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Mutualisms as Consumer-Resource Interactions

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Recognition that predator-prey interactions involve consumer-resource interactions has served as a conceptual foundation for mechanistic understanding of the influences of predation on patterns and processes in ecology and evolutionary biology. Conversely, although mutualism is increasingly recognized as important in nature, it is still often perceived as an eccentric case of interspecific interactions with little relevance to major patterns and processes in ecology. This perspective stems, in part, from the paucity of general principles that can unify mutualistic systems varying greatly in natural history. In this chapter, we develop one such principle, which is that mutualism, like predator-prey interactions, is a consumer-resource interaction.

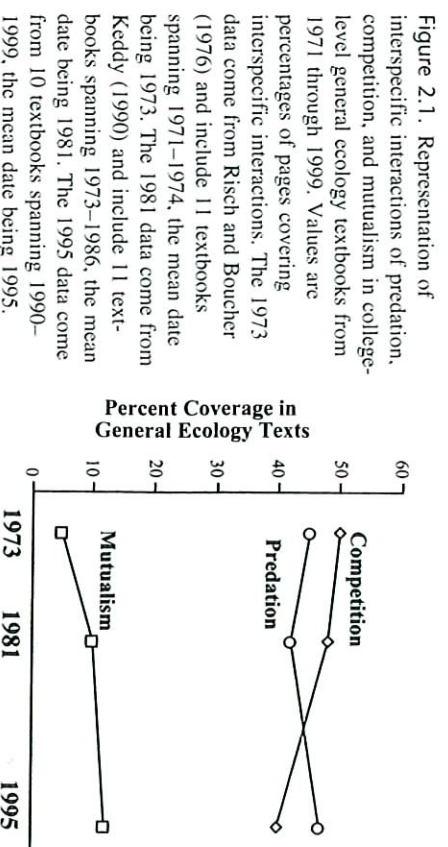
Almost all mutualisms involve the transfer of energy and nutrients between individuals of two species; one species functions as a consumer and the other as a resource. Yet mutualism differs from predator-prey interactions in that the outcome of the consumer-resource interaction results in a net positive effect on per capita reproduction, survival of both populations, or both. We identify three ways in which consumer-resource interactions take place within mutualisms: two-way consumer-resource, one-way consumer-resource, and indirect interactions. We examine many different mutualistic systems, identifying which of these three means of consumer-resource interaction each exemplifies. Using case examples, we discuss why the exchange of resources and services leads to mutualism, rather than to predation or competition. We further discuss how consumer-resource mutualisms are often context-dependent, varying with the supply of an extrinsic resource or with the presence or abundance of a predator or parasite of one of the mutualists. The consumer-resource interaction between individuals of mutualists' populations may often generate the mechanism underlying the interaction's effects on population-level attributes, such as the growth or size of a population.

Interspecific interactions play key roles in the ecological and evolutionary dynamics of populations, as well as in the structure and dynamics of food webs, communities, and ecosystems (Jones and Lawton 1995, Polis and Winemiller 1996, Fox et al. 2001). Historically, predation and competition has received much more attention than mutualism. This bias is exemplified in the attention given to interspecific interactions in ecology textbooks. Over the past 30 years, the focus on predation has remained fairly constant, coverage of competition has decreased, and coverage of mutualism has increased (Figure 2.1). Nevertheless, mutualism currently represents only 12% of text pages devoted to interspecific interactions, while predation and competition each represent over 40%. Moreover, recent monographs on population dynamics thoroughly explore the roles of predation and competition, but barely address mutualism (Murdock et al. 2003, Turchin 2003).

Despite this relatively poor coverage, mutualisms are becoming increasingly recognized as fundamental to the structure and function of biological systems worldwide. Examples of some key mutualists in habitats throughout the world include pollinators and seed dispersers in tropical forests, nitrogen-fixing bacteria in deserts and agroecosystems, mycorrhizal fungi in grasslands, lichens in tundras, corals in marine systems, and microbes in deep-sea vents. Influences of mutualism transcend multiple levels of biological organization, ranging from cells to populations, communities, and ecosystems. For example, mutualism may have been key to the origin of eukaryotic cells and to the radiation of angiosperms (Margulis 1975, Crepet 1983). Mutualism can be critical to the reproduction and survival of many plants and animals, and to the cycling of nutrients. Moreover, the ecosystem services that mutualists provide, such as C, N, and P cycles associated with plant-microbial systems, are leading them to be increasingly considered a conservation priority (Costanza et al. 1997, Naban and Buchmann 1997, Wall and Moore 1999).

Our understanding of mutualism has been hindered by the relative lack of general principles that generate predictions and syntheses across mutualistic systems that differ greatly in their natural history. This lack may partially explain why treatments of mutualism in textbooks and monographs are often short and focus on natural history stories of particular systems, rather than on broad ecological and evolutionary concepts, which occur more commonly in discussions of predation and competition. Turchin (2003, p. 30) suggests that mutualisms are not necessarily unimportant, "but unlike trophic [or consumer-resource] interactions, mutualisms do not seem to be of universal importance." "Mutualism could be the most important interaction in some specific population systems," Turchin explains, "but all organisms are consumers of something, and most are also a resource to some other species." Turchin (2003) suggests that the attention of researchers is devoted to trophic and consumer-resource interactions, rather than to mutualism, because such interactions appear most important to population dynamics. Indeed, the consumer-resource dichotomy has been central to understanding predator-prey interactions and competition (MacArthur 1972, Abrams 1980, Tilman 1982, Murdoch et al. 2003, Turchin 2003).

The point has generally been missed, however, that mutualism also involves trophic interactions that reflect a consumer-resource dichotomy. In this chapter, we argue that consumer-resource interactions are central to nearly all mutualisms, and that this mechanism of interaction between individuals can potentially unify our understand-



ing of mutualistic systems differing greatly in their natural history. Moreover, linking three interspecific interactions that fundamentally differ in outcome (mutualism, predation, and competition) offers both a challenge and a reward. By recognizing that consumer-resource interactions are central not only to predation and competition, but also to mutualisms, we may be taking a step toward generalizing the influences of interspecific interactions, and mutualism in particular, on population processes. We hope the consumer-resource approach will encourage the application of the large body of theoretical studies developed in the context of predation and competition to provide new insights into the study of mutualism. Below, we discuss the general applicability of a consumer-resource framework to interspecific interactions. We then show that mutualistic interspecific interactions can be characterized in one of three ways under a consumer-resource framework. We discuss how mutualisms are often context-dependent, varying with the supply of an extrinsic resource, with the presence or abundance of a consumer of one of the mutualists, or with both. We conclude by discussing some of the advantages and limitations of treating mutualisms as consumer-resource interactions.

Consumer-Resource Interactions

Interactions between populations occur when the actions, traits, or density of individuals of one population result in a change in some attribute of another species' population (Abrams 1987). Population attributes may include per capita reproduction or survival, population growth, population size or density, and mean character values of individuals. Population interactions can be classified in two general ways (Abrams 1987). First, interactions can be characterized according to effects or outcomes of the interaction between individuals. Thus, (+, -), (+, 0), (-, -), and (+, +), with +, 0, and - signs refer to positive, neutral, or negative effects, respectively, on the population attribute of interest. Second, interactions can be characterized according

to the mechanism, that is, the ways in which individuals interact (e.g., a predator eating a prey, or an animal consuming nectar and pollinating a flower).

Consumer-resource interactions were primarily incorporated into the study of predation and competition in order to provide a mechanistic perspective on interactions among individuals and the resulting effects on population attributes (MacArthur and Levins 1967, MacArthur 1972, Abrams 1980, Tilman 1980, Tilman 1982). However, the consumer-resource interaction is currently used as often in an outcome-based context as in a mechanism-based context. Consumer-resource interactions have become almost synonymous with a +, - outcome of trophic interactions, including predator-prey, parasite-host, parasitoid-host, and herbivore-plant interactions. If consumer-resource interactions are classified based on +, - interaction outcomes, then by definition any interaction not resulting in a +, - outcome is not a consumer-resource interaction. Yet consumer-resource interactions are not limited to trophic interactions. They can include interactions between populations and abiotic resources, such as plant uptake of nutrients or detritivore use of decaying vegetation. Moreover, consumer-resource interactions do not always result in +, - outcomes. For example, two or more species using the same limited resource can lead to exploitative competition -, -. Competitors may include multiple predator species (consumers) using the same prey species (resource), or multiple plant species (consumers) using the same limited nutrient (resource). Similarly, as we will show, nearly all mutualisms +, + involve consumers and resources. Hence, consumer-resource interactions are a common feature of most interspecific interactions. The simple transfer of energy or nutrients between individuals of two populations does not necessarily mean the interaction outcome is +, -. Here, we suggest that the consumer-resource interaction is a general mechanism by which individuals of two different populations interact, often contributing to effects on population-level attributes.

Mutualism: Consumer-Resource Interactions

Mutualism has been characterized in terms of both the mechanism by which individuals interact and the effect or outcome on populations. The outcome definition of mutualism is simply that both species benefit. Nearly all mutualisms, however, involve both benefits and costs to both interacting species. Benefits result from acquiring a resource, often nutritional, or a service, often dispersal or protection, from a partner. Costs arise as a consequence of providing a resource or service to a partner. Both benefits and costs are implicitly understood to increase or decrease reproduction or survival (or both), or possibly some energetic currency, as these are the fundamental units for ecological and evolutionary processes (Brown 1995). Hence, the outcome of mutualism can be more precisely defined as net positive effects on per capita reproduction and/or survival of both interacting populations, with the understanding that interaction strengths are not simply (+, 0, -), but vary along a continuum (Paine 1980, Paine 1992). We must point out, however, that at this stage in the study of mutualism we do not really know how large the costs are of mutualism.

Mutualisms can also be characterized by how individuals interact. This characterization centers around the three most common benefits that mutualists provide one

another: nutrition, transportation of gametes or progeny, and protection from natural enemies or the abiotic environment (Boucher et al. 1982). Although these characterizations have great utility for explaining mutualism, they are based on the perspective of only one of two interacting mutualists. For example, plant-pollinator interactions are classic examples of "transportation mutualisms," but this classification is obviously phyto-centric, because the pollinator gains a food resource of nectar and/or pollen while the plant gains in reproduction and transportation of gametes. As we will show, nearly all mutualisms involve food, or nutrition, exchange in one or both directions.

We emphasize consumer-resource interactions in mutualisms as a way to describe the effects of the interaction on population-level attributes. We identify three ways in which consumer-resource interactions take place in mutualisms: two-way consumer-resource interactions, one-way consumer-resource interactions, and indirect interactions. We discuss each of these mechanisms of interaction and their relationships with the benefits and costs of mutualism. We define these mechanisms of interaction in Table 2.1, depict each of them graphically in Figure 2.2, and provide examples in Table 2.2.

Mutualisms with Two-Way Consumer-Resource Interactions

In one group of mutualistic interactions, individuals of each of the two species consume a resource provided by the other (Table 2.2; Figure 2.2A,B). We refer to these as *two-way consumer-resource mutualisms*. Familiar examples include lichens, corals, digestive symbioses, and plant-rhizobial interactions (Table 2.2; Figure 2.2A,B). Resources may be either produced by one mutualist and consumed by the other, or harvested from the environment by one mutualist and consumed by the other. In two-way consumer-resource mutualisms, each mutualist benefits from resources provided by its partner, and each mutualist incurs a cost of provisioning resources to its partner. Mutualistic outcomes occur when benefits of consuming the resource provided by each partner exceed costs of providing resources. Recently, Hoeksema and Schwartz (Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2001, Hoeksema and Schwartz 2002) have shown that mutualisms can be characterized by the net benefit to each partner. Table 2.1. Three Means by Which Consumer-Resource Interactions Are Embedded within Mutualisms

Two-Way Consumer-Resource Mutualisms

Two species each consume a resource provided by the other. Resources may either be a product of one species, or be harvested by that species and then provided to the other. The interaction is mutualistic when benefits received by each species from the acquired resource exceed costs of providing a resource to the partner.

One-Way Consumer-Resource Mutualisms

Only one species consumes a resource provided or harvested by its partner; in return, the resource provider receives some service (dispersal or protection) from its partner, which directly benefits reproduction, survival, or both. The interaction is mutualistic when costs of producing or harvesting the resource do not exceed the benefits of receiving that service, and vice versa.

Indirect Mutualisms via a Third-Species Consumer or Resource

Two species, neither of which is a consumer or resource of the other, form an indirect mutualism via a third species that is a consumer or resource of one or both of the other two.

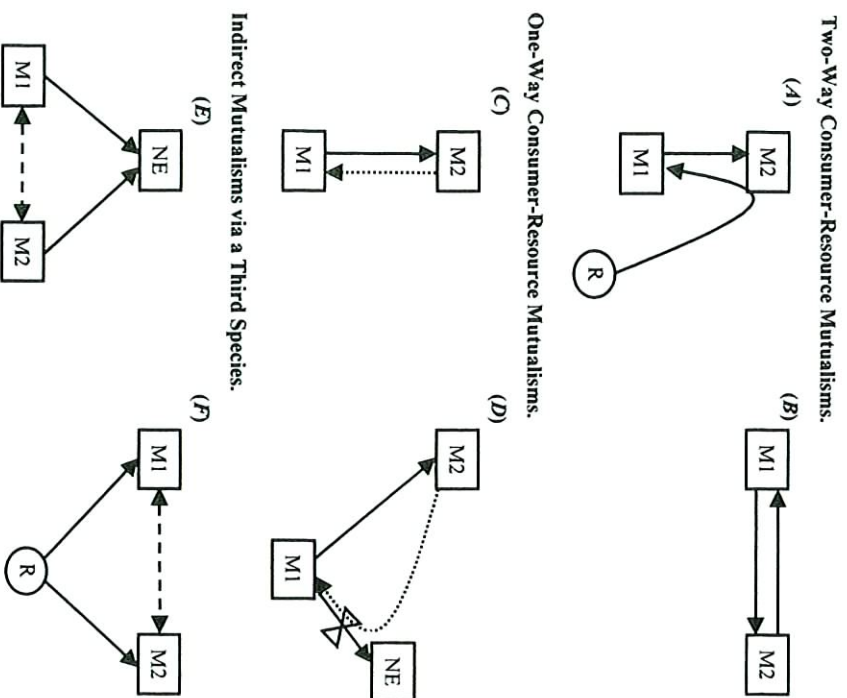


Figure 2.2. Graphical depictions (using topological approaches of food web diagrams) of the three means by which consumer-resource interactions are embedded within mutualisms: two-way consumer-resource (A,B), one-way consumer-resource (C,D), and indirect mutualistic interactions (E,F). Boxes with M1 and M2 represent mutualist species 1 and 2. A circle with R is a resource extrinsic to the pairwise interaction; the resource could be a third species or an abiotic nutrient. A box with NE is a natural enemy, such as predator or parasitoid. A solid, one-headed arrow is a consumer-resource interaction; the arrow points from the resource to the consumer and is the direction of energy flow or nutrient movement. A dotted arrow is a nontrophic, service (e.g., dispersal or protection). The arrow points from the mutualist providing the service to the mutualist receiving the service. A double-headed dashed arrow is a two-way indirect mutualistic interaction between M1 and M2 that arises via a third-party consumer or resource. In protection mutualisms (D), the service is provided by M2 by modifying the rate at which M1 interacts with NE. Joined triangles indicate rate modifier.

Table 2.2. Examples of Mutualistic Systems in Nature

Mutualism	Partners	Figure 2.2	Consumer
1. Two-Way Consumer-Resource Mutualisms			
Lichen	Fungi, algae	A	Fungi
Coral	Coral, Zooxanthellae	A	Algae
Mycorrhizal	Plant, mycorrhizal fungi	A	Coral
Nitrogen fixation	Plant, rhizobial bacteria	A	Zooxanthellae
Myrmecotrophy	Plants, ants	A	Plants
Ant agriculture	Ants, fungi	A	Mycorrhizae
Digestive symbioses	Aphid-bacteria	B	Plants
	Ruminant, bacteria/protozoa	B	Rhizobium
	Termite, protozoa	B	Ants
			Ants
			Fungi
			Aphids
			Bacteria
			Ruminants
			Bacteria/Protozoa
			Termites
			Protozoa
2. One-Way Consumer-Resource Mutualisms			
Dispersal	Plant (pollen), animal	C	Animals
	Plant (pollen), pollinator/seed-eater	C	Pollinator progeny
	Fungus (spores), beetles	C	Beetle
	Plants (seed), vertebrates	C	Vertebrate
	Plants (seed), insects	C	Ants
	Plants, ants	D	Ants
	Ant-Lycenid caterpillar	D	Ants
	Ant-Homopteran	D	Ants
	Plants, fungal endophytes	D	Fungal endophytes
3. Indirect Mutualisms via a Third Species Consumer or Resource			
Cleaning	Cleaner-fish, client fish	F	Cleaner-fish
Müllerian mimicry	Two or more mimicking species	E	Predator of mimics
Mixed-species foraging groups	Two or more vertebrate species	E	Predators
Honey guide	Honey guide bird, honey badger	F	Bird, badger

Note: Figure 2.2 provides topological depictions of these examples. This table is intended to provide examples; it is not an exhaustive list.

2003) showed how what we identify as two-way consumer-resource mutualisms can be favored, given the comparative advantage of resource acquisition and trade. Although their theory and models are rooted in economics rather than in ecological consumer-resource theory, both approaches to mutualism involve similar principles.

The nitrogen-fixing interaction occurring between plants and rhizobial bacteria (Douglas 1994) is a two-way consumer-resource mutualism (Table 2.2; Figure 2.2A). Nitrogen is a limiting nutrient for plants in many ecosystems. Plants typically cannot convert atmospheric nitrogen to a chemical form that can be taken up by roots.

although rhizobia can. Rhizobia form nodules on roots where they receive photosynthates from plants; in exchange they provide plants with fixed nitrogen (Douglas 1994). In the broad sense, plants consume nitrogen that has been altered to a usable form by the bacteria, and bacteria consume photosynthates produced by plants. Hence, both plants and bacteria function as both consumers and resources. Plant-rhizobial mutualisms are in many ways similar to plant-mycorrhizal mutualisms, in which plants and fungi exchange photosynthates and nutrients, typically phosphorus or nitrogen. In this case, however, the nutrient is a harvested resource rather than a synthesized resource (Smith and Read 1997). Another example is the agricultural mutualism involving fungi and leaf-cutter ants (Currie 2001; Table 2.2; Figure 2.2A). Ants do not produce a resource consumed by fungi. Rather, they harvest a resource (leaf tissue), which they then provide to fungi. Fungi grow exclusively on the leaf tissue in ant nests, and, in turn, ants eat hyphae produced by fungi. Thus, as in plant-rhizobial interactions, both partners function as both consumers and resources.

Digestive symbioses also are examples of two-way consumer-resource interactions. Examples include interactions between termites and certain gut-inhabiting protozoa, and between ruminant mammals and certain bacteria and protozoa living within their rumen (Douglas 1994). Digestive symbionts, one partner in the mutualism, are provided with food as a result of the foraging of their hosts, the second partner (Douglas 1994). Yet hosts cannot utilize that food resource until it has been chemically altered by symbionts. Digestive symbioses differ from other two-way consumer-resource mutualisms in that both partners use a single resource that the host harvests from its environment. Because the host and symbiont utilize the same resource, they are depicted in Figure 2.2B as occupying the same trophic level. In contrast, other consumer-resource mutualisms involve mutualists on separate trophic levels (Figure 2.2A,C,D).

Mutualisms with One-Way Consumer-Resource Interactions

In *one-way consumer-resource mutualisms* (Table 2.2; Figure 2.2C,D), only one of the two interacting species consumes a resource produced by its partner. The consumer species benefits from the resource produced by the resource species, and producing the resource generally is a cost to the resource-providing species. Such interactions can result in a mutualistic outcome, because the consumer provides the resource species with a service, such as dispersal of the resource species' gametes or progeny (Table 2.2; Figure 2.2C) or protection from natural enemies or the abiotic environment (Table 2.2; Figure 2.2D). The interaction is mutualistic when benefits (resources) acquired by the consumer species outweigh costs of providing the service, *and* when benefits of the consumer species outweigh costs of producing resources.

Pollination mutualisms are one-way consumer-resource interactions in which the pollinator is the consumer and the plant is the resource. The pollinator benefits from receiving the resource of nectar or pollen (or both), while the resource-providing plant benefits from reproduction and gamete dispersal resulting from the consumer's actions (Table 2.2; Figure 2.2C). The interaction is mutualistic when benefits of nectar consumption to the animal pollen vector outweigh costs of pollen transport *and* when

benefits to plant reproduction and pollen dispersal outweigh costs of producing nectar. Seed dispersal by frugivorous vertebrates or ants is another example of a one-way consumer-resource mutualism involving plants and their visitors, but in this case dispersal increases propagule survival rather than reproduction of the visited plant. In these interactions, a food resource associated with the seeds (fleshy fruit or elaiosome) is produced by plants and consumed by dispersers.

Another kind of one-way consumer-resource mutualism is the interaction between lycaenid caterpillars and protective ants (Table 2.2; Figure 2.2D). Here, ants consume food secretions produced by lycaenid larvae, while larvae benefit when ants protect them by modifying the rate at which natural enemies interact with larvae (Pierce et al. 2002). This ant-lycaenid interaction is representative of many other protection mutualisms, including ant-plant protection, in which ants consume a food resource produced by plants and plants benefit from reduced herbivory resulting from ant protection (Heil and McKey 2003).

Indirect Mutualisms via an Intermediate Consumer or Resource

We have defined interactions between populations of two species as those in which the actions, traits, or density of individuals of one population cause a change in some attribute of another population. Such interactions are *direct* in nature. *Indirect* interactions between two populations differ in that changes in attributes of the two indirectly interacting species result from the actions, traits, or abundance of a third species or resource, this third party being a consumer or resource of one or both of the other two species (Holt 1977, Schoener 1993, Abrams et al. 1996, Werner and Peacor 2003).

Two common examples of indirect interactions are exploitative competition and apparent competition. Exploitative competition occurs between two species sharing a limiting resource. The resource could be another species or a limited nutrient. The two competitive species may not directly interact with one another, but each may have negative effects on the other's population density by reducing the abundance of the shared resource. Apparent competition occurs between two prey species and is mediated through a shared natural enemy (Holt 1977). The two prey species do not directly interact, but may have negative effects on each other's population density by contributing to their natural enemy's abundance (cf. Abrams et al. 1998). Similarly, indirect mutualisms can arise via a third species that may be either a consumer or resource of one or both mutualists (e.g., Boucher et al. 1982, Kawabuchi et al. 1993, Woolton 1994, Abrams et al. 1998; Tables 2.1 and 2.2; Figure 2.2E,F).

Two species, neither of which is a consumer or resource of the other, can form an indirect mutualism via a third species that consumes one or both of them. Müllerian mimicry is one such example (Turner and Speed 1999). In these interactions, two species interact indirectly in the presence of a third species that is a predator of both (Table 2.2; Figure 2.2E), when the prey species share a color pattern that accurately advertises to the predator that each is toxic. The indirect interaction is mutualistic when predators learn the distasteful color pattern more quickly than when they interact with a population of only one of the prey species. The mimic species benefit by indirectly increasing each other's survival rates. A similar indirect mutualism is

believed to occur between bird species feeding in mixed-species foraging groups (Hino 1998). Each species reduces per capita investment in vigilance for predators while increasing foraging intensity, thereby minimizing mortality risk while maximizing energy intake.

Cleaning mutualisms between fish (Poulin and Grutter 1996) also fit into this category of indirect interactions. Cleaner-fish consume ectoparasites of their client fish. Cleaners benefit by obtaining a food resource, while the client may benefit from reduced parasite loads. Even though close behavioral associations occur between cleaner-fish and client fish (Bshary and Grutter 2002), the cleaner-client interaction is an indirect mutualistic interaction mediated via ectoparasites. It differs from the previous two examples in that the mutualistic effect arises through a trophic cascade, exemplifying the adage that an enemy of one's enemy can be one's friend.

Indirect mutualistic interactions may occur when a third species is a shared resource, rather than a natural enemy of two species (Figure 2.2F). The mutualism between honeyguide birds and honey badgers (as well as humans) is one such example (Short and Horne 2002). Both birds and badgers use bee nests as food resources (wax and honey, respectively). However, honeyguides cannot gain access to the resource until the honey badger (or human) has first disrupted the nest and dislodged the bees. Honeyguides, in turn, have excellent spatial memories of local bee nests and through characteristic calling, flying, and perching behaviors are able to lead badgers and humans to those nests. Thus, birds and badgers benefit by sharing of a common resource, which neither could efficiently access without the other.

In these examples, indirect mutualistic effects are entirely mediated by a third-party consumer or resource (Figure 2.2E,F). Two-way and one-way consumer-resource mutualisms (Figure 2.2A–D) differ in that they involve direct consumer-resource interactions between two species (M1 and M2). As is shown in Figure 2.2A and D, however, even in direct mutualisms, a third-party resource (R) or natural enemy (NE) sometimes contributes to the mutualistic outcome of the interaction between M1 and M2. Indeed, as we will further discuss below, mutualisms are often context-dependent, varying with the presence or abundance of R and NE. Yet such context dependency differs from indirect interactions in which no direct consumer-resource relationship occurs between M1 and M2. For example, consider one-way consumer-resource mutualisms involving protection (Figure 2.2D). Effects of M1 on M2 are not mediated through NE. The M2 consumes a food resource produced by M1. Thus, populations interact directly, but the outcome of this interaction for M1 depends upon the service M2 provides by modifying the interaction between NE and M1. This example is similar to plant-mycorrhizal interactions, in which the mutualism arises in part through an extrinsic resource, R, rather than a natural enemy, provided to plants by fungi, but fungi directly consume photosynthates.

In many ways, as the examples we have offered demonstrate, our description of indirect mutualistic interactions is analogous to Connor's (1995) conceptual framework for mutualism of by-product benefits—the important difference being that we explicitly recognize that this type of mutualistic interaction is indirect, arising via a third species that is a consumer or resource of one or both of the indirectly interacting mutualistic species. Furthermore, the conceptual framework of benefits and costs arising via consumer-resource interactions is fundamentally different from that of

Connor (1995) in that the consumer-resource framework focuses on the ecological mechanism (or mechanisms) by which mutualistic interactions arise. In contrast, Connor's conceptual framework focuses on the origin and subsequent evolution of different types of benefits of mutualism. Below, we present examples of indirect mutualisms, many of which are the same examples of by-product mutualisms described by Connor (1995). We then contrast indirect mutualisms with direct consumer-resource mutualisms that also involve a resource or consumer extrinsic to the pairwise mutualistic interaction.

Context Dependency of Consumer-Resource Interactions

Effects of interspecific interactions on population attributes are rarely, if ever, static in space or time. Like predation and competition, strengths and outcomes of mutualistic interactions can vary with many factors, including life history traits, life stage or age, and density of interacting mutualists (Thompson 1988, Bronstein 1994a). Indeed, predatory lifestyles under appropriate circumstances may transition to omnivory (see Eubanks, ch. 1 in this volume). Here, we emphasize how mutualistic outcomes of consumer-resource interactions can depend on resources and predators (consumers) extrinsic to the pairwise mutualistic interaction (see also Bronstein and Barbosa 2002).

Two-way consumer-resource mutualisms can shift to commensalism or predation if M1 substantially reduces its production of resources for M2, or vice versa (Figure 2.2A,B). If ambient conditions are poor, such that M2 is able to provide little to no resources to M1, then M1 may either withdraw from the interaction, or reduce its reciprocal provision of resources to M2. In theory, any two-way consumer-resource interaction in which resource provision is potentially limited by environmental supply should be subject to this form of context dependency. Plant-mycorrhizal interactions are one well-studied example (Smith and Read 1997), because the supply of phosphorus provided to plants by mycorrhizae may vary with phosphorus availability in soil.

One-way consumer-resource mutualisms can be context-dependent, depending on the presence or abundance of natural enemies. In protection mutualisms (Figure 2.2D), if natural enemies are absent or rare, then the benefits of protection provided by M2 may not exceed the costs incurred by M2 in producing a resource for M1. In such cases, the interaction between M1 and M2 may shift to a commensal or parasitic consumer-resource interaction. However, M1 may also modify its production of resources for M2 in response to changes in its own requirement for protection. Examples include ant-defended plants that increase extrafloral nectar production in response to herbivory (Heil et al. 2001, Ness 2003) and ant-tended lycacid caterpillars that offer secreted rewards at a greater rate after simulated predator attacks (Agrawal and Fordyce 2000), thereby attracting more mutualistic consumers. There is also evidence that resource-provisioning rates can increase in the presence of other, perhaps competing, reward-producers (Del-Claro and Oliveira 1993), or decrease in the absence of reward collection (Heil et al. 2000). Resource-supply rates, which are costs for M1 and benefits to M2, can thus be as varied in space and time as the natural enemies that necessitate protection.

Mutualisms also can have effects on consumer-resource dynamics of predator-prey interactions. When a mutualist is a prey item for a natural enemy and its protecting partner varies in space, time, or effectiveness, then the interaction between predator and prey (NE and M1) can similarly vary. For example, mutualist ant species can differ greatly in density, foraging pattern, aggressiveness, and effectiveness in deterring the natural enemies of their partner mutualist (Fraser et al. 2001). Thus, these characteristics mediate the interaction between natural enemy and prey (i.e., the mutualist).

The nature of consumer-resource interactions also can shift between being nominally predatory and mutualistic. For example, the likelihood that ants will consume individuals in a homopteran aggregation rather than protect them from natural enemies has been predicted to increase with the foraging distance required to collect the honeydew resource provided by Homoptera, the quality of rewards offered by Homoptera, and the relative need of those ant colonies for carbohydrates versus protein (Moya-Raygoza and Nault 2000, Cushman 1991, Fischer et al. 2001, Offenberger 2001). This context-dependent, qualitative change in consumer-resource interactions, from mutualism to predation, may even stabilize homopteran populations, given that their populations appear regulated in the presence of ants but explode or crash in their absence (Larsen et al. 2001). In assisting low-density populations and pruning high-density populations, the ants may be highly effective regulators of homopteran populations. Interactions typically interpreted as having (+, -) outcomes can also become mutualistic under some circumstances. For example, herbivory is typically classified as a (+, -) consumer-resource interaction. However, in some cases (e.g., large mammal grazers of African grasslands), some level of herbivory may increase biomass production and plant fitness (McNaughton 1979, de Mazancourt et al. 1998, de Mazancourt et al. 2001).

Discussion

Studies of mutualism have historically focused on details of interactions between particular partner species. The great diversity in natural history among mutualistic systems has obscured the many similarities among them and, consequently, has hampered recognition of the general influence mutualism has on patterns and processes in ecology. In the past two decades, however, the study of mutualisms has begun to be unified under a number of organizing principles (Addicott 1984, Janzen 1985, Cushman and Beattie 1991, Bronstein 1994b, Schwartz and Hoeksma 1998, Bronstein 2001, Bronstein and Barbosa 2002, Holland et al. 2002). In this chapter, we continue this unification by proposing that, like predator-prey interactions, nearly all mutualisms have consumer-resource interactions embedded within them. Indeed, we have shown that mutualists almost always interact via one of the three types of consumer-resource interactions. These consumer-resource interactions between individuals are often the mechanism resulting in changes in population-level attributes, such as per capita reproduction, survival, population growth, population size or density, and mean trait values of individuals of a population. Furthermore, these three types of consumer-resource interaction explicitly incorporate the (reproductive and survival) services

of dispersal and protection, as well as the benefits and costs of mutualism, which are some of the few general features of mutualisms. One advantage of examining the consumer-resource mechanism by which individuals of mutualistic populations interact is that it simplifies the diversity in natural histories of mutualists. Almost all of the many mutualistic systems occurring in nature appear to fit into only one of the three consumer-resource interactions (Tables 2.1 and 2.2), and nearly all mutualistic systems can be described by only one of a few topological diagrams of the consumer-resource interaction (Figure 2.2; Table 2.2). The very few exceptions include, for example, pollination mutualisms in which the pollinator does not consume a plant product but collects some substance to attract mates (e.g., some euglossine bees and orchids; Roubik 1989). By appreciating the ubiquity of consumer-resource interactions, ecologists can understand mutualisms as diverse as ant-fungus agriculture; plant-nitrogen fixing bacteria; and plant-mycorrhizal, coral, and lichen systems as reciprocal resource exchange mutualisms. Similarly, nearly all dispersal and protection mutualisms are one-way consumer-resource interactions, each with its own topological diagram that circumvents the past need to subdivide them into further categories based on interacting taxa and natural history.

Recognition that mutualisms have consumer-resource interactions embedded in them can lead to new thinking and perspectives in studies of mutualism. As an example, consider Turchin's (2003) conclusion based on a review of empirical studies of population dynamics. He suggested that trophic and consumer-resource interactions may be the most important mechanisms governing population dynamics. The rationale is that energy and nutrients obtained from food are the basic currency underlying many population processes. If Turchin's rationale is correct, then its extension to mutualism suggests that population dynamics of species that interact as consumers with their mutualist partners may be more influenced by the population changes of their partners than are species that receive services from their mutualists, such as dispersal or protection. The relative influence of one mutualistic population on another may be either enhanced or buffered, depending on which partners consume and which provide resources. One of the contributions that a consumer-resource framework may bring to the study of mutualism is a context in which to understand and frame our study of asymmetric influences of interacting species on one another. Further, mutualistic interactions may provide an opportunity to evaluate the importance ascribed to consumer-resource interactions, precisely because they include these interactions but are not limited to them.

We have argued that nearly all mutualistic interactions can fit into only one of three categories of consumer-resource mutualisms (Table 2.1), and into only one of six general interaction topologies (Figure 2.2). However, when a mutualistic system involves multiple forms of benefits and costs, other topologies can occur. This alternative will be particularly prevalent for mutualistic systems in which one of the interacting partners incurs benefits both through the acquisition of a resource and through a service such as dispersal or protection. One example may be the ant-fungus agriculture mutualism. We previously described this mutualism as a two-way consumer-resource interaction with the topology shown in Figure 2.2A. However, ants provide fungi not only with a resource (leaf tissues), but with dispersal; when ants leave their resident nests to establish new colonies, they take some fungi with

them. This mutualism is a two-way consumer-resource interaction in either case, but the topology may be more accurately diagrammed by adding in Figure 2.2A a dotted arrow going from M2 (the ants) to M1 (the fungus) to represent the additional benefit of the ants' dispersing the fungus. As benefits and costs are more fully integrated into the consumer-resource approach to mutualistic interactions, more topologies may be needed to depict the full range of effects of M1 and M2 on one another.

Another concern with topological diagrams of consumer-resource mutualisms involves the ability to accurately discern trophic levels. In traditional food web diagrams, solid arrows typically connect consumers with resources. The consumer is placed above the resource in the diagram, reflecting that the consumer occupies a higher trophic level. Representing two-way consumer-resource mutualisms in this way may be difficult. Because both mutualists provide one another with a resource, it can be argued that both mutualists are on the same trophic level (Figure 2.2B). Yet, in many two-way consumer-resource mutualisms, one partner is accurately depicted as occupying a trophic level above its partner (Figure 2.2A), as with bacteria or fungi that consume photosynthates from plant roots. On the other hand, hosts and endosymbionts involved in digestive symbioses are probably best depicted as being on the same trophic level, because they both utilize the same resource harvested from the environment by the host species.

Similar issues may arise when one is discerning whether a resource is intrinsic or extrinsic to a pairwise mutualistic interaction (e.g., R in Figure 2.2A). Some ecologists may prefer that diagrams of digestive symbioses explicitly include an extrinsic resource, though not depicted in our Figure 2.2B, because the host harvests the resource from the environment. However, one could argue that the extrinsic resource of Figure 2.2A be removed from the topological diagram, because the extrinsic resource may be altered chemically before becoming available to M1. The questions whether to include the extrinsic resource in the topology and how to trophically depict mutualistic partners involved in two-way consumer-resource interaction are issues perhaps best left to the judgments of individual researchers.

Despite these few limitations, we believe the application of the consumer-resource paradigm to mutualism represents an advance in the study of mutualism. Furthermore, we hope that the qualitative, verbal arguments we have presented here will encourage more theoretical and quantitative research on the population ecology of mutualistic systems. The remarkable diversity of natural histories that result in mutualisms make them some of the most fascinating interactions, yet this very diversity has perhaps hampered an understanding of the general mechanics of interacting mutualistic populations. It is our hope that, by recognizing that almost all mutualisms involve consumer-resource interactions, the study of mutualism, like that of predation, will become a more unified and synthetic discipline.

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Table 2.2 Examples of mutualistic systems in nature which represent each of the three means by which consumer-resource interactions are embedded within mutualisms. Fig. 2.2 provides topological depictions of these examples. This is not intended to be an exhaustive list.

MUTUALISM	PARTNERS		FIG. 2.2 CONSUMER RESOURCE			
(1) Two-Way Consumer-Resource Mutualisms.						
	Lichen	Fungi, Algae	A	Fungi	Algal Photosynthates	
				Algae	Nutrients, Water	
	Coral	Coral, Zooxanthellae	A	Coral	Algal Photosynthates	
				Zooxanthellae	Nutrients, Nitrogen	
	Mycorrhizal	Plant, Mycorrhizal Fungi	A	Plant	Nutrients, Phosphorus	
				Mycorrhizae	Root Exudates, Carbon	
	Nitrogen Fixation	Plant, Rhizobial Bacteria	A	Plant	Nitrogen	
				Rhizobium	Root, Exudates, Carbon	
	Myrmecotrophy	Plants, Ants	A	Plant	Debris-derived Nitrogen	
				plant food rewards		
	Ant Agriculture	Ant, Fungus	A	Ant	Fungus	
				Fungus	Ant-collected leaves	
	Digestive Symbioses	Aphid-Bacteria	B	Aphid	Synthesized Amino Acids	
				Bacteria	Aphid Ingested Food	
				Ruminant	Bact/Prot Digest. Food	
		Ruminant, Bacteria/Protozoa	B	Bacteria/Protozoa	Ruminant Ingested Food	
				Termite	Protozoa Digested Food	
		Termite, Protozoa	B	Protozoa	Termite Ingested Cellulose	
(2) One-Way Consumer-Resource Mutualisms.						
	Dispersal	Plant (pollen), animal	C	Animal	Nectar and/or Pollen	
		Plant (pollen), Pollinator/Seed-eater	C	Pollinator Progeny	Seeds, Fruit Tissue	
		Fungus (spores), Beetle	C	Beetle	Fungal Tissue	
		Plant (seed), Vertebrate	C	Vertebrate	Fruit	
		Plant (seed), Insect	C	Ants	Elaiosome	
	Protection	Plant, Ant	D	Ant	Nectar, Food Bodies	
		Ant-Lycanid Caterpillar	D	Ant	Caterpillar Secretions	
		Ant-Homopteran	D	Ant	Homopteran Excretions	
		Plant, Fungal Endophytes	D	Fungal Endophyte	Carbon	
(3) Indirect Mutualisms via a Third Species Consumer or Resource.						
	Cleaning	Cleaner Fish, Client Fish	n/a	Cleaner Fish	Client Ectoparasites	
	Müllerian Mimicry	Two or More Mimicking Species	E	Predator of Mimics	Mimics	
	Mixed Species Foraging Groups	Two or More Vertebrate Species	E	Predators	Foraging Species	
	Honey Guide	Honey Guide Bird, Honey Badger	F	Bird, Badger	Bee larvae and honey	

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