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THE ECOLOGY OF MUTUALISM

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INTRODUCTION

Elementary ecology texts tell us that organisms interact in three fundamental ways, generally given the names competition, predation, and mutualism. The third member has gotten short shrift (264), and even its name is not generally agreed on. Terms that may be considered synonyms, in whole or part, are symbiosis, commensalism, cooperation, protocooperation, mutual aid, facilitation, reciprocal altruism, and *entraide*. We use the term *mutualism,* defined as "an interaction between species that is beneficial to both," since it has both historical priority (311) and general currency. *Symbiosis* is "the living together of two organisms in close association," and modifiers are used to specify dependence on the interaction (*facultative* or *obligate*) and the range of species that can take part (*oligophilic* or *polyphilic*). We make the normal apologies concerning forcing continuous variation and diverse interactions into simple dichotomous classifications, for these and all subsequent definitions.

Thus mutualism can be defined, in brief, as a $+/+$ interaction, while competition, predation, and commensalism are respectively $-/-$, $-/+$, and $+/0$. There remains, however, the question of how to define "benefit to the

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species" without evoking group selection. Two definitions have coexisted for decades. In one, benefit is defined on the individual level, in terms of the relative fitness of organisms that do and do not participate in the interaction. This definition seems particularly appropriate for questions of evolution, but is inadequate when considering population-level phenomena involving a balance of positive and negative fitnesses. For example, many frugivorous animals destroy some of the seeds they consume and disperse others; the net result of these individual predations and mutualisms may be either an increase or a decrease in the plant population. The second definition considers this population-level effect, and is the definition tacitly assumed in applying models such as Lotka-Volterra equations to mutualism (as well as competition and predation). Thus the individual-level definition uses change in the fitness, W_1 of individuals of species 1 when they interact with individuals of species 2, while the population-level definition uses the change in dN_1/dt, the growth rate of population 1, as N_2 changes. We will not attempt to enshrine one or the other of these definitions.

We cover first direct mutualism, in which the two species interact physically, and then indirect mutualism, in which each species benefits from the other's presence but there is no direct contact. Direct mutualisms are divided into symbiotic and nonsymbiotic mutualism, using physiological integration as the basic criterion. This approach is artificial but convenient. It has little general usefulness: other divisions of mutualism (289) do not align neatly on a symbiotic/nonsymbiotic dichotomy. Although exceptions abound, symbiotic mutualisms tend to be coevolved and obligate, while facultative mutualisms are frequently nonsymbiotic and not coevolved.

Using these definitions, we start with two observations. On the one hand, an enormous number of ecologically and economically important interactions, found throughout the biosphere, would seem to be mutualistic. On the other hand, few studies have actually demonstrated increases in either fitness or population growth rate by both of the species in an interaction. Interactions have generally been shown to be mutualisms by describing what is exchanged. Mutualism may be everywhere, but its existence remains practically unproven.

HISTORY

The history of the study of mutualism by ecologists is akin to Sherlock Holmes's case of the barking dog, in which the point of interest was that the dog did not in fact bark. It is notable that despite promising early beginnings and wide recognition of mutualistic interactions, ecologists have devoted little time and energy to this subject (264).

Although discussions of the subject of mutualism typically start with DeBary's book on symbiosis (69), apparently the first use of the term "mutualism" is in Pierre van Beneden's 1875 book *Les Commensaux et les Parasites* (311), published simultaneously in German and English (as *Animal Parasites and Mess-Mates*). This was a popular work, and van Beneden was perhaps the foremost Belgian biologist of his time, with a bibliography ranging from worms to whales (172). In his youth he was active in the revolution of 1830, which won Belgian independence. He became celebrated in later years for his parasitological work, on which *Les Commensaux et les Parasites* concentrates. But he felt that since, in addition to parasites, "we find others who mutually provide each other services, it would be most unflattering to call them all parasites or commensals. We consider it fairer to call them *Mutualists,* and thus mutualism takes its place beside *commensalism* and *parasitism*" [(27); italics in original]. The capitalization of "Mutualists" is probably an indirect reference to the "Mutualité" societies organized by workers in France and Belgium to support each other financially, and indeed analogies to human society are common throughout the book.

Only two years later, van Beneden's definitions were critically discussed by Alfred Espinas in a doctoral thesis at the University of Paris entitled *Des Sociétés Animales.* This work, which shocked the university authorities by discussing the philosophy of Auguste Comte, "whom no one at that time dared to mention" (80), is concerned with the question "what is the essence of society?" Espinas discusses mutualism in a chapter on "Accidental societies between animals of different species: Parasites, Commensals, Mutualists." The treatment concentrates on domestication as one kind of mutualism, but also discusses such relationships as tick-birds and rhinoceroses, mixed species bird flocks, and ant-aphid associations.

By 1893 the subject was sufficiently developed to deserve a review article in the *American Naturalist* by Roscoe Pound (250). Pound recognized most of the major kinds of mutualism we study today, including pollination, legume root-nodulation, and various animal examples. By the turn of the century one could count literally hundreds of articles on one mutualism or another (273). More importantly, there seems to have been a general recognition of the fundamental similarity of interactions ranging from mycorrhizae to cleaner-fish.

The analogy of mutualism to cooperation in human society, never absent in previous work, was made a political issue in 1902 with the publication of *Mutual Aid: A Factor in Evolution,* by the anarchist Peter Kropotkin (178). This best-selling work was a rebuttal of the Social Darwinists and cited examples of cooperation in the natural world, to counter the contention that nature proved the inevitability of cutthroat competition. With

Kropotkin's book, mutualism became well known in lay society, and it continued to be discussed among biologists in the following decades. But in comparison to the rapid growth of the rest of ecology in the 20th century (76, 340), mutualism lost ground. While the construction of a theoretical base for studies of competition and predation in the 1920s and 1930s gave these subjects a strong boost, (93, 94, 194, 277, 318) the theoretical work of Kostitzin on mutualism (177) was amost totally ignored.

Kostitzin led a fascinating life (276, 277): After fighting in the Russian Revolutions of 1905 and 1917, he became head of the Soviet Union's Geophysics Institute. In the mid-1920s he moved to France, where he lived till his death in 1963. He collaborated with Vito Volterra, and published on topics ranging from single-species population dynamics to glaciation and the evolution of the atmosphere.

Mutualism figures prominently in the work of Warder C. Allee, a Quaker and pacifist, who wrote extensively on human and animal cooperation and coauthored the textbook *Principles of Animal Ecology* (6). This work was for many years the fundamental text in animal ecology, and it devotes considerably more space to mutualism than most contemporary ecology books. Yet it revealed the lack of progress made since the 19th century. Allee et al's collection of examples is longer than Pound's, their presentation of the analogy between natural mutualisms and cooperation in human society is subtler than Kropotkin's, but the treatment contains little that is new.

Only in the 1970s has mutualism finally begun to compete with other interactions as a subject for ecologists' consideration. To judge by citations, their work has relied little on that of their predecessors; during the period 1965–1979, van Beneden's book was cited almost exclusively by parasitologists, Kropotkin's mostly by social scientists and sociobiologists (often unfavorably), and Pound's article hardly at all (145). Interestingly, several recent theoretical treatments of mutualism have depicted it by means of the same graph, though with little cross-referencing (41, 84, 139, 213, 288, 315, 316). Mutualism's time seems finally to have arrived.

Two points emerge from this brief historical survey: the lack of interest in mutualism among ecologists for most of the 20th century, and the involvement of many of those who did study it with what at the time were left-wing causes. We suggest as an hypothesis for historians of science that mutualism has been avoided during most of the 20th century because of its association with left-wing politics (perhaps especially with Kropotkin).

DIRECT MUTUALISM

Mutualisms have long been seen as exchanges of benefits, of which one can identify a few main types: (*a*) nutritional: either the breakdown of compounds by digestion for the partner, or supply of growth factors or nutrients

by synthesis or concentration; (b) supply of energy, generally from photosynthesis; (c) protection, either from environmental variation or from enemies; and (d) transport, either from unsuitable to suitable environments or by dispersal of gametes or propagules. Symbiotic mutualists generally exchange the first two services, sometimes the third, and rarely the fourth. Nonsymbiotic mutualisms can involve all four.

Symbiotic Mutualisms

TYPES   Most symbiotic mutualisms involve the supply of energy from one partner to the other, whether autotroph to heterotroph (284) or between heterotrophs (e.g. gut microbes). A number of benefits may be provided in exchange: (a) breakdown of compounds, facilitating digestion; (b) supply or concentration of nutrients; (c) environmental constancy; and (d) bioluminescence.

Gut flora are involved in breaking down cellulose and related substances in mutualism with many vertebrates (134, 136), as well as with termites (304) and other arthropods (51, 291). Urea is broken down and its nitrogen recycled by rumen bacteria (134) and by the fungal components of some lichens (4). Toxic secondary plant compounds are also degraded in caeca and rumens by microbial symbionts (134).

The synthesis of compounds, including vitamins and amino acids, is performed by gut microbes in numerous associations (12, 48, 51, 77, 123, 134, 174). Ruminant microbes, and those in other animals, synthesize all of the B-complex vitamins, vitamin K, and the sulfur-containing amino acids. The breakdown of urea results in ammonia and carbon dioxide, and the ammonia is used by the bacteria to make amino acids, which are later obtained by the animal (134). Similar activities take place in lichens in which ammonia is incorporated by algae into amino acids and vitamins, and vitamins are secreted by the algae (4). An endozoic alga has been found to be the major source of fatty acids to its host flatworm, in a case in which the flatworm has lost the ability to synthesize these substances (215). Mycorrhizal fungi also produce growth factors, in this case plant hormones (42).

Symbiotic nitrogen fixation is known to take place in root nodules of leguminous plants (31, 71, 228, 256, 339) and in some nonlegumes (38, 53, 267, 303). In the legumes, the bacteria of the genus *Rhizobium* are the endosymbionts, and in the others, Actinomycetes, except for a recently discovered *Rhizobium*-Ulmaceae association (23, 308, 309). Blue-green algae fix nitrogen in both roots and above-ground parts of other woody plants, such as cycads, *Gunnera,* and various Rubiaceae (256). Symbiotic nitrogen fixation has also been discovered in lichens whose algal components are blue-green algae (4, 216), sphagnum moss (107), aquatic ferns (197), grasses

(43, 227), sponges (333), sea urchins (112), shipworms (55), and termites (25, 44). A disadvantage is that the cost of nitrogen to a plant with symbionts is greater than to a plant that acquires nitrogen in the form of nitrate (113).

Mutualisms involving the concentrating of nutrients include mycorrhizae and a few other instances involving algae and bacteria. Mycorrhizal fungi can take up nutrients at low concentrations, improve water uptake, and confer resistance to pathogens upon their hosts (42, 62, 87, 146, 147, 257). Plants benefit most when soil nutrient concentrations are low. In some circumstances, normally mutualistic fungi can be parasitic, and in rare instances of high phosphate levels the increased uptake caused by mycorrhizae can cause phosphate poisoning (42). Nutrient uptake by endozoic algae has been found in coral zooxanthellae, which take up ammonia from seawater (222), and in green hydra, whose bacterial symbionts increase uptake of phosphate from the medium (332). Endozoic algae in general take up waste products from their hosts and use them for their own growth. In corals, nitrogenous wastes have been traced from zooplankton to polyp to algae, in what constitutes a recycling of nutrients within the association (224, 248). Leaf-cutting ants (Attini), macrotermitine termites, and a variety of beetles culture fungi (20, 21, 92, 255, 327, 337). They feed, protect, and distribute the fungus, consuming parts of it (which are often specialized for the purpose) in return. The fungi seem in many cases to be incapable of independent existence. These interactions are best considered symbiotic even though the fungi are external to the ants and physically encountered by them only during culture: They share the colony's nest, and the biochemical and behavioral interactions are complex (255, 337).

Green plants are also "fed" by ants that inhabit the plant and bring debris into their nests, which decomposes and is available for uptake by the plant (140, 141, 146, 265). In "ant-gardens," the ants place the plants' seeds in their nests, where they germinate and take up nutrients from the nest wall (173). In at least one species, when the ants are absent the plant stops producing the food bodies on which the ants feed (266).

The provision of a constant environment, or a place in which to lead a sheltered existence, is found in mutualisms involving endozoic algae and in lichens. Endozoic algae generally have thinner cell walls than free-living algae, a characteristic that may be due to the physical protection gained by living within another organism (201, 294). Similarly, the algae found in lichens are frequently unable to survive where the lichen is found growing, suggesting that living with fungi improves resistance to injury and desiccation (4). There are trade-offs, however; symbiotic species of algae grow more slowly when inside animals than when cultured in vitro, and more slowly still than nonsymbiotic species (324).

Symbioses with bioluminescent microorganisms are found in a variety of animals (126, 207, 226). While bioluminescence may have originated as an oxygen detoxification system (207), it now has a wide variety of functions, including prey attraction, protection, communication, and mate attraction. In many cases the function is not yet understood. This is thus a "grab-bag" category in which many different benefits share a common biochemistry.

EVOLUTION   The evolution of symbiotic mutualisms is generally thought to begin through proximity of the organisms involved. We discuss how associations are initiated, what sorts of adjustments and adaptations must be made en route to mutualism, and the selective pressures for these changes.

Parasitism is one possible starting point (271, 274, 327). In this case the problem of first infection has been taken care of, and one needs only to consider how parasitism could change to mutualism. A model system is the experimental demonstration of reduction of virulence of a bacterial infection of an *Amoeba,* which ultimately became dependent on the bacteria (160). Reduction of detrimental effects of the parasite on the host must be accompanied by development of host dependency on the parasite, which is already dependent on the host. Scott (274, 275) gives two routes to the evolution of dependence. The first is through a parasite-relationship of low virulence in which the parasite leaks nutrients, increasing host survival and thus its own fitness. Alternatively, an increase in ecologically imposed limitations, which the parasite helps overcome, can select for closer dependence.

Ingestion as a starting point is thought to be appropriate for mutualisms involving algae, gut microbes, and some eukaryotic organelles (205, 206, 207). Selection pressure for resistance to digestion would be strong, and the ingesting animal would have to develop a means of recognizing the alga as a nonfood item, and also as nonforeign. Carbohydrate diffusion from the alga would place some value on retention of the intact alga. Another necessary alteration is the regulation of growth rates of the algae (223). Currently algae are found in vacuoles or in the cytoplasm, and some are reduced to little more than chloroplasts (283, 325).

In cases starting as symbiotic commensalisms, the evolution of mutualism may proceed by the commensal's providing some benefit that would be selected for if it increased the host's chances of survival and/or decreased the likelihood of the host's attempting to get rid of the commensal. Alternatively, a change in ecological circumstances or the presence of an ecological opportunity could transform the relationship into a mutualism if the commensal happens to render the host better able to survive or take advantage of the situation.

A driving force behind the evolution of symbiotic mutualisms is expressed by Dubos & Kessler (73), who argue that as more needs of the association are met by the combined abilities of the mutualists, the intensity of competition on those partners from ecologically similar species will diminish. This proceeds by selection of one symbiont to increase its fitness through changes that increase the fitness of the other symbiont.

Nonsymbiotic Mutualisms

Nonsymbiotic mutualisms are those in which the two species are physically unconnected. While there may be some physiological habituation to the mutualist, as in the anemone-dwelling fishes (89), there are no direct physiological links. Various mutualisms involving ants, including myrmecophytes and the leaf-cutter ant–fungus relationship, offer ample material for arguments about classification; having considered nutritional aspects above, we deal with protection in this section.

TRANSPORT   Pollination and dispersal have enjoyed a recent surge of interest and have accumulated a large literature to which we cannot do justice in the scope of this paper (but see reviews by Howe, Regal, and Dressler in this volume). Both involve the transport of particles involved in reproduction, and for both there are nonmutualistic alternatives. In both interactions, transport is effected in exchange either for some sugar-rich substance (nectar, ovarian tissue of fruits) or the consumption of some of the particles to be transported (pollen, nuts). In the case of pollination, in which the "target" area is very limited, the transport will generally be either successful or totally unsuccessful. In dispersal, on the other hand, the difference between outcomes is not as absolute, and the target is large and diffuse (328). Finally, both interactions are important to the genetic structure of the population.

Pollination by mutualism with animals is critical to sexual reproduction in the majority of flowering plants. The advantage of the mutualistic solution may be reduced pollen waste, longer transport, or increased probability of success at low density (290). After initiation with insect species in the Coleoptera and Diptera, the mutualism has been developed in several other orders, most notably the Hymenoptera (110, 127, 129, 158, 252, 297). There is a variety of vertebrates involved, including birds, bats, monkeys (148), lemurs (293), rodents (331) and other mammals.

Dispersal of seeds, fungal spores (19, 88, 95, 210), and other propagules may not be as critical as pollination; offspring could simply grow up beneath their parent and replace it. However, dispersal would appear to offer the (seldom proven) advantages of colonization of other sites, increased outcrossing, and escape from predators (124, 125, 231, 243). Since some of

those predators may be the dispersers themselves, the interaction can shift between mutualism and predation depending on plant and predator/disperser densities (39). Many animal taxa act as dispersers, including birds, (135, 200), bats (85), large mammals (159), ants (22, 30, 66, 119, 124, 125, 133, 195, 231, 253, 298), *Drosophila* (95), beetles (19), tortoises (262), and fish (105).

PROTECTION Protection from predators, parasites, diseases, toxins (161), and occasionally competitors is provided by many organisms. The other partner may be animal or plant, and may provide food (*sensu lato*), reciprocal protection, housing, or some combination.

Ant-plant protective mutualisms range from symbiotic obligate systems in which the plants house and feed the ants [e.g. *Acacia* (24, 149); *Cecropia* (150)] to housing ants without food provided [e.g. rubiaceous myrmecophytes (29, 140, 141); *Barteria* (154)] and food provided without nest sites [chiefly extrafloral nectar-producing species (27, 82, 342)]. In all cases, aggressive and predatory ant behavior serves to reduce damage to the plant (26, 27, 28, 35, 70, 132, 141, 143, 149, 150, 154, 163, 165, 167, 168, 171, 176, 229, 239).

Ants and other insects are also mutualists with some herbivorous and sap-feeding insects, the ants providing protection in return for honeydew, a sugary secretion extruded through the anus or glands (1, 2, 9, 46, 130, 241, 270, 323). Homoptera and Lepidoptera seem to be the main taxa involved. Related mutualisms are some cases of phoresy in which insects transport other insects or mites on their backs. The "riders" are brought to sources of food and in return may protect the insects against parasites (336). Similar benefits may occur with nest-sharing insects (337).

There are numerous examples of protection mutualisms among marine animals, including burrow-sharing by gobies and shrimp (89, 111, 192), anemones living on crab shells (15, 269), and cleaning mutualisms (77, 83, 106, 131, 188, 190, 191, 193, 282). Both the goby-shrimp and crab-anemone mutualisms allow the partners to occupy areas they otherwise could not (89, 269). Cleaning interactions are a set of potential mutualisms that have been a matter of some controversy (131, 190, 191, 193, 282). Cleaners are known from a variety of marine habitats, and there are many species apparently adapted to the role. Their removal only sometimes has negative effects on the host fishes. Losey (193) questions the mutualistic nature of some cleaning relationships, noting that parasite load shows little correlation to tendency to solicit cleaning, and that scales and mucus are also taken by cleaner fishes.

Other interactions involve mutual protection, which may appear as a simple consequence of living together. Protection against starfish predation

is provided to corals, scallops, and clams by xanthid crabs, sponges, and diverse epibionts, respectively (36, 102, 313). The epibionts and sponges are in turn less vulnerable to predation, and the crabs gain both protection and energy-rich mucus. Further benefits are provided in the mutualism between sea-anemones and the fish (*Amphiprion*) that live inside them (89, 208). The anemone gains protection, food, and is cleansed of waste and necrotic tissues, while the fish is protected and suffers less parasitism and disease. In other invertebrates, such protection mutualisms can help species in competition for space as well (52, 232). This aid can allow both partners to extend their habitat ranges, and also, for example, permits the bryozoan *Celleporia* to dominate the community, which it does not do in the absence of the mutualistic hydroid *Zanclea* (232).

Both increased food and protection may be involved in mixed-species aggregations; but, which is more important, and indeed the mutualistic character of the phenomenon itself, are controversial. Mixed aggregation is known in delphinid whales (61, 245), fishes (192), birds (58, 90, 217, 218, 221), sea urchins (74) and terrestrial mammals (11, 32). The two principal hypotheses relating to the formation of heterospecific groups are that they enjoy an increased efficiency of foraging and that they are better able to to detect and avoid predators. Bird flocks have been the most thoroughly studied.

Increased foraging efficiency by flocking has been proposed by Moynihan (220) and Cody (59). Flocking tends to occur when food availability is low (59, 217). However, individual birds in flocks spend less time watching and more time feeding, suggesting that protection from predators is the primary reason for flocking, and improved feeding is a secondary consequence (104, 181). The theories of Vine (317) and Hamilton (118) show that individuals can reduce their chances of being eaten if they cluster together. This helps explain the origin of flocking for predator avoidance but not its specifically mutualistic (multi-species) nature. The motivation for mixed grouping is vaguer for monkeys than for birds. Mixed troops of monkeys travel and feed together (32), and the different species recognize one another's alarm calls (209). Baboons and impalas or bushbucks benefit from each other's presence by mutual recognition of alarm calls (11, 78, 321). In association, the impalas enter types of vegetation they do not use when unaccompanied by baboons (78).

APPARENT PREDATION   A third class of nonsymbiotic mutualism, somewhat miscellaneous and in many cases speculative, consists of apparently predatory interactions in which the "prey" actually benefits. Porter (247) has shown that some algae absorb phosphorus from the gut of zooplankton as they are "eaten" and usually pass through unharmed; similar

benefits may occur in copepods (79). Enhanced availability of nutrients to plants upon grazing has been suggested by Owen & Wiegert (235, 236) and by Stenseth (292), while growth-enhancing factors in grasshopper and bison saliva have been studied with mixed results (75, 128). Grazers may also retard succession and thus preserve the plants of the successional stages they prefer (56, 301).

Other predators may reduce allocation of resources to offspring unlikely to survive and thus make their prey more efficient in reproduction (310). Similarly, herbivores may change the growth patterns of their prey and possibly decrease vulnerability to physical damage (281). As these cases indicate, what is now a mutualism may have arisen from some adaptation of the prey to predation, which makes it inefficient when the predator is absent. But whatever the origin, the interaction must be seen as mutualistic if fitness and/or population growth are reduced without it. The same principles apply to nontrophic interactions that appear to be +/−, such as cowbirds' laying eggs in other birds' nests or epiphytes weighing down trees' branches: The negative impact may be exceeded by benefits such as parasite removal (285, 286) or nitrogen fixation and trapping of nutrients the tree can use (225). These cases, while often speculative, are fundamentally similar to those of pollen-feeding pollinators or nut-consuming dispersers: There is a balance of positive and negative effects on the "prey" that may shift with environmental conditions (39, 341).

THEORIES OF MUTUALISM

Ecological theory about mutualism, excluding Kostitzin's book (177), dates only from the last decade, and has been directed at two main questions: (a) When will mutualisms develop (note that we do not say "evolve") and in what sorts of species and environments will they be found? (b) When will a community involving mutualists persist (again, we do not say "be stable")?

Excluding theories concerning indirect mutualism, to be dealt with in a later section, four kinds of model can be distinguished: (a) those of individual selection, which are often of a cost-benefit type; (b) population dynamics models, with two, three, or many species; (c) models of shifts of interactions from mutualistic to predatory or competitive; and finally (d) the "keystone mutualist" concept.

Individual selection models (13, 170, 249, 271, 335, 336), though different in details, come to similar conclusions. They generally find that intimacy or symbiosis favors mutualism because the number of competitors receiving benefits is restricted. However, Wilson's (336) model shows that mutualism can evolve even with large trait groups. Roughgarden (271) and Keeler

(170) each find that major fitness gains are critical. Axelrod & Hamilton (13) do not consider games with differing payoffs (the equivalent of changes in fitness), but it seems clear that even within the "prisoner's dilemma" payoff matrix the greater the reward for mutual cooperation relative to noncooperation the more likely is cooperation. Mutualism is expected when it is valuable [e.g. protection in areas of high predation pressure (15), nodulation under competition for soil nitrogen (40)] and when it is cheap and efficient [e.g. extrafloral nectaries when ants and sunlight are abundant (170)]. What is still lacking is a theory that will predict when mutualistic solutions are preferred to nonmutualistic ones, assuming both are possible (but see 113, 260).

The population dynamics models, most starting from Lotka-Volterra competition theory and reversing the sign of the coefficients, are to some extent replies to the early contention that mutualism has a destabilizing effect on communities (211, 212, 213) and therefore should be rare. It has been shown that mutualism can be stabilized by a variety of means: strong negative density-dependence (103, 116, 183, 249, 315), curvilinearities (3, 116, 213, 288, 315, 329), frequency dependence (183), or predation (125). Furthermore, mutualism demonstrates situations in which models without either stable or feasible equilibrium points nevertheless have both species persisting indefinitely (315). Thus the criteria for stability, though widely used, are probably irrelevant to existence in the real world (315), and even highly unstable models with both mutualism and positive density-dependence may be biologically reasonable (D. H. Boucher, in preparation). Lotka-Volterra models also indicate that mutualisms with stable equilibria tend to show out-of-phase oscillations (100).

Post, Travis & DeAngelis have shown how the mathematical theory of M-matrixes can be used to examine communities in which all the interactions are mutualistic (68, 249, 305, 306). This theory may prove useful— even though communities of even three species in which all interactions are mutualistic are probably rare—since the theory also applies to communities with certain combinations of mutualistic and competitive interaction.

Other theories of mutualism are less mathematical. Boucher (39) has developed a graphic model of seed consumption to predict the population densities at which mutualism will turn into predation; the model successfully predicts the relative densities of nut-producing trees. Gilbert's concept of a "keystone mutualist" (98) whose demise would produce major shifts in community structure is analogous to the earlier "keystone predator" idea of Paine (237).

Indeed, one approach to generating predictions about the effect of mutualism would be simply to reverse predictions concerning predators or competitors. For example, if removal of a predator on a competitively dominant

species should decrease diversity, removal of its mutualist should increase it. Mutualism theory is still at a stage in which simple modifications of competition and predation models may provide unexpected insights.

We can also suggest several questions about mutualism that theorists have not considered. When will mutualisms tend to be asymmetric or symmetric (46)? If one mutualist can interact with each of two others, when will the two "compete" for it, and how? When will the fitness and population-dynamics definitions of mutualisms conflict (288)? Finally, theory that gives quantitative predictions about mutualism is almost totally lacking. Theoretically, the field is wide open.

THE DISTRIBUTION OF MUTUALISM

There are clear differences among communities in the abundances of some mutualisms. For example, angiosperms of tropical rainforests and tropical deciduous forests are almost entirely animal-pollinated (162), while the dominant species of temperate deciduous forests are wind-pollinated (= nonmutualist). Desert and tundra have numerous animal-pollinated species (81), while temperate grasslands, frequently 90% graminoids by canopy coverage, have little animal pollination. Boreal forests are similarly dominated by wind-pollinated trees. Comparable patterns hold for seed dispersal.

Myrmecophytes—plants inhabited by ants—appear to be confined to the tropics (29, 141, 149, 150). Janzen (149) found ant-acacias to be limited by the length of the dry season; a healthy ant colony required continuous leaf production by the plant. There are other peculiar patterns: Both ants and acacias are numerous and important in Australia, but ant-inhabited acacias do not occur there (132).

Ant-plant mutualism at extrafloral nectaries, while having many of the same properties, is much less specialized and more widespread. Both temperate and tropical plants are known to possess extrafloral nectaries (27, 166, 342). Existing data are incomplete but suggest that the majority of such species are tropical. Keeler (170) has recently summarized the data on cover by plants with extrafloral nectaries; it ranges from nearly 100% to zero but a temperate-tropical comparison would be premature. Most studies (27, 164, 166, 170) have found positive correlations between abundance of extrafloral nectaries and ant abundance at the site.

Ant dispersal of seeds is widespread, but some regions [e.g. Australia (30, 66)] are particularly rich. Beattie & Culver (22) found a significant correlation between the number of species with ant-dispered seeds and ant abundance at West Virginia sites, but cover by myrmecochorous plants was independent of ant abundance. Although myrmecochory is best known in

temperate plants, several tropical myrmecochores have recently been reported (133, 195), suggesting that current biogeographic information is incomplete.

Similar temperate-tropical differences show up for other mutualisms. Cleaner-fish mutualisms, fungus-gardening invertebrates, and symbiotic corals seem to be confined to the tropics. Nitrogen-fixing mutualisms, on the other hand, seem to contradict the pattern, with actinomycete-nodulated plants being rather boreal and the most tropical of the legume subfamilies (Caesalpinoideae) having only about one fourth of its genera known to nodulate. The proportions for the more temperate Papilionoidae and Mimosoideae are about 90% (7).

Mutualisms thus seem more prominent in tropical communities (213), although there are some major exceptions. However, there are several problems in interpreting this trend ecologically. There are major phylogenetic influences, and the mutualisms are by no means independent. [To add another example, Gilbert (97) notes the inverse correlation of ant-plant and ant-insect protection mutualisms.] Most fundamentally, the data in most cases are absolute abundances and not proportions. While mutualism increases toward the equator, so do species richness, productivity, biomass, and perhaps predation pressure. Thus without data on *proportions* of taxa or individuals that are mutualistic, we can say little.

Two other claims have been made concerning the distribution of mutualisms: that they require environmental stability (91, 261), and that they allow survival in marginal habitats (187). The apparent contradiction is somewhat reconciled by the fact that the first claim applies more to nonsymbiotic mutualisms and the second to symbioses. It is true that many plant colonists of disturbed areas do not form relationships with mycorrhizal fungi (146, 147), and many weedy plants are selfing or apomictic (122). However, light-gap species are frequently mutualistic (26, 230, 299).

It has also been suggested that mutualisms will allow survival in marginal habitats. The nutritional aspect is of greatest ecological importance here, with the mutualistic association better able to survive in nutrient-poor habitats (187) and on lower quality diets than the same species living separately. This can be thought of as an example of division of labor, with the elimination of redundant metabolic pathways within the association. The association is like a microcosm, having its own nutrient cycling mechanisms, which tend to keep essentials within the system rather than let them flow through in an unrestricted fashion. Consequently, the mutualists are able to thrive in circumstances, such as the nutrient-poor waters of tropical and subtropical seas or the poor soils of tropical rain forests, where nutrient loss is a severe problem (8).

Whatever the patterns of distribution, there is no doubt that mutualisms are important to the organization of many communities and the diversity of many taxa. Prime examples are the angiosperms, whose diversity and dominance expanded in tandem with those of their pollinators and, to a lesser extent, their dispersers (50, 108, 242, 259, 290). The result has been a hundred-fold increase in vascular plant richness since the early Cretaceous (50), as well as major radiations among insects, particularly Hymenoptera. Mycorrhizae may have been involved in another major evolutionary event, the invasion of the land by plants (246), and the diversity of modern fungi owes a great deal to mycorrhizal and lichenous taxa (4). The existence of coral reefs depends both on endozoic algae (238, 248, 294) and on protection mutualisms (102), while the large herbivores of grasslands generally depend on ruminant bacteria to maintain their high densities in these cellulose-rich habitats (202). Deep-sea vent communities may also depend on mutualism (57).

All these arguments for the importance of mutualism in ecosystems as we know them seem a bit trivial when we turn our attention to the likelihood that eukaryotic cells are the descendants of intracellular symbionts (205, 206, 207, 326). The serial endosymbiosis theory holds that mitochondria, chloroplasts, and other organelles are derived from symbiotic prokaryotes. Recent discoveries lending credence to this theory are reviewed by Whatley et al (326), Margulis (207), and Taylor (295).

Mutualisms are known in all kingdoms of organisms, and there is a tendency for the partners to come from different kingdoms (45). This is particularly true for obligate and symbiotic mutualisms, and may simply be a reflection of nutritional complementarity. Some taxa seem particularly likely to enter into mutualisms—e.g. *Nostoc, Trebouxia, Symbiodinium,* and *Chlorella* (207), and at a higher level, ants, coelenterates, and legumes. Some taxa participate in several mutualisms simultaneously: *Acacia collinsii,* for example, has pollination by bees, dispersal by birds, protection by ants, and probably mycorrhizae and *Rhizobium* nodules (and is also a weedy species).

THE NUMBER OF PARTNERS

Three sorts of specificity can be distinguished in examining the interaction of a mutualist with its partners—the numbers of species, of individuals, and of genomes involved. Each of these raises different questions, and all three are different from the questions of obligacy and symbiosis. However, certain correlations seem to emerge.

We call the interaction of a single pair of species "monophily." An example is the pollination of *Yucca glauca* by *Tegeticula yuccasella* (5, 251). "Oligophily" is the presence of a few species in each role—say less than five. Examples of this interaction are found in, for example, curved-beak hummingbirds and the specialized flowers they pollinate. Finally, "polyphilic" mutualisms involve multiple taxa simultaneously—e.g. yellow composites and their pollinators (flies, bees, butterflies).

Many of the most celebrated mutualisms are monophilic: in pollination [*Yucca* (5, 251), figs and fig wasps (128, 158), solitary bees and their hosts (81, 152, 244)]; ant-plant protection mutualisms [*Barteria* and *Pachysima* (154), *Cecropia* and *Azteca* (150)]; nutritive mutualisms [*Atta* and its fungi (255, 337), fungus-gardening beetles (21), at least some lichens (206), invertebrate-alga interactions (207, 222)], and others. Monophily is often hard to understand: Two species with clearly separate genomes (jumping genes notwithstanding) and independent evolutionary histories interact cooperatively. When monophily is obligate and symbiotic, the two species are often considered as one. Certainly, the pair ceases to have two sets of interactions: Interaction with one species requires interaction with the other. These are the species for which high evolutionary risk has long been proclaimed. They have given up their "freedom" and depend, evolutionarily and ecologically, on the presence of a species whose genome evolves independently. They cannot exchange genes with it, are subject to its mutability or lack of mutability, and must endure situations imperiling its survival. Selection will occur, of course, but the mutualist is a victim of the fitness of its partner, rather than a direct participant.

The conventional wisdom about monophilic obligate mutualists given above is an overstatement, of course. Species generally lumber along with numerous incomplete adaptations to today's unreliable environment, only indifferently adapted to any particular danger. Perhaps mutualistic interdependence does not engender major risks very often; whether it raises the risks of extinction over the long run is also unclear. Investigation of the population dynamics of a monophilic mutualism as compared to oligophilic congeners would be informative.

Monophilic facultative mutualisms are unknown to us. A self-compatible and self-fertilizing *Yucca* would constitute one, if such a plant existed. Since such things are by no means impossible, but only unknown, we conclude that they are selected against, perhaps for the reasons mentioned above. There are also mutualisms in which only two species interact at a given site but the pairs may vary. For example, *Acacia collinsii* forms ant-acacias with *Pseudomyrmex belti, P. ferruginea,* and *P. nigrophilosa* in western Costa Rica (149). On an individual level this might be considered monophilic, but on the population level it is certainly oligophilic.

Oligophilic mutualists would appear to have the "best of both worlds." Oligophily is the compromise between the risks entailed by specialization and the inefficiency of generalist interactions; it is common in both facultative and obligate, symbiotic and nonsymbiotic mutualisms. Much of pollination falls into this category, as well as many mycorrhizal associations, nitrogen-fixation, and mixed feeding flocks of birds.

Polyphilic obligate symbiotic mutualism is rare. Invertebrate interactions with *Chlorella* may qualify (101, 189, 307); but the taxonomy of symbiotic algae is extremely difficult, so these results may change. Most mutualist taxa are probably polyphilic facultative mutualists, simply because these broad interactions encompass so many species. Generalist pollination, extrafloral nectaries (163, 171), myrmecochory and other animal dispersal of seeds (200, 243), vesicular-arbuscular mychorrhizae (204), and vertebrates and their gut flora are examples. Obligate mutualism would appear to operate differently from facultative mutualism, with the former tending to be monophilic or oligophilic, the latter oligophilic or polyphilic. Judging from the abundance of different types, it would seem that facultative mutualisms are readily established between species but that significant coevolution is rare. The mutualisms remain casual and generalized. In a few cases, coevolution leads to major fitness gains for the partners, perhaps followed by obligacy and/or symbiosis.

This view is quite different from the one given previously, which suggested that symbiotic mutualism evolves from intimate interactions that are parasitic or commensal. It seems likely that both processes have occurred. Perhaps detailed comparison of the (presumed) histories of a variety of mutualisms would tell us about the conditions selecting for symbiosis.

In order to take full advantage of the opportunities available once the partnership is established, the interacting species must have solved the critical problems of (a) one mutualism and two sets of limiting factors and (b) finding the partner. Often the first problem is solved by the establishment of the interaction itself. It is also frequently solved by symbiosis: Living together, both species have the same set of experiences, even if they do not necessarily react similarly. Thus the symbiotic pair, confronted with the predator of one, is jointly faced with producing antipredator defenses or perishing. The nonsymbiont, on the other hand (imagine a pollinator), may return to find its partner devoured. The problem of finding the partner can also be solved by symbiosis: Putting both mutualists into each propagule (whether calf or hydra bud) is an efficient way to maintain the mutualism. Consequently, many (but not all) "highly successful" mutualists are symbiotic.

The numbers of individuals with which one partner is mutualistic ranges from one to millions (158). Wilson (336) has discussed this in the light of

"the classical group selection problem," that of the mutualist's helping its competitors as well as itself. Competition for mutualism has been found both within and between species (2, 175, 319), and the within-species competition would seem a major obstacle for the evolution of mutualism. Wilson shows that spatial heterogeneity of interaction (demes structured into trait-groups) can provide a solution; Post et al's (249) model of mutualist-commensalist competition gives the same sort of result.

The ratio of numbers of individuals of the two species interacting is an important consideration, particularly in symbiosis, and it would seem that the optimum ratio would not necessarily be the same for both species. Synchronization of reproduction can be seen as a way to maintain a more or less constant ratio (205, 223), but little is known about how such ratios vary or the role of conflicts in them.

Symbiotic mutualisms tend to create new "organisms" with two or more distinct genomes, and the cellular endosymbiosis theory suggests that all eukaryotes are such organisms (207). The dependency involved if the symbiosis is obligate implies that coordination between genomes, with elimination of redundancy, should be beneficial to the association; but this would seem to conflict with a strict "selfish gene" view. Some examples of coordination are elegant; for example, leghemoglobin in *Rhibozium* nodules is synthesized partly on the bacterial template (heme) and partly on the plant template (globin) (63). Furthermore, the structure of leghemoglobin is remarkably similar to those of animal hemoglobins. Such cases of mutualism may provide useful tests for theories of genetic selfishness.

FORMATION AND BREAKDOWN

While some mutualisms are undoubtedly highly coevolved (5, 96, 141, 149, 158, 215, 224, 251, 255, 266), and past (and the present) authors have emphasized evolutionary processes, mutualisms can easily be formed without evolution (157). Species may be preadapted to forming a new mutualism through traits presumably evolved with different partners elsewhere; e.g. the extrafloral nectaries of introduced *Vicia* in California attract the introduced ant *Iridomyrmex* (176), and cattle egrets pick ticks off deer (117). However, other apparent mutualisms have been observed to develop rapidly with little preadaptation [e.g. dogs and langurs (280), amoebae and bacteria (160)]. Given the facultative, polyphilic nature of many mutualisms, it would be an error always to interpret them in coevolutionary terms.

Once a mutualism exists, it is subject to "parasitism" in two senses. First, the association may provide a novel resource on which to prey, such as root nodules or *Acacia* thorns. Second, either partner, or a third species, may

take one of the benefits normally provided, without giving anything in return. Nectar-robbing insects (18, 19, 81, 144), ants preying on their aphids (323), cleaner-fish biting their "hosts" (106), and unaggressive ants inhabiting acacias (149) are just a few examples. Acacia-ants may take nectar from other sources (169), indicating the beginnings of either breakdown of the mutualism or oligophily. Invasion of islands, in which one partner may be left behind, often leads to the loss of coevolved traits (155, 263).

Extinction of one partner ought to have drastic effects on the other if there has been substantial coevolution; by the same token, it may result in rapid extinction of the partner and thus leave little evidence behind. In fact, despite the potential importance of this phenomenon (98), few good cases are known (296, but see 234). Loss of a substantial seed disperser community may simply result in new dispersers' taking over (159). Neither highly obligate nor highly facultative mutualisms are likely to give good evidence of extinction caused by loss of mutualist.

INDIRECT MUTUALISM

Several recent theoretical studies (180, 184, 185, 314, 320, 335, 336) have indicated that species that never come into physical contact may nevertheless positively affect each other's fitnesses or population growth rates. Data sustain these assertions in a substantial number of cases. Nevertheless, most of the following "indirect mutualisms" should be seen as speculative, interesting, and perhaps indicative of the need to revise accepted views of communities (261, 336).

Consumer-Resource

Using MacArthur's (198) consumer-resource equations, Levine (184) and Vandermeer (314) have shown how two consumers, by reducing competition and preventing competitive exclusion among the resources they eat, can benefit each other. This type of mutualism is a consequence of the interaction of two well-accepted ecological phenomena: competition, which can lead to reduced niche overlap (14, 34, 120, 138, 175, 198, 199, 213, 219, 240, 254, 312, 329, 330), and the keystone predator effect (60, 65, 99, 121, 122, 151, 182, 329). An intriguing aspect of this mutualism is that it follows directly from competition and predation. Thus it should be taken seriously by ecologists who believe competition and predation to be important in structuring communities.

An obvious consequence of the model of Levine (184) is that indirect mutualism is unlikely to occur in adjacent trophic levels. Plants' resources do not compete, therefore the plants are not able to engage in this kind of

mutualism, and are more likely to be in competition with one another. Herbivores could be indirect mutualists, but this would mean that the animals which feed on those herbivores would not be.

A promising system for the verification of a case of indirect mutualism exists in subalpine ponds in Colorado (72). The distribution of a midge larva (*Chaoborus*) in these ponds has been shown to depend on the presence of a larval salamander (*Ambystoma*), apparently through interactions between the large and small species of *Daphnia,* which are eaten by *Ambystoma* and *Chaoborus,* respectively. Large *Daphnia* were present in small numbers and small *Daphnia* in large numbers in ponds where the salamander lived. Since absence of salamanders is correlated with absence of small *Daphnia,* midges can only survive in ponds inhabitated by salamanders. Up to this point, the system appears to fit the requirements for indirect mutualism outlined above: The two consumers have different feeding habits and the resource species probably compete for food (both *Daphnia* are herbivores). To demonstrate mutualism it remains to manipulate population densities of all four species in controlled conditions.

Possible consumer-resource indirect mutualisms also exist among terrestrial herbivores. Two herbivorous rodents studied by Cameron (54) were subjected to removal experiments. Results indicated a mutualistic relationship, as survivorship and reproduction were lower in both experimental populations than in control populations, but the mechanism was not determined. On the Serengeti plain in Africa, where wildebeest, Thompson's gazelle, and zebra are the large herbivores, there is another possible case of indirect mutualism. Stomach contents indicate a dietary separation among the three (114). Thompson's gazelles prefer to feed in areas where wildebeest have grazed one month previously, since these regions have greater plant biomass (202). No data on the effects of gazelle grazing on the quantity of grasses to be eaten by wildebeest are available. This appears to be a promising case, but the full story is not yet told.

Enemies' Enemies

Indirect mutualism may also occur among competing species, as shown by Lawlor (180). If species A competes with B, and B with C, the net interaction between A and C may be mutualistic, and the principle can be generalized to multispecies communities. Lawlor's (180) analysis of niche overlap matrixes for bird communities indicates such mutualism, and Seifert & Seifert (278) found mutualisms in *Heliconia* bract invertebrate communities through removal experiments. The principle of "two negatives may create a positive" can be extended to communities containing any kind of interaction, using Levins's loop analysis techniques (185). Here again, species with

no direct interaction may affect each other's growth rates positively. The method is particularly powerful in that it generates testable predictions using only knowledge of the signs of interactions.

Friends' Friends

The reverse of the above situation can also exist: if A and C are both mutualistic with B, A and C can benefit each other indirectly. This possibility, which also can be derived from loop analysis, is indicated in a number of pollination systems. Mimicry among flowers in limited populations, such as those found in alpine areas, could enlarge the population size perceived by pollinators. This has been proposed by Macior (203) for a number of sympatric, synchronously blooming species that resemble one another and share a pollinator. Several subalpine species in Colorado, all of which are pollinated by butterflies, share an ultraviolet reflectance pattern (322). Brown & Kodric-Brown (49) have described a system in which seven species with flowers similar in appearance place pollen on different parts of the pollinators, in this case humingbirds. If mimicry did not occur, constant pollinators would switch from rare species to rare species upon perceiving that each is insufficiently rewarding, until they landed on a common species with which they would stay, to the detriment of the rare species (37). Some pollen is wasted when pollinators move between mimics, but this may favor a plant more than not being visited at all.

While competition for pollinators is thought to explain divergent flowering times (219, 319), the consequences of divergence may be a form of indirect mutualism (16, 18, 272). This has been demonstrated by Waser & Real (320) on the same species studied in the competition experiments of Waser (319). When the number of flowers on the early-flowering species was reduced, the seed set of the later-flowering species declined. In the short run, this works in one direction, to the benefit of the later-flowering species. In the long view, both species support the pollinator population, and it is reasonable to hypothesize that removing either species will reduce future pollination by reducing the resources available to the pollinators. While the above example is from the temperate zone, the phenomenon may be widespread; Schemske (272) describes "pollinator sharing" in tropical herbs. The general principle is that the increase in pollination must outweigh the loss of pollen in interspecific transfers. Mutualist maintenance over longer periods or in higher densities than would occur if fewer mutualistic species were present may indeed apply to many other systems (18, 147).

This raises another question: When does sharing a mutualist result in competition and when does it result in indirect mutualism among the

sharers? Either is possible; and at present we have little knowledge, either theoretical or empirical, with which to answer.

Not all the interactions in a "friends' friend" mutualism need be positive. Somewhat more complicated cases are found when ant protection of aphids also results in protection of the plants on which they feed (214). The important point is that the ants protect the plant and the plant indirectly (via the aphid) feeds the ants. One could extend this to systems in which the ants simply prey on insects found on the plant and thus protect it, without any direct mutualism between ant and herbivore at all. This results in "green islands" of protected plants in the vicinity of wood ant nests (179). Indeed Price et al (251a) suggest that the role of plant defenses is often indirect, through making herbivores more vulnerable to predation and parasitism; thus "Enemies should be considered as mutualists with plants."

Protection without Interaction

A final class of indirect mutualism involves species whose interactions with third species tend to reduce predation on each other. The third species may be a predator whose rate of predation on each of two prey is reduced when both are present. This may be due to such phenomena as Müllerian mimicry or predator satiation (153). It may also result from chemical protection, such as in the "plant defense guilds" proposed by Atsatt & O'Dowd (10). In all these cases, a simple safety-in-numbers (whatever the species to which the "numbers" belong) is all that is necessary to produce indirect mutualism by reducing the probability that a given prey individual is eaten.

A more complicated situation is described by Lubchenco (196) in rocky intertidal communities. A green crab eats young periwinkles, which fed upon the alga *Enteromorpha*. *Enteromorpha* provides good cover for the crabs, hiding them from gulls. Where periwinkles are not held in check, the alga *Chondrus* becomes dominant, but crabs cannot hide well in this alga. There is no known direct interaction of crab and *Enteromorpha*, so this is an indirect mutualism.

While we have no reason to believe that new evolutionary theories will be necessary to explain the evolution of any kind of indirect mutualism, it is appropriate to point out the work of Wilson in this connection (335, 336). Wilson's model depends on the existence of spatial variation within communities and thus differential feedback through loops of interactions. This condition satisfied, two genotypes may be differently affected by their interactions with other elements of the community. Thus species or genotypes can be selected to increase the abundance of other species or genotypes if this brings positive feedback. Clearly, this could result in the evolution of indirect mutualisms, and in simulations it produces many mutualistic in-

teractions (336). The question that remains is whether Wilson's model accounts for anything existing in the real world. This brings us back to the need for more information on the abundance of mutualistic interactions, particularly those that appear to be coincidental or the outcome of evolution driven by other processes.

FUTURE DIRECTIONS

Different approaches to ecology have emphasized different interactions and levels of organization. Ecosystem studies tend to look at the interconnectedness of the species in a community with respect to their roles in energy flow and nutrient cycles. This emphasizes wholeness and beneficial relationships, or at least takes a positive view of negative interactions as part of ecosystem functioning. The other major school of thought in ecology is much more individualistic in approach and has risen to preeminence with the decline of the "community as superorganism" view. After a period of being hauled out of the past and held up as a bad example of scientific practice, the organismic school has been given a tentative pardon in a commentary by Richardson (261). Richardson proposes that the organismic view is supported by evidence of the existence of "multispecies group mutualisms," or of species that play a key role in giving a community its distinctness. It remains to be seen whether future work on mutualism will help to reconcile the organismic and individualistic views. When some workers see mutualism as an integrating mechanism for whole communities (261, 336), and others view it as the endpoint of a "mutually exploitative arms race" (67), there is obviously a philosophical gap of some size to be bridged.

   What is clear is that the study of mutualism has made major advances in just the past decade. Theorists have successfully defended mutualism against the charges of being destabilizing (211, 212) and group-selectionist (333), while field studies have shown it to be widespread and important to many population and community characteristics (17, 33, 85, 96, 108, 109, 115, 152, 244, 258, 287, 300, 327, 337, 338). Given the importance of many mutualisms to human welfare (40, 51, 87, 98, 134, 136, 204, 210, 256, 339), not to mention their elegance and beauty, we can only hope that the rapid growth of interest in mutualism will continue.

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