

# Mutualism in a community context

Todd M. Palmer, Elizabeth G. Pringle, Adrian Stier, and Robert D. Holt

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## 9.1 Introduction

In the highlands of East Africa, a giraffe ambles through a savanna dotted with *Acacia drepanolobium* trees, which stand half the giraffe's height and bristle with spines and bulbous hollow structures known colloquially as whistling thorns. The trees are myrmecophytes, or ant-plants, members of an iconic class of protection mutualisms first elucidated by Janzen (1966) nearly fifty years ago. As the giraffe lowers its head to feed from a tree, ants stream from the hollow domatia and attack its lips and nostrils. Surprisingly, the giraffe is unperturbed: it continues to browse, using its long prehensile tongue to wipe the ants away. Closer inspection reveals another surprise: the *Crematogaster nigriceps* ants that occupy this plant have methodically pruned it, sterilizing the tree by destroying the buds that would have developed into flowers and fruits. This is all occurring even as the tree pays heavily to support *C. nigriceps*, channeling energy into the production of extrafloral nectar that feeds the ants and domatia that house them. Indeed, the metabolic cost of these investments is sufficient to reduce the plant's growth rate. From the classic pairwise perspective of species interactions, therefore, *C. nigriceps* appears to be a parasite of its host plant, imposing multiple costs while providing no obvious benefit. Yet we now know that this relationship is in fact mutualistic, providing both growth and reproductive benefits to host trees (Palmer et al. 2010). How can this be the case?

The answer lies in the community context of the interaction. To fully understand the ecology and evolution of mutualism, we must consider other

partners in the mutualism, and also the many non-mutualistic interactors in the community. And so in turn we must broaden both the spatial and temporal scopes of mutualism studies: for *A. drepanolobium*, the balance sheet of costs and benefits may be kept for 150 years or longer, and lifetime fitness is the only currency that matters in the end.

By taking a community-based, long-term perspective, we can unpack the apparent paradox of this *A. drepanolobium*–*C. nigriceps* interaction. In terms of defense, *C. nigriceps* is not very effective at defending host plants from chronic giraffe herbivory (Stanton and Palmer 2011), but it is highly effective against rare but potentially lethal elephant herbivory (Goheen and Palmer 2010). Indeed, long-term studies of the interaction have shown that elephants appear to be a driving force in the evolution of this association (Stanton and Palmer 2011). In terms of sterilization, *C. nigriceps* is but one of four ant species that compete intensely for exclusive occupancy of the tree, and it is the only ant that sterilizes the tree. As a subordinate ant in the competitive hierarchy, *C. nigriceps* persists in part by being a strong colonizer of new host plants. It therefore tends to occupy plants at early life stages, when reproductive potential is low. For young plants, protection from elephants is more important for lifetime fitness than squeezing out a few seeds: it is better for the individual to survive to reproduce at a larger, less vulnerable, and more fecund stage. As plants mature, competitively superior, non-sterilizing ant species supplant *C. nigriceps*, releasing the plant from reproductive suppression. However, these other ants do not defend the tree as effectively against elephants. In the context of

long-term community dynamics, therefore, *C. nigriceps* enhances the tree's lifetime fitness by conferring increased survival at the vulnerable early stage. Moreover, the cost to the trees occupied by *C. nigriceps* in terms of current reproduction is outweighed by the sum of future offspring (Palmer et al. 2010).

Although the *Acacia drepanolobium*–ant mutualism is a highly specialized and geographically restricted interaction, it shares common features with many of the world's mutualisms. Mutualisms nearly always include a diversity of interacting species (Box 9.1, by Michael Stat, highlights the diversity within coral–algal symbioses), variation in the costs imposed and benefits provided by different mutualist partners, and interactions between mutualists and non-mutualist members

of the broader community. In this chapter, we elaborate on the themes underpinning the ant–acacia example, arguing that much recent progress in our understanding of mutualism has been made by carefully considering spatiotemporal heterogeneity of the broader communities in which mutualisms are embedded. We begin by discussing the complexity inherent in mutualisms, which typically consist of multiple species on one or both sides of the interaction. We then move on to consider the role of the broader community in shaping mutualisms, briefly discussing how mutualisms arise from and are changed by the interactions with the organisms that surround them. Finally, we consider how mutualisms themselves feedback to modify the structure and stability of the communities in which they occur.

### Box 9.1 The community ecology of coral–algal mutualism

#### Michael Stat

Many corals form a mutually beneficial interaction with single-celled algae belonging to the dinoflagellate genus *Symbiodinium*. The association is primarily defined by the exchange of nutritional compounds that increases the metabolic capacity of the partners in the otherwise nutrient-poor oligotrophic ocean waters where corals are found (Muscatine and Porter 1977). The animal host receives organic carbon fixed through algal photosynthesis as well as amino acids, while the dinoflagellate symbiont receives inorganic compounds as a byproduct of host respiration. This highly efficient cycling of nutrients between the partners is made possible by the spatially intimate localization of the symbionts that are housed within the gastrodermal tissue of the animal, and ultimately results in the growth of corals and formation of reef ecosystems (Box 9.1 Figure 1).

In coral–algal mutualism, it has become evident that a dynamic interaction between the host and a diverse community of dinoflagellate symbionts occurs. This discovery was made possible with the application of molecular tools to identify different populations of *Symbiodinium*. In contrast to the limited morphological variation among *Symbiodinium* algae that contributed to the earlier perception of a single species within the genus inhabiting all corals (and other animal hosts), molecular techniques have revealed a relatively large amount of genetic diversity within this taxonomic

group as compared to other dinoflagellate genera. To date, nine divergent evolutionary lineages that have been called clades A–I have been identified in the genus, with each lineage containing varying numbers of strains or subclade symbiont types (Pochon and Gates 2010). The importance of the genetic diversity among members of *Symbiodinium* is recognized by the functional diversity displayed by different symbiont types and their effect on host fitness. For example, differences among *Symbiodinium* strains in photophysiology, thermal tolerance, and carbon fixation and translocation to the host, and their subsequent effect on coral growth rates have been observed (Little et al. 2004, Rowan 2004, Cantin et al. 2009).

The majority of corals associate with a single dominant strain of *Symbiodinium*. However, recent research has now shown that most, if not all, corals also harbor a diversity of cryptic symbionts or *Symbiodinium* strains in very low numbers (Silverstein et al. 2012). While there are biogeographic and host specificity patterns in the distribution of the dominant symbionts of corals, providing evidence for an evolutionary influence on host–symbiont assemblages (LaJeunesse 2005), the functional role and interaction of cryptic symbionts with corals and their contribution to the stability and overall persistence of the symbiosis is unclear. Interestingly, changes in the community composition of *Symbiodinium* in corals away from the dominant homologous symbiont have

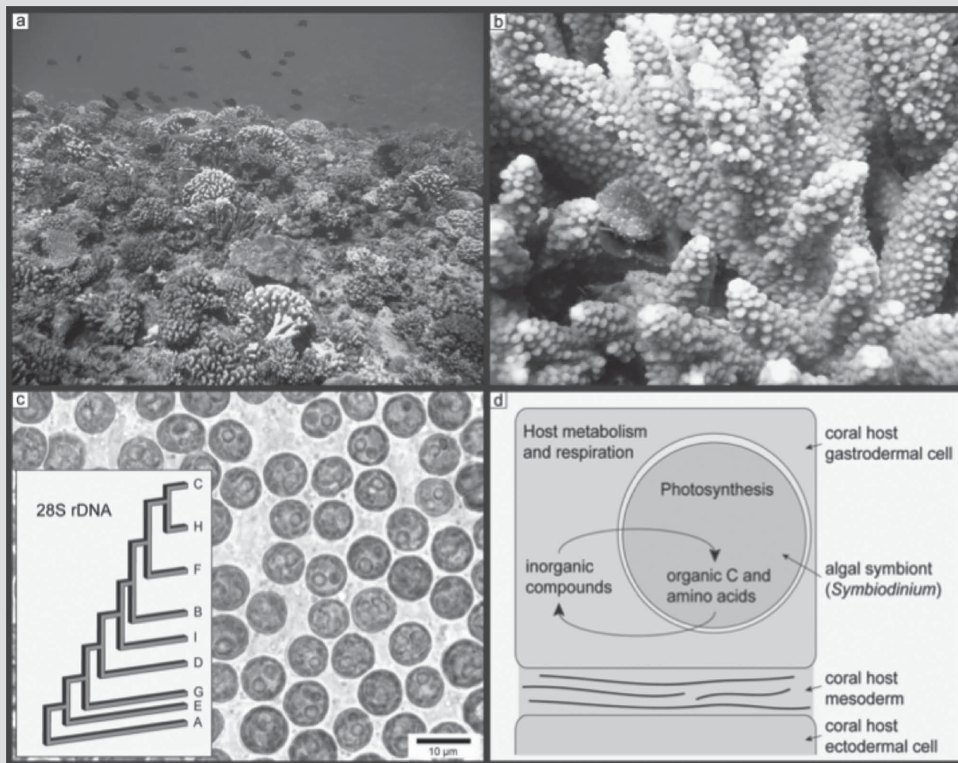
**Box 9.1** *Continued*

been observed during ontogeny of the coral and in response to local environmental changes.

Coral-algal symbioses are very sensitive to variation and changes in the environment. Elevated seawater temperature (and a variety of other abiotic factors) can cause a breakdown in the symbiosis between corals and their dinoflagellate algae, leading to the expulsion of the algal complement from the host tissue, and resulting in the phenotype described as coral bleaching (Hoegh-Guldberg and Smith 1989). Prolonged exposure to temperature increases as little as 1 °C above the local average maximum can potentially lead to coral bleaching and mortality. During thermal stress

(and other factors that affect the symbiosis), however, a disruption in the symbiotic interaction between the partners provides the opportunity for different *Symbiodinium* strains to proliferate and occupy the coral host environment (i.e. opportunistic symbionts). For some corals, shifts toward a more thermally tolerant symbiont population during ocean warming have been shown to occur, buffering the coral against the stress event and increasing their resistance to bleaching (Jones et al. 2008).

While changes in the symbiont community to thermally tolerant *Symbiodinium* may provide a rapid mechanism of acclimatization for corals, there is a trade-off to such



**Figure 1** (a) The corals on the forereef of Moorea, French Polynesia, that grow and thrive as a result of the mutualistic association between corals and algae belonging to the genus *Symbiodinium*. (b) A close-up of a coral colony of a branching species of *Acropora*. (c) A bright-field microscope view of dinoflagellate algae in the genus *Symbiodinium* that form a mutualistic symbiosis with corals (image courtesy of Peta Clode, CMCA, The University of Western Australia). The inset shows a cartoon representation of the phylogeny of *Symbiodinium* and the evolutionary relationship of the nine lineages (clades A–I) within the genus based on the sequence of partial nuclear ribosomal DNA. (d) The localization of the algal symbionts that are housed within the gastrodermal cells of the coral host and the cycling of nutrients between the partners. See Plate 6 for color version.

*continued*

**Box 9.1** *Continued*

symbiont transitions. Community shifts to thermally tolerant algae result in shifts away from the homologous symbionts of corals, and a breakdown in the host-specific patterns that have been observed. These altered coral-algal assemblages are not likely to be as productive as those developed over evolutionary time scales. Indeed, recent evidence shows thermally tolerant symbionts produce and translocate less carbon to their coral hosts as compared to heat-sensitive symbionts, resulting in slower coral growth rates (Little et al. 2004, Cantin et al. 2009, Jones and Berkelmans 2010). How these altered associations also affect other aspects of coral biology such as reproductive output is unknown. The role of cryptic, opportunistic, and thermally tolerant symbionts to the perpetuation and resilience of coral-algal symbioses is an area of current research, and may shed light on how this mutualism has persisted for millions of years.

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**9.2 Complexity within mutualism**

Early studies of mutualism focused on species pairs, but we now know that mutualisms are usually interactions between guilds of multiple partner species (Stanton 2003). We consider such mutualisms to be “complex.” Importantly, not all partners within such mutualisms are equal. Per capita effects of a given partner on its mutualist can range from strongly positive to mostly negative (in which case the partner is an exploiter rather than a mutualist; see Chapter 6). In addition, even partners that have similar per capita effects on a mutualist can vary in abundance, and hence in the magnitude of their population-level effects. There may also be interactions among the co-occurring species within a partner guild. Such interactions can dramatically

modify the community structure of the partner species (i.e., the identity, diversity, and density of partners) and the performance of the other mutualist. Going back to our earlier *C. nigriceps* example, it was necessary to understand the interactions among the different acacia ant species in order to explain spatiotemporal patterns in both ant community structure and host tree performance.

In this section, we focus on three important questions that arise from our recognition of the ubiquitous complexity in mutualism. First, what maintains the diversity of potential mutualistic partners? Second, how does such complexity influence the fitness and performance outcomes of these interactions for the mutualists? Finally, can we understand multispecies mutualisms by studying their constituent pairwise associations, or do the

collective interactions lead to emergent properties that require us to study all partners at once? Below we address each of these questions in turn.

### 9.2.1 Maintenance of mutualist diversity

Addressing what generates and maintains mutualist species diversity first requires us to define our terms. Mutualism is a very broad class of interactions (involving benefits such as seed dispersal, pollination, nutrition, and protection; see Chapter 1), and the mechanisms that mediate diversity in each of these interactions could be very different. Drawing generalities about how species diversity is maintained in diffuse, free-living mutualisms will probably be particularly challenging because the partners in such mutualisms are often taxonomically disparate. For example, in dispersal mutualisms, the seeds of a particular tree species may be primarily or secondarily dispersed by birds, primates, insects, and rodents, and species diversity in each guild may be maintained by different mechanisms. However, the theories of island biogeography, metapopulation dynamics, and metacommunities seem to offer useful conceptual frameworks for explaining diversity in interactions where a mutualist serves as a discrete island (host) for one or more partner species (e.g., coral-algal, plant-ant, plant-endophyte, and other mutualistic symbioses).

Drawing from these theories, diversity in antagonistic interactions, such as host-pathogen relationships, is thought to arise from variability within both individuals and communities, among populations, and through time (Holt and Dobson 2006). Individual hosts act as islands, which first serve as venues for pathogen colonization and later for local extinction. The success of colonization, and the likelihood of extinction, can be determined by competitive interactions among pathogens that share the same host(s). Similarly, when mutualists serve as hosts for multiple symbionts, processes of colonization and extinction, as well as competition among symbionts, should play key roles in mediating partner diversity and abundance. For example, 20 cm-diameter corals in the South Pacific can be inhabited simultaneously by assemblages of more than ten species of crabs that collectively defend the coral from predatory seastars. Adult crabs do not

tolerate other adults of the same species on a single coral head, and this negative intraspecific density dependence creates opportunities for stable coexistence of multiple partner crabs on a single host coral (Stier et al. 2012). In another marine example, gutless polychaete *Osedax* worms that colonize “whale-fall” (carcasses that have fallen to the ocean floor) host nutritional endosymbiotic bacteria whose diversity appears to be determined by the interplay of ocean depth (and associated abundance of the horizontally transmitted bacteria in the environment), host individual, host ontogenetic stage, and competitive interactions among the bacteria (Verna et al. 2010).

Do certain conditions generally favor low- versus high-diversity mutualist guilds? In the simplest case, strong partner choice by a mutualist can effectively screen out other potential partners, leading to high specificity within the interaction. But in other cases, the ecological and evolutionary factors that generate the observed continuum from monospecific dominance in some interactions to diverse guilds in others are not as obvious. One possibility is that the strength of competition among mutualist partners controls the diversity of the partner community. For example, intraspecific competition within guilds of partner species should increase diversity, as in the coral-crab mutualism described above, and interspecific competition should decrease diversity, as has been reported for plant-mycorrhizal mutualisms (Jansa et al. 2008). Alternatively, when different partners provide complementary benefits to mutualists, those partners may foster diversity by becoming indirect mutualists of one another. For example, the gastropods *Anachis lafresnayi* and *Mitrella lunata* remove different types of fouling epibionts from the red algae *Chondrus crispus*, and both gastropod species are required for the algae to grow, which protects the gastropods from crab predation (Stachowicz and Whitlatch 2005). When selection on competing partner species to reduce niche overlap leads to functional complementarity in the benefits they provide to their mutualist, positive relationships between partner diversity and mutualism stability can arise and affect entire networks (Bastolla et al. 2009). A key remaining question is whether particular types of mutualisms are more conducive than others to



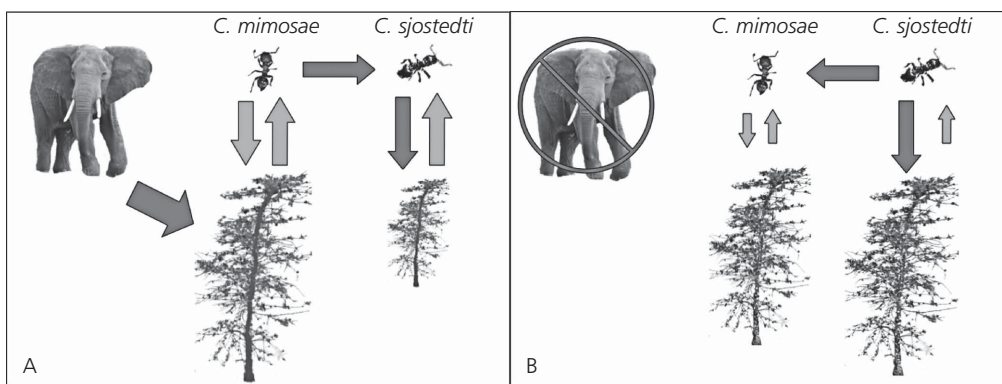
spatial and/or temporal niche partitioning among their partners. Whatever the ultimate causes of mutualist partner diversity, it is clear that this complexity has pervasive consequences for the performance and fitness outcomes of mutualistic interactions.

### 9.2.2 Consequences of diversity for mutualistic outcomes

When mutualists interact with many partner species, either serially or simultaneously, differences in partner identity and/or composition can substantially alter the performance of the other mutualist in at least two ways. First, when the total number of partners is constrained by a limiting resource supplied by the other mutualist (e.g., plant carbohydrates for mycorrhizal associates, Kiers et al. 2011), the resource-supplying mutualist is harmed by interactions with less-beneficial partners because they deplete the resource and reduce the potential for future interactions with better partners. In such cases, changes in the community of partner species, or more specifically in the proportion of partners of different quality, should alter the performance of the other mutualist. For example, the loss of large herbivores in an African savanna has caused *A. drepanolobium* trees to reduce the overall quantity of rewards for ants (Figure 9.1). This led

to a shift in the community of ant associates of *A. drepanolobium* from more- to less-beneficial species, which, in turn, reduced rates of plant growth and increased plant mortality (Palmer et al. 2008). Second, changes in the partner community can shift the balance between cooperative and antagonistic interactions among partners, with a range of indirect consequences for the other mutualist. For example, van der Heijden et al. (1998) found a positive correlation between mycorrhizal fungal diversity and plant productivity in an old-field community. This positive correlation could be driven either by complementarity, if different mycorrhizal species perform non-redundant functions, or, possibly, by cooperative interactions among the mycorrhizal species themselves (Jansa et al. 2008). Quantifying the mechanisms underlying the effects of changes in partner diversity is an important future step in mutualism ecology. Importantly, understanding these mechanisms could help elucidate how anthropogenic disturbance to ecological communities will affect ecosystem function.

Despite the recognition that partner diversity can strongly affect the performance of mutualists (In Box 9.2, Daniel Doak shows how guilds of poor mutualists may benefit their partner as a group), however, we do not yet know whether there is any general pattern in the direction of outcomes



**Figure 9.1** Effects of large mammal extinction on an ant–*Acacia* mutualism in East Africa. Browsing by large mammals (Panel A) induces high levels of nectar production in *Acacia drepanolobium*, which favors the competitive dominance of the strongly mutualistic and nectar-dependent *Crematogaster mimosae* over its competitor *C. sjostedti*, an antagonist of the host plant which does not depend on host plant nectar. Following the extinction of large mammals (Panel B), host plants reduce their production of extrafloral nectar, shifting the balance of competition among ant species towards dominance by the antagonistic *C. sjostedti*. Increased occupancy of host plants by *C. sjostedti* results in slower rates of tree growth and dramatically increased host plant mortality (Palmer et al. 2008).

produced by higher partner diversity (Morris et al. 2007). Expanding the temporal scales of mutualism studies seems particularly critical to assessing this question. For one, the magnitude of benefits derived from different partner species may vary with environmental conditions (Kersch and Fonseca 2005). For another, variation in the year-to-year reliability of a particular partner species may modify the “value” of alternate partners to the mutualist (Palmer et al. 2003). For example, a highly beneficial partner whose populations are

highly variable will not confer many benefits to its mutualist in years when its densities are low. In general, the impact of partner diversity on host performance is probably highly context dependent (see Chapter 10), and a significant challenge is to identify the mechanisms underlying this variability. Moreover, we must consider to what extent we can actually quantify the overall outcomes of complex mutualistic webs by studying the individual, experimentally amenable components of a given mutualism.

### Box 9.2 How imperfect relationships with multiple, exploiting partners can lead to mutualistic success

#### Daniel F. Doak

For a relationship between individuals of two species to be a mutualism, each partner must gain more benefits than it loses. If one partner is, on balance, hurt by the interaction and the interacting species is also supplanting the role of what we would otherwise consider a mutualist, we would generally classify it as an “exploiter” (see Chapter 6). While using the criterion that a mutualism is based on net positive effects for both partners is simple in theory, in many mutualisms the time span of the relationship and the longevity of at least one of the partners can conspire to make the net effects of the interaction quite difficult to unravel. In particular, these complications can allow guilds of poor mutualists to benefit their partner as a group, even when each alone would clearly be considered an exploiter.

Principles of stochastic demography (Tuljapourkar 1990, Doak et al. 2005) suggest that in the most simple circumstances three conditions must be met for an individual of species A to be sustained and even benefited by multiple, imperfect partners of a mutualist guild B (partners B1, B2, B3, etc.). Namely: (1) each alternate B partner must increase some aspects of A’s fitness, even if diminishing fitness in other ways; (2) the different B partners must contribute contrasting costs and benefits to A; and (3) an individual of A must have a good chance of experiencing different B partners over its lifetime, either randomly or in a more ordered sequence. In essence, from A’s perspective, association with different Bs creates different environments that have negatively correlated effects on different aspects of fitness—if these negative correlations are strong enough, association with multiple Bs can in some cases dramatically elevate A’s

fitness. Associating with diverse guilds of exploiters is most likely to produce benefits when interactions are relatively prolonged because this creates the opportunity for guild B to influence multiple aspects of species A’s fitness. A good example is the relationship described at the outset of this chapter between myrmecophytic trees and ants, where trees are inhabited by many ant species over their long lifetimes (Palmer et al. 2010), and ants can influence the survival, reproduction, and growth of their hosts.

It is easiest to understand these effects with a simple model. Consider a myrmecophyte A with three life stages (seeds, juveniles, and adult plants) that associates with one of two ant species, B1 or B2. B1 is a highly effective defender of its plants, which leads to high survival rates of both juveniles and adults, but B1 also feeds on flower buds, which reduces reproductive success. In contrast, B2 is a poor defender of its plants, which leads to low survival, but it increases fruiting success, perhaps by pollinating or by fertilizing the plant with discarded insect prey. We can make two stage-structured demographic models, one for the demography of A individuals associated with B1, and one for A individuals associated with B2. These demographic transition models are in the standard form, showing transitions between the three stages of the plant’s life cycle:

$$A_{B1} = \begin{pmatrix} 0 & 0.06 & 0.45 \\ 0.2 & 0 & 0 \\ 0 & 0.6 & 0.9 \end{pmatrix}, A_{B2} = \begin{pmatrix} 0 & 0.6 & 6 \\ 0.2 & 0 & 0 \\ 0 & 0.2 & 0.6 \end{pmatrix}$$

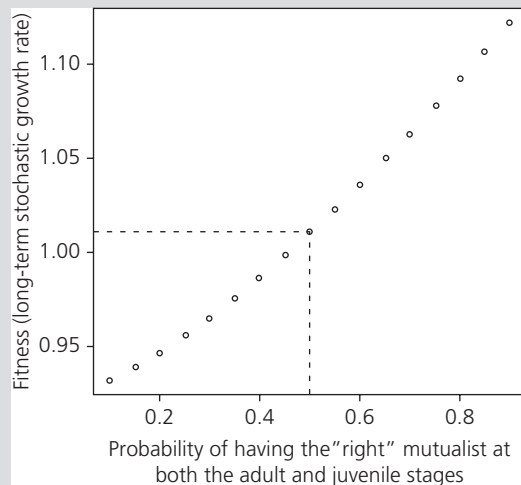
For our example, the annual growth rates of plants associated with B1 and B2 are  $\lambda = 0.96$  and  $\lambda = 0.93$ ,

*continued*

**Box 9.2** *Continued*

respectively. In other words, in both cases a lineage of plants associated with only one ant species will rapidly decline. However, if each year a plant has an equal probability of associating with one or the other of the two ant species, the annual population growth rate (which is also a measure of individual fitness) is a little over 1.01—a growing lineage. Each ant in isolation is harmful, but in combination, they can have strong benefits for their common partner.

While this ability to benefit from two poor mutualists is striking, the scenario we have just described is not the optimal one for the plant. The reproductive costs of the B1 ant are small for the always low-reproducing juvenile plants, whereas the advantage of surviving to be an adult is high; for adults, the relative importance of reproduction is far higher. Thus, selection should favor the plant's ability to manipulate which ant is most likely to occupy it at each of these two life stages. At the extreme, if the plant can manipulate



**Figure 1** Control of the frequency of association with different mutualists at different life stages can yield strong benefits. In the text, we discuss how randomly alternating association with two partner species can yield benefits for a plant. Here we show results when juvenile plants have increasing probabilities of associating with B1, and adults have the same increasing probabilities of associating with B2. Compared to the random probability that juvenile or adult will have a 50% chance of hosting B1 or B2, there are enormous gains in biasing associations for each life stage of the plant.

its associations such that juveniles mostly have B1 ants, and adults mostly have B2s, the plant achieves dramatically higher fitness (see Box 9.2 Figure 1). In one real study system we have seen signs of just such advantageous differential occupancy by alternate mutualists at different life stages (Palmer et al. 2010), and we expect similar patterns can be found in other systems.

Here we've focused on the advantages of interactions with different partners in the case where alternative partners can be considered exploiters. It is worth noting that the same general advantage of association with multiple partners should also in theory occur when alternative partners do not have net negative effects in isolation, but do still have contrasting effects on different aspects of fitness (e.g., a plant associating with nitrogen fixers and with protective ants, or lichen fungi that maintain both nitrogen-fixing bacteria and more photosynthetically efficient green algae).

As our simple analyses show, the line between good mutualists, poor mutualists, and exploiters can be a gray one, and depends on the patterns of association between each species and the entire suite of alternate partners. These examples also show that we should be clear that short-term "exploitation" may not accurately reflect the lifetime costs and benefits of associating with any one partner, when multiple partners interact with single individuals over their lives. Finally, these results point to the interesting hypothesis that mutualists can achieve strong fitness advantages by manipulating the sequence of partners they associate with during different life stages. This is a particularly fascinating question for systems more complex than the one we modeled, where both partners have some control over the interaction.

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### 9.2.3 Approaches to studying complex mutualisms

Speciose mutualist networks, like all diverse interaction webs, are inherently complex. There are two main approaches to the study of such complexity. We can either focus on a module of interactions among a small number of key players and build up to larger communities, or we can characterize community-wide interaction patterns holistically with network metrics (see Chapter 11). In recent decades, three- to four-species community modules (McCann 2012) have been the staple units for theoretical and experimental investigation of indirect and higher-order interactions (e.g., the non-additive effects of multiple predators or mutualists, apparent competition, intraguild predation, and competitive networks). Two factors motivate the use of community modules. First, modules are empirically manageable and analytically tractable structures within diverse interaction networks. Second, many networks are compartmentalized (Chapter 11), which may make it possible to quantify interactions at the module level and then scale up to entire networks. Although this latter rationale sounds good in theory, the logistical constraints of factorially manipulating more than a few species at a time have so far limited our ability to combine module-level studies in order to elucidate interactions within diverse networks.

When experiments become too onerous, network analyses provide an appealing alternative approach to studying complex webs of mutualistic interactions (Chapter 11). Recently, theoretical ecologists have begun to integrate classic food web theory with mutualistic network theory (Fontaine et al. 2011). Despite the appeal of network analyses, however, community-module studies suggest that the abundance of higher-order interactions in real communities will complicate our efforts to understand them using networks alone (Cohen et al. 2009). Higher-order interactions, in which the properties of a system emerge non-additively, make it difficult to recapitulate the dynamics, structure, and stability of complex systems by analyzing their parts. For example, experimental studies of predator-prey interactions have found that the combined effects of two or more predator species frequently differ

from those predicted for a single predator (Vance-Chalcraft et al. 2007). These studies evaluate if effects are independent (i.e., the predator species do not interact), synergistic (i.e., effect on prey is greater than additive), or antagonistic (i.e., effect on prey is less than additive). In many cases, multiple predator effects are sub-additive, as a result of interference among different predator species competing for the same prey. A comparable framework could be employed to study the effects of multiple mutualists (Stier et al. 2012), using experiments to evaluate how the presence of multiple partners influences the net benefits of mutualism, relative to the benefits that result from pairwise interactions alone. If higher-order interactions are indeed common in mutualistic networks, then determining when these interactions are antagonistic and when they are synergistic, and by what mechanisms, will provide insight into how mutualists will respond to shifts in the density and diversity of their partners. For example, it has been suggested that antagonism among pollinator species reduces the pollination of plants by competitively subordinate pollinators (Palmer et al. 2003). If these subordinate competitors provide superior pollination service, interference between pollinators has the potential to influence plant fitness sub-additively.

Recent studies have suggested that higher-order interactions may indeed be of general importance to the structure and stability of mutualistic networks. For example, “nurse” plant species that increase the survival of heterospecific seedlings (e.g., by ameliorating evaporative stress) promote a stable, nested network structure, wherein some nurse-plant species facilitate many more seedling species than others (Verdu and Valiente-Banuet 2008). Kefi et al. (2012) demonstrated that such higher-order, non-trophic interactions among plants can both stabilize competitive interactions and increase network diversity. Despite these findings, many important questions remain unanswered. We do not know, for example, how higher-order interactions modify mutualistic coevolution, nor how variation in the frequency and strength of higher-order interactions affect mutualistic networks. Such questions deserve further study.

Approaches designed to understand complexity within mutualisms may be similarly useful in

beginning to expand our view outwards, toward the broader community. Mutualisms, of course, are not interactions occurring in a vacuum; they occur within diverse, interacting ecological communities, which both affect and are affected by the mutualisms themselves. Next, we consider the impacts of the broader community on mutualisms.

### 9.3 How communities influence mutualisms

Comparable to the impact of multiple mutualists (Stanton 2003), species in the community that are external to the focal mutualism, i.e., third-party species, can drive context-dependent outcomes of mutualisms across time and space (Bronstein and Barbosa 2002). Many good examples of the importance of third-party species come from studies of pollination. Strauss (1997) argued that leaf-eating herbivores could alter floral traits, with consequences for pollinator attraction. We now know that herbivores can alter not only floral number and morphology, but also chemical traits and phenology, with strong indirect effects on pollinators (Gómez et al. 2009, Kessler et al. 2011). Additionally, there is evidence that plants benefit from pollination only in the absence of herbivores when herbivores preferentially attack plants with more flowers (Herrera et al. 2002), that induced defense traits reduce pollination more in the presence of other nectar-providing plant species (Gegear et al. 2007), and that such interactions can alter macroevolutionary patterns in flowering plants (Armbruster et al. 2009). Competitive interactions can also affect pollination mutualisms. For instance, in herbaceous plants, light competition from the woody overstory can indirectly reduce flowering success by lowering the average temperature, which decreases pollinator activity (Kilkenny and Galloway 2008). At an evolutionary scale, this may explain why herbaceous species in deciduous forests tend to flower in the spring and fall, when light penetrates well to the forest floor, and not in the summer (Schemske et al. 1978).

Recognition of mutualisms as integral components of larger interaction webs was a vital step forward for community ecology (Fontaine et al.

2011), and recent studies have begun to integrate trophic and mutualistic higher-order interactions into network theory (Stouffer 2010). Nevertheless, studying mutualistic interactions, themselves quite complex, in the context of all of the other potential interactions in a given community raises the spectre of overwhelming contingency (see Chapter 11). With this challenge in mind, we suggest a systematic approach to studying how third-party species affect mutualisms. Specifically, we must: (1) establish which third-party species exert the strongest effects on a given mutualist complex; (2) evaluate the importance of variation—both spatial and temporal—in the effects of third-party species on mutualists; and (3) incorporate metapopulation and metacommunity theory, in combination with molecular tools, to test whether there are predictable patterns of (co)evolution in such interactions.

Below, we first consider how third-party species can exert effects on mutualism. We then discuss potentially fruitful approaches to studying the importance of third-party species in the outcomes of a given mutualism, revisiting the three steps above.

#### 9.3.1 Mechanisms of third-party effects

All mutualisms are affected by third-party species. A substantial subset of mutualisms—those that involve protection from competitors or natural enemies—are mutualistic precisely *because* of the presence of third-party antagonists. The influence of third parties on the dynamics of other mutualisms can be subtle. For example, dispersal mutualists may transport propagules to sites where competition and/or seed predation is reduced, but the benefits of this service will depend on the abundance of each community's competitors and consumers. As another example, the benefits of pollination mutualisms depend on the relative importance of sexual versus vegetative reproduction, which itself may depend on the intensity of the co-evolutionary arms races between plants and their pathogens (Seger 1988).

Third-party species shape the outcomes of mutualisms via interactions, both direct and indirect, with the mutualists. Interactions with a third party can alter mutualistic outcomes by changing: (1) the

density of mutualists (e.g., Knight et al. 2005); (2) the rewards offered by one mutualist to another (Strauss 1997, Palmer et al. 2008); and/or (3) the costs of reward production or receipt (Strauss 1997). For example, ant visitation to flowers can decrease bumblebee pollination, presumably because bees both reduce flower visits (lower density) and spend less time on flowers (reduced perceived rewards) when subject to the possible costs of ant harassment or attack (Cembrowski et al. 2014). The substantial interest in the balance of trade between mutualistic partners (i.e., the continuum of outcomes between net benefits and net costs) has resulted in more research on how traits influence mutualism, and thus on how third-party species can alter such traits, than on how third-party species affect the population densities of mutualists (Bronstein 1998). Although empirical studies of how third parties alter mutualist densities are necessary, they will be challenging because such effects play out over multiple generations (Knight et al. 2006). In addition, we note that there is still very little specific information on the costs of mutualism, which limits our ability to infer how third-party species might affect such costs. For example, although herbivory leads to increased plant toxins in both flower nectar (Strauss 1997) and fruit pulp (Whitehead and Bowers 2013), the fitness effects of toxin allocation are rarely measured in plants and are even less understood for pollinators and seed dispersers.

Bronstein and Barbosa (2002) summarize several specific pathways by which a third species can affect mutualistic outcomes, including effects caused by antagonists, other mutualists, and exploiters of the mutualism. As in most interaction networks, however, the relative importance of direct versus indirect effects of third-party species on mutualists remains unclear (but see Menge 1995 for efforts to understand the balance of these effects in food webs). In one of the rare examples of indirect effects of third-party species on mutualism, Knight et al. (2005) showed that fish increase the benefits of a pollination mutualism to a plant by reducing densities of dragonflies, which eat the plant's pollinators. Examples of direct interactions between mutualists and third-party species are more common, and these can be comparable in strength to

the interactions between the mutualists themselves, even causing the net benefits of the original mutualism to disappear (Palmer et al. 2008). It seems unlikely that a single indirect interaction could have an equally strong effect, but again, such studies will require a better understanding of how third-party species affect the population dynamics of mutualist species.

Finally, third-party species also affect mutualisms by modifying the environment. For example, falling tree branches that damage myrmecophytic *Leonardoxa* plants create the disturbance regime necessary for the coexistence of two symbiotic ant species, because one ant species is a strong colonist of damaged plants, whereas the other forms larger, more competitive colonies (Debout et al. 2009). Other examples include subterranean termites that shift the competitive balance among defensive ant species in acacia trees by increasing local primary and secondary productivity (Palmer 2003), and soil microbial communities that alter phosphorus availability, with cascading effects on plant-mycorrhizal mutualisms (Johnson et al. 2010). Such environmental effects by third-party species are doubtless pervasive, but deserve more explicit study. Spatiotemporal variation in such effects will also generate substantial variation in the dynamics of mutualism across space and time.

### 9.3.2 How do we study the effects of third-party species?

To understand the cumulative effects of third-party species on mutualisms, we return to our three goals from above. To establish which third-party species have the strongest effects, we must determine how much of the community must be considered explicitly to understand the outcomes of a particular mutualism. There is reason to hope that it will suffice to consider relatively small numbers of associated species. Similar to the way in which omnivory shortens the length of the average interaction chain in food webs (Menge 1995), third parties can affect both mutualistic partners simultaneously. For example, a grazing ungulate can both eat plants and reduce mycorrhizae by compacting soil (Eom et al. 2001). In addition, some important non-mutualistic interactions may involve the same species that function

as mutualists: seed dispersers can eat defensive ants (Janzen 1966), defensive ants can deter pollinators (Ness 2006), and pollinators can also eat the plants they pollinate (Adler and Bronstein 2004). Finally, there are usually keystone third-party species with disproportionate effects on any given mutualism (Gómez et al. 2009), limiting the fraction of the community that may need to be studied in detail to understand a given mutualism. Of course, one of the primary challenges for establishing generality is that many effects of third parties will be strongly context dependent (Chapter 10).

An important step toward understanding context-dependent outcomes will be to investigate the role of third-party species in shaping the community-scale diversity of potential mutualists (see Section 9.2). The theoretical framework of evolving metacommunities (Leibold et al. 2004, Urban and Skelly 2006) predicts that communities are shaped by local and regional processes, linked by the dispersal of interacting, evolving populations. The processes of community assembly predicted by metacommunity theory can profitably be applied to mutualisms and third-party interactors. Dispersal, colonization, and local extinction lead to heterogeneity in local mutualist communities, which may be driven by competition–colonization trade-offs (“patch dynamics”), the effects of heterogeneity in local environmental conditions on the outcomes of competition (“species sorting”), and the persistence of populations that would otherwise be unsuited to local conditions by means of persistent dispersal (“mass effects”; see Mihaljevic 2012 for a recent exploration of this theme). Importantly, these forms of spatial dynamics have been shown to stabilize models of obligate mutualisms (Hoopes et al. 2005) by ensuring species persistence at larger spatial scales (i.e., the scale of the metacommunity).

Conversely, mutualisms themselves play important and little-studied roles in metacommunity dynamics. Most fundamentally, pollination and dispersal mutualisms provide the essential services of transporting genes and individuals across space. Mutualisms can also alter the balance of competition within trophic levels (Clay and Holah 1999) or the strength of interactions across trophic levels, and increase spatial heterogeneity in communities (Mihaljevic 2012). This heterogeneity, in turn,

can play an important role in species coexistence by shifting competitive balance and/or creating enemy-free space (Hoopes et al. 2005). Incorporating mutualisms into both theoretical and empirical analyses of spatiotemporal heterogeneity in interaction webs (Gómez et al. 2009) is in our view crucial for gauging the role of the community in shaping mutualisms, and in turn of mutualisms in altering the broader community, as we will discuss below.

Moving forward, the complementary use of meta-community theory and molecular tools will help to elucidate spatiotemporal variability in community assembly and its cascading effects on the ecology and evolution of species interactions. For example, phylogeographic studies of mutualist species can be used to estimate gene flow among metapopulations and to compare historical demographies to investigate codispersal of interacting species (e.g., Smith et al. 2011). By identifying similar phylogeographic patterns of yucca plants and moth pollinators that indicated historical connections, Smith et al. (2011) were able to investigate and rule out the possibility that plants had experienced historical dispersal limitation due to the extinction of their megafaunal seed dispersers. As molecular tools continue to develop, it may soon be possible to move beyond studies of neutral loci to investigate loci under selection in geographic mosaics (Vermeer et al. 2011) and to associate these loci with phenotypic traits that are relevant to a given mutualism (Kloth et al. 2012). These studies will require in-depth knowledge of the selective pressures on traits that can only come from increased effort to investigate interactions experimentally and measure traits of interest in the field.

What are the traits that mediate interactions between mutualists and third parties? In the special case of protection mutualisms, the importance of third-party natural enemies may be quantified indirectly in reward production, a trait of the protected species. For example, lycaenid caterpillars secrete nearly double the amount of nectar for attending ants when threatened by simulated enemy attack (Leimar and Axen 1993). Conversely, when enemies or competitors are absent, we should expect the disappearance of rewards, either plastically or adaptively. For example, Palmer et al. (2008)

demonstrated that these circumstances can lead to the disappearance of mutualistic rewards offered by the protected species on ecological time scales. In many mutualisms, the traits of interest will be behavioral: pollination, dispersal, and protection mutualisms all involve an exchange of resources for mutualistic services, and services usually depend on behaviors. Behavioral traits have been less studied in the context of mutualistic coevolution than other phenotypic traits, perhaps because they are more difficult to quantify, but they are no less important. For example, studies have shown that predators strongly affect pollination mutualisms not only by directly consuming pollinators, but also by reducing pollinator visitation rates and the time spent on flowers (Romero et al. 2011). Gómez et al. (2009) provide an example of how structural equation modeling can be used to identify strongly interacting third-party species and their effects on the evolution of plant morphological traits in a diffuse pollination spatial mosaic. An important next step will be to look simultaneously at pollinator traits in this network, and to do so will require behavioral studies.

It is our hope that the steps above provide a tractable roadmap for deepening our understanding of how the broader ecological community affects mutualism outcomes. We now turn our attention to the converse problem: how do mutualisms affect their broader communities?

## 9.4 How mutualisms affect communities

Because virtually every species on earth is involved in at least one mutualistic partnership, and because so many species rely on mutualisms for reproduction and/or survival, mutualism clearly plays a central role in the assembly, structure, and persistence of ecological communities. However, our understanding of how mutualisms affect communities is still limited. Here we will explore a few of the many important questions that remain unanswered. First, what determines whether mutualisms modify community diversity, and can we predict a priori whether they will increase or decrease species richness? Then, what is the role of mutualism in delineating species ranges, which are important determinants of community assembly

and membership? Finally, do mutualisms tend to stabilize or destabilize the dynamics of species' populations that comprise communities?

### 9.4.1 Effects of mutualisms on community diversity

Mutualisms can reduce species diversity by enhancing the performance, and therefore the competitive dominance, of their partner species. These effects may in turn reduce diversity at other trophic levels (e.g., Ringel et al. 1996). A notable example of this phenomenon is found in specialized plant-endophyte mutualisms (Rudgers and Clay 2008). Alkaloid-producing fungal endophytes that live in tall fescue grass (*Lolium arundinaceum*) enhance the grass's competitive dominance by reducing herbivory, which results in strong suppression of both plant and arthropod species richness in the broader community (Rudgers and Clay 2008, but see Faeth 2010). Similarly, the presence of arbuscular mycorrhizae can disproportionately benefit the invasive and more mycotrophic grass species spotted knapweed, reducing prairie grass diversity (Harner et al. 2010), and the aggressive acacia ants from our opening example suppress elephant herbivory, which contributes to the monodominance of *A. drepanolobium* trees at ecosystem scales (Goheen and Palmer 2010). Indeed, these processes can have dramatic effects on entire ecosystems. In Hawaii, invasion of lowland forests by *Falcateria moluccana* trees that engage with nitrogen-fixing bacterial symbionts has dramatically increased the availability of limiting nitrogen in the soil. This in turn has facilitated the growth and spread of several invasive plant species, transforming lowland forests that had formerly been dominated by native plants (Hughes and Denslow 2005).

The above examples come from highly specialized mutualisms, but of course mutualisms do not have to be specialized to reduce community diversity. In fact, it is the diffuse, generalized nature of many mutualisms that has frequently allowed invasive species to establish new mutualistic partnerships that allow them to spread in introduced areas (Richardson et al. 2000). Although variation in partner quality is the norm within speciose mutualisms, we know relatively little about how the availability



of any given partner affects the abundance or diversity of other partners on the same side of the mutualism. In some instances, a particular partner species may provide such attractive rewards or services that it effectively “steals” mutualists away from other members of its guild. For example, plant species that provide large rewards to mutualistic pollinators can increase the degree of pollen limitation in other plants (Traveset and Richardson 2006), although we know little about the consequences of these effects at the population or community level. Again, invasion ecology can provide insights into the mechanisms behind such effects. In central Europe, for example, the invasive annual *Impatiens glandulifera* produces superabundant floral nectar, drawing pollinators away from native plants and reducing the native-plant seed set (Chittka and Schurkens 2001).

Mutualism can also clearly increase community diversity in both evolutionary and ecological time. Among the most striking examples of this are mutualisms that enable the persistence of foundational (e.g., coral-zooxanthellae mutualisms) or keystone species (e.g., figs and their pollinating wasps), which in turn provide critical habitat, food, or other resources for myriad species. Mutualisms can also foster species diversity simply by permitting rare species to persist at lower densities or in harsher environments than they would without mutualism. For example, mixed-species flocks of foraging birds may permit some species to persist in low-resource conditions (e.g., northern winters for insectivorous birds) where otherwise they might disappear (Morse 1970). In addition, flocking provides protection from predation, which should weaken top-down effects, e.g., of raptors and other specialized bird predators. As another example, animals can facilitate long-distance dispersal, which can be important for species persistence at the metacommunity scale when local populations suffer recurrent extinctions. Mutualism also promotes diversity through other, less direct pathways. In Box 9.3, Charlotte Lee, Brian Inouye and Tom Miller discuss how interactions between competing partners and their shared mutualist can promote coexistence of the competitors. Additionally, mutualism can exert “equalizing” (Chesson 2000) effects on species coexistence when inferior competitors are preferentially

chosen by superior mutualists (Bever 2002), or when superior competitors facilitate inferior competitors more than they harm them (Schmitt and Holbrook 2003).

An important unanswered question is whether we can predict the strength and direction of the effects on community diversity of different types of mutualisms (e.g., pollination, dispersal, nutrition, protection) that are more or less specialized. For example, are generalized mutualisms more likely to increase community diversity over ecological or evolutionary time scales since many species can openly access the resources exchanged? Conversely, are highly specialized mutualisms more likely to decrease diversity by conferring advantages to only certain mutualist species (e.g., Rudgers and Clay 2008)? Or are highly specialized mutualisms more “compartmentalized,” reducing the impact of these interactions on the broader community? In general, while numerous studies have documented the positive and negative effects of mutualism on guild- or community-level diversity, we still lack a mechanistic understanding of how these effects are wrought. In the future, eradication programs for invasives may provide excellent large-scale experimental templates for understanding how particular mutualists drive changes in community diversity. In addition, the widespread, anthropogenically driven loss of particular guilds of mutualists, such as the loss of large mammalian dispersers caused by overhunting in tropical forests, is unfortunately providing opportunities to test how mutualists influence the structure of entire communities (Terborgh et al. 2008). Changes in seed-disperser communities affect how far juvenile plants can disperse from their parents, and other types of mutualisms also play important roles in establishing range limits.

#### 9.4.2 Mutualism and species range limits

We know much less about the role of mutualism in determining species range limits than we know about the roles of abiotic factors and other biotic interactions (e.g., competition, Sexton et al. 2009). Local communities are assembled from the regional species pool, which itself is comprised of species with overlapping ranges. The factors that determine range limits are therefore important in

### Box 9.3 Mutualism alters competition: coexistence of mutualists and exploiters

**Charlotte T. Lee, Brian D. Inouye,  
and Tom E. X. Miller**

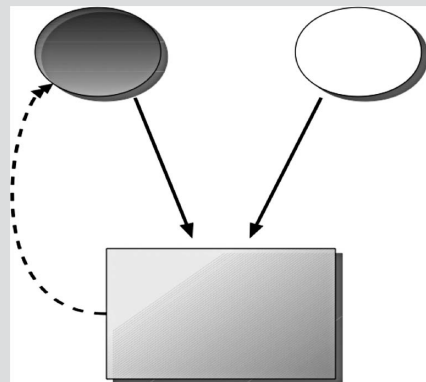
The existence of exploiters is a prominent problem in the community ecology of mutualism (e.g., Bronstein 2001, Morris et al. 2003; see Chapter 6). Competition plays a central role in this problem because an exploiter might be expected to enjoy a competitive advantage as a result of not paying the costs of providing mutualistic benefits to a partner species. Why don't exploiters always disrupt mutualisms by driving one of the partners extinct through competitive exclusion? One possible answer to this question is that mutualism can alter the dynamics of competition in ways that promote coexistence of the mutualistic and exploitative competitors.

Recent theoretical work shows that the inclusion of key demographic detail in competition models can enable coexistence between competitors that differ in their effects on their resource species (Lee and Inouye 2010, Lee et al. 2011). This includes the case when one competitor is a mutualist and the other an exploiter (Box 9.3 Figure 1); no restrictive assumptions about competitive asymmetries, trade-offs, or spatial or temporal heterogeneity are required to enable coexistence. When interactions between individuals are prolonged and exclusive, such as those between ant-adapted plants and the ant colonies that nest in them, competitors' differing influences over the vital rates of their resources can alone enable coexistence. When interactions are shorter in duration, competitors' effects on their resource can enable coexistence through interaction with age or stage structure in the resource species. We discuss examples of each case below. In both, the novel stabilizing effect of mutualism arises when each competitor influences the resource population in a way that benefits the other species, i.e. in a way harmful to itself.

Mutualisms between ants and ant-adapted plants (myrmecophytes) provide excellent examples of prolonged interactions. In ant–myrmecophyte mutualisms, multiple ant species may compete to establish colonies within specialized plant structures. If ant colonies cannot be displaced once established, competition follows the lottery model (Sale 1977). The key departure from basic lottery competition is that ant colonies may protect their host plant from herbivores and/or competitors, which can “feed back” to the space they occupy by increasing plant vital rates such as survival, growth, and reproduction (e.g., Vasconcelos 1991, Palmer et al. 2010). These benefits feed

back to affect the number and type of plants available to ants, altering the dynamics of competition between ant species (Lee and Inouye 2010). Stable coexistence is most likely when one ant species has greater rates of colony reproduction but less effectively protects plant survival and fecundity (and thus is an exploiter), and the other species has higher persistence on plants and lower reproductive rates, while promoting stronger plant performance (and thus is a mutualist).

Many mutualists do not form long-term relationships, but instead collect food from their hosts on a short-term basis (Holland and DeAngelis 2010). Prominent examples include the many animals that collect nectar, food bodies, or pollen from plants while pollinating or protecting them. Plant survival, growth, and reproductive rates not only are influenced by these activities, but also typically vary between plant size classes or life history stages. Numerous studies document effects of animals on stage-specific plant vital rates that can be expected to alter the dynamics of the host population (e.g., Maron and Crone 2006, Underwood and Halpern 2012). As in the longer-lasting associations described above, competitors' effects on plant demographic rates can feed back to stabilize coexistence (Lee et al. 2011). The competitors must differ in their effects on the plant population, in



**Figure 1** A mutualist (gray circle) and an exploiter (white circle) compete (black arrows) for resources supplied by a resource species (gray rectangle), but the resource species benefits from the mutualistic competitor (dashed arrow) at a cost to that competitor. This simple diagram highlights the importance of competition to the problem exploiters pose to mutualisms, but suppresses key demographic detail which can promote the coexistence of the two competitors.

*continued*

**Box 9.3** *Continued*

the same way as competing mutualists and exploiters do above. Due to the shorter duration of interactions, however, it is also necessary for the resource population to exhibit some underlying age or stage structure, so that via their effects on resource demography, the competitors can shift the relative abundance of resource stages in ways that favor their competitors.

That mutualism could be ecologically vulnerable to invasion by an exploiter, yet not vulnerable to extirpation by that exploiter, emerges from two different models appropriate to mutualisms that involve prolonged symbiosis and short-term interaction, respectively. The key similarity in the models is that the underlying mechanisms of both mutualism and competition be expressed explicitly—by a careful accounting of competitors' direct effects on one another and indirect effects mediated through their impact on their shared resource's demography. When this is accomplished, mutualism and competition can interact in ways that can yield coexistence surprisingly easily.

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- determining community membership. Mutualistic interactions probably help to delimit species' ranges because of their role in metacommunity dynamics, as discussed previously. Strong interdependence in more specialized interactions means that the range limits of either partner can be constrained by the availability/dispersal limitation of the other. Both colonization and extinction could thus be strongly influenced by the presence or absence of mutualist partners.
- We are just beginning to characterize the mechanisms by which interdependence between mutualists determines species' ranges. For example, plant species with a strong degree of pollen limitation may be limited at range edges by the availability or performance of their dominant pollinators (Chalcoff et al. 2012). Nutritional mutualisms between plants and their belowground microbial associates may be similarly important to spatial distributions: although many of these interactions are generalized, there is evidence that a lack of sufficient mycorrhizal or rhizobial partners can limit both the spread of invasive species (Parker et al. 2006) and the distribution of native species (Stanton-Geddes and Anderson 2011). For example, pines were slow to invade the southern hemisphere, where there are no native ectomycorrhizal partners (Richardson et al. 2000), until introduced fungal networks (e.g., from pine plantations) accumulated sufficiently to insure inoculation. At a more local scale, Terwilliger and Pastor (1999) suggested that black spruce (*Picea mariana*) were slow to colonize meadows located in old beaver ponds because of the compounded effects of absent mutualisms. The tree requires

ectomycorrhizal fungi to grow, and the fungi cannot tolerate submergence at the initial stages of beaver pond succession. In addition, the animal that disperses the fungus, the redbacked vole (*Clethrionomys gapperi*), is prevented from entering the meadows by the dominant rodent in meadows, the meadow vole (*Microtus pennsylvanicus*; Terwilliger and Pastor 1999). Thus, abiotic conditions and competitive interactions between dispersers together limit the spatial distribution of a host that requires specialized mutualisms.

Seed-dispersal mutualisms also play a pivotal role in determining species ranges (Svenning and Skov 2007), but we know very little about whether and how dispersal mutualisms are degraded or altered at range edges. These dynamics will be important to understand because they affect the plasticity of plant responses to future climate change. The establishment and persistence of plant populations depends in large part on the frequency and timing of dispersal events, which provide opportunities for range expansion and “rescue” from local extinction. Case et al. (2005) suggest that gradients in the abundance of generalist animal dispersal agents could lead to range limits in plant species; any factor that reduces colonization relative to extinction could generate a range limit. Long-distance dispersal events in particular can play a powerful role in shaping plant distributions, but the rarity of these events poses challenges to empirical assessments of how much dispersal mutualisms constrain species ranges. Seed addition experiments, in which seeds are planted into novel habitats beyond range edges, will be informative in assessing the relative importance of dispersal limitation (Clark et al. 2007) versus factors such as habitat availability. Such studies can be paired with more mechanistic studies to evaluate how disperser guilds and plant performance vary from range centers to boundaries.

### 9.4.3 Mutualism and community stability

Ecologists are beginning to recognize an important role for mutualism in determining community stability. Recent models suggest that diverse interaction types, including mutualism, competition, and predation, stabilize the population dynamics of species within communities (Mougi and

Kondoh 2012). This of course suggests that positive interactions play a crucial role in maintaining community-wide stability, contrary to classic models in which the positive feedbacks inherent in mutualism were considered to be destabilizing (May 1981). Yet the biological mechanisms that underlie the stabilizing effects of mutualism remain unclear. Are mutualisms stabilizing because they introduce positive feedbacks between constituent species that are otherwise vulnerable to overexploitation by predators or extirpation by competitors? Does the diffuse nature of most mutualistic interaction networks cause weak interactions, which enforce stability, to dominate (Emmerson and Yearsley 2004)? Or does the disparate nature of the broad class of interactions that we identify as mutualisms, and the multiple mechanisms that therefore underlie them, preclude any meaningful generality?

One profitable research avenue will be to explore the effects of mutualism on the stability of community modules that lie somewhere between highly simplified two-species studies, and the (largely phenomenological) modeling studies that embrace entire ecological communities across multiple trophic levels. For example, Benadi et al. (2012) recently modeled the effects of pollinators on the stability of the guild of plants they pollinate. They found that whether pollinators stabilized plant guilds depended on both the extent to which plant resource use overlapped, and the degree of pollinator specialization. When plant species had overlapping resource niches, pollinators strongly destabilized plant guilds irrespective of the degree of pollinator specialization; in effect, rarer plants received lower levels of conspecific pollen transfer than more common species, decreasing their relative contribution to the seed bank in each successive year. However, when plant species had very low levels of niche overlap (contributing “stabilizing” effects to coexistence, Chesson 2000), pollinators stabilized plant guilds in all cases except for instances in which pollinators were completely generalized (Benadi et al. 2012). Importantly, this study considered the stability of the pollination network in a broader context, evaluating both variation in the pollination mutualism and the degree of resource competition among plant species. Because niche overlap among coexisting plant species is often high, the results from this

study suggest that other mechanisms in addition to niche overlap may need to be invoked to explain coexistence of plant species that share pollinators. Nevertheless, this work provides an excellent example of how viewing mutualism within a broader community context can shed light on the extent to which mutualism, in concert with other species interactions, influences the stability of ecological communities.

Empirical studies of the effects of mutualism on community stability are scarce, but one emerging generality seems to be that the mechanisms by which the mutualists interact with the broader community determine whether these interactions stabilize or destabilize community dynamics. For example, nutritional mutualisms that fuel species' dominance are likely to stabilize communities where such dominants provide heterogeneous habitats (e.g., corals, Hay et al. 2004), but destabilize communities where these dominants exert strong competitive effects on other guild members (e.g., invasive ants, Shik and Silverman 2013). The effects of protection mutualisms on communities may also depend in part on the trophic level of the protected partner. If the protected species is an autotroph, mutualism can stabilize communities by buffering plants from consumption, for example where ants stabilize tree cover by protecting their acacia hosts from catastrophic elephant herbivory (Goheen and Palmer 2010). Contrastingly, in cases where the protected species is a consumer, mutualism may lead to strong cycles of exploitation and recovery. For example, Morales et al. (2008) showed that when aphids were protected by ant mutualists from predation, they exerted strong consumptive effects on plants, with destabilizing effects on the food web. More generally, where protection mutualisms simplify the trophic structure of communities, the likelihood of strong trophic interactions could potentially increase, with destabilizing effects on communities. These ideas provide testable propositions for empirical work.

## 9.5 Conclusions and future directions

Over the past thirty years, a groundswell of interest in interspecific cooperation has greatly increased our understanding of the ecology and evolution of

these ubiquitous interactions. We have learned that mutualisms are themselves complex associations of interacting species, that third-party species greatly modify the outcomes of interactions between mutualist guilds, and that mutualisms transform communities by creating foundational habitat, extending species ranges, and linking populations across space, through time, and via webs of interactions. Yet in many ways, our understanding of mutualism is still in its infancy: relative to interactions such as competition and predation, there remains a great need for research—both theoretical and empirical—on the interplay between mutualisms and the broader communities in which they are embedded. We have highlighted recent research that illustrates some general phenomena about feedbacks between mutualisms and their community context, but many questions remain. Below, we highlight a number of unanswered questions (by no means exhaustive) that we think are important to consider as the field moves forward.

1. Because the benefits of mutualism vary with abiotic and biotic context, the ranking of the “best” partners for a particular mutualist may also vary from year to year, or from one place to another. In light of this, does partner diversity buffer mutualism from temporal and spatial environmental variation (Box 9.1)? Are there abiotic conditions which foster the efflorescence of mutualisms, or conversely hamper their formation or retention?
2. How does species diversity in mutualistic assemblages, whereby a given mutualist interacts with multiple partners either serially or simultaneously, integrate to influence long-term fitness of each participant (Box 9.2)? Because natural selection operates on lifetime fitness, this is a particularly critical area of study for understanding the maintenance of cooperation (and related traits and behaviors), particularly among partners differing in generation length and dispersal range.
3. When a mutualist interacts sequentially with a number of partners, how does the timing, duration, or sequence of partnerships influence fitness? Does the rank order of the quality of partners remain constant or change in the course of mutualist ontogeny?



4. How important are indirect effects provided by third parties to the structure and functioning of mutualistic interactions (e.g., Knight et al. 2005), and do third parties tend to have stronger effects on mutualisms by changing mutualist traits or population densities?
5. Are mutualisms, which often result in transport of genes and individuals, disproportionately important to metacommunity dynamics, relative to interactions such as competition or predation? How does the degree of specialization in mutualism influence the persistence of the participant species within metacommunities?
6. Especially for obligate mutualisms, to what degree do the costs of mutualism constrain the range limits of species?
7. To what degree can a quantitative, theoretical framework for the community ecology of mutualisms be devised, comparable to say niche partitioning or food-web models? To what extent does the broad natural history of mutualisms, from mycorrhizae to seed dispersal, preclude the development of generalized models?
8. How can an understanding of mutualism in community settings inform issues in applied ecology? For example, can we use trait-based approaches to predict the success of invasive mutualists in novel habitats (see also Chapter 13)? Can one make strong predictions about how communities and ecosystems will change when mutualisms dissipate or disappear? For example, the loss of specialized pollinators will lead to plant extinctions, but what other broad-scale community-wide or ecosystem-level consequences (discussed in Chapter 14) will there be?

We began this chapter by highlighting how the acacia ant *Crematogaster nigriceps*, an apparent sterilization “parasite” of the East African ant-plant *Acacia drepanolobium*, actually exerts strong positive effects on the lifetime fitness of these acacias. Yet this positive effect only emerged by considering the broader community in which this particular pairwise association is embedded. To illuminate the mutualistic role of this species, it was necessary to understand the dynamics of competition among the various ant partners, the impact of a broad suite of herbivores and other mortality factors on the plant, the

costs and benefits of different ant-plant pairings across acacia ontogeny, and the long-term demography of the host plant. In essence, broadening the spatial and temporal scope of the study of this mutualism yielded insights that would not have been possible using more conventional pairwise, single-life-stage study approaches. In the same way, a recurrent theme throughout this chapter is the need to identify the mechanisms underlying the interactions between mutualists and their communities. Expanding our studies of mutualism to consider the surrounding community and longer temporal scales—and linking ecological and evolutionary processes over different spatial and temporal scales—will be crucial for identifying such mechanisms. As we expand the scope of our studies to include broader ecological contexts, mutualism will continue to claim an overdue and more prominent role in community ecology.

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