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Review article

# Coming to Terms with a Field: Words and Concepts in Symbiosis

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## Abstract

More than a century after de Bary (1879) adopted the term ***symbiosis***, biologists still disagree about the word's meaning. Many researchers define symbiosis in the sense of de Bary, as an intimate, outcome-independent interaction between species; others use symbiosis as a synonym for mutualistic or non-parasitic associations. This varied usage arises in part from the absence of a language for describing both symbiotic and non-symbiotic mutualistic interactions; the complexity of many "mutualistic" endosymbioses poses a particular descriptive difficulty. Expropriation of "symbiosis" to identify these mutualistic associations is an understandable, but ultimately confusing, and conceptually limiting solution to this problem. Retention of the broad, outcome-independent sense of symbiosis is urged. Alternate terms, including ***chronic endosymbiosis***, are proposed for apparently benign symbioses which are too poorly known, or too complex, to categorize comfortably as "mutualistic."

In addition to outcome-independent investigations of symbiotic phenomena, questions of the evolutionary significance of symbioses are difficult, but important problems. Thus, terms which address particular outcomes for host or symbiont – e.g., parasitism, commensalism and mutualism, "costs," "benefits," fitness, and related terms – also have a place in the language of symbiosis research.

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> Habits of language... mold habits of thought.
>
> Paul Weiss, 1969

> It follows that the present confusion necessitates the definition of the term [symbiosis] whenever it is used.
>
> M.Hertig, W.H. Taliaferro
> and B. Schwartz, 1937

> ...much time and space has previously been taken up by semantic discussion of the words, *symbiosis* and *mutualism*. I would like to hope that what follows will be the last word but am under no illusions that this will be the case!.
>
> D.H. Lewis, 1985

As might be expected of any new field of study, symbiosis research is still defining the language and conceptual framework of its questions. The most telling symptom of this emergent state is the fact that its central concept – the definition of symbiosis itself – is also its most conspicuously and chronically troublesome dilemma. More than a century after Anton de Bary adopted the term *symbiosis*, students of symbiosis still hold divergent views of the word's meaning, and thus the field's scope. The persistence of this muddle suggests that it is not merely a tiresome grammatical difficulty, but instead a problem which touches on substantive issues in the field. I examine here the current status of the semantic confusion about "symbiosis," consider the roots of the problem, and suggest some ways to clarify some of the conceptual issues which this problem raises.

## 1. Definitions of Symbiosis

De Bary (1879) defined symbiosis as "des Zusammenlebens ungleichnamiger Organismen," the living together of dissimilarly named organisms. Put another way, symbiosis is an intimate association between two or more species; it includes mutualistic, parasitic and commensal associations. From the conceptual perspective of de Bary, therefore, symbiosis is an association defined by intimacy of interaction, rather than by the consequences of that interaction.

Defining a given interaction as "intimate" is not always easy, but biologists at least share a general understanding of the word. Endobiotic associations are generally accepted as intimate interactions, because the life of one organism inside another obviously involves morphological and physiological intimacy between the participants. Characterizing short-term associations and ectosymbiotic interactions can be more problematic, since "intimacy" in these cases is a matter of perspective, and thus open to debate: Where does the transient presence of an ingested microorganism in an animal's gut end, and an intestinal symbiosis begin? Where does specialized insect herbivory end, and insect-plant ectosymbiosis begin? A crisp distinction between intimate and non-intimate inter-species interactions is often difficult to draw. Nevertheless, the definition of intimacy as protracted physical contact between the species partners (Margulis, 1991) at least provides an explicit criterion for differentiating "intimate" from "non-intimate" interactions.

However, there still is no agreement on the role that *ecological consequences or outcomes* of inter-species intimacy should play in definitions of symbiosis. In the most common alternative to de Bary's definition, symbiosis is sometimes used as a synonym for mutualism or an antonym to parasitism. This outcome-dependent alternative is partly based on the habits of popular language, which commonly uses "symbiosis" to describe mutualistic relations between colleagues, political allies or teammates, or (for manufacturers of cars or perfumes) the mutually beneficial, synergistic relationship between product and customer. But most confusion over the meaning of symbiosis is perpetrated by biologists themselves. Five current American texts in general biology (Campbell, 1990; Curtis and Barnes, 1989; Keeton and Gould, 1986; Raven and Johnson, 1992; Wessells and Hopson, 1988) do define symbiosis clearly in the sense of de Bary. But among more advanced texts in ecology and evolutionary biology there is less consensus. While several recent texts (Howe and Westley, 1988; Ehrlich and Roughgarden, 1987; Begon et al., 1990; Stiling, 1992) use de Bary's concept of symbiosis, others do not define symbiosis formally (Kormondy, 1984; Futuyma, 1986; Odum, 1989; Ricklefs, 1990), or they equate symbiosis with mutually beneficial associations (McNaughton and Wolf, 1979; Avers, 1989) or non-parasitic (Pianka, 1988) ones.

Remarkably, symbiosis terminology seems most variable in the specialized research literature on the phenomenon. Although most researchers (e.g., Hertig et al., 1937; Goff, 1982; Lewis, 1985; Ahmadjian and Paracer, 1986; Schmidt and Roberts, 1989) seem to use symbiosis as did de Bary, this usage is neither universal nor consistent, even among the most distinguished students of the field. Several well-known monographs (Caullery, 1922; Whitfield, 1979) have explicitly defined symbiosis as symbiotic *mutualism*. Others have considered de Bary's definition vague and "outdated" (Lewin, 1982) or too broad to be useful (Smith, 1989). Several authors formally embrace (Smith and Douglas, 1987), or even promote (Margulis, 1990, p. 673; 1991) de Bary's outcome-independent usage of symbiosis, but then focus on cooperative, benign, or non-pathological instances of symbiosis in ways which implicitly (Smith and Douglas, 1987; Margulis, 1990, p. 675) or explicitly (Douglas and Smith, 1989; Smith, 1989) exclude parasitism or pathogenic associations from the purview of symbiologists. Why does this confusion persist?

## 2. Confusing Symbiosis with Mutualism: Some Causes of the Problem and Some Suggested Solutions

Some of the early semantic difficulties with symbiosis arose from misunderstanding by several biologists of de Bary's original usage. As Pound (1893) and Hertig et al. (1937) noted, a number of the 19th– and early 20th–century authors (including Caullery, 1922) mistakenly inferred that de Bary's definition of symbiosis designated only mutually beneficial associations. Since then, however, several biologists (e.g., Hertig et al., 1937; Goff, 1982; Lewin, 1982; Ahmadjian and Paracer, 1986; Smith and Douglas, 1987; Margulis, 1991) have reaffirmed the clear, outcome-independent sense of de Bary's definition.

Thus, the current confusion does not stem from misunderstanding de Bary. It arises instead because we do not have a language to discuss benign or mutualistic interspecies interactions, including "mutualistic" symbiosis; with this deficiency, we tend to preempt the larger term for this restricted use. Until recently we have been culturally and scientifically conditioned to the view that most interspecies interactions are antagonistic (Boucher, 1985). Parasitologists thus have worked within a generally accepted biological paradigm and a well developed conceptual framework. Biologists studying mutualistic or other non-pathological symbioses have not had this advantage.

Two circumstances exacerbate the situation. First, until very recently, parasitologists and students of "mutualistic" symbioses have not interacted closely. Second, the best-known proponents of "symbiosis" as a field of research typically have studied non-parasitic symbioses. Symposia and conferences on symbiosis have usually been dominated by "mutualistic" topics, with parasites relegated to a minor presence or even neglected entirely. By the same token, parasitology meetings tend to give short shrift to "mutualistic" topics. Thus, there has been a tendency for students of non-pathological symbioses to see their field as something apart from, and even in contrast to, parasitology.

Why is "mutualistic symbiosis", or a comparably restrictive term, not used more widely to describe explicitly non-parasitic symbioses? One reason may be that for many students of "mutualistic" endosymbioses (e.g., Saffo, 1991a,b), mere "mutualism" often seems a simplistic way to describe the complex dynamics of the particular phenomena which they study.

For their hosts (with some exceptions, as noted below), infection with "mutualistic" endosymbionts is apparently benign, and sometimes demonstrably beneficial or even obligate. However, benefits of "mutualistic" symbiosis to the endosymbiont are usually less clear. Drawing upon their own excellent empirical work on algal-heterotroph associations and other endosymbioses, as well as on the work of others, Douglas and Smith (1989) have noted that there is little critical evidence that the endosymbionts in many "mutualistic" endosymbioses benefit along with their hosts. Some authors have even speculated that in some cases (e.g., lichens, algal-invertebrate associations) endosymbionts actually might be parasitized by their "mutualistic" hosts (Schwendener, 1867, in Cooke, 1977; Ahmadjian and Jacobs, 1982; Ahmadjian and Jacobs, 1983). Much of this uncertainty regarding endosymbiont benefits arises from lack of study; in many cases of "mutualistic" endosymbiosis, the effect of symbiosis on the endosymbionts is simply unknown (Saffo, 1991b).

For most such symbioses, "mutualism" seems an inadequate or at least premature term. Still, the absence of obvious pathological effects on the host does seem to distinguish some symbioses in important ways from parasitisms. Smith has used the acronym "POLLNPIA" (permanent or long-lived non-parasitic intimate association: Smith, 1989) or simply "endosymbiosis" (Douglas and Smith, 1989) to describe these benign associations. Unfortunately, neither term is very useful. The first of these terms is accurate but unwieldy; the second is confusing in its authors' explicit exclusion of parasitism from symbiosis. Also, the concept behind both these proposed terms does not address those cases of "mutualistic" endosymbioses, such as the molgulid-*Nephromyces* symbiosis (Saffo, 1991a,b) or the endosymbiosis between dicyemids and benthid cephalopods (Hochberg, 1983; Saffo, 1991a) where symbiosis seems clearly obligate for the *endosymbiont*, but is of uncertain or complex consequence for its animal hosts.

One approach to distinguishing apparently benign symbioses from parasitisms is a negative one: to refer to the former associations as "non-parasitic" or "non-pathological" symbioses. Another approach is more positive: to invent a term that avoids assertions of benefit, obligateness, or selective outcome and instead addresses other differences between parasitisms and "mutualistic" endosymbioses. One of these differences is *prevalence* – that is, the percentage of individuals of a given host species that are infected with a given endosymbiont (Margulis et al., 1982). Parasites typically infect less than 100% of a given host population. Although antagonistic symbionts can sometimes infect as much as

100% of several *populations* of a host species (Kuris et al., 1991), I have found no reports of parasites, parasitoids, or pathogens infecting 100% of individuals throughout an entire host *species.* In contrast, the prevalence of "mutualistic" endosymbionts among individuals of a host species *typically* is 100%; sometimes 100% prevalence can extend even through higher categories of host taxa, with endosymbionts infecting all individuals of entire genera, families, orders, classes or even phyla (e.g., Malloch, Pirozynski and Raven, 1980; Smith and Douglas, 1987; Saffo, 1982, 1991a, 1992; McFall-Ngai, 1991; Nardon and Grenier, 1991). Uninfected hosts of "mutualistic" endosymbioses are usually limited to unusual or temporary natural conditions and to artificial conditions such as laboratory culture, fertilized agricultural land, or transplants of hosts to new habitats (Saffo and Davis, 1982; Harley, 1984). In further contrast to parasitism, it is clear in at least some cases, such as coral bleaching (L. Roberts, 1987; Bunkley-Williams and Williams, 1990); Glynn and Weerdt, 1991), that even "naturally" aposymbiotic hosts may not necessarily thrive. I have dubbed symbioses with 100% prevalence of endosymbionts in a given host taxon *chronic endosymbioses* (Saffo, 1991a). Almost all of the apparently benign endosymbioses either demonstrated or suspected to be mutualisms can be included in the category of chronic endosymbioses.

## 3. The Importance of Both Outcome-Independent and Outcome-Dependent Terminology in Symbiosis Research

Whitfield (1979) has rightly said that symbiosis biology should be primarily concerned with "the phenomenological investigation of processes" rather than with definitions. But words do matter, because they mold the way we think. Synonymy of symbiosis with only mutualism or "non-parasitism" is an unfortunate usage, because it limits our thinking and our questions. De Bary's broad definition does not limit its usefulness, despite the concerns of some investigators (Lewin, 1982; Smith, 1989; Douglas and Smith, 1989). It is, in fact, the very breadth of de Bary's "beautifully general term" (Whitfield, 1979) that makes it experimentally and conceptually fruitful, the best descriptor of the entire phenomenon addressed by students of the field.

There is a real need for an outcome-independent term to describe intimate associations between species. First, for many symbioses, the evolutionary consequences for one or both of the partners of the association are unknown. This is especially true of newly described or little-studied symbioses, including endosymbiotic associations between heterotrophic prokaryotes and eukaryotic hosts such as sea star larvae (Bosch, 1992), brittle stars (Walker and Lesser, 1989), bryozoans (Zimmer and Woollacott, 1983), earthworms (Buchner, 1965), sponges (Vacelet, 1975; Santavy et al., 1990), placozoans (Grell, 1981; Grell and Benwitz, 1981), vesicular-arbuscular mycorrhizal fungi (Scannerini and Bonfante-Fasolo, 1991), and the symbiotic protist *Nephromyces* (Saffo, 1990). The evolutionary dynamics of better-studied symbioses can also elude understanding, even when other aspects of these host-symbiont interactions have been resolved. For instance, there have been extensive biochemical, morphological, ecological, and taxonomic studies of lichens, and experimental dissociation and syntheses of lichens in the laboratory have been carried out (Ahmadjian and Jacobs, 1982, 1983; Smith and Douglas, 1987; Galun, 1988). But even after more than a century of research, basic aspects of lichen dynamics remain poorly understood. There is still debate (Ahmadjian and Jacobs, 1982, 1983 vs. Hawksworth, 1988a,b; Honegger, 1991; Kendrick, 1991) about the parasitic or mutualistic nature of lichen symbioses, in part because definitive laboratory and field experiments to resolve the issue have not been done. Additionally, as noted earlier, there are several chronic endosymbioses – such as legume-rhizobial symbioses, algal-invertebrate associations, and associations of marine fish and cephalopods with luminescent bacteria – where the beneficial effects of symbiosis on the hosts have been established, but the consequence of the symbiosis for the endosymbiont remains unclear.

Secondly, it is often hard to draw a distinct line between antagonistic and mutualistic symbiosis. Even when their dynamics are fairly well understood, many symbiotic associations are still too complex to pigeonhole into the simple categories of parasitism, mutualism, and commensalism. In some cases, a single association incorporates both antagonistic and mutualistic components. For instance, several insects pollinate plants such as figs (Janzen, 1979) and yuccas (Howe and Westley, 1988) by parasitizing the plant ovules; thus, as John Thompson has put it (Saffo, 1991b), such insects are paradoxically mutualists only when they are parasites. Three-partner interactions, too, can include both antagonistically and mutualistically interacting pairs. For example, in several mutualistic symbioses (fungal endophytes of grasses, epibiotic bacteria on crustacean embryos), symbionts benefit their host by enhancing host defenses against predators or pathogens (Clay, 1988; Gil-Turner et al., 1989; Gil-Turner and Fenical, 1992).

The effect of an endosymbiont on its host may vary with changes in such abiotic and biotic environmental factors as the host species, developmental stage of host, and the availability of light or ambient nutrient concentrations (Saffo, 1991a). Basidiomycetes such as *Armillaria mellea* and *Rhizoctonia* spp. (harley, 1984) form host-benefiting mycorrhizae with orchids and *Monotropa* but have unambiguously pathogenic effects on other host plants. Similarly, the tobacco leaf pathogen *Pseudomonas syringae* pv. *tabaci* causes death in oats, but it enhances host plant growth and symbiotic, rhizobia-mediated nitrogen fixation in legumes (Knight and Langston-Unkefer, 1988).

"Mutualistic" endosymbiotic effects can vary even within the same host species. This variation can arise not only from genetic-based differences, such as differential susceptibility of host genotypes to parasitic or pathogen infection, but also can be correlated with variation in the ambient environment (Saffo, 1991a,b). For example, although vesicular-arbuscular mycorrhizae (VAM) are usually considered mutualistic symbioses, VAM fungi can parasitize their hosts in certain environmental circumstances. VAM fungi enhance plant growth in low-phosphorus soils (Bethlenfalvay et al., 1982a,b, 1983; Miller et al., 1987), but can reduce plant growth in high-phosphorus soil (Bethlenfalvay et al., 1983), or in conditions, such as low irradiance, that inhibit photosynthesis (Daft and El-Giahmi, 1978). At moderate phosphorus levels, VAM effects on plant growth can vary with the developmental stage of the plant and the relative fungal biomass (Bethlenfalvay et al., 1982a,c). Similarly, in the light, symbiotic green hydras (a) grow faster than their aposymbiotic counterparts in the absence of organic nutrients and (b) grow as fast as aposymbiotic green hydras in the presence of organic nutrients. But in the dark and with organic nutrients, symbiotic green hydras grow more slowly than aposymbiotic animals (Douglas and Smith, 1983). These outcome-variable interactions seem especially apparent in cyclically reestablished (horizontally transmitted), chronic endosymbioses (Saffo, 1991b).

The outcome of some basically antagonistic associations can also be shifted by environmental factors. For instance, avian brood parasitism is ordinarily harmful to the host offspring. However, in circumstances favoring infection of host nests with botfly larvae, cowbird chicks can enhance their hosts' reproductive rate compared to that in cowbird-free nests; they do so by removing botfly larvae from their host nest mates (Smith, 1968).

Finally, the apparent distinction between net harm (parasitism) and net mutual benefit (mutualism) can be very small. The costs of mutualism to hosts and endosymbionts – in reproductive rate, energy, or diversion of nutrients – are sometimes very high, while, conversely, parasites do not always cause much harm. For instance, Gill and colleagues (Rennie, 1992) have found that newts infested with high concentrations of trypanosomes ($10^6$ parasites/ml blood) may show no increased mortality or decreased reproductive rate compared to uninfected newts. Even while they cause net harm to the host, parasites can benefit hosts in some ways. For example, the presence of *Plasmodium* and other parasites has been linked to suppression of auto-immune disease in infected mammals, including humans. Even more strikingly (Desowitz, 1981), laboratory mice infected with *Trypanosoma* spp. and *Trichinella spiralis* have higher body weights and longer average life spans than uninfected controls, possibly because the parasites provide thiamine, pantothenate and pyridoxine to their hosts.

"Symbiosis" – living together – is the right word to discuss *all* the above complex phenomena. "Living together" is the essence of the matter and the root of most of our questions. Using this larger definition of symbiosis facilitates investigations unprejudiced by preconceptions about outcomes. And, in encouraging us to see the many similarities between mutualistic and parasitic interactions, it also invigorates the conceptual underpinnings of symbiosis research.

But this outcome-independent perspective should not preclude the use of words like parasitism, commensalism, mutualistic symbiosis, and other outcome-dependent terms, when they are appropriate, to describe the dynamics of particular symbiotic interactions. In informal discussion, and occasionally in print, several colleagues – faced with the misuse of symbiosis as only mutualism, or dismayed by weak arguments about the selective effects of symbiosis on particular symbionts or hosts – occasionally have suggested that questions of outcome are undesirable or futile foci for symbiosis research. They dismiss discussions of ecological consequences, "costs and benefits," and effects on fitness or selective outcomes, as "impossible" to prove (Margulis, 1990, p. 674) or simply not important. But just as we restrict ourselves unduly by defining symbiosis *only* as mutualistic outcomes, so also do we constrict our field by barring questions about outcome from investigations of symbiotic interactions. The former perspective limits inquiry by suggesting that the evolutionary dynamics of symbiosis are already understood; the latter limits inquiry by suggesting that evolutionary questions cannot be solved or should not even be asked.

But questions of benefit *do* matter, because fitness matters. One need not indulge simplistic excesses of the "adaptationist programme" (Gould and Lewontin, 1979) to recognize that symbionts that harm their hosts are likely to spread through a host population at different rates, and possibly in different ways, than do those that benefit their hosts. By the same token, it is appropriate to investigate whether the long-term evolutionary dynamics of a symbiotic interaction are influenced by the effects of symbiosis on the fitness of both host and symbiont.

Even within a single taxon, measuring fitness is a difficult task. Measurement of fitness and related parameters (such as "benefit," "cost," "harm," and "reproductive success") is an even more daunting challenge for symbiotic associations, not only because they involve several taxa, but also because the interactions of symbiotic partners with each other and with the outside environment are complex and usually poorly understood. But because fitness is hard to measure does not mean that it is not worth measuring. Addressing such questions in any system requires sophisticated, multidisciplinary approaches, but it can be done (cf. Watt and Boggs, 1987; Watt, 1990). Such questions can be tackled in symbiosis research once the tools and perspectives of population genetics and evolutionary biology can be incorporated into studies of symbiotic interactions.

Inclusion of questions of evolutionary mechanisms will enhance not only symbiosis but also evolutionary biology itself. Particularly, symbiosis can offer evolutionary biology a new set of provocative and testable models for investigating coevolutionary questions. These models can help define ways in which variation in *interactions* between genomes – not just genomic variation *per se* – might affect evolutionary change, and they can expand the conceptual and ecological scope of questions about the relative roles that antagonistic and mutualistic interspecies interactions play in structuring communities.

The study of symbiosis is a field virtually defined by connections and interactions, not only between species but also between investigative disciplines. Probing the full biological significance of intimate interactions between species requires new research approaches drawn from the experimental and conceptual tools of several fields, including modern evolutionary biology and ecology, as well as physiological, cellular, and molecular biology. The effort will demand conceptual clarity and experimental patience. But it will not only invigorate the study of symbiosis; it will also enlarge the impact of symbiosis research on all of biology.

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