

Mutualism

J N Holland, Rice University, Houston, TX, USA

J L Bronstein, University of Arizona, Tucson, AZ, USA

© 2008 Elsevier B.V. All rights reserved.

Introduction

Mutualism Defined

Historical Study of Mutualism

Benefits and Costs of Mutualism

Functional Responses and Population Dynamics

Conditional and Context-Dependent Outcomes

Evolutionary Ecology of Mutualism

Further Reading

Introduction

Fundamental to the discipline of ecology is understanding how and why interactions between populations of different species (i.e., interspecific interactions, species interactions) influence the growth, abundance, dynamics, and stability of the interacting populations. Interspecific interactions occur when the actions, traits, or density of individuals of one population result in a change in some attribute of another species' population. Population attributes may include, for example, (per capita) reproduction, survival, recruitment, mortality, population growth, population size, population density, and mean character (trait) values of individuals comprising the population. Almost all, if not all, species are involved in at least one interspecific interaction, and most are involved in multiple interspecific interactions at any one time. For example, an individual plant may simultaneously interact with pollinators, seed dispersers, root symbionts, herbivores, and plant competitors.

Interspecific interactions are most commonly classified according to the outcomes or effects of interactions between individuals of different species. The effect or outcome of any given interaction on a population attribute can be positive (+), negative (−), or neutral (0). Thus, there are six different pairwise outcomes: predation (+, −), competition (−, −), mutualism (+, +), commensalism (+, 0), neutralism (0, 0), and amensalism (−, 0) (Figure 1). Although this classification is based on discrete (+, −, 0) effects on each of the interacting populations, as Figure 1 depicts, they actually range continuously among one another; for example, a very small positive effect (+) ranges into a neutral (0) and then a negative (−) effect.

Mutualisms are increasingly recognized as fundamental to patterns and processes of ecological systems. Mutualisms occur in habitats throughout the world, and ecologists now acknowledge that almost every species on Earth is involved directly or indirectly in one or more mutualism (Table 1). Examples include animal-mediated pollination and seed dispersal, which can be particularly

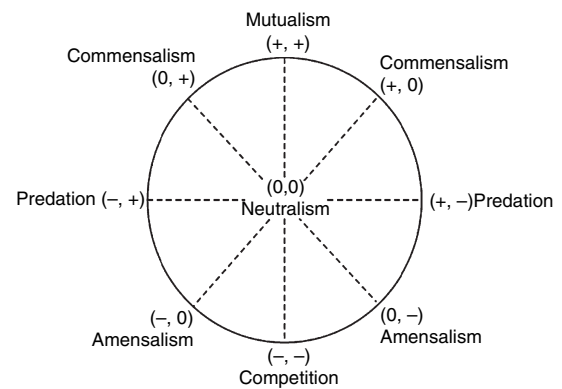


Figure 1 A compass of interaction outcomes that classifies interspecific interactions into one of six general forms based on their effects or outcomes on the interacting populations. Moving from the center toward the periphery of the compass increases the strength or magnitude of the interaction outcome, but does not alter the sign of the effect of the interaction for either of the interacting species. On the other hand, moving around the periphery of the circumference changes the sign and type of interspecific interaction.

prominent in tropical forests; the plants benefit by having pollen and seeds transported by animals, while the animals are generally attracted to and rewarded by food (nectar and fruit, respectively). Nitrogen-fixation mutualisms are important in many habitats, notably including deserts and agroecosystems. In these interactions, root-associated bacteria fix nitrogen to a form that can be used by plants, and obtain carbon from the plants in return. Nutrient exchanges also occur between root-associated mycorrhizal fungi and plants in grasslands, which are common in grasslands; between fungi and algae that constitute lichens (prominent in tundras and early successional communities); between coral and the zooxanthellae that inhabit them in marine systems; and between microbes in deep-sea vents of oceans. Other common mutualisms involve relationships between animals that protect plants or other animals from harsh abiotic environments and from natural enemies. For example, ants defend many plants from attack by herbivores, in

Table 1 Some examples of mutualisms, types of species involved in the interactions, and associated benefits and costs

<i>Mutualism</i>	<i>Partners</i>	<i>Benefits</i>	<i>Costs</i>
Lichen	Fungi Algae	Algal photosynthates Nutrients, water	Nutrients, water Algal photosynthates
Coral	Corals Zooxanthellae	Algal photosynthates Nutrients, nitrogen	Nutrients, nitrogen Algal photosynthates
Mycorrhizal	Plants Mycorrhizae	Nutrients, phosphorus Root exudates, carbon	Root exudates, carbon Nutrients, phosphorus
Nitrogen Fixation	Plants Rhizobia	Nitrogen Root exudates, carbon	Root exudates, carbon Nitrogen
Ant agriculture	Ants Fungus	Fungus-food resource Ant-collected leaves	Ant-collected leaves Fungus-food resource
Digestive symbiosis	Termites Protozoa	Protozoa-digested food Termite-ingested cellulose	Food for termites (?) Digesting food (?)
Pollination	Plants Animals	Pollen dispersal, pollination Nectar and/or pollen	Nectar and/or pollen Time/energy
Seed dispersal	Plants Animals	Seedling recruitment Seed/fruit food resource	Disperser food resource Time/energy
Ant-plant protection	Plants Ants	Herbivore protection Nectar, food bodies	Nectar, food bodies Time/energy protecting
Ant-insect protection	Insects ^a Ants	Natural enemy protection Insect food provision	Food secretions/excretions Time/energy protecting

^aLycaenid caterpillars, homopterans.

exchange for food and living space. These mutualisms are particularly well known in tropical environments, although they occur in habitats worldwide.

Influences of mutualism transcend levels of biological organization from cells to populations, communities, and ecosystems. Mutualisms are now thought to have been key to the origin of eukaryotic cells, as both chloroplasts and mitochondria were once free-living microbes. Mutualisms are crucial to the reproduction and survival of many plants and animals, and to nutrient cycles in ecosystems. Moreover, the ecosystem services mutualists provide (e.g., seed dispersal, pollination, and carbon, nitrogen, and phosphorus cycles resulting from plant-microbe interactions) are leading mutualisms to be increasingly considered a conservation priority.

Mutualism Defined

Mutualism is most commonly defined in a way that reflects the positive signs characterizing the outcome of their interactions, that is, as interactions between individuals of different species that benefit both of them. However, mutualism can be more precisely defined as an interaction between individuals of different species that results in positive (beneficial) effects on per capita reproduction and/or survival of the interacting populations. As in other interspecific interactions, the degree of dependency of each mutualist upon the other ranges from obligate to facultative; hence, they can be obligate-obligate, obligate-facultative, or facultative-facultative interactions. Facultative mutualists are ones whose populations persist

in the absence of a mutualist, whereas obligate mutualists are ones whose populations go extinct in the absence of a mutualist. In species-specific mutualisms, only a single partner species confers mutualistic benefits, whereas in generalized mutualisms, an array of species can provide the necessary benefit. For example, a plant that cannot produce seeds in the absence of a single pollinator species is engaged in a species-specific, obligate mutualism, while a plant that can self-pollinate to some extent and that can be pollinated by multiple flower-visitors is involved in a facultative, generalized mutualism.

The term mutualism is not synonymous with symbiosis, cooperation, or facilitation, although ecological and evolutionary parallels do occur among these forms of interaction. The term symbiosis identifies an intimate, close association between species in which the large majority or entire life cycle of one species occurs within or in very close association with another. Often, one species (the symbiont) is not free-living, but inhabits the body of another species (the host). A mutualism can also be a symbiosis, and many symbioses are also mutualistic, but not all symbioses are mutualisms and not all mutualisms are symbioses. Interactions between algae and fungi that comprise lichens and between termites and the protozoa that inhabit their digestive systems are examples of mutualistic symbioses. In contrast, plant-pollinator mutualisms are not symbiotic, as both partner species are free-living. Other symbioses are parasitic rather than mutualistic, including, for example, interactions between humans and protozoa that cause malaria.

While mutualism is an interspecific interaction, the term cooperation is generally used to describe mutually

beneficial interactions between individuals of the same species, often involving social interactions. Examples of species in which cooperation is an important feature include naked mole rats and honeybees and other social insects. Finally, facilitation differs from mutualism in that, while it does involve positive feedback, it is not necessarily an interspecific interaction. Facilitation typically refers to the modification of some component of the abiotic or biotic environment by one species that then enhances colonization, recruitment, and establishment of another species, such as occurs during succession.

Historical Study of Mutualism

Observations that we can now associate with mutualism date back many centuries to natural history descriptions of species interactions by Herodotus, Aristotle, Cicero, Pliny, and others. Yet, the term mutualism was not used in a biological context until 1873, when Belgian zoologist Pierre van Beneden coined the term, stating that “there is mutual aid in many species, with services being repaid with good behavior or in kind.” Even though much of his focus was on competition and struggle within and among species, Charles Darwin was probably one of the first to give substantial attention to mutualism, especially pollination. Darwin pointed out that mutualistic interactions presented a significant challenge to his theory: individual organisms would not be expected to provide services or rewards for the sole benefit of individuals of another species, for such traits could not have evolved through natural selection. To resolve this dilemma, Darwin showed how plant traits that benefit animals, such as fruit and nectar, function first to increase a plant’s own reproductive fitness. He pointed to cases in which the interests of mutualists could come into conflict, leading to cheating behaviors such as nectar robbing (the collection of nectar by flower-visitors that do not pick up or deposit pollen). In showing that mutualisms could emerge in nature strictly by selfish actions, limited by costs and driven by conflicts of interest between partners, Darwin laid much of the groundwork for current studies of the evolutionary ecology of mutualistic interactions.

Natural history lore about mutualisms may have accumulated for centuries, but a deeper ecological understanding of these interactions has lagged behind that of predation and competition. First, much more attention has been paid to mutualism from evolutionary biologists than from population and community ecologists. As identified in Darwin’s work, mutualism does present many interesting evolutionary issues, and mutualistic species do indeed exhibit many uniquely evolved morphological and behavioral traits resulting from their interactions. A second reason for the lag in understanding relates to historical development of theory for the

population dynamics and ecological stability of mutualism, compared with that of predation and competition. During the first two decades of the twentieth century, scientists such as A. J. Lotka and V. Volterra began theoretical investigations into how competition and predation influenced the stability and dynamics of interacting populations. Even though there are many recognized limitations to early results and mathematical approaches, they nevertheless provided ecologists of the time with a foundation upon which to build further theory and empirical research.

The history of theoretical research on the ecological dynamics of mutualism is quite different, however. Mutualism did not begin to be investigated theoretically until the mid-1930s. These models indicated that mutualism was either unstable, leading to unbounded population growth, or when stable, a very weak interaction having little influence on the dynamics of mutualistic populations. In the 1960s and 1970s, more theoretical investigations of mutualism began to emerge. However, these models largely replicated the results of earlier studies, and indicated that mutualisms were unstable, leading either to extinction or never-ending positive feedback and unbounded population growth. Since the 1980s, however, there has been much growth in the study of mutualism. Biologically realistic theory has accumulated that indicates that mutualism is not inherently unstable. The primary generalization to emerge from these models is that for mutualism to be stable, some factor must limit the positive feedback of the interaction on a population’s growth rate. Factors incorporated into theory that have generated some stability include intra- and interspecific competition, predation, frequency dependence, spatial structure, and benefit and cost functional responses, most all of which involve some form of negative density dependence. Along with these theoretical studies, empirical studies of mutualism have continued to increase in the past 20 years; these studies clearly indicate that mutualisms are common in nature and their populations do not in fact grow unbounded. Nonetheless, one of the most fundamental questions continuing to be asked about mutualism is what biological mechanisms prevent the inherent positive feedback of mutualism from leading to unbounded population growth.

Although there has been much growth in theoretical and empirical research on mutualism in recent years, there are still few generalizations and little conceptual unification across mutualistic interactions, which are indeed highly diverse and differ greatly in natural history (Table 1). As one indication of this, in current ecology textbooks, over 85% of the pages devoted to mutualism present natural history examples rather than concepts or theory. Despite such shortcomings, progress is being made on the ecology of mutualism. A few generalizations have emerged, including that nearly all mutualisms

involve both benefits and costs; benefits and costs are themselves often density dependent, exhibiting functional responses; the outcome of interactions are often context dependent; and mutualisms often inherently entail conflicts of interests. Each of these generalizations is discussed below.

Benefits and Costs of Mutualism

Ecologists now recognize that one of the few generalizations that can be made about mutualisms is that nearly all of them involve both benefits and costs for each interacting species (Table 1). Mutualistic outcomes arise when the benefits of an interaction outweigh costs for both interacting species, such that the net effects of the interaction equal benefits minus costs. Currencies used as measures of benefits and costs often vary among mutualisms, but commonly include physiological or behavioral responses to various direct and indirect measures of growth, survival, and reproduction. Whatever currency is used to measure benefits and costs, they both are implicitly understood to ultimately affect reproduction and/or survival, or possibly some energetic currency, as these are the fundamental units for ecological and evolutionary processes.

Benefits are goods and services that a mutualistic species cannot obtain affordably, or at all, in the absence of its partner(s). Three general classes of benefits occur among mutualisms: transportation, protection, and food/nutritional resources (Table 1). Transportation involves the movement of oneself or one's gametes, including, for example, pollen dispersal by pollinators and seed dispersal by frugivores. Benefits of protection involve the defense, guarding, or shelter of a mutualist from natural enemies (e.g., predators, herbivores, parasites, parasitoids) or the abiotic environment. Examples include ant protection of plants from herbivores and of certain other insects from predators and parasitoids. Benefits may also include nutritional resources, ranging from nutrient and carbon exchanges in plant/mycorrhizal interactions to food substances provided by plants in return for protection by ants.

Although most of the benefits that mutualists provide one another have long been known, it has only recently been recognized that mutualistic interactions also involve costs. Costs of mutualism arise as a consequence of the provision of resources and services to partner(s). Costs include investments in structures and substances to reward mutualists (e.g., nectar) and the energy and time spent obtaining those rewards (Table 1). In most cases, there is interspecific exchange of benefits and costs, such that the benefits accruing to one mutualist translate into the costs experienced by its partner and vice versa. For instance, the plant invests in the production of nectar at

some cost to itself; that nectar is the benefit received from a floral visit by the pollinator. The pollinator also experiences a cost, in terms of time and energy spent obtaining that nectar. Time and energy costs can be difficult to measure; also, they are only incurred in cases where the interaction actually takes place. In contrast, other costs are incurred whether or not an individual does in fact interact with its mutualistic partner(s). For example, nectar is generally produced by plants regardless of whether pollinators actually visit a flower.

Functional Responses and Population Dynamics

Benefits and costs are rarely fixed attributes of species interactions, but rather vary with the abundance or population density of mutualistic partners. In other words, benefits and costs of mutualism exhibit functional responses. In its most general application, a functional response represents how the rate of change of one population varies with the density or abundance of individuals of another population. Historically, most models of mutualism simply used linear or saturating type 2 functional responses, with little consideration of the underlying biological mechanisms. Expressing functional responses of mutualism in terms of benefits and costs provides a mechanistic basis for understanding mutualism's influence on the intrinsic growth rate and population dynamics of interacting species.

The difference between benefit (B) and cost (C) functional responses equals the net effect (NE) functional response of mutualism on the rate of change in the size of a mutualist's population (i.e., $NE = B - C$). Many different scenarios are theoretically plausible for functional responses of benefits and costs, and hence for net effect functional responses (Figure 2). Figure 2a presents the scenario in which net effects to a mutualistic population, mutualist 2, increase linearly with the population density of its mutualistic partner, mutualist 1. That is, the more mutualists there are, the better and better a partner fares. It is this ever increasing net effect functional response that gives rise to the unrealistic result of unbounded population growth that was typical of early theoretical studies. In nature, however, many different limitations prevent net effect functional responses from increasing continually. Benefit and/or cost functional responses to mutualist 2 may saturate or diminish with increasing population density of mutualist 1, such that net effect functional responses saturate or diminish as well. Figures 2b–2f represent examples of how benefit and cost functional responses may vary with one another, and hence give rise to different net effect functional responses. Other shapes of benefit and cost functional response are feasible as well.

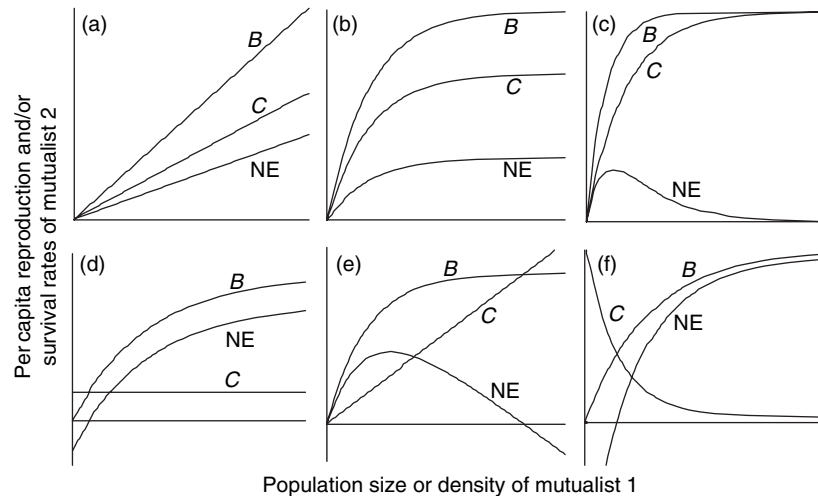


Figure 2 (a–f) Examples of potential functional response curves in terms of benefits (B), costs (C), and net effects (NE) on the per capita rate of reproduction and/or survival of a mutualist population, mutualist 2, as a function of its partner's population size, mutualist 1. Benefits positively affect the rate of reproduction and/or survival, while costs negatively affect the rate of reproduction and/or survival, such that $NE = B - C$.

The well-known mutualism between yucca plants and yucca moths serves as one example of how benefit, cost, and net effect functional responses to one mutualist (the plant) vary with the population size or density of its pollinating insect partner (the moth). This example is graphically depicted by **Figure 2c**. Yucca moths both pollinate yucca flowers and lay their eggs into them. Eggs hatch to produce larvae that consume developing seeds. Thus, both benefits and costs of yucca moths affect plant reproduction, via their effects on seed production: it is increased through moth pollination, and decreased through the consumption of developing seeds by the pollinator's offspring. If moth density is low, then the benefits of pollination to plant reproduction are small (B in **Figure 2c**). As moth density increases, more flowers are pollinated. However, at some point, moths are sufficiently abundant that all flowers become pollinated; that is, the benefit functional response of moths to plants saturates (B in **Figure 2c**). Further increases in moth density do not lead to greater seed production. Rates of oviposition, and hence costs of seed consumption, follow a similar pattern, except that, given the biology of yucca moths, oviposition occurs at a lower rate than pollination. If moth density is high, then costs of larval seed consumption to plant reproduction are large, such that nearly all seeds are consumed by larvae of eggs laid in flowers (C in **Figure 2c**). Thus, the net effect functional response for plant reproduction via seed production, $NE = B - C$, is a unimodal function of moth density.

Two-species models that incorporate benefit and cost functional responses show that the dynamics and stability properties of populations involved in mutualisms can differ greatly depending upon the shapes of these

functional response curves. As indicated above, the great diversity in natural history and in associated benefits and costs among mutualisms has hampered development of generalizations about these interactions. Expressing functional responses in terms of benefits and costs provides one general theory for mechanistic understanding of how mutualism influences the growth, dynamics, and ecological stability of interacting species. Nevertheless, as yet we know little about the shapes of these relationships in nature.

Conditional and Context-Dependent Outcomes

The outcomes of interspecific interactions are not simply $(+, 0, -)$, but instead vary along a continuum. Mutualism, like predation and competition, is in many cases not a fixed attribute or outcome of the interacting species. For example, the upper half of **Figure 1** shows that mutualism can grade into commensalism $(+, 0)$ and then predation $(+, -)$ as the effect on one of the two partners changes. This variation in the strength and outcome has become known as conditionality or context dependency of mutualism. Mutualistic outcomes can vary depending upon numerous factors, including the abundance of predators and competitors, the supply of resources such as nutrients, the density and distribution of mutualists, and the size, stage, or age classes of interacting species. All of these factors can lead to spatial and temporal variation in the community and environmental context of mutualistic interactions. Gradation of mutualism into other interaction outcomes arises mechanistically via changes in the

relative magnitudes of benefits and costs associated with spatial and temporal changes in these above factors.

Mutualisms are often contingent upon external factors, such as the availability of limiting resources or the presence and/or density of a predator or competitor. The protection mutualism between ants and treehoppers (plant-feeding insects) exemplifies how outcomes can vary with predator density. In a high-predator year or location, treehoppers are decimated by predators if not protected by ants. In contrast, at places and times where predators are few, the interaction is commensal or even parasitic: ant protection is not necessary, yet treehoppers still must pay the cost of providing food resources to the ants. Thus, variation in the magnitude of benefits of the mutualism to treehoppers generates a shift in the outcome of the interaction: it is conditional upon the abundance of predators.

The interaction between plants and root-associated mycorrhizal fungi represents an example of how the outcome of mutualistic interactions can be conditional upon nutrient availability. Mycorrhizal fungi increase the availability of soil phosphorus for the host plants; in turn, the plants provide mycorrhizae with carbon resources (root exudates). When plants are grown in phosphorus-rich habitats, the cost of providing mycorrhizae with carbon can exceed the benefits of the phosphorus obtained from mycorrhizae. Consequently, some plants can reduce their mycorrhizal infections under these conditions, even excluding mycorrhizae from their roots altogether.

In addition to spatiotemporal variation in environmental resources and predators, variation in benefits and costs associated with functional responses can lead to conditional outcomes of mutualism. As shown in the yucca/moth example above, irrespective of the particular species involved, the strength and outcome of a mutualism will vary with the densities of interacting partners. If mutualist densities occur at which costs equal or exceed benefits (Figure 2), then the outcome of an interaction will degrade into commensalism or predation (Figures 1 and 2). Thus, it is feasible for one 'mutualistic' species to have positive net effects on its partner at some population densities, and commensal or parasitic net effects at other densities. These examples demonstrate how complex mutualisms can be, and how dependent their outcomes are on the biotic and abiotic environment in which they occur.

Evolutionary Ecology of Mutualism

Much of the current research on mutualism centers on the ecology and population dynamics of mutualism, but, as indicated above, the evolution of these interactions has attracted considerable attention as well. Issues central to the study of the evolutionary ecology of mutualism include: their evolutionary origin and stability, the evolution of specificity and obligacy, and natural selection and the

evolution of mutualistic traits. While evolutionary biologists study these and many other topics concerning mutualism, evolutionary ecologists have focused much of their attention in recent years on one question in particular: what are the biological mechanisms that may prevent overexploitation of one mutualistic species by another, thereby averting the degradation of mutualism into parasitism or predation?

Mutualism inherently involves conflicts of interest between interacting species when there is interspecific linkage of benefits and costs. Overexploitation and conflicts of interest can lead to the ecological and evolutionary destabilization of mutualism. In benefiting by extracting a cost from its partner, a species might increase its own benefit and its partner's cost to the point at which the partner no longer has a net benefit. For example, yucca moths may pollinate and deposit eggs in yucca flowers, but if moths deposit so many eggs that most or all seeds are consumed by larvae, then the costs of seed consumption may converge with the benefits of seed production. In either case, if a species increases its benefit and as a result, its partner's cost increases beyond its limits of tolerance, it could cause extinction of the partner. If interactions are obligate, this could mean extinction of both species. Destabilization of mutualism through conflicts of interest may arise independent of the evolution of cheater genotypes within either of the populations of partner species.

Theoretically, the evolutionary stability of mutualism requires that a conspecific 'cheater' genotype, within either partner species, not be able to spread to fixation and eliminate the 'mutualistic' genotype. This problem mirrors similar barriers to the evolution of intraspecific cooperation. Cheaters are individuals that increase their fitness, relative to their conspecifics, by reducing their cost:benefit ratio and thereby the benefit:cost ratio of their partner. They can do so by reducing benefits provided to their partner (and costs to themselves), or by increasing their own benefits (and costs to their partner). In either case, theory predicts that cheater fitness will increase and the cheater phenotype may spread to fixation, reducing mutualism to parasitism.

Mutualism has also been suggested to be destabilized if a species extracts a benefit from a mutualistic species without returning benefits to that species, though, by definition, such interactions involving cheater species are not mutualistic. For example, some bees pierce holes in flowers to extract nectar without ever exhibiting behaviors that pollinating insects display. Such nectar-robbing insects are also often referred to as 'cheater' species, as they extract benefits without returning them. As another example, certain close relatives of yucca moths lay their eggs in yucca flowers and developing fruit, but have lost the morphological and behavioral traits that confer benefits on yucca plants. These moths function as seed predators and the interaction is by definition parasitism rather than mutualism.

Despite the strong negative effects that they can inflict, there is no evidence that such parasites and cheaters necessarily lead to the destabilization of mutualisms. In fact, given the ubiquity of mutualism in nature, the implication is either that parasites and cheaters are somehow held in check, or that such cheating rarely arises in nature. There is growing recognition that at least in some mutualisms, certain traits or behaviors of one or both mutualists act to reduce or inhibit such parasites and cheaters. As one example, many flowers exhibit structural features that protect nectar from floral visitors that do not contact the stigmas and stamens while feeding. As another example, plants may be able to curtail the growth of mycorrhizae to reduce the benefits they extract, and thereby prevent their costs from exceeding benefits. Such topics of evolutionary stability, conflicts of interests, and cheating within mutualisms remain in great debate.

See also: Coevolution; Cooperation; Pollination; Seed Dispersal.

Further Reading

- Boucher DH (1985) *The Biology of Mutualism*. New York: Oxford University Press.
- Bronstein JL (1994) Our current understanding of mutualism. *Quarterly Review of Biology* 69: 31–51.
- Bronstein JL (1994) Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution* 9: 214–217.
- Bronstein JL (2001) Mutualism. In: Fox CW, Roff DA, and Fairbairn DJ (eds.) *Evolutionary Ecology: Concepts and Case Studies*, pp. 315–330. New York: Oxford University Press.
- Bronstein JL (2001) The exploitation of mutualisms. *Ecology Letters* 4: 277–287.
- Connor RC (1995) The benefits of mutualism – A conceptual framework. *Biological Reviews of the Cambridge Philosophical Society* 70: 427–457.
- Hoeksema JD and Bruna EM (2000) Pursuing the big questions about interspecific mutualism: A review of theoretical approaches. *Oecologia* 125: 321–330.
- Holland JN, DeAngelis DL, and Bronstein JL (2002) Population dynamics and mutualism: Functional responses of benefits and costs. *American Naturalist* 159: 231–244.
- Holland JN, DeAngelis DL, and Schultz ST (2004) Evolutionary stability of mutualism: Interspecific population regulation as an evolutionarily stable strategy. *Proceedings of the Royal Society of London B* 271: 1807–1814.
- Holland JN, Ness JH, Boyle AL, and Bronstein JL (2005) Mutualisms as consumer–resource interactions. In: Barbosa P and Castellanos I (eds.) *Ecology of Predator–Prey Interactions*, pp. 17–33. New York: Oxford University Press.
- Schwartz MW and Hoeksema JD (1998) Specialization and resource trade: Biological markets as a model of mutualisms. *Ecology* 79: 1029–1038.
- Stanton ML (2003) Interacting guilds: Moving beyond the pairwise perspective on mutualisms. *American Naturalist* 162: S10–S23.
- Vázquez DP, Morris WF, and Jordano P (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters* 8: 1088–1094.