Oecologia (2000) 125:321–330
DOI 10.1007/s004420000496

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Pursuing the big questions about interspecific mutualism: a review of theoretical approaches

Received: 3 January 2000 / Accepted: 17 July 2000 / Published online: 31 August 2000
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Abstract Along with increases in empirical information about interspecific mutualisms have come both new and refined questions about them. These questions have spurred diversification in the theoretical approaches being applied to interspecific mutualism. This theoretical literature has become large and potentially confusing, but as a whole is very relevant to answering the current important questions about mutualism. We first present three important questions about mutualisms raised by recent empirical results. (1) What factors control whether interactions become mutualistic or parasitic? (2) Why are highly specialized mutualisms rare and what are the implications of this observation? (3) What is the impact of trophic complexity on the functioning of mutualisms? Second, we highlight results of recent models of mutualism that address at least one of the three questions, and point to potentially rewarding avenues of exploration for these modeling approaches. This review should be useful to both empiricists and theorists as a roadmap to both the variety of theory currently being applied to mutualisms and to results that are in need of additional theoretical and empirical exploration.

Key words Mutualism · Parasitism · Virulence · Biological markets · Prisoner's dilemma

Introduction

Interspecific mutualisms represent some of the most important and widely studied interactions in ecology. Under the global heading of "mutualism" are found partners and interactions as diverse as hummingbirds and the flowers they pollinate, gut symbionts in the digestive tracts of animals, ants that protect plants from herbivory, and mycorrhizal fungi that exchange carbohydrates and nutrients with plants. Mutualisms are also ubiquitous geographically and evolutionarily, with mutualist partners found in all organismal kingdoms and in all ecosystems (Boucher 1985a). This abundance and diversity, coupled with their potential role in structuring communities (e.g., van der Heijden et al. 1998) and promoting coevolution (Thompson 1994), have made mutualisms the focus of many empirical studies (Bronstein 1994). From these studies, a sizable body of knowledge has accumulated regarding the natural history of mutualisms, the benefits for species involved in them, and the conditions under which they operate.

Along with increases in understanding of mutualisms have come a number of questions about how mutualistic interactions evolve, remain mutualistic, and are affected by the complex community within which they exist. Recently, a wide variety of theoretical techniques has been used to explore these questions, such as game theory [especially the iterated prisoner's dilemma (IPD); see Appendix], population dynamic models, biological market models, and models of the evolution of virulence. This surge of varied approaches to modeling mutualisms has resulted in a large and potentially confusing literature that is relevant to answering the current important questions regarding how mutualisms operate.

The specific goals of this review are therefore twofold. We present three important questions about mutualisms raised by recent empirical results. Then, for each question, we highlight results from recent theoretical models elucidating the question, and suggest new directions for theory. For empiricists, this review should serve as a roadmap to mutualism theory that may suggest which theoretical results need to be tested. For theorists, this review should foster a broader perspective regarding the approaches being used by other theorists and should highlight important empirical results that need to be explored theoretically.

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Question 1: the balance of trade in mutualisms – what factors determine if a species evolves to or behaves as a mutualist or a parasite?

Continuous variation is inherent in all aspects of mutualisms, including the effectiveness of different partner species or individuals within a species in conferring benefits (e.g., Schemske and Horvitz 1984; Parker 1995). Furthermore, most mutualisms are also characterized by apparent asymmetry in benefits received by the two sides of the interaction (Jordano 1987; Bronstein 1994). That is, in a mutualism between two species, one species often appears to benefit from the interaction much more than the other. For example, in plant-bird seed dispersal systems, when a plant is very dependent on a single bird species for the dispersal of its seeds, the bird usually utilizes seeds from many other plants and is thus not very dependent on that single plant species (Jordano 1987). Recent work has shown that when this asymmetry becomes exacerbated, a previously mutualistic interaction can become a parasitic one, and some interactions have been shown to slide back and forth between the two. One example is the plant-mycorrhizal interaction, in which some species of fungi act as strong mutualists, some as weak mutualists or weak parasites, and some can even act as strong parasites (Smith and Smith 1996; Johnson et al. 1997). Furthermore, the same species can act as a mutualist or a parasite depending on soil nutrient levels (Smith and Smith 1996; Johnson et al. 1997). Over the short term (i.e., the time scale of plasticity and behavior), the placement of potential partner species along the mutualism-parasitism continuum appears to be controlled by a "balance of trade" among the resources or services being exchanged. If environmental conditions change the costs or benefits of the interaction such that costs are greater than benefits for one of the partners, an interaction can become parasitic. However, through the course of evolution of these interactions, the mechanisms that promote the stable existence of interactions near the mutualism/parasitism boundary are not clear.

Theoretical progress and future directions: modeling interactions along the mutualism/parasitism continuum

The balance of trade: IPD models

Although continuous variation in the quantity of rewards is a feature inherent to most mutualisms, the costs and benefits to an individual are fixed and discrete in many mutualism models. In classic IPD models, for example, an organism receives a certain amount of "payoff" for cooperating with a cooperator, a certain amount for cheating a cooperator, and so on (Appendix). Furthermore, the decision to cheat or not to cheat is based only on these payoffs, according to predetermined behavioral strategies. Models with such an all-or-nothing structure cannot explore the gradual evolution from parasitism to mutualism, nor can they analyze how interactions may slide (through plasticity or behavior) along the gradient between mutualism and parasitism in response to changing environmental conditions.

Some recent IPD models take important steps toward tackling this issue, however. At least six recent papers (Leimar 1997; Doebeli and Knowlton 1998; Roberts and Sherratt 1998; Killingback et al. 1999; Wahl and Nowak 1999a, 1999b) introduce models that allow continuous variation in the payoffs associated with mutualism that can vary over the course of the game. This is an important step, giving this framework the potential for exploring the gradual movement of interactions between mutualism and parasitism. These models differ in the mechanism allowing varying payoffs, but in all of them, players' decisions about how much to invest in a partner are based in some quantitative way on a perception of the quality of their partner. The model of Doebeli and Knowlton (1998) is more appropriate than the other models for analyzing interspecific mutualisms, since it separates players into two local, intraspecifically competing classes (i.e., species), between which the potentially mutualistic interaction takes place. All other IPD models assume that all players are in the same class and could potentially compete or interact mutualistically with any other player. The only difference among players in the IPD has been, classically, in their strategies with respect to when they cooperate versus defect. Doebeli and Knowlton (1998) assume that the amount invested by an individual varies with the payoff received in the previous iteration, assuming that "healthy organisms have more to offer their partners," and they allow these investment decisions to evolve as mutations periodically arise. Under these conditions, they find that long-term persistence of mutualism is possible, though it is characterized by large fluctuations in the costs and benefits of the interaction. An interesting result is that strong asymmetry in the interaction always evolved when the two species differed in rate of evolution: the partner with the relatively higher rate of evolution always evolved to experience a relatively lower level of benefit from mutualism. This result is intuitively surprising, since one might expect a species with a higher rate of evolution to have, usually, the upper hand in an evolutionary arms race. However, it is consistent with observations of some obligate symbiotic mutualisms (Smith and Douglas 1987). Of interest would be to investigate whether this peculiar result is due to the obligate nature of the interaction assumed in this model, by allowing one or both of the species the possibility of existing or even reproducing apart from the other. Such a system might facilitate the selection of genotypes better able to punish relatively poor partners by terminating the association.

Doebeli and Knowlton (1998) suggest that future work should incorporate fluctuations in population sizes. This step would be useful, given the potential influence of population size on the benefits received from mutualism (Addicott 1984; Breton and Addicott 1992; Pellmyr and Huth 1994) and the potential influence of this rela-

tionship on the population stability of the two species (Bull and Rice 1991). This multiscale approach could be particularly powerful for understanding interspecific mutualisms, by allowing exploration of the impact of individual-level costs and benefits on population-level processes. When population dynamics are incorporated into the IPD framework, it will be interesting to see whether results of the models begin to converge on those of previous population dynamic models. Specifically, diminishing benefits from mutualism at higher population sizes would be expected to increase the stability of mutualism (see Boucher 1985b).

The balance of trade: biological market models

Biological market models show promise for addressing the balance of trade in mutualisms (question 1), since their central mechanism necessarily places interactions along a continuum from mutualism to parasitism. The basis of biological market models is that the decisions to cooperate, and with whom to cooperate, are based on a comparison of the potential benefits offered by a number of different potential partners attempting to outbid each other for the right to participate in the interaction (Noë 1990; Noë et al. 1991; Noë and Hammerstein 1994, 1995). A price of trade is determined by the balance between supply of and demand for the benefits being exchanged, and the price locates the interaction along the mutualism-parasitism continuum: a price that is very favorable for one species but not for the other is indicative of a more parasitic relationship than if the price is favorable for both species. Theoretically, this "partner-choice" mechanism can be important in determining the dynamics of a potentially mutualistic interaction (Bull and Rice 1991; Noë et al. 1991; Noë and Hammerstein 1994). A major question, however, is how often interspecific interactions actually function as biological markets. The yucca-yucca moth interaction has been suggested to sometimes exhibit partner choice (Pellmyr and Huth 1994), and partner choice, in principle, has the potential to operate in any mutualistic interaction involving multiple potential partners on either side (as most do: Howe 1984; Bronstein 1994; Waser et al. 1996; Kearns et al. 1998). In reality, however, a number of factors may dilute a classic market structure in commerce among nations (see e.g., Chacholiades 1973) as well as in interspecific biological interactions (Noë et al. 1991; Noë and Hammerstein 1994). Thus, an important question to ask is not whether a system is functioning as a biological market or not, but the *extent* to which it is doing so. Most interactions probably exist somewhere between a pure biological market and a pure non-market.

Biological market models may be particularly useful for understanding the prevalence of asymmetry in mutualisms, in which one species or partner benefits from the interaction much more than the other (Noë et al. 1991). The partner choice mechanism is consistent with the maintenance of such skewed relationships, based on a supply-and-demand argument. As long as a commodity controlled by an individual on one side of the interaction is in high demand by individuals on the other side, the individuals in control of that commodity can "bargain" for the best offering "price" among the individuals needing it. In doing so, it can choose to interact with those individuals offering the best price, or return benefit (Noë et al. 1991). Thus, an asymmetrical relationship, in which one species benefits much more than the other from the interaction, can develop when one species controls a commodity in high demand by the other (Noë et al. 1991).

One recent example of a market model of mutualistic interactions is that presented by Schwartz and Hoeksema (1998) and extended by Hoeksema and Schwartz (in press). They develop a model for two species that both need the same two resources, using the example of a mycorrhizal fungus and a plant, both of which need carbon and phosphorus. The main mechanism of their model is that whenever two species need each of two resources, and differ in their abilities to obtain at least one of those resources, they will always benefit by specializing in the acquisition of the resource they obtain more efficiently and trading with the other species for the other resource. This model is potentially useful in exploring how mutualisms may fluctuate across the mutualism/parasitism boundary in ecological time. It can be analyzed along a continuum of resource availabilities and thus can make predictions about when the interaction will shift from mutualism to parasitism along a gradient of resource availability.

An important next step will be to test predictions of this model by collecting data on resource acquisition by potential mutualists, both in association with and in isolation from each other, along gradients of resource availability. These data could be used to paramaterize the graphical approach employed by Schwartz and Hoeksema (1998), in order to test whether the pure biological market approach accurately predicts the ecological behavior of the potentially mutualistic organisms. If it does not, then the interaction departs to some extent from a strict market structure. For example, an ideal experiment to test the basic model of Schwartz and Hoeksema (1998) would be to grow facultatively ectomycorrhizal plants and fungi along gradients of soil nutrient availability as well as atmospheric CO_2 availability. One would collect data on cumulative nutrient and carbon acquisition by both the plants and the fungi, as well as surrogates for fitness of the plants and the fungi. Figure 1 shows, using a hypothetical subset of such data, how the market conditions for a potentially mutualistic interaction could be paramaterized.

The basic economic theory of international trade among nations, upon which the model of Schwartz and Hoeksema (1998) is based, makes one potentially useful prediction that has not been explored in the biological market framework to date. As discussed by Leighton (1970), in some situations, two nations can each benefit from specialization and trade even if they do not differ in

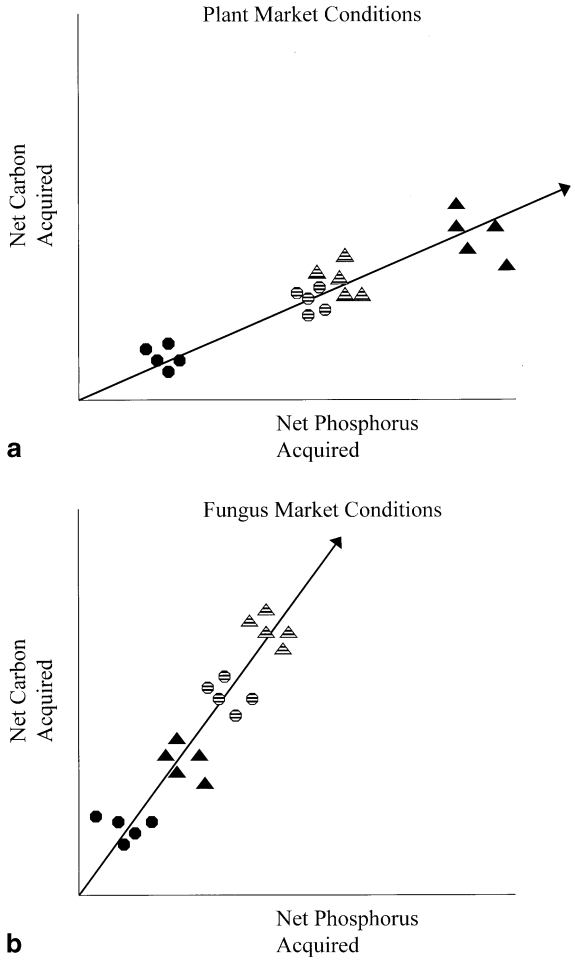

Fig. 1 Market conditions for a plant (**A**) and a mycorrhizal fungus (**B**), parameterized using hypothetical data from a two-by-two factorial experiment: high or low phosphorus (P) availability, and plant and fungus grown separately (in "isolation") or together (with "trade"). Data are cumulative carbon and phosphorus accumulation by individual plants or fungus genets (*closed triangles* high P availability, isolation; *hatched triangle* high P availability, trade; *closed circles* low P availability, isolation; *hatched circles* low P availability, trade). The *arrows* represent the preferred set of combinations of the two nutrients acquired by the two species, and correspond to the optimal consumption vector of Schwartz and Hoeksema (1998). Note that the arrow of the fungus is steeper than that of the plant, suggesting that the fungus prefers to acquire a higher ratio of carbon to phosphorus than does the plant. The market model of Schwartz and Hoeksema (1998) suggests that species will always benefit from specializing in the acquisition of the resource for which they perceive a relative acquisition advantage, and trading that resource to the other species for the other resource. However, the basic theory of international trade (e.g., Leighton 1970) suggests that different preferences by two nations, as exhibited here between the fungus and the plant, are sufficient for two nations to benefit from trade even if they have the same relative abilities to produce or acquire two commodities

their relative abilities to produce two commodities. As long as the two nations differ in their relative *preferences* or needs for two commodities, they can still profit from specialization and trade. In a biological market, this situation would be analogous to two species having different relative preferences for two different nutrients, for example. In that case, each species, in isolation from trade, would perceive a higher price for the nutrient that they "prefer." With the possibility of specialization and trade, each species should specialize in acquisition of the nutrient that they do not prefer, and trade for the one that they prefer. This mechanism allows a benefit from specialization and trade even if two species have identical abilities to acquire two resources. As a result of this mechanism, a surprising prediction emerges. If two species differ in both their relative preferences for two resources and their relative abilities to acquire those resources, in some cases they may each benefit from specializing in the acquisition and trade of the resource for which they perceive a relative acquisition *disadvantage*. Thus, differences between species in their preferences for two resources may facilitate the location of their interaction along the mutualism portion of the continuum from mutualism to parasitism. Figure 1 illustrates a hypothetical scenario in which two species, a plant and a mycorrhizal fungus, differ in their relative preferences for two resources, carbon and phosphorus.

The balance of trade: virulence models

Models of the evolution of virulence in host-parasite systems may also help us answer question 1. These models usually consider the continuum from strong to weak parasitism (high to low virulence), and occasionally model interactions fluctuating or evolving along the full continuum from parasitism to mutualism. A common prediction that emerges from this literature is that the evolution of low virulence (commensalism) and the potential for mutualism is unlikely under most conditions, but that an intermediate level of virulence will be selected for (e.g., Lenski and May 1994; van Baalen and Sabelis 1995). This conclusion is based on the assumption that highly virulent strains reproduce at a higher rate in their hosts, and thus more propagules of these strains are likely to be released during any one episode of transmission. Highly virulent strains experience a tradeoff, however, because host longevity, and hence the probability of an episode of transfer to a new host, is negatively affected by higher virulence. Thus an optimal level of virulence maximizes transmission efficiency and host longevity. Low virulence, and hence the possibility of a benign or even mutualistic interaction, will only be selected when this tradeoff is not experienced, i.e., when transmission of the pathogen is very dependent on the prolonged health or reproductive success of the host, and transmission efficiency is not maximized by high virulence.

The most extreme case in which a tradeoff between transmission efficiency and host success is not experienced is that of vertical transmission, in which the pathogen is dispersed directly from a host to the host's offspring. In this situation, the pathogen's success is directly tied to the reproductive success of the host, and there should be strong selection against a highly virulent pathogen strain that kills its host before the host has re-

produced (Ewald 1987). If we assume that host-parasite interactions exhibiting low virulence are more likely to evolve into mutualistic interactions, then the host-parasite literature suggests that models exploring the evolution of interactions across the boundary between mutualism and parasitism should consider mode of transmission as a potentially important factor. In fact, a few previous models of the evolution of mutualism from parasitism have relied heavily on vertical transmission of the parasite for stable mutualism to be possible (Yamamura 1993, 1996; Maynard Smith and Szathmáry 1995). A prediction that emerges from these models is that in potentially mutualistic systems, cheaters (parasites) should be less prevalent or successful the more they are transmitted vertically. A fascinating example of a host-pathogen system that seems to fit these predictions is described by Herre (1993). In a system of nematodes parasitizing fig wasps, the degree of virulence of the nematodes was closely correlated with the degree of horizontal relative to vertical transmission. One example of a mutualism that may be stabilized by vertical transmission is the interaction between endophytic fungi and their grass hosts (Clay 1990). These fungi are transmitted in the seeds of their host plants, and benefit their hosts in a number of ways including increased resistance to herbivores.

Two recent models outline the conditions under which the evolution of mutualism from parasitism can occur in the absence of vertical transmission (Matsuda and Shimada 1993; Genkai-Kato and Yamamura 1999). Both depend on the assumption of the evolution of by-product benefits from the parasite to the host, for which the parasite experiences no cost. The model of Genkai-Kato and Yamamura (1999) also requires, for the evolution of mutualism, that the host exhibit some ability to punish overly exploitative parasites (i.e., partner choice). Thus, models of host-parasite interactions along the continuum from mutualism to parasitism suggest that in general we expect mutualism to be favored to the extent that transmission of the symbiont depends intimately on the prolonged health or reproductive success of the host, as in vertical transmission. In the absence of such conditions, by-product benefits and partner choice for the host may be required for mutualism to evolve.

An extensive survey of the mechanisms of benefit exchange by mutualists (Connor 1995) supports the notion that by-product benefits should be extremely important in the evolution of mutualisms from parasitisms. Connor suggests that two of the most commonly studied types of mutualism, between plants and their animal pollinators and seed dispersers, began as parasitisms of the plant by the animal. In some instances, the plant received a sufficient by-product benefit from the animal (pollination, seed dispersal) for the interaction to function as a mutualism. Since the origin of these interactions, many plants have evolved investments in the interaction, such as nectar for pollinators or the fruit surrounding the seed in seed dispersal interactions. A logical direction for models of the evolution of mutualism from parasitism via by-product benefits would be to allow for the possible evolution of investment by the partners. As discussed above, recent IPD models allow investments to evolve, but do not consider by-product benefits. We are not aware of any models that simultaneously consider by-product benefits and allow the evolution of investment.

Question 2: why are highly specialized mutualisms so rare in nature, and what are the implications of this observation?

Highly host specific mutualisms are extremely rare in nature (Howe 1984; Bronstein 1994; Waser et al. 1996; Kearns et al. 1998) and, in fact, multiple species usually participate on both sides of the interaction (e.g., Fig. 2; see also Horvitz and Schemske 1990; Thompson and Pellmyr 1992; Pellmyr and Thompson 1996). For example, in the interaction between plants and arbuscular-mycorrhizal fungi, most systems are characterized by many plant species and many fungal species, with most of the possible plant-fungus pairs of species interacting to some degree (Smith and Read 1997). The generalized nature of most mutualisms may have important implications for the response of species to changes in the abundance of or benefits offered by their partners. For example, a simple two-species model of a one-to-one mutualism might predict that decreased abundance in one of the species would necessarily hurt the partner on the other side of the interaction. If there are multiple competing species on one side of a mutualism, however, then decreased abundance of one of these species could simply result in increased abundance of an alternative acceptable species, with no negative impact on species on the other side of the interaction (e.g., Davidson et al. 1989). The lack of specificity in many mutualisms may also affect the evolution of these interactions (Janzen 1980; Thompson 1994; Waser et al. 1996; Pellmyr et al. 1997). For example, even if specific species pairs are more efficient mutualists with each other than with other potential partners, a diverse community of potential partners may

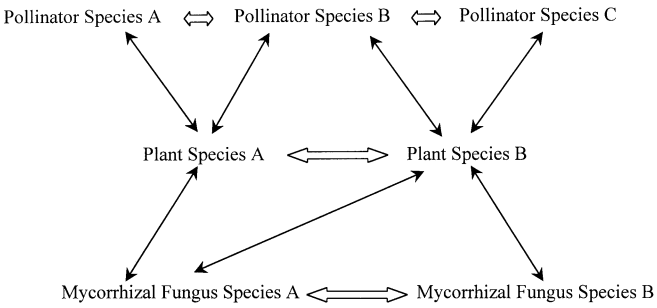

Fig. 2 A hypothetical community involving two plant species engaged in two types of mutualism (mycorrhizal and pollination). This is probably a very common situation in nature. Solid black arrows (↔) represent interactions that are usually mutualistic, while hollow arrows (⇔) represent interactions that are usually competitive

result in a selective regime that is too diffuse to allow tight coevolution between two of the species.

Theoretical approaches and future directions: lack of specificity in mutualism

Lack of specificity: a simple mean-variance model

What selective forces encourage the development of generalization in mutualisms? Waser et al. (1996) develop a simple model for pollination systems that makes a number of predictions along these lines. Most important, it suggests that while plants and pollinators may gain temporary advantages by specializing on partnerships that are particularly efficient, temporal or spatial variation in the presence of potential partner species will select against the evolution of very specific interactions. For example, the relative abundances of flowering plant species at a site can vary significantly over time, such that the evolution of specialization on any one plant species would not be advantageous in the long term (Waser et al. 1996). In fact, a negative effect of partner or resource unpredictability on the evolution of specialization is nearly ubiquitous in models of the evolution of specialization (Futuyma and Moreno 1988; Hoeksema 1999).

Lack of specificity: virulence models

Unique predictions about the evolution of generalization emerge from models of the evolution of virulence in symbiotic interactions. A question that is commonly asked by these models is: how do diverse cohorts of mutualist species coexist? Both simple models of the evolution of symbiosis (e.g., Maynard Smith and Szathmáry 1995) and epidemiological models of the evolution of virulence in the interaction between a host and multiple parasite strains or species (e.g., Bremerman and Pickering 1983) predict a competitive exclusion principle where there will always be selection for a more virulent (i.e., less mutualistic) strain or species, since virulence is expected to be positively correlated with the reproductive rate of the parasite. Thus, all else being equal, a cheater should always be able to invade and replace mutualist species. This idea is analogous to the principle of competitive exclusion in ecological communities of competing species where one resource is limiting (Gause 1934).

Two recent models independently proposed a similar mechanism that may allow coexistence of benign parasites (or mutualists) with virulent parasites (or cheaters). Nowak and May (1994; see also May and Nowak 1994) present a model of "superinfection" and the evolution of parasite virulence that is similar mathematically to a metapopulation model presented by Tilman (1994). Superinfection is the process by which a more virulent parasite strain colonizes a host and outcompetes a less virulent strain if there is one present. New, uninfected hosts replace hosts that die, at a rate sufficient to maintain a stable host population. These authors find that if we assume a tradeoff between competitive ability within a host/patch (which is positively associated with virulence) and transmission rate (through better colonization ability or through allowing the host to live longer), multiple strains can coexist that vary in their level of virulence, though the overall level of virulence is higher than in the absence of superinfection. While mutualism per se is not included in these models, the ability of low-virulence strains to persist in the presence of high-virulence strains at least allows for the possibility of the evolution of mutualism through the gain of a by-product benefit by the host.

Despite the potential for competition/colonization tradeoffs to explain the maintenance of diversity in systems of competing species, few complete data sets have been collected with which to test these predictions, especially for communities of competing mutualists. One system that may be amenable to such empirical tests is the interaction between trees and ectomycorrhizal fungi. These trees have large root systems that usually harbor a diversity of fungal species. Root tips, the site of fungus colonization, are continuously dying and being replaced by new root tips. These new root tips are colonized by fungi growing from spores or from nearby, colonized root tips. If the better colonizers are the poorer competitors for root tips, then individual root tips could function as hosts in the models of May and Nowak. Fungal diversity would be maintained because new root tips are produced fast enough to allow the better colonizers to escape being outcompeted by the better competitors. "Early-stage" ectomycorrhizal fungi such as *Hebeloma* and *Laccaria* species have been suggested to be relatively better colonizers of tree seedling roots than so-called "late-stage" ectomycorrhizal fungi such as *Cortinarius* and *Russula* species (see e.g., Bowen 1994). Are the better colonizers poorer competitors? Pairwise fungus-fungus competition experiments could be used to determine a competitive hierarchy, and colonization ability could be estimated through observations of fungal colonization of newly field-planted, previously uncolonized host plants. If competitive ability is found to be inversely correlated with colonization ability, then these parameters could be combined with data describing root turnover in a superinfection model to determine whether competition/colonization tradeoffs are sufficient to explain the coexistence of ectomycorrhizal fungi in a root tip metapopulation.

Lack of specificity: IPD models

While IPD models to date have not addressed generalization in mutualisms, in the sense that they have not explicitly incorporated multiple competing species on either side of a potentially mutualistic interaction, we see no reason why they cannot. Doebeli and Knowlton's

(1998) IPD model of mutualism went so far as to subdivide the individuals in the model into two guilds, within which intraspecific competition takes place, and between which potential mutualism occurs. Including multiple species in the guilds on either side of the interaction, with each individual interacting with more than one species at a time, would allow exploration of the impact of generality on mutualisms in this very useful modeling framework. While Doebeli and Knowlton's (1998) model predicts that long-term persistence of mutualism is possible, we might predict, based on the results of host-parasite models (e.g., Nowak and May 1994; see discussion above), that the average interaction might evolve to be relatively less mutualistic when multiple varying symbionts are competing within individual hosts.

The incorporation of multiple potential partners into any modeling framework will allow greater understanding of the role of cheating in mutualisms because of the impact of generality on the options available to both the cheating species and the species being cheated. The decision to cheat, in which an individual receives benefits but does not reciprocate to its partner, may be affected by the risk of ending the relationship entirely. This risk may be greater when a cheated individual has the opportunity to switch to an alternative partner, as in partner choice models (Noë and Hammerstein 1995). Dugatkin and Wilson (1991) and Enquist and Leimar (1993) present patchy IPD models that allow exploitative individuals to switch from patch to patch in search of generous, exploitable, partners. As discussed by Noë and Hammerstein (1995), this partner switching is only one possible partner choice strategy. A full partner choice model would also include the ability to choose a new partner based on the relative quality of a number of potential partners. The impact of cheating will also be affected by whether or not the cheater has the option of switching to alternative potential partners. If the species being cheated becomes too scarce (due to being cheated) to provide sufficient resources for the cheater, the cheater may switch to an alternative partner before driving the first partner to extinction. This situation allows the cheated species a chance to increase again in numbers, but also prevents sanctions against strong cheaters. These predictions would be profitably explored in a game-theoretical context.

Question 3: how does trophic complexity influence the persistence of mutualism?

Mutualisms can be strongly influenced by the presence of additional trophic levels, often in ways that are not immediately obvious. For example, they may not be mediated by changes in density or biomass of the species being affected. Werner and co-workers have repeatedly demonstrated the prevalence of "trait-mediated" indirect effects of predators on the interaction between other species in animal communities (e.g., Eklov and Werner 2000; Peacor and Werner 1997), whereby the behavior and resulting interaction strength between two species (e.g., competing herbivores) can be modified by the presence of additional species in other trophic levels. Though this example does not involve mutualism, it illustrates the potential for species in other trophic levels to influence interactions in a subtle way. In one recent example involving mutualism, Strauss et al. (1999) found that damage from herbivores can have negative effects on the ability of *Brassica rapa* plants to attract pollinators. The herbivore can potentially disrupt the plant-pollinator mutualism, and once again the effect is not density mediated. There is no reason to think that such effects are not prevalent in systems involving mutualistic interactions, but this issue has been little explored empirically or theoretically.

Many species may be involved simultaneously in more than one type of mutualism (Fig. 2). As a result, a potentially limiting resource may have to be allocated to traits associated with different partners. If allocating resources to one of these partners results in a decrease in allocation to another (as would be expected if energy budgets are limited), then variations in the current strength of one interaction may influence the outcome of another one. Furthermore, the predicted effects of such a tradeoff will differ depending on the shape of the tradeoff function, i.e., whether the total amount allocated varies with the proportion allocated to different recipients. For example, a plant may have to allocate carbon to mycorrhizal fungi, *Rhizobium* bacteria, and to fruit or nectar for seed dispersers and pollinators. If increased soil nutrient availability decreases allocation to the mycorrhizal mutualism (Smith and Read 1997), more resources may be available to invest in a seed or pollen dispersal mutualism. However, physiological constraints may prevent perfect redistribution of the resource (carbon) such that a unit of carbon previously allocated to mycorrhizal fungi is not completely available for allocation to pollination. Although tradeoffs between different mutualisms have not been specifically investigated empirically or theoretically, studies have demonstrated the presence of allocation tradeoffs involving, for example, plant defense and reproduction (Koptur 1985; Agrawal et al. 1999).

Theoretical progress and future directions: trophic complexity and mutualisms

Trophic complexity: interaction web models

Interaction web models based on sets of differential equations could seemingly be readily used to explore the impact of trophic complexity on the population dynamics of mutualists. An interaction web model simultaneously considers the effects of multiple species on one or both sides of a potentially mutualistic interaction, as well as the effect of species in additional trophic levels. Unfortunately, this modeling approach has yet to be explored adequately with regards to mutualisms – most complex interaction web models are pure "food web"

models, including only interactions in which organisms consume one another (Polis and Winemiller 1996). While some of the benefits exchanged in mutualisms fit this description, many do not, and these are necessarily excluded from a strict food web. In one example of an interaction web model involving mutualism, Ringel et al. (1996) introduce a four-species differential-equation model that includes two plants, an insect that pollinates both plants, and a predator of the insect. They find that the addition of a second mutualist increases the local stability and community persistence of the model, compared to the model with just one mutualist. This result contrasts with typical two-species models, which tend to be unstable unless they include some mechanism for diminishing returns at higher densities of the mutualists (Boucher 1985b). Although the study of Ringel et al. (1996) would have been stronger if they had explored a wider range of parameter values for interactions between the species involved, these results suggest that the difficulty of stabilizing mutualism in two-species analyses may be misleading when not considered in a wider community context. These conclusions should caution us from overinterpretation of the results of simple models because they show that by increasing the complexity of a model system only slightly, we can produce model conclusions that are dramatically different. The few examples of complex interaction web models including mutualisms (e.g., Heithaus et al. 1980; Ringel et al. 1996) have yielded some promising results, but these should still be considered preliminary, as this approach has not been adequately explored.

Trophic complexity: biological market models

A difficult challenge for the biological market framework would be to develop models that examine the interaction between species simultaneously involved in multiple types of mutualism, e.g., a plant interacting both with pollinating animals and mycorrhizal fungi (Fig. 2). This structure would be analogous to the inclusion of more than two nations in basic models of international trade, which would not fundamentally change the mathematics involved (see e.g., Chacholiades 1973). As in the simple two-nation models, each nation simply imports goods that it does not produce itself, and exports goods that can be sold for profit on the world market. All nations that perceive a relative production advantage for a commodity can profit by trading that commodity on the international market. A biological market model such as that presented by Schwartz and Hoeksema (1998) could be extended in this manner to include three or more species exchanging three or more resources. For example, a plant could simultaneously be trading carbon to both a mycorrhizal fungus and *Rhizobium* bacteria. The mycorrhizal fungus trades mineral phosphorus to the plant for carbon, while the bacterium trades mineral nitrogen. The price of carbon for either the fungus or the bacterium would be partially determined by the demand of the other. The graphical approach utilized by Schwartz and Hoeksema (1998) could still be employed, with a graph of market conditions being drawn for each of the three species. So far, the extension of this approach to more than two types of mutualism seems simple. However, basic theory of international economics tells us that relaxations of some key assumptions of the pure theory of trade quickly complicate analyses of global trade among more than two nations (Leighton 1970; Chacholiades 1973; Grubel 1977). For example, the pure theory assumes perfect competition among all nations involved. However, in reality, extremely large output of a commodity by a highly developed nation can outweigh the comparative advantage for that commodity held by a smaller, less-developed nation, allowing the larger nation to undersell the smaller nation. In biological markets, this may mean that while a smaller or less abundant species in a guild holds a theoretical comparative advantage for a certain resource, which should allow it to profit from specialization and trade, a larger or more abundant species may in effect "unfairly" outcompete the smaller species by underselling it, preventing the smaller species from profiting through trade.

Conclusion

This review has highlighted recent theoretical progress in answering important questions about mutualistic interactions. The various modeling approaches discussed here were developed to answer different types of questions, and so in some sense comparing their utility in answering the same questions is inappropriate. However, with respect to the three questions about mutualism highlighted here, no one modeling approach is expected to be a panacea – each has strengths as well as inherent weaknesses. We have tried to suggest how each approach can take advantage of its strengths and push the boundaries of its weaknesses to contribute to answering some important questions about mutualism. We recognize that extremely realistic models may be analytically cumbersome, and may not be general (Levins 1966), but we hope that, as in some other cases, the most general models can also be the most realistic (Orzack and Sober 1993).

The three questions about mutualism presented here are clearly not mutually exclusive. For example, determining the factors responsible for the balance of trade in mutualisms (question 1) and understanding the impact of the complex community context of mutualisms (questions 2 and 3) will both lead to greater understanding of the potential impact of cheaters on mutualisms, as discussed above.

None of the theoretical literature we have reviewed, and little of the empirical work, thoroughly relates specific costs and benefits exchanged in a potentially mutualistic interaction to components of fitness of the organisms involved. While we recognize that empirical researchers have struggled to accomplish this task with

limited success, we encourage continued efforts in this direction. With the goal of linking specific costs and benefits of mutualisms to success of the organisms involved in mind, empiricists should attempt to budget specific costs and benefits exchanged in their systems and keep track of how these costs and benefits are related to the fitness of the organisms involved.

It has been argued (Kareiva 1989; Steinberg and Kareiva 1997) that there are great benefits to be reaped through a more thorough dialogue between theoretical and empirical research. We hope that this review is successful in furthering this dialogue in the investigation of mutualistic interactions.

Acknowledgements We thank the following for helpful discussion and/or comments on earlier drafts of this paper: L.S. Adler, R. Monson, W. Morris, M. Sanchez, M.W. Schwartz, J.A. Umbanhowar, and D.P. de Valpine. This material is based upon work supported by National Science Foundation Graduate Fellowships.

Appendix 1 The iterated prisoner's dilemma

The iterated prisoner's dilemma (IPD) is a specific case of a repeated two-player game, the characteristics of which are given by the payoff matrix

	C	D
C	R	S
D	T	P

During each round of the game, each player can cooperate (C) or defect (D) and receive a payoff based on its own choice (rows of the matrix) and the opponent's choice (columns). If both players choose to cooperate, they both receive R units of payoff. If both choose to defect, they both receive P units of payoff. If one player cooperates and the other defects, the cooperator receives S and the defector receives T. The two general conditions of the game are that $R > P$ and $R > \min(S,T)$.

If $T > R$ and $P > S$, then we have the specific scenario that has been dubbed the prisoner's dilemma, in which the short-term payoff is always larger for defection than for cooperation. One common extension of the prisoner's dilemma is that in which the interaction is repeated and participants remember the outcome of prior interactions, known as the iterated prisoner's dilemma. In an IPD, mutual cooperation can be maintained if the players use specific strategies for choosing whether to cooperate or defect. One such strategy is called "tit for tat," which dictates that players cooperate on the first play and then do what the opponent did on the previous play (Axelrod and Hamilton 1981).

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