CHAPTER 1

The Significance of Symbiosis

INDIVIDUALS OF DIFFERENT SPECIES form persistent associations from
which they all benefit. These relationships are symbioses. The core pur-
pose of this book is to assess the biological significance of symbioses
and to investigate the processes by which symbioses are formed and
persist in both evolutionary and ecological time. Symbioses are biologi-
cally important because they are widespread and dominate the biota
of many habitats. I address this aspect of the biological significance
of symbiosis later in this chapter. For the present, I suggest that any
doubting readers should "look out of the window" and list every or-
ganism they can see. I can guarantee that most, probably all, organisms
on the list are a product of symbiosis. The prevalence of symbioses is
not, however, the only reason why symbioses should be important to
biologists. An additional reason is that symbiosis challenges two widely
accepted tenets of biology: the universality of descent with modifica-
tion in evolution, and the primacy of antagonism in interactions among
organisms. I will start by explaining these challenges.

1.1 SYMBIOSIS AS A SOURCE OF NOVEL TRAITS

The core expectations of evolution by descent with modification are
that morphological, physiological, and other traits of an organism are
derived from traits in the ancestors of the organism, and that changes
in these traits can be described by multiple, small steps with each inter-
mediate condition viable. Most traits can be explained in this way, but
there is unambiguous evidence that some traits of great evolutionary
and ecological importance have been gained laterally from different,
often phylogenetically distant, taxa. Some laterally acquired traits are
novel for the recipient organism and they can be evolutionary innova-
tions, i.e., "newly acquired structures or properties which permit the
assumption of a new function" (Mayr 1960, p. 351)].

There are two routes for the lateral acquisition of traits: symbiosis
and horizontal gene transfer. Entire organisms are acquired by sym-
biosis and so the traits gained can be genetically, biochemically, and
even behaviorally more complex than those obtained by horizontal

transfer of isolated genes. Two very different types of symbiosis illustrate this point. The eukaryotic cells that acquired the cyanobacterial ancestor of plastids gained the capacity for oxygenic photosynthesis as a single package, including many correctly expressed genes, the integrated molecular and cellular machinery for the assembly of multi-component photosystems in photosynthetic membranes, and the enzymatic machinery for carbon fixation. Similarly, an *Acacia* tree that is protected from herbivores by a resident colony of ants has acquired a morphologically and behaviorally complex defense capable of responding appropriately to herbivore attacks of variable magnitude and type.

The appreciation that descent with modification is an inadequate evolutionary explanation does not mean that symbioses contradict current understanding of evolutionary processes. Symbioses are subject to natural selection and, contrary to some claims (e.g., Ryan 2003), they have no discernible dynamic independent of natural selection.

1.2 Symbiosis as a Type of Biological Alliance

Interactions among organisms are routinely portrayed as principally antagonistic, dominated by competition, predation, and parasitism. The history of life has even been described as "a four billion year war" (Marjerus et al. 1996). This perspective is not wrong, but it is incomplete. Organisms have repeatedly responded to antagonists (predators, competitors, etc.) and abiotic stresses such as low nutrient availability by forming alliances, i.e., interactions with other organisms, resulting in enhanced fitness and ecological success of all the participants. As with alliances among people, political parties, and nation states, the persistence of many biological alliances depends on the continued presence of the antagonist, and the benefit gained from the alliance can vary with the identity of the participants and environmental conditions. I return to this issue in section 1.3.

Most alliances are founded on reciprocity, that it is advantageous to help another organism only if the favor is returned. In a two-organism system, reciprocity requires that each of the organisms places a higher value on what it receives (benefit) than what it gives (cost) (figure 1-1a). For example, the relationship between mycorrhizal fungi and plant roots is underpinned by the transfer of photosynthetic sugars from plant to fungus, and of phosphate in the reverse direction. Photosynthetic carbon is cheap for the plant to produce but a critical resource for the fungus, which cannot utilize the polymeric carbon sources in soil. Inorganic phosphate is relatively immobile in soils, and is acquired more readily by the fine, branching fungal hyphae than by the relatively

(a)

$$X \quad \begin{array}{c} -10 \longrightarrow +30 \\ +30 \longleftarrow -10 \end{array} \quad Y$$

net	+20		+20

NUMBER OF SPECIES

(b)

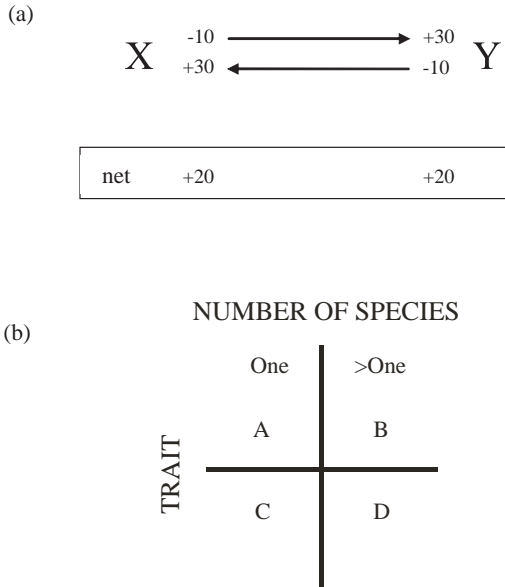|	One	>One
TRAIT	A	B
	C	D

Figure 1-1   Biological alliances. (a) Most alliances are underpinned by reciprocity between the two participating organisms, X and Y. Each organism provides a service at cost of 10 arbitrary units and receives a benefit of 30 units, yielding net benefit of 20 units. (b) Alliances are classified according to the number of species and traits involved. Examples of each type of alliance include (A) roosting bats huddling together, sharing their uniform trait of heat production; (B) mixed-species flocks of passerine birds foraging for food in winter; (C) bartering of goods between humans; and (D) consortia of multiple microbial species that, through their complementary metabolic capabilities, degrade otherwise recalcitrant organic compounds. [Figure 1-1a modified from figure 1 of Douglas (2008)]

massive plant roots with short, nonbranching root hairs. The one situation where reciprocity as depicted in figure 1-1a does not apply is between closely related organisms. Here, kin selection is important: genotypes that help relatives (i.e., individuals with many genes in common) increase in frequency and are at a selective advantage over genotypes that do not help.

Many organisms in alliances display cooperative traits, i.e., traits that are advantageous to another organism (the recipient) and that have evolved because of their beneficial effect on the recipient. The *Acacia* trees introduced in section 1.1 display cooperative traits that benefit their resident ants: swollen, hollow thorns which provide domatia (nest sites) for the ants, and extrafloral nectar and highly nutritious antbodies on which the ants feed (figure 1-2). In return, various behavioral
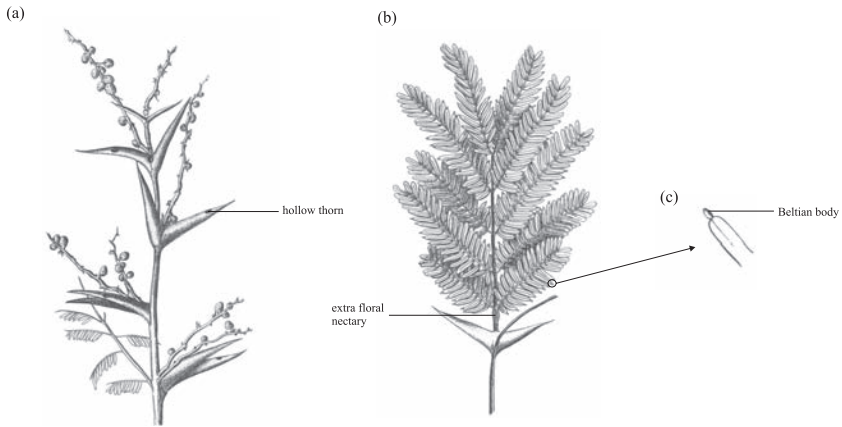
(a)　　　　　　　　　　　　　　(b)

Figure 1-2   Adaptations of *Acacia sphaerocephala* for symbiosis with protective ants of the genus *Pseudomyrmex*. (a) Hollow thorns that provide domatia (nest sites) for ants. (b) Extrafloral nectary at base of leaf. (c) Lipid-rich ant-body at tip of leaflet. [Reproduced from figure 4-18 of E. O. Wilson (1971) *The Insect Societies*. Harvard University Press]

traits of the ants are advantageous to the plant, including patroling the plant to protect against herbivores and removing fungal spores at the breakpoint of the ant-bodies to prevent fungal infection of the plant. As a contrary example, the food in the gut of an animal infected by a tapeworm is not a cooperative trait because, although the tapeworm benefits from the food, animals have not evolved the habit of eating for the benefit of tapeworms.

Alliances can be classified according to whether they involve one or multiple species displaying the same or different traits, and this two-way classification generates four categories (figure 1-1b). The focus of this book is category D in figure 1-1b, alliances between different species with different traits. These alliances are also known as mutualisms, which are formally defined as relationships from which all participants derive benefit. In this book, I consider symbioses as a type of mutualism, specifically mutualisms in which the participants are in persistent contact.

This brings me to the most frustrating difficulty in the field of symbiosis—the lack of a single universally accepted definition. Disagreement over definitions has led to disputes about which relationships are symbioses and, consequently, a lack of consensus about the common features of symbiotic systems. Two alternative definitions of symbiosis, neither fully satisfactory, have dominated the literature for many decades: "symbiosis as any association" and "symbiosis as a persistent mu-

tualism." Here, I digress briefly from the core topic of this chapter, the significance of symbioses, to address the thorny problem of definitions.

1.3 Definitions of Symbiosis

1.3.1 Symbiosis As Any Association

The term symbiosis was coined originally by Anton de Bary in 1879 to mean **any association between different species**, with the implication that the organisms are in persistent contact but that the relationship need not be advantageous to all the participants. De Bary explicitly included pathogenic and parasitic associations as examples of symbioses. Many symbiosis researchers use this definition and, without doubt, some colleagues steeped in the symbiosis literature will have objected to the opening two sentences of this book.

One key advantage of the definition of de Bary is that it promotes a broad context for research into symbioses. It acts as a reminder that it is important to investigate both the costs and the benefits to an organism of entering into a symbiosis (see figure 1-1a); and it is reasonable to expect some of the processes underlying relationships that are classified as mutualistic and antagonistic to be similar. For example, just as the persistence of certain antagonistic interactions depends on one organism failing to recognize the antagonist as a foreign organism, so some organisms may be accepted into symbioses because they fail to trigger the defense systems of their partner and not because they are positively recognized as mutualists.

Nevertheless, the definition of de Bary has two serious shortcomings. First and very importantly, the definition is not accepted by most general biologists or nonbiologists today, and so fails to communicate effectively. Most people do not describe the current malaria pandemic or the potato blight that caused the Irish famine of the 1840s as examples of symbiosis. Second, there are few principles generally applicable to symbioses, as defined by de Bary, but inapplicable to other biological systems. As a result, the "symbiosis as any association" definition is something of a catch-all category. Although this definition does promote further enquiry and insight into symbioses, any insights obtained are unlikely to be common to all symbioses defined in this way.

1.3.2 Symbiosis As a Persistent Mutualism

The definition of symbiosis widely accepted among both general biologists and the lexicographers who prepare English dictionaries is **an association between different species from which all participating**

organisms benefit. I subscribe to this definition even though it is not without difficulties.

The "symbiosis as a persistent mutualism" definition requires a formal assessment of the benefit derived by the organisms in the association. The standard approach to identify benefit is to compare an organism's performance (survival, growth, reproductive output, etc.) in the presence and absence of its partner. If the organism performs better with the partner, it benefits from the relationship and if it performs better in isolation, then it is harmed by the association. Although the methodology appears straightforward, it is unsuitable for many associations.

There are two types of problem. First, for some associations, there are formidable practical difficulties. Consider the deep-sea symbioses, such as the chemosynthetic bacteria in the tissues of pogonophoran worms at hydrothermal vents and the luminescent bacteria in the lure of deep-sea angler fish. It is difficult to envisage how bacteria-free pogonophorans and angler fish could be generated experimentally and how the performance of the bacteria-free individuals could be monitored reliably in habitats so inaccessible to humans.

The second and more fundamental problem is the variability of real associations, such that benefit is not a fixed trait of some relationships but varies, especially with environmental circumstance. To illustrate this issue, let us consider hermit crabs of the genus *Pagurus*. Hermit crabs live in empty shells of gastropods that are often colonized by benthic cnidarians, such as sea anemones and hydroids. Generally, the cnidarian benefits from settling onto a shell inhabited by a hermit crab because it has ready access to scraps of food produced when the crab eats and because the mobility of the crab in its shell introduces the cnidarian to different habitats that may increase food availability and reduce the risk of burial in sediment. The hermit crab is widely believed to benefit because the cnidarian can act as a bodyguard, protecting it from predators by firing deterrent and often toxic nematocysts from its tentacles. For example, the sea anemone *Calliactis parasitica* effectively deters octopus predation of *Pagurus* species (Ross 1971). The protective value of hydroids is, however, variable. Predation rates of hermit crabs can be elevated or depressed by hydroids, depending on the predator species, and the underlying factors are complex. For example, Buckley and Ebersole (1994) investigated *Pagurus longicarpus* inhabiting shells colonized by the hydroid *Hydractinia* spp. and subject to attack by the blue crab *Callinectes sapidus*. In aquarium trials, hermit crabs in shells bearing hydroids were significantly more likely than those in hydroid-free shells to be eaten by blue crabs (figure 1-3a). The difference arose because it took longer for the blue crabs to crush the hydroid-free shells, often giving the resident hermit crab time to escape. Further analysis of Buckley
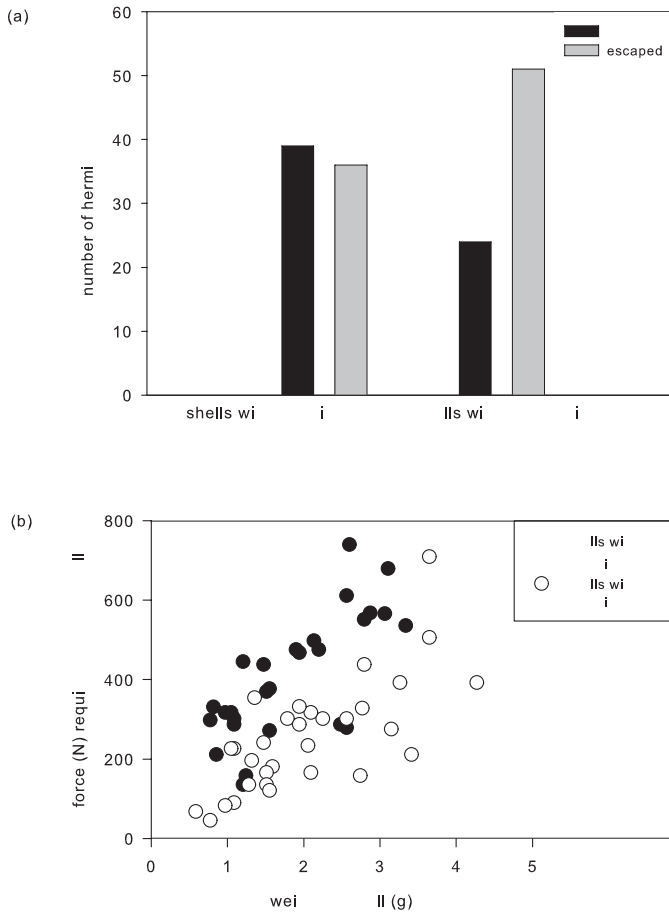
Figure 1-3   Impact of the association with hydroids on the susceptibility of the hermit crab *Pagurus longicarpus* to predation by *Callinectes sapidus*. (a) Occupation of hydroid-bearing shells significantly depressed the frequency of *P. longicarpus* that escaped from *C. sapidus* attack ($\chi^2 = 6.158$, $p < 0.05$). (b) Mechanical strength of shells inhabited by *P. longicarpus*, either colonized by hydroids (open symbols) or lacking hydroids (closed symbols). [Redrawn from data in Buckley and Ebersole (1994)]

and Ebersole (1994) revealed that shells bearing the hydroids were more likely than hydroid-free shells to be colonized by burrowing polychaete worms (*Polydora* species), and the tunnels of these worms significantly depressed the mechanical strength of the shells (figure 1-3b).

This complex multiway interaction between hermit crabs, hydroids, burrowing polychaete worms, and the predatory blue crabs raises a

question: why do the hermit crabs ever use shells bearing the hydroids? One possible explanation is that the hydroids may protect the shell from colonization by large sessile animals, such as slipper limpets or bivalves, which would make the shell very heavy and unbalanced for the hermit crab. Based on these considerations, do hermit crabs benefit from associating with hydroids? The answer is that "it all depends"—on the incidence of burrowing worms, the identity and abundance of predators, and the incidence of settling limpets. All of these factors are anticipated to vary with site and season.

As the hermit crab association illustrates, many real associations are complex and variable. This does not undermine the definition of symbiosis as a mutually beneficial association, provided the definition refers to the interaction between the organisms, not the organisms themselves. An organism that enters into a mutually beneficial relationship is symbiotic in the context of that relationship; but if, through a change in environmental circumstance or other factors, the relationship becomes antagonistic, then it is no longer a symbiosis. In this way, associations with variable outcomes for the participating organisms are transformed from a problem for the definition of symbiosis to an opportunity to explore the factors that affect the incidence of symbiotic (i.e., mutually beneficial) interactions.

The fluidity of some biological interactions is particularly apparent for some organisms that were originally identified as parasites but are now realized to be harmless or even advantageous to partners under certain circumstances. For example, the fungus *Colletotrichum magna* was first identified as a virulent pathogen of certain plant species (figure 1-4a) but its impact on plant growth was subsequently found to depend on the plant species and even cultivar, such that the fungal infection promotes the growth of some plants (figure 1-4b) and can provide protection from drought or pathogens (Redman et al. 2001). Similarly, the bacterium *Helicobacter pylori* in the human stomach is best known as the cause of ulcers and gastric cancer in adults, especially older people, but in children and young people, *H. pylori* is harmless and may even be beneficial, providing protection against diarrhoea and asthma (Blaser and Atherton 2004). In the same way, organisms which are usually harmless or beneficial can be deleterious to their partners under certain circumstances. The tiny mite *Demodex folliculorum*, <0.5 mm long, is a commensal of humans. It lives exclusively in hair follicles, including the roots of eyelashes, and reproduces sexually with a generation time of 2–3 weeks. It occurs in most adults and many children, and it is generally harmless. Occasionally, however, the infections are heavy and deleterious, causing itching and swelling. Similarly, the arbuscular mycorrhizal fungi are usually beneficial symbionts of plant roots but they can,
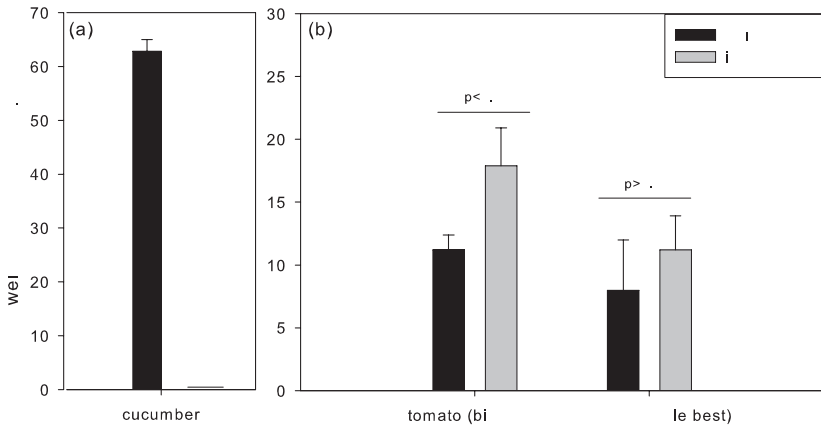
Figure 1-4 Impact of the fungus *Colletotrichum magna* (strain L2.5) on plant growth: (a) pathogenic on cucumber; (b) beneficial and apparently neutral for two tomato cultivars. s.e. indicates standard error. [Drawn from data in Redman et al. (2001)]

occasionally, be harmful to the plants. For example, *Glomus macrocarpum* causes a stunting disease of tobacco plants (Modjo and Hendrix 1986).

I favor the definition of symbiosis as a persistent mutualism because its scope provides a meaningful biological framework for one of the key questions explored in this book: How do mutually beneficial interactions between different species evolve and persist?

1.3.3 Duration of Contact

For how long should the partners in an interaction be in contact for the relationship to be called a symbiosis? It is widely, but not unanimously, accepted that the answer is: at least a substantial proportion of the lifespan of the interacting organisms. It has only rarely been argued that the predation of gazelles by lions, the rapid death of people infected by the Ebola virus, and the pollination of plants by fleeting visitations of foraging butterflies are symbioses (e.g., Lewis 1985).

Some examples bring into focus the problem posed by the definition of symbiosis as a persistent association. Let us consider first the relationship between humans and honeyguide birds, two species that share a taste for honey. The bird cannot access the honey from most bee colonies, but appears to have a better knowledge than people of the location of the colonies. In their study of the Boran people in Kenya, Isack and Reyer (1989) found that the honeyguide leads people to bee nests by calling and flying short distances ever closer to the nest, and

then changes its call and flight pattern in the immediate vicinity of the nest. The people open up the nest to harvest the honey, and the bird feeds on the honeycomb fragments that are too small for the people to harvest. The participants in this relationship do not make contact and so the relationship is not a symbiosis.

At the other extreme of persistence are the vertically transmitted microorganisms in some animals, where contact persists beyond the lifespan of an individual host. The complement of intracellular bacteria in some insects is acquired exclusively from the mother insect, usually by transfer from the cells housing the bacteria to the ovaries and insertion into the unfertilized egg. Obligate vertical transmission can result in associations persisting continuously over long evolutionary timescales. As an example, there is good phylogenetic evidence that the bacterium *Buchnera aphidicola*, the vertically transmitted symbiont of aphids, has persisted through generations of its insect hosts for at least 160 million years (Moran et al. 1993); and the mitochondria have been transmitted vertically for up to 2000 million years (Embley and Martin 2006).

The difficulties for a definition of symbiosis as a persistent association arise for relationships with an intermediate duration of contact. This is illustrated by insect pollination of plants. For many plants, contact with the pollinator is brief, as little as a few seconds, while the insect collects nectar or pollen. As already considered, these interactions are not usually deemed to be symbioses. Among orchids, however, the duration of contact may be prolonged to minutes to hours, often with elaborate mechanisms to ensure pollen transfer to a specific location on the insect. This condition relates to the fact that the pollen grains of orchids are not separate but held in compact structures called pollinia, such that an orchid flower is dependent on a single insect for pollen transfer. An exceptional example is the orchid *Coryanthes*. As Barth (1991) describes, the complex *Coryanthes* flowers (figure 1-5) trap their pollinating bees, *Eulaema*, for long periods. The narrow base of the flower lip exudes a liquid scent, which the bee collects by scratching with its forelegs. It often slips off the lip, into the bucket below. The bucket contains a watery solution, exuded from the column of the flower, and the bee swims about in the water. The only exit is via a narrow hole at the apex of the lip, and it may take the bee half an hour or more to escape. If the bee is carrying pollinia from another flower, the pollinia are transferred to the stigma; and the pollinia from the current flower are transferred to the abdomen of the first bee to take this route through the flower. Even more persistent plant-pollinator contact is displayed by the plants with brood-site pollination, including the figs (*Ficus*) pollinated by agaonid wasps and *Yucca* species pollinated by moths. In these systems (discussed further in chapter 3, section 3.2.2), pollination is linked to insect
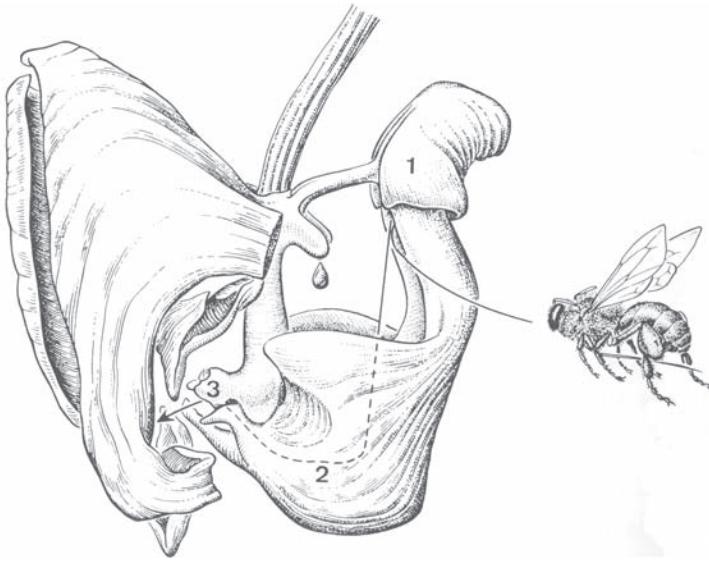
Figure 1-5   The flower of *Coryanthes* orchid. Arrows show the course of the pollinating insect. See text for details. [Redrawn from figure 7.27 of Barth (1991)]

deposition of an egg into some of the flower ovules. Seed set in the ovules bearing insect eggs is aborted and the insect offspring develops, to adulthood for the pollinators of *Ficus* and through larval development for the *Yucca* pollinators (which pupate in the soil).

A similar continuum in the duration of contact is displayed by the microbiota in animal guts. Members of the gut microbiota vary greatly in their persistence, from transients, entering and leaving the gut with the food, to residents, retained for much of the animal lifespan. A classic illustration is the study of *Escherichia coli* serotypes in a single human volunteer over 11 months. Of the 53 types identified, most persisted for one to a few days and just two types persisted for the full duration of the experiment (Caugant et al. 1981).

Among the *E. coli* types that vary in their persistence in the guts of humans and among the various pollination systems described above, there is no minimal residence time that can be used meaningfully as a criterion for symbiosis. In other words, it is biologically unrealistic to create a simple dichotomy based on duration of contact between relationships that are, and are not, symbioses. These issues have a bearing on the framework for this book. Although I will conform to the convention that relationships with no or fleeting physical contact are not symbioses, I will use these relationships as examples to illustrate and develop ideas that are relevant to symbioses.

Let us now return from the digression into definitions to the main purpose of this chapter: the significance of symbiosis. In the following section, I provide a brief primer on the evolutionary and ecological significance of some symbioses.

1.4   THE BIOLOGICAL SIGNIFICANCE OF SYMBIOSES

1.4.1   *Misunderstandings about the Significance of Symbioses*

The biological importance of symbioses is central to current understanding of these relationships. This opening sentence could not have been written throughout the greater part of the twentieth century, when mutually beneficial symbioses were treated as curiosities of nature that were ecologically unstable and evolutionarily transient (Sapp 1994). The ecological argument for the instability of symbioses was that, by Lotka-Volterra equations, mutually beneficial interactions lead to uncontrolled population increase while antagonistic interactions tend to stabilize populations (figure 1-6). The evolutionary argument was that genotypes which confer benefit on non-kin are at a selective disadvantage relative to selfish genotypes which provide no benefit. The implication is that symbioses fail in ecological time because they are too mutualistic and in evolutionary time because of the selection pressure to be less mutualistic. Both perspectives cannot be right and, in reality, both are wrong. The reasoning underlying each perspective is based on the erroneous assumption that symbioses are perfectly mutualistic. In reality, the partners in symbioses are often in conflict, but the conflict is managed and controlled. These issues are explored in chapter 3. Here, I consider the biological significance of symbioses in three respects: as a source of novel capabilities, in the evolution of eukaryotes, and as a determinant of the ecological success of some plants and animals.

1.4.2   *Symbiosis As a Source of Novel Capabilities*

For many symbioses, one organism provides a benefit that is different from any preexisting trait in its partner. As considered in section 1.1, such a benefit can be an evolutionary innovation. The novel capabilities gained in this way are very diverse but many can be classified as one of four functions: access to a novel metabolic capability, protection from antagonists (predators, pathogens, etc.), mobility (including dispersal), and agriculture. Table 1-1 provides some examples of symbioses and other mutualisms according to these functions.

For symbioses that involve reciprocal exchange of services, the benefits gained by the different partners can be functionally distinct or vary
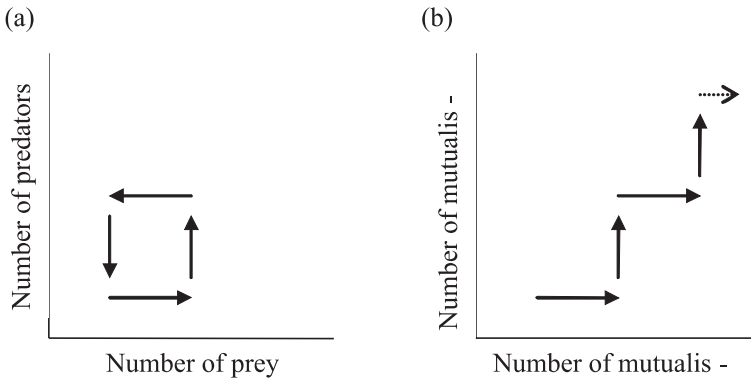
Figure 1-6   Projected population size of interacting organisms in (a) an antagonistic interaction such as a predator-prey relationship and (b) interaction between populations of two mutualists, here labeled as 1 and 2.

with circumstance. The *Acacia*-ant symbiosis illustrated in figure 1-2 involves the reciprocal exchange of food for protection as provided by the plant and ants, respectively. As considered earlier in this chapter (section 1.2), the mycorrhizal symbiosis between plant roots and fungi is primarily nutritional under most environmental conditions, with the plant gaining mineral nutrients from the fungus, and the fungus gaining photosynthetic sugars from the plant; but the interactions are not uniform. For example, the principal advantage of this symbiosis for natural populations of the plant *Vulpia ciliata* is protection from fungal pathogens (Newsham et al. 1995).

Animal behavior is central to the capabilities acquired by some symbiotic organisms. This applies particularly to animal-mediated dispersal, agriculture, and some instances of protection from predators (see table 1-1). Agriculture is of particular interest in this context. Agriculture can be defined as the cultivation of a different species and the consumption of a proportion of that organism or its products. It involves inoculating a suitable substratum with the cultivated organism, which is then tended to ensure its growth and protection from competitors and pathogens. Linked to the complex behavior required, farming has a very restricted distribution, largely limited to humans, ants, termites, and beetles. Fungi are farmed by attine ants, termites of the subfamily Macrotermitinae, and various beetles, including the ambrosia beetles (Platypodinae and some Scolytinae) (Wilding et al. 1989; Farrell et al. 2001). Some symbioses between ants and hemipteran insects also have the traits of agriculture, with the hemipterans farmed by ants for their honeydew (see chapter 5, section 5.2.1).

TABLE 1-1
Survey of Benefits Gained from Symbioses and Nonpersistent Mutualisms

Relationship	Examples
(a) Access to metabolic capability	
Inorganic carbon fixation	Cyanobacteria-derived plastids in algae and plants Algae/cyanobacteria in lichenized fungi, protists, and animals Mycorrhizal and endophytic fungi associated with plants Chemosynthetic bacteria in animals
Aerobic respiration	Bacteria-derived mitochondria in eukaryotes
Nitrogen fixation	Bacteria (e.g., rhizobia, *Frankia*, cyanobacteria) in plants Cyanobacteria in lichenized fungi Bacteria in a few insects (e.g., termites)
Cellulose degradation	Bacteria in vertebrates Protists in a few insects (e.g., "lower" termites, woodroaches) Fungi in Macrotermitidae
Nutrient biosynthesis (e.g., vitamins, essential amino acids)	Bacteria or fungi in animals, especially insects, and in protists
Degradation of toxins	Bacteria in animal guts
Toxin production	Bacteria in animals (e.g., insects, bryozoans, sponges) Fungi in plants
Hydrogen consumption	Methanogenic bacteria in anaerobic protists
Luminescence	Bacteria in some fish and squid
(b) Protection from antagonists	
Protection from herbivores	Ants associated with plants remove or deter herbivores
Protection from predators	Ants deter predators/parasitoids of hemipteran insects and lycaenids Sea anemone/hydroids protect hermit crabs
Removal of ectoparasites	From client fish by cleaner fish; from ungulates (e.g., gazelle) by pecking birds
Protection from pathogens	Microbiota in animal guts and plant rhizosphere (immediate environs of roots)

TABLE 1-1 (*cont.*)

Relationship	Examples
(c) Dispersal/mobility	
Biotic pollination	Male gamete (pollen) transported to stigma of plants by insects, birds, mammals
Biotic seed dispersal[1]	Seeds transported away from parent plant by birds, mammals, ants
Ant-tended hemipterans	Transport to suitable feeding sites on host plants
(d) Agriculture[2]	Cultivation of fungi by bark and ambrosia beetles, termites, and attinine ants Cultivation of hemipteran insects by some ants

[1] This category refers to seed dispersal by animals that forage for (a) seeds but fail to eat them all or (b) plant products associated with seeds, e.g., fruits consumed by various birds and mammals, elaiosomes (lipid-rich structures) consumed by ants. Seeds that become attached to the surface of animals (e.g., hooked seeds on the fur of mammals) are excluded because the interaction is passive and functionally comparable to wind dispersal (Herrera 2002).

[2] Defined as the cultivation of another organism and consumption of the cultivated organism or its products.

In many symbioses, the contrasting traits of the participating organisms are underpinned by a difference in their metabolic capabilities. The capabilities are complementary, with two or more organisms contributing different elements of a common metabolic pathway, resulting in the net synthesis or degradation of certain compounds. For example, bacteria of the genera *Clavibacter* and *Pseudomonas* can degrade the toxic herbicide atrazine to carbon dioxide and ammonia when cultured together but not individually (De Souza et al. 1998) because they have complementary metabolic capabilities (figure 1-7). These bacteria comprise a consortium, meaning that the interacting bacteria perform more complex capabilities than either displays on its own. In this particular system, the collective capabilities of the consortium are enhanced by cross-feeding of metabolites between the partners.

In other symbioses, the metabolic capabilities of the organisms are unequal, with one organism gaining access to capabilities present only in its partners. These associations generally involve eukaryotes, which, as a group, are metabolically impoverished relative to bacteria. The lineage that gave rise to the eukaryotes lacked the capacity for aerobic respiration, photosynthesis, and nitrogen fixation; many eukaryotes that
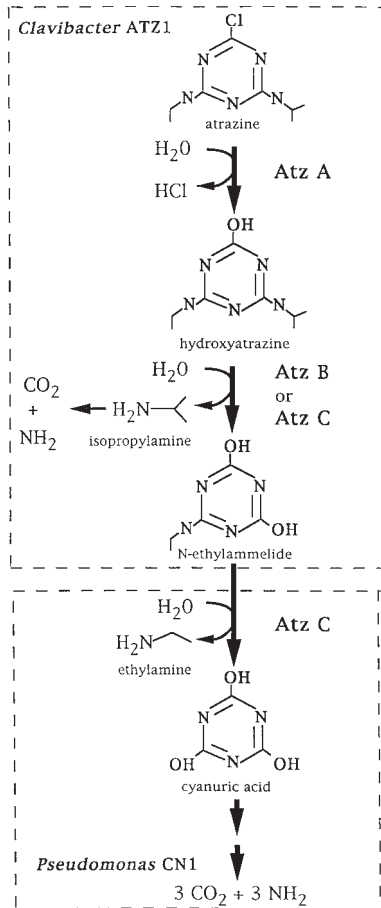
Figure 1-7 Degradation of the *s*-triazine herbicide atrazine to carbon dioxide and ammonia by a consortium of *Clavibacter* spp. and *Pseudomonas* spp. [Reproduced from figure 6 of de Souza et al. (1998) with permission from the American Society for Microbiology]

feed holozoically, including all animals, additionally cannot synthesize 9 of the 20 amino acids that make up protein (the essential amino acids) and various coenzymes essential to the function of enzymes central to metabolism (vitamins, such as biotin); vertebrates additionally lack the capacity to degrade the cellulose and related polysaccharides that account for 90% or more of plant material; and arthropods cannot synthesize sterols, including cholesterol which is an essential component of eukaryotic membranes. On multiple evolutionary occasions, eukaryotes have acquired these metabolic capabilities by entering into

relationships with microorganisms. For example, various plants gain access to nitrogen fixation by associating with nitrogen-fixing bacteria; some animals, such as corals, and the lichen fungi gain photosynthesis by associating with algae; and other animals derive specific nutrients, including essential amino acids and B vitamins, from symbiotic bacteria. The services provided in these symbioses are nutritional.

Some organisms benefit from symbioses with partners which can synthesize secondary compounds that deter or are toxic to natural enemies. A well-known example among plants is the protection from herbivores gained by many grasses from alkaloid-producing endophytic fungi in their tissues (Schardl 1996; see also chapter 2, section 2.2.3). The incidence of these symbioses between animals and microorganisms is uncertain, and only a few examples have been explored in detail. They include the production of compounds known as bryostatins by the bacterium *Endobugula sertula* in the marine bryozoan *Bugula neritina* (Davidson et al. 2001) and the polyketide pederin by uncultured pseudomonads in both beetles of the genus *Pederus* and sponges, including *Theonella swinhoei* (Piel 2002; Piel et al. 2004). There is evidence, direct for *Pederus* and circumstantial for the bryozoans and sponges, that these compounds protect the animals from predators (Kellner and Dettner 1996; McGovern and Hellberg 2003).

The complexity of some symbioses involving microorganisms with a defensive function is illustrated by two highly specific associations between insects and streptomycete bacteria. One is the relationship between beewolves (bees of the family Crabanidae) and Candidatus *Streptomyces philantii* located in glands on the antennae of the adult beewolf (Kaltenpoth et al. 2005). The adult female transfers an inoculum of bacteria to the brood cell, in which eggs are deposited. In due course, the larval offspring collect the bacteria from the brood cell and apply them to the silk of their cocoon within which they subsequently pupate in the soil. Behavioral and bioassay data indicate that the streptomycete produces antibiotics which protect the pupa from fungal attack. Streptomycetes are also crucial for leaf-cutting ants. These ants maintain fungal gardens of a specific basidiomycete fungus on which the ants feed. The fungus is susceptible to a specific fungal pathogen *Escovopsis*, and *Escovopsis* infections are kept in check by antibiotics produced by streptomycete associated with the ventral surface of the ants (Currie et al. 2003).

Bioactive compounds synthesized by a symbiotic partner can also be exploited in offense, as is illustrated by antlions, predatory larvae of the insect family Myrmeleontidae within the order Neuroptera (the lacewings). Antlions subdue their prey by injecting toxic saliva via their piercing mouthparts. The salivary toxin which paralyzes the prey of *Myrmeleon bore* larvae is a protein, GroEL, produced by the bacterial

symbiont *Enterobacter aerogenes* (Yoshida et al. 2001). GroEL is a well-known bacterial protein that functions as a chaperonin, i.e. it promotes the correct folding of proteins. It appears that the GroEL of *E. aerogenes* has adopted a second function as a toxin while retaining its chaperonin function. Four amino acid residues have been identified as critical to the toxicity of the protein; they are absent from the GroEL of other bacteria, including *E. coli* (the *E. coli* GroEL is not toxic). The mode of action of the GroEL from the antlion symbiont is not known, but it appears to be relatively specific causing paralysis of other insects, including cockroaches, but not of mice. How the antlion avoids the toxic effects of the protein is also unknown.

Some microorganisms protect plants and animals from toxic organic compounds and metals in the environment. One of the most remarkable examples relates to the potent neurotoxin methylmercury, the pollutant which caused large-scale poisoning of the human population of Minamata, Japan in the 1950s. Methylmercury is absorbed very efficiently across the gut wall of animals because it forms a complex with the amino acid cysteine that mimics another amino acid, methionine, resulting in its transport throughout the body (Clarkson et al. 2003). Bacteria in the gut of mammals can degrade methylmercury by de-methylating it to elemental mercury and mercuric ions, both of which are eliminated via the feces (Rowland 1999). This reaction in the symbiotic bacteria has provided people with a degree of protection against methylmercury contamination of foods.

1.4.3   Symbiosis and the Biology of Eukaryotes

The eukaryotic condition is fundamentally symbiotic. The basis of this statement is that all eukaryotes either bear mitochondria or are derived from mitochondriate ancestors; and mitochondria have evolved from symbiotic bacteria. The evidence for a symbiotic origin of mitochondria is overwhelming. Mitochondria are produced exclusively by division of preexisting mitochondria, i.e., eukaryotic cells cannot generate mitochondria *de novo*, and virtually all mitochondria have their own genome including genes of sequence allied to those of α-proteobacteria, specifically rickettsias (Gray et al. 1999). Certain anaerobic protists including the diplomonads, metamonads, and microsporidians have proven to be crucial to our understanding of the centrality of symbiosis to eukaryotes. These protists bear no structures readily identifiable with mitochondria but, where studied, they have genes of sequence allied unambiguously to mitochondrion-derived genes. The interpretation that these organisms have mitochondriate ancestors is supported by careful cytological analysis revealing tiny membrane-bound organ-

elles, known as mitosomes, with the characteristics of relict mitochondria (e.g., Tovar et al. 2003).

The eukaryote-mitochondrial relationship probably had a single evolutionary origin at least 1.45 billion and perhaps 2 billion years ago (Embley and Martin 2006), meaning that all modern eukaryotes have evolved in the context of a long-standing intimate symbiosis with a foreign organism in their cytoplasm. The implications are considerable, as can be illustrated by programmed cell death in eukaryotes. An essential early step in the commitment of eukaryotic cells to die is signal exchange between the cytoplasm and the mitochondrion, resulting in the release of the mitochondrial protein cytochrome c from the mitochondrial matrix to the cytoplasm. Why should an organelle with primary function in aerobic metabolism be central to cell suicide? One possibility is that programmed cell death is an evolutionary modification of antagonistic interactions between the eukaryotic nucleocytoplasm and the bacterial ancestor of mitochondria. It is not suggested that programmed cell death is an expression of virulence in modern mitochondria, but that the central role of mitochondria in programmed cell death may have evolved from such an interaction. I consider this interaction further in the context of the evolution of mitochondria in chapter 3, section 3.6.3.

It is widely accepted that the selective advantage to the eukaryote of associating with the bacterial ancestor of mitochondria was access to the bacterial trait of aerobic respiration. The ancestral eukaryotes also apparently could not fix inorganic carbon from CO_2 or nitrogen from elemental nitrogen, N_2. Various eukaryotic lineages have repeatedly acquired these latter capabilities by symbiosis with bacteria possessing these capabilities. The plastids/chloroplasts of all photosynthetic eukaryotes (the plants and algae) are derived ultimately from symbiotic cyanobacteria capable of oxygenic photosynthesis. There are various symbioses between eukaryotes and nitrogen-fixing bacteria (Kneip et al. 2007), but we have no entirely satisfactory explanation for the apparent absence of nitrogen-fixing organelles in eukaryotes (see chapter 3, section 3.6.5).

1.4.4 Symbiosis and the Ecological Significance of Some Plants and Animals

Plants and animals live in a microbial world. Their surfaces are colonized by microorganisms (bacteria and protists) from which they generally derive no substantial harm. Some plants and animals, however, live in specific and coevolved relationships with particular microorganisms, and these associations have profound impacts on the ecology and

evolution of the taxa involved and, in some instances, also on entire
ecosystems. In particular, animal or plant symbioses with microorgan-
isms dominate most terrestrial landscapes, certain coastal environments
and the immediate environs of deep-sea hydrothermal vents.

The roots of more than 75% of plant taxa are susceptible to infec-
tion by mycorrhizal fungi (Newman and Reddell 1987) which gener-
ally promote plant mineral nutrition. Molecular and paleontological
data suggest that the association with one type of mycorrhizal fungi,
the arbuscular mycorrhizal fungi, is very ancient, probably evolving
ca. 400 million years ago at the time of the origin of land plants (Simon
et al. 1993). It has been argued that the symbiosis and the resultant en-
hanced capacity of early plants to acquire nutrients from the substra-
tum was a prerequisite for the evolutionary transition of plants from
aquatic to terrestrial habitats. Furthermore, these fungi produce a gly-
coprotein known as glomalin which can account for up to 5% of soil
carbon and nitrogen and promotes soil structure (Rillig 2004; Treseder
and Turner 2007). The implication is that, if mycorrhizal associations
had not evolved, then terrestrial landscapes would probably have been
dominated by microbial mats and crusts, especially of cyanobacteria.
Certainly, mycorrhizal infection is the norm in the vegetation in most
habitats today, including tropical rainforests, temperate and boreal for-
ests, savannah, and temperate grasslands (Treseder and Cross 2006).
One important type of vegetation that is not founded on mycorrhizas is
land used for annual crop production, where plowing and related prac-
tices generate a highly disturbed soil environment in which mycorrhizal
fungal networks cannot establish fully. This is one factor contributing
to the requirement of conventional crop production for high nutrient
inputs.

Wave-resistant calcareous reefs are a characteristic feature of many
shallow, clear waters at low latitudes (<ca. 35°). Although these reefs
account for just 2% of the area of coastal waters, they are of immense
ecological and economic importance. They are renowned as ecosystems
of high biodiversity and productivity, and they support fishing and
tourism industries crucial to the economy of many countries, as well as
providing coastal defense against storms (Cesar et al. 2003). The reefs
are generated predominantly from the skeletons of scleractinian cor-
als bearing dinoflagellate microalgae of the genus *Symbiodinium* (also
known as zooxanthellae) in their tissues; and there is strong experi-
mental evidence that coral skeletogenesis by shallow-water corals is
promoted by the photosynthetic activity of the zooxanthellae (Moya
et al. 2006). The coral-zooxanthella symbiosis is, thus, the architectural
foundation of shallow-water coral reef ecosystems. Furthermore, there
is evidence that reef building by scleractinian corals in shallow waters

depended on the prior evolution of the algal symbiosis. This issue is considered further in chapter 5 (section 5.2.1).

The importance of microbial symbioses in shaping ecological communities is also illustrated by the fauna associated with deep-sea hydrothermal vents, where hot waters enriched with reduced inorganic compounds are released into the water column at areas of sea floor spreading. One would expect such habitats to be dominated by microorganisms, especially chemoautotrophic bacteria which can harness the energy generated by oxidation of reduced inorganic compounds to carbon dioxide fixation. Most hydrothermal vents, however, are also richly colonized by a diverse invertebrate fauna, in some locations including vestimentiferan tube-worms up to 2 m long and large bivalve mollusks. The basis of this exceptional fauna is symbiosis: the animals derive fixed carbon compounds from chemoautotrophic bacteria in their tissues (Van Dover 2000). These communities are unique in their independence from solar energy. They could persist for millenia in the absence of the sun (but not indefinitely because they require oxygen, derived ultimately from oxygenic photosynthesis). Taxonomically allied worms and bivalves also occur in marine sediments, hydrocarbon seeps, and whalefalls, i.e., the decaying carcasses of whales on the sea bottom (Van Dover 2000; Baco and Smith 2003). Symbiosis with chemoautotrophs has expanded the metabolic repertoire of these animals, enabling them to exploit habitats that would otherwise be available only to microorganisms.

In addition to the many symbioses with microorganisms, a wide diversity of animals and plants associate with other animals, e.g., mites and ants with plants; shrimps, crabs, and fish with corals and sea anemones. These symbioses have traditionally been treated as ecologically trivial but useful model systems to study the behavioral and morphological consequences of coevolutionary processes and biological specialization. Recent research on both some marine relationships and ant associations with plants and hemipteran insects suggests that these associations are of far greater ecological significance than traditionally believed. In particular, some have substantial impacts on the wider community structure, including the promotion of species diversity (e.g., Heil and McKey 2003; Hay et al. 2004).

1.5 The Structure of This Book

In this chapter, I have introduced and illustrated two key points. First, we live in a symbiosis-rich world, in which the symbiotic habit is widespread and abundant. Second, symbioses contribute to the real

complexity and variability in biotic interactions. In particular, the prevalence of symbioses demonstrates that the natural world is not driven exclusively by antagonistic interactions; and the acquisition of novel traits by symbiosis is an important exception to the generality that evolutionary change is mediated by multiple, sequential mutations, each with a small phenotypic effect. Altogether, symbiosis is a biological phenomenon of first-order importance.

As stated at the beginning of this chapter, the central purpose of this book is to explore the symbiotic habit, including how symbioses are formed and persist in both evolutionary and physiological time. Symbioses pose genuine biological problems. As the many twentieth-century biologists who regarded symbioses as trivial would argue, symbiosis appears to be improbable because the benefits that symbiotic organisms confer on their partners are often costly to provide, and the participants often compete for a common resource. How is it that, despite these conflicts, symbioses are prevalent and persistent? The answer comes in three parts, explored in chapters 2–4.

In chapter 2, "The Evolutionary Origins and Fates of Organisms in Symbiosis," I consider the evolutionary relationships between symbiotic organisms and organisms with different lifestyles. It is widely assumed, especially among biologists modeling the evolution of co-operation and symbiosis (e.g., Johnstone and Bshary, 2002; Hauert et al., 2006; Traulsen and Novak 2006; Taylor et al. 2007) that symbioses have evolved from antagonistic relationships and are prone to revert to antagonism. The review of the evolutionary history of symbioses in chapter 2 yields a very different picture. Although evolutionary transitions between antagonistic and mutualistic relationships certainly have occurred, the evolutionary origins of symbioses are diverse, and many real symbioses are derived from casual relationships or involve mutualists derived from different symbioses.

Whatever the evolutionary origin of symbioses, their persistence implies that conflicts among the partners do not necessarily lead to symbiosis breakdown within the lifespan of an individual organism or over short evolutionary timescales. In chapter 3, "Conflict and Conflict Resolution," I review the incidence of conflict and some of the routes by which conflict can be managed. Potentially widespread mechanisms of conflict resolution involve asymmetry among the symbiotic organisms, with one in control and enforcing the good behavior of its partners. Although symbioses are mutualistic, they are not necessarily cooperatives of coequals. This is illustrated particularly by organelles that are controlled almost totally by the host. I argue that the evolutionary transition to organelles is the consequence of one route to conflict resolution.

Conflict among organisms in symbiosis is heightened when one partner fails to provide a service or consumes common resources excessively. Symbiotic organisms that avoid such unsuitable partners are expected to encounter lower levels of conflict with their partners. Partner choice is a sufficiently important topic to merit a full chapter on its own. In chapter 4, "Choosing and Chosen in Symbiosis," I explore the mechanisms by which organisms identify cooperative partners, discriminate against ineffective organisms and persist together in apparent harmony. Many of the putative mechanisms are widely perceived as preexisting defenses against antagonists that are recruited, often with modification, for symbiotic function. However, with the recognition of the antiquity and pervasiveness of the symbiotic habit, we should consider alternative possibilities. Perhaps, mechanisms that have evolved for the management of organismal interactions can be applied to both beneficial and antagonistic relationships; and they are labeled as defensive responses only because of the greater research effort on antagonistic than on mutualistic associations.

In chapter 5, "The Success of Symbiosis," I apply understanding of the formation and persistence of symbioses, as explored in chapters 2–4, to investigate the basis of the significance of the symbiotic habit. Symbioses are important not just because they are widespread and abundant (as considered in this chapter) but also because the acquisition of symbiosis can dramatically alter the evolutionary history of some lineages and change the structure of ecological communities. I also consider the success of symbioses in the context of human activities. There are both threats and opportunities: threats to symbioses arising from anthropogenic impacts, and opportunities where we can harness symbioses to our advantage, especially in medicine and pest control strategies. Understanding of the processes underlying the symbiotic habit (chapters 2–4) can contribute to the amelioration of these threats and the successful exploitation of various associations.

In the concluding chapter 6, "Perspectives," I explore the opportunity for future research on symbiosis and some outstanding questions that can be resolved best by analysis across many symbioses.

The structure of this book is founded on the perspective that a grasp of multiple systems can promote our understanding of the symbiotic habit. Most of the systems that I use to illustrate and develop themes are symbioses, but I also address parasitic or pathogenic interactions and nonpersistent mutualistic relationships where they can contribute to my argument.