously to exploit its host varies greatly between different types of association.
Hence, such 'mutualistic' aspects are of only secondary importance in consid-
ering the general phenomenon of symbiosis.

If a general definition of symbiosis is required, it is better constructed in
terms of its being a contrasting condition to parasitism. In parasitism, hosts
are exploited by parasites; in symbiosis, hosts always exploit their symbionts,
although simultaneous exploitation of host by symbiont may occur in certain
associations.

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