

# Competition and Coexistence: Exploring Mechanisms That Restrict and Maintain Diversity within Mutualist Guilds

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**ABSTRACT:** Mutualistic interactions are diverse and widespread and often involve multispecies guilds of mutualists competing for access to one or more partner species. Despite the ubiquity of these interactions, we know little about the dynamics of competition and coexistence within these guilds or how interactions between mutualists and their shared resource (the partner species) may influence these dynamics. In this article, we review the evidence for interspecific competition for partners within mutualist guilds in both plant-pollinator and ant-myrmecophyte systems. We then review evidence for the operation of different coexistence mechanisms within these guilds and discuss how the dynamics of competition and coexistence may be uniquely shaped by multispecies mutualist interactions. In particular, we note that adaptive and plastic responses by mutualists to variation in partner quality are likely to play an important role in determining these dynamics. We summarize by considering the ecological conditions that are likely to restrict or promote species coexistence within mutualist guilds. We suggest that these guilds may provide powerful model systems for exploring multiple mechanisms of species coexistence, and we discuss how these mechanisms may be modified by evolutionary adaptation.

*Keywords:* competition for partners, mutualism, species coexistence, patch dynamics, limiting resources, competition-colonization trade-offs, ant-plant symbiosis, pollination, specialization, generalist, myrmecophyte, resource partitioning.

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Within the past decade, the paradigm of mutualisms as highly specific and tightly coevolved interactions has faded and is being replaced by the recognition that most mutualisms involve multiple species interacting with one or more potential partner species (Howe 1984; Bronstein

1994; Waser et al. 1996). Species diversity within mutualistic interactions has broad ecological and evolutionary consequences, including variation in the benefits of mutualist services (Janzen 1975; Oliveira et al. 1987; Davidson et al. 1991; Longino 1991; Young et al. 1997; Bronstein 1998), the potential for complex interactions within diverse mutualist assemblages (e.g., see Hoeksema and Bruna 2000; Stanton 2003), and the evolution of parasitism within previously mutualistic associations (reviewed in Yu 2001). While the consequences of mutualist guild diversity are becoming evident, the mechanisms that stabilize these associations are poorly understood. How do multiple species coexist within guilds of mutualists in the face of potentially strong competition? While many studies have addressed species coexistence within trophic communities (reviewed in Tokeshi 1999; Chesson 2000), coexistence mechanisms have rarely been examined in the context of mutualistic interactions (but see Palmer et al. 2000; Yu 2001; Hoeksema and Kummel 2003).

Despite a great deal of progress in the study of species coexistence over the past century, few studies have experimentally tested multiple competing hypotheses within a single ecological system (e.g., Palmer 2001; Yu et al. 2001). Mutualist guilds provide powerful model systems for understanding the mechanisms underlying species coexistence for several reasons. First, among groups of mutualists that share partner species, strong competition for those partners is not uncommon (e.g., among pollinators for floral resources, among ants for myrmecophytic host plants). Second, the resources for which mutualist guilds compete are often individuals that are stationary and discrete (e.g., myrmecophytic plants, flowers, plant roots), making these systems unusually tractable for the study of coexistence mechanisms. Third, mutualisms are widespread and potentially critical determinants of community structure (e.g., Bronstein 1994; Kiers et al. 2000; Christian 2001). Finally, because members of mutualist guilds compete for a dynamic resource that may be under reciprocal selection with its partners, studies within these guilds may provide insight into novel coexistence mechanisms.

We have several objectives in this article. First, we review

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four classes of coexistence mechanism for which broad empirical and theoretical support exists and that seem likely to operate either singly or in combination to support diversity within guilds of mutualists. Second, we discuss the evidence for partner limitation and competition for partners in two well-studied mutualisms: the usually diffuse interactions between plants and their pollinators and the often more tightly coevolved associations between ants and their myrmecophytic host plants. We also review evidence for the operation of these different coexistence mechanisms within these mutualisms and suggest research agendas that can accelerate our understanding of the factors that stabilize and/or destabilize species diversity within mutualisms. Finally, we consider the ways in which mechanisms of species coexistence among mutualists may differ qualitatively from coexistence within other guilds, given the dynamic nature of the mutualist-partner interaction. In each section, we call attention to potential research directions.

#### Competition among Groups of Mutualists

In the absence of competition, mechanisms of coexistence need not be invoked to explain species diversity within guilds. It is therefore important to determine whether or not partners or their services represent a limiting resource for mutualist populations. Interspecific competition occurs when one species reduces the access of another species to a necessary resource that is in limited supply. Ideally, one would like to demonstrate the existence of partner limitation at the population level by showing that the density or growth rate of a mutualist population is increased either by removal of competitors or by enhancing the supply of partners, the putatively limiting resource. However, this has rarely been achieved in any mutualistic system, and we know little about the extent to which mutualist populations are limited by their partners or their services (Addicott 1986; Bronstein 1994; Stanton 2003). In the absence of such data, we often assume that if the average performance (e.g., foraging rate, fertility) of individual mutualists is increased by greater access to partners, then the availability of partners represents a limiting resource. It is unlikely that in any given mutualism, both guilds are limited by each other. If they were, the populations of both would increase until one guild becomes limited by another, extrinsic factor.

#### Some Well-Supported Mechanisms of Species Coexistence

Of the myriad coexistence mechanisms that have been proposed, only a subset have won broad acceptance among

ecologists. Here we discuss several of these mechanisms, which we divide into four nonexclusive categories.

#### *Environmental Heterogeneity and Trade-Offs*

The majority of coexistence mechanisms may be codified as forms of niche partitioning within heterogeneous environments (Cody and Diamond 1975; Whittaker 1975; Chesson 1991) by allowing that niches include both spatial and temporal axes of environmental heterogeneity. In this scenario, trade-offs in performance under differing physical and/or biotic conditions allow species to coexist, with each species dominating in different locations, with different partners, or at different times (reviewed in Tokeshi 1999).

#### *Patch Dynamics and Colonization-Competition Trade-Offs*

Coexistence within guilds may be facilitated when species exhibit trade-offs between competition and colonization abilities. In the absence of environmental heterogeneity, these trade-offs can facilitate species coexistence under restrictive conditions (Levins and Culver 1971; Tilman et al. 1994): when both propagules of competitive dominants can displace adults of inferior competitors and adults cannot successfully reproduce locally while they are being displaced (Yu and Wilson 2001). While trade-offs in colonization and competitive ability occur across a wide variety of taxa (Wilson 1971; Werner and Platt 1976; Roughgarden et al. 1988; Gleeson and Tilman 1990; Tilman 1990; Tilman and Wedin 1991; Haukialmi and Henttonen 1993), only a subset of ecological systems (reviewed in Yu and Wilson 2001) conform to these assumptions (e.g., see Holmes and Wilson 1998; Adler and Mosquera 2000; Yu and Wilson 2001; Levine and Rees 2002).

A more common ecological scenario is represented by lottery models, where competition is restricted to propagules (e.g., juveniles) and adult mortality is independent of the outcome of juvenile competition (e.g., Sale 1977; Chesson and Warner 1981). In this case, colonization-competition trade-offs promote species coexistence only when environmental heterogeneity confers to each species the highest population growth rate at some place or time (Chesson and Warner 1981; Comins and Noble 1985). This "replacement competition" (Yu and Wilson 2001) mechanism is essentially a form of niche partitioning, where environmental heterogeneity is partitioned into different resources (Abrams 1988; Yu and Wilson 2001).

#### *Recruitment Limitation and Aggregation*

A third class of coexistence models addresses systems in which recruitment limitation or aggregation minimize the

effects of interspecific competition. Strong dispersal limitation either may result in intraspecific aggregation of competitors (e.g., Rees 1996; Pacala and Levin 1997) or may allow species to win sites by forfeit, lessening the effects of competitive asymmetries (e.g., Hurtt and Pacala 1995). Intraspecific aggregation may also result from patterns of mate-searching behavior among invertebrates (e.g., Ives 1991). Evidence for multispecies coexistence via aggregation comes from both plant (Rees et al. 1996; Rejmanek 2002) and animal communities (reviewed in Wertheim et al. 2000), and winning by forfeit appears to play an important role in the coexistence of some tropical forest tree assemblages (e.g., Hubbell et al. 1999).

#### *Tritrophic Models*

Competitive coexistence may also be facilitated when predators, disease agents, or parasites disproportionately target the most abundant species (e.g., Jones 1933; Janzen 1970; Connell 1971; Lubchenco 1978; Tscharrntke 1992).

#### *Multiple Mechanisms*

While there is abundant empirical and theoretical evidence for the operation of these mechanisms in guilds of trophic competitors, we wish to stress that the presence of one mechanism does not obviate the operation of others in natural systems. For example, in a guild of East African acacia ants, patch dynamics (Stanton et al. 2002), two forms of priority effects (Stanton et al. 1999; Palmer et al. 2002), habitat heterogeneity (Palmer et al. 2000; Palmer, in press), disturbance (T. M. Palmer, M. L. Stanton, and T. P. Young, unpublished data), and temporal environmental variability (T. M. Palmer, M. L. Stanton, and T. P. Young, unpublished manuscript) all appear to contribute to species coexistence. Thus, a key question is not whether each of these mechanisms plays a role in diversity maintenance but to what extent. Further, within the context of mutualisms, what roles do plastic or adaptive responses by partner populations play in mediating coexistence within mutualist guilds? We now turn to the question of species coexistence within two well-studied mutualist systems: plants and their pollinators, and ants and their myrmecophytic hosts.

### **Competition, Coexistence, and Adaptation in Pollination Guilds**

Along with seed dispersal mutualisms, pollination systems are among the most diffuse mutualistic interactions. Most often, observers find that any given plant is visited by multiple species of pollinators and that pollinators, both at the species and individual level, visit flowers on multiple

plant species (reviewed in Waser et al. 1996; but see Johnson and Steiner 2000). Pollination associations tend to be redundant: in the absence of one mutualist partner species, another can often provide food resources or pollination services (e.g., Compton and McCormack 1999; Fleming et al. 2001; but see Bond 1994; Kearns et al. 1998). However, even in diffuse pollination mutualisms, flowering plants and pollinators are typically obligate participants in the overall mutualism, and there may be strong competition among members of each guild for access to the resources or services its partners provide.

#### *Limitation of Pollinator Populations by Floral Resources*

Population-level limitation by access to partners is critical to the issue of species coexistence within mutualist guilds, but as in many other mutualistic associations, we know relatively little about the factors that limit pollinator populations. In some systems, it has been shown that floral resources are in surplus supply and are unlikely to constrain local pollinator densities (e.g., Nefdt and Compton 1996; Addicott 1998), but the sources of those external constraints are rarely identified (Addicott 1986). Limitation of pollinator populations by floral resources is consistent with, but not proven by, correlative studies showing higher rates of pollinator activity in sites with historically greater densities of flowers (e.g., Frank 1998; Steffan-Dewenter and Tscharrntke 2000).

A number of studies have used correlation, experimentation, and/or comparative analysis to test for the existence of interspecific competition for shared floral resources among pollinator species. Typically, experimental studies document competition-induced changes in the performance of individual pollinators rather than in pollinator population density (but see Bowers 1986), forcing us to assume (for our purposes) that there is a correlation between individual- and population-level responses (Addicott 1986).

The most direct demonstrations of competition within natural pollinator communities have used field manipulations to reduce the density of one or more pollinator species and then have documented changes in the behavior of pollinators remaining at the site. Typically, competitively subordinate pollinators respond to release from competition by broadening of the spectrum of flower species they visit (Primack and Howe 1975; Inouye 1978; Bowers 1986) and/or by increasing time spent visiting high-yield flowers and patches (Morse 1982; Hingston and McQuillan 1999). Conversely, natural or experimental introductions of competitively dominant pollinator species can restrict patterns of flower visitation and even reduce the population densities of native pollinators (Roubik 1978; Evertz 1993; but see Steffan-Dewenter and Tscharrntke 2000; Roubik and

Wolda 2001). An alternative but underused experimental approach is to increase or decrease the amounts of floral reward available within a site and then measure changes in pollinator behavior or performance that are (or are not) consistent with competition for naturally occurring floral resources. For example, providing superabundant nectar with artificial feeders can reduce the intensity with which hummingbirds exclude pollinators of other species from their territories (Powers and McKee 1994).

Our ability to generalize about the importance of competition within pollination guilds is limited by the few manipulative studies that have been published and by the possibility that published results are biased toward those demonstrating competition. We believe that this is a fertile area of research for investigators interested in multispecies mutualisms. Field manipulations can be a powerful way to reveal the existence of competition for floral resources and also to document competitive inequalities among members of a pollinator guild (Bowers 1986; Nagamitsu and Inoue 1997; Sandlin 2000).

#### *Potential Mechanisms of Coexistence among Competing Pollinators*

Given how little we know about population limitation and competition among copollinators, it might seem premature to speculate about mechanisms that could maintain species diversity within pollination guilds. However, we believe that ecological theories on species coexistence can be used to guide analyses of multispecies pollinator communities. Pollinator coexistence is not only of theoretical importance. Many conservation biologists are concerned about the spread of invasive pollinators such as honeybees and some bumblebees, which can reduce populations of native pollinators (e.g., Dafni and Shmida 1996; Hingston and McQuillan 1998; Kato et al. 1999; Gross 2001). Both fundamental and applied investigations will be better informed if we can learn what makes certain pollinators invasive competitive dominants (e.g., Corbet et al. 1995) and what conditions favor the persistence of competitively subordinate species.

*Environmental Heterogeneity and Trade-Offs.* Resource partitioning among copollinators may be a widespread phenomenon that minimizes interspecific competition for floral resources and that facilitates the persistence of pollinators that are not competitively dominant. There is a vast literature describing variation in the spectra of flowers used by different species of co-occurring pollinators. We only touch on that literature here to make the point that pollinators within the same guild may partition resources along at least three axes of heterogeneity: spatial, temporal, and/or floral. First, co-occurring pollinator species can vary in the

way they utilize habitats that are spatially heterogeneous with respect to edaphic factors (Herrera 1988) or reward density (Johnson and Hubbell 1975; Kwak 1987; Cotton 1998; Mayfield 1998). For example, species within many guilds of tropical hummingbirds display a consistent set of foraging strategies ranging from territorial species that dominate dense flower patches to trap-lining foragers that can more efficiently utilize widely scattered, low-reward flowers (Feinsinger 1976; Feinsinger and Colwell 1978; Tiebout 1992). Second, a number of investigators have found that members of a pollinating guild tend to forage during different portions of the season (Feinsinger 1980; Ginsberg 1983) or at different times of the day (Paton 1993; Cotton 1998). Some competitively subordinate pollinators are temporal fugitives that can sustainably use the dregs of pollen and nectar left in flowers that have been fully exploited and then abandoned by more competitive species (e.g., Heinrich 1976).

Despite the many studies demonstrating resource partitioning among co-occurring pollinator species, we still have a poor understanding of how these patterns influence, or are shaped by, competition for floral resources. Comparative studies can provide some support for alternative mechanisms. For example, finding that one pollinator species visits a narrower range of available flower species in sites it shares with another pollinator is highly suggestive of hierarchical competitive displacement rather than fixed preference (e.g., Inouye 1978; Johnson 1986; Kato et al. 1999). Even more convincing evidence of competitive displacement comes from experiments in which the removal of one pollinator results immediately in an expanded foraging repertoire for subordinate pollinator species (Primack and Howe 1975; Inouye 1978; Laverty and Plowright 1985; Soltz 1987). As the body of experimental evidence grows, we may find that in guilds with hierarchical competition, the foraging preferences of competitively dominant pollinators are determined primarily by maximization of foraging efficiency rather than by the presence of competitors (e.g., Pimm et al. 1985). In contrast, subordinate pollinators may frequently be restricted to suboptimal flower species because of the presence of dominant competitors. Accordingly, it will be important to monitor how multiple species within the pollinating guild respond to manipulations of competitors or resources rather than considering just one or two focal species (Macnally 1983).

*Patch Dynamics and Colonization-Competition Trade-Offs.* Because flowers are relatively immobile resources that are patchily distributed over space, patch dynamics may contribute to the persistence of competitive subordinates in multispecies pollination guilds. In pollination mutualisms, new resource patches are constantly being created as new flowering species come into bloom or, at a smaller spatial

scale, by the opening of new flowers. A number of investigators have reported that competitively subordinate pollinators tend to arrive at new flowers before competitive dominants, a pattern that is reminiscent of competition-colonization trade-offs (Roubik 1980; Paton 1993; Nagamitsu and Inoue 1997). Alternatively, nonterritorial subordinates may persist because they are better at recognizing novel flower types as nectar sources or at finding cryptic flowers (Tiebout 1996).

*Selection and Coexistence.* Even when we document diverse foraging patterns within pollinator guilds, further analysis is needed to determine whether the use of different habitats, temporal periods, or flower species actually facilitates coexistence among pollinator species. If resource partitioning promotes coexistence among pollinators, then we would predict that those (subordinate) individuals displaying behaviors or morphologies that increase niche overlap with dominant competitors should be at a selective disadvantage. For example, in a guild of bees that shows interspecific variation in proboscis length, individual bees with mouthpart lengths more similar to those of competitive dominants may be at a disadvantage in competition. A potentially complementary approach would be to manipulate the floral resource base for a pollination guild to limit opportunities for niche partitioning, for example, by reducing the diversity of flowering species, thinning flowers to reduce spatial heterogeneity in density, or increasing overlap in flowering phenology (e.g., Waser 1978a). The responses of local pollinator populations to such treatments could reveal a great deal about the importance of resource partitioning for competition and species coexistence.

The community ecology literature is replete with models and hypotheses that can be mined productively by pollination biologists, but we have not yet mentioned them. For example, the persistence of competitively subordinate pollinators could be enhanced by spatial aggregation (reducing the ratio of interspecific to intraspecific interactions they experience), reduced susceptibility to natural enemies, or an ability to remain dormant in years when flower resources are scarce. These possibilities remain largely unexplored in pollination guilds, and they represent fertile ground for research.

#### *The Role of Adaptive Responses in Promoting Coexistence among Plants That Share Pollinators*

There is an extensive literature showing that interactions among plant species sharing pollinators can range from facilitative to competitive, depending on overlap in flowering phenology, how frequently pollinators move pollen between species, and the degree to which pollinator pop-

ulations are limited by, or attracted to, floral resources (e.g., Levin and Anderson 1970; Schemske et al. 1978; Waser 1983; Campbell 1985; Motten 1986; Rathcke 1988; Stone et al. 1996). Here, we emphasize only a few major points. First, we note that the two types of pollination service for which coflowering plant species potentially compete, pollinator visits and effective pollen transfer, have different consequences for coexistence within the plant guild. Competition for pollinator visits can directly affect plant densities only when two conditions are met: seed set is pollen-limited and plant population sizes are limited by seed recruitment. In contrast, natural selection within populations of coflowering plants may be influenced by competition for pollinator visits and/or for effective pollen transfer to conspecifics under a broad range of ecological conditions. Here, we focus on adaptive responses to competition that may facilitate coexistence within guilds of coflowering species.

In mixed plant communities with limited access to pollinators, the presence of more attractive flowers can reduce pollinator visits to less attractive members of the plant guild, decreasing their average seed production and possibly their population densities. In the face of such asymmetric competitive ability, selection within populations of plants that are inferior exploitative competitors for pollinator visits may favor traits that can reduce the negative effects of competition. These may include traits that increase the effectiveness of infrequent pollinator visits (Motten 1986; Medan and Basilio 2001) or that facilitate self-fertilization (Randall and Hilu 1990; Fishman and Wyatt 1999).

The consequences of competition via interspecific pollen transfer for selection on plant traits should be strongly influenced by at least two factors: a species' local frequency within a coflowering community and the degree to which individual pollinators show fidelity to its flowers. If pollinators move at random between coflowering plants and interspecific pollen transfer leads to reductions in seed production, species that are relatively rare within the community may be vulnerable to competitive exclusion (Levin and Anderson 1970; Waser 1978b). This is because visits to rare flower types are likely to be followed by pollen-wasting visits to other species, and pollinators arriving at the flowers of rare species are likely to be carrying mostly extraspecific pollen grains. Rarity disadvantage due to interspecific pollen movement could be a potent force acting to homogenize communities of coflowering plants, and so it is important for biologists to study how minority populations can persist in the face of this type of competition.

In plant populations that share pollinators with coflowering species, natural selection should favor traits that reduce the negative effects of interspecific pollinator movements and that reduce the probability of such movements

(also see Waser 1983). These adaptations should coincidentally facilitate the persistence of minority species.

Less common plant species within a coflowering guild may experience selection for traits that ameliorate the competitive impact of pollinator movements between different species. For example, fecundity losses due to post-deposition interference by foreign pollen might be ameliorated by changes in stigma chemistry or morphology. Another possible response, which could be viewed as spatial partitioning of the pollinator's body surfaces, would be to evolve a floral morphology that increases the precision of pollen transfer from anthers to stigmas of the same species and minimizes pollen deposition on heterospecific flowers during pollinator movements between species. Intraguild differences in floral tube length and in the placement of anthers and stigmas have often been interpreted in this light (e.g., Brown and Kodric-Brown 1979; Feinsinger et al. 1986; Armbruster et al. 1994; but see Murcia and Feinsinger 1996). Recent studies have shown that precise pollen placement can enhance male and female reproductive success within plant populations (reviewed in Barrett 2002; see also Darwin 1862), but we lack quantitative studies of how selection on such traits may be molded by the frequencies and morphologies of coflowering species.

Reproductive losses due to interspecific pollen transfer may also select for traits that reduce the numbers of interspecific transitions made by pollinators. For example, species at low frequency within a coflowering plant community may undergo adaptive alterations in phenology that minimize overlap in flowering time with more abundant competitors, a form of temporal resource partitioning. This is an idea that has inspired many investigators, but it has proven difficult to demonstrate whether flowering phenologies within pollination guilds are significantly hyperdispersed and, more importantly, whether staggered flowering times are an adaptation to reduce competition for pollination services (reviewed in Waser 1983). If interspecific pollen transfer favors reductions in phenological overlap, then we should see stronger selection for individuals with divergent flowering times in species that are minority members of a pollinator-sharing guild. To our knowledge, this is an idea that has not been tested.

Adaptation can also lead to reduced interspecific pollinator movements if evolved floral traits increase the tendency of pollinators to show fidelity to a single species of flower. Traditionally, pollination biologists have emphasized the selective advantages of having specialized pollinator species, but this view is now being reexamined because of the apparent rarity of inflexibly specialized pollinators and the high risks of reproductive failure for plants that can be pollinated by just one or a few species (reviewed in Waser et al. 1996). A similar but alternative

view is that interspecific pollen transfer selects for traits that encourage individual pollinators to move principally among flowers of the same species within a foraging bout (Levin and Anderson 1970; Straw 1972; Waser 1978*b*; Kunin and Iwasa 1996; Chittka et al. 1999). Short-term floral constancy is common in bumblebees and honeybees (reviewed in Waser 1986), and recent studies have lent support to the long-held idea that constancy can increase the efficiency of pollinators because of the dynamics of their sensory and memory systems (Chittka and Thomson 1997; Chittka et al. 1999; Barrett 2002). Pollinators tend to show greater levels of constancy to rewarding flowers and are also less likely to make interspecific transitions when coflowering species differ dramatically in color and/or morphology (Chittka et al. 1997; Gegear and Laverly 1998), and they may therefore select for individual plants with high rewards and unusual floral morphologies. In plant populations where reproductive success is reduced by interspecific pollen transfer, such adaptations should facilitate coexistence among coflowering species. It may be productive to view this coexistence mechanism as a form of temporal aggregation in which interspecific contacts, mediated through pollinator movements, are minimized.

Taken together, these arguments suggest some new research priorities for investigators interested in competition and coexistence in guilds of plants that share pollinators. First, we need more integrative studies of the extent to which pollination limits plant population densities. Few investigators have attempted to document whether both pollen limitation of seed production and seed limitation of recruitment are occurring within the same plant population (but see Pavlik et al. 1993; Ackerman et al. 1996), but these are precisely the data we need to assess the impact of pollinators on plant population and community dynamics. Second, we see a need for more experimental studies documenting how fitness interactions between coflowering species may be mediated by pollination. Last, there are great opportunities for using intraspecific floral variation to understand how interspecific competition for pollination services exerts selection pressures within pollination guilds. Many of the hypotheses presented here can be tested by analyzing patterns of phenotypic selection on floral traits (Lande and Arnold 1983) in concert with manipulations of flower density and diversity within coflowering plant communities (e.g., Campbell et al. 1997).

#### Competition and Coexistence in Ant-Myrmecophyte Systems

Species in more than 141 plant genera worldwide have been found in either obligate or facultative relationships with plant-ants (Davidson and McKey 1993). In a few cases, pairwise mutualism between a particular ant and

plant species have been reported (McKey 1984, 1991; Chenuil and McKey 1996; Yu and Davidson 1997; Fiala et al. 1999; Brouat et al. 2001). However, in most cases, plant-ants and/or their myrmecophytic hosts are associated with multiple partner species (Davidson and McKey 1993).

For specialized myrmecophytes and symbiotic plant-ants, participation in the overall mutualism is often obligatory. Myrmecophytic plants provide a number of potential benefits to ants, including nesting space and food rewards (Janzen 1966, 1975; Vasconcelos 1991). In return, ants may provide protection from herbivory (Janzen 1966; Davidson and McKey 1993; Fonseca 1994; Federle et al. 1998), pruning of neighboring plants (Janzen 1966; Benson 1985; Davidson and McKey 1993; Federle et al. 1998), nutrient enrichment (Janzen 1966; Treseder et al. 1995), or some combination of these services. In most of these systems, it is rare to find myrmecophytes that attain maturity without having hosted a symbiotic ant colony, and plant-ant colonies succeed only if they can retain possession of a host. However, this mutual dependence does not necessarily mean that either guild of mutualists is limited by the other.

#### *Limitation of Plant-Ants by Host Plants*

Obligate plant-ant colonies depend completely on host plants for their establishment and survival, suggesting the potential for strong competition among different ant species using the same host plant species. Although direct experimental evidence for this competition is rare (Palmer et al. 2000), a number of observations suggest that competition for host plants may be common. For example, plant-ants often saturate the available nest space provided by myrmecophytes (e.g., Fonseca 1993, 1999; Palmer et al. 2000). Further, newly recruiting host plants are often colonized by multiple queens (Janzen 1975; McKey 1984; Perlman 1992; Vasconcelos 1993; Maschwitz and Fiala 1995; Yu and Davidson 1997; Stanton et al. 2002), whereas mature plants are typically occupied by only a single colony (Janzen 1975; Davidson and McKey 1993). Interference competition for host-plants may also be important at later stages of colony development. For example, aggressive displacement of colonies of subordinate species by more dominant species has been reported (e.g., Young et al. 1997; Palmer et al. 2000). In addition, interspecific turnover of ant species on host plants over time has been documented for a number of myrmecophyte genera (reviewed in Davidson and McKey 1993), potentially reflecting competitive displacement of inferior competitors by more aggressive species (e.g., Janzen 1975; McKey 1984; Davidson et al. 1989; Palmer et al. 2000).

Despite an abundance of correlative and inferential evi-

dence indicating competition for host plants within plant-ant guilds, few experiments have confirmed the existence of competition or identified its mechanisms. Such experiments are necessary to understand the precise nature of competition and coexistence among plant-ants, because host plants are a complex resource comprising both food and nest sites. For example, do correlations between habitat productivity and patterns of plant-ant species occupancy (e.g., Davidson and Fisher 1991; Davidson et al. 1991; Davidson and McKey 1993; Yu and Davidson 1997; Palmer, in press) result from asymmetries among ant species in the degree of resource limitation, space limitation, or some combination of these factors? In ant-myrmecophyte systems, these factors are often readily amenable to experimentation. For example, resource production and domatia volume might be supplemented on host plants in a factorial experiment to determine whether ant colony size or fecundity is limited by space or food resources and whether ant species vary in response to these manipulations.

#### *Potential Mechanisms of Coexistence among Competing Plant-Ants*

*Environmental Heterogeneity and Trade-Offs.* Environmental heterogeneity may take a number of forms, with differing expectations for the mechanisms supporting species coexistence in each. Spatial variation in resource quantity or quality may facilitate coexistence if there are interspecific trade-offs in the ability of species to exploit resource-rich versus resource-poor patches (e.g., Kotler and Brown 1988; Hanski 1989) and/or differences in species' tolerance for low resource conditions (e.g., Grime 1979). Davidson and colleagues have suggested that variation in habitat productivity may play a role in species coexistence within ant-plant systems in the Neotropics and Asia on the basis of observations and experiments demonstrating that competitive dominants tend to occupy faster-growing hosts and more productive habitats, while subordinates are generally restricted to slower-growing hosts and less productive habitats (Davidson and Fisher 1991; Davidson et al. 1991; Davidson and McKey 1993; Yu and Davidson 1997; but see Vasconcelos and Davidson 2000).

In the *Acacia drepanolobium* ant system in tropical Africa, Palmer (2001, in press) demonstrated that a productivity mosaic is spatially correlated with the outcome of competition among acacia ant species for host trees. In productive microsites, competitively dominant ant species are more likely to supplant subordinates, whereas the likelihood of subordinates replacing dominants on host trees increases with distance from these hot spots (Palmer, in press). High-productivity areas favor rapid colony growth in dominant species and subsequent takeovers of neighboring trees, whereas dominant species appear to be less

persistent on host trees in lower-productivity areas. Overall, the apparent generality of competitive trade-offs among ants (Davidson 1998) suggests that habitat-driven spatial variation in resource quality or productivity may play an important role in promoting coexistence within plant-ant guilds.

*Patch Dynamics and Colonization-Competition Trade-Offs.* Interspecific trade-offs in colonization and competitive abilities or in dispersal ability and fecundity appear to be important in maintaining species diversity within some specialized ant-plant symbioses. For example, Stanton et al. (2002) document a complete reversal in the competitive hierarchy among four acacia ants between two stages of colony development. Species that dominate in fights between foundress queens during early stages of host-plant colonization are competitively subordinate in interspecific battles between mature colonies for the possession of host trees. Yu (2001) provides a cogent and detailed review of the contribution of patch dynamics to coexistence within ant-myrmecophyte systems, which we will not duplicate here. Instead, we emphasize that, since plant-ants are essentially sessile organisms that compete strongly for space, they provide fertile ground for testing patch dynamics theory within animal communities. One question that might be profitably examined in these systems is whether successional diversity results from strong dispersal limitation of competitive dominants (e.g., Janzen 1975) or from trade-offs in the ability to exploit early versus later successional environments (e.g., the “niche hypothesis”; Pacala and Rees 1998; Stanton et al. 2002). Investigating the precise nature of the trade-offs supporting species diversity is important for understanding the generality of mechanisms such as the competition-colonization trade-off in natural systems (see Yu and Wilson 2001; Levine and Rees 2002) as well as for evaluating the robustness of predictions from models that rely on these trade-offs (e.g., the extinction-debt model; Tilman et al. 1994).

In plant-ant guilds characterized by colonization-competition trade-offs and competition among mature colonies, priority effects may slow the rate at which competitively subordinate plant-ants are displaced from guilds. In East Africa, for example, the competitively subordinate plant-ants *Crematogaster nigriceps* and *Tetraoponera penzigi* are efficient colonists that both modify *A. drepanolobium* host plant architecture in ways that reduce the likelihood that their colonies will be aggressively displaced by superior competitors on neighboring trees (Young et al. 1997; Stanton et al. 1999; Palmer et al. 2002).

*Recruitment Limitation and Aggregation.* In relatively uniform habitats, theory suggests that competing species may coexist through intraspecific aggregation (e.g., Hanski and

Cambefort 1991; Ives 1991; Bolker and Pacala 1999), which increases the intensity of intraspecific relative to interspecific competition. To our knowledge, no evidence for this mechanism exists in the ant-plant literature, which has generally ignored intraspecific competition. Even so, because plant-ant colonies interact most strongly with near neighbors (e.g., Palmer et al. 2000), they may be strong candidates for testing the applicability of spatial coexistence mechanisms in animal communities.

*Tritrophic Models.* Although ant populations are generally regarded as being limited by competition (Holldobler and Wilson 1990), parasitism may nonetheless play a key role in supporting species diversity. The viability of this mechanism hinges on whether parasites disproportionately target the queens or colonies of more abundant species. There is evidence that parasites may be a major source of queen mortality and may cause disproportionate mortality among host ant species as a result of both habitat and host specificity (Davidson and Fisher 1991; Yu and Davidson 1997; Yu and Pierce 1998; M. L. Stanton, unpublished data). However, the quantitative contribution of parasitism to ant guild coexistence is not well known (but see Yu and Quicke 1997; Yu et al. 2001).

*Can Host-Plants Affect the Outcome of Competition among Plant-Ants?* Characteristics of the resources offered by myrmecophytes may also influence competitive dynamics among plant-ants. For example, changing the rate, timing, or composition (e.g., C:N ratios) of resource supply in host plants may favor particular ant-plant species over others (Davidson and McKey 1993; Davidson 1997; Yu and Davidson 1997). Experimentally augmenting nectar rewards on *A. drepanolobium* host plants increases the likelihood of takeover attempts by a competitively dominant plant-ant, suggesting that plant traits can influence the outcome of competition among potential partners (Palmer et al. 2002). If myrmecophytes display variation in the production (e.g., Folgarait et al. 1994), availability (e.g., Izzo and Vasconcelos 2002), or composition of provisioned resources, their impact on ant coexistence may be profound (also see “Discussion”).

While characteristics of plant rewards may influence ant guild dynamics, we have little quantitative information about the fitness benefits of myrmecophyte rewards to plant-ants (Bronstein 1998). Studies demonstrating correlations between ant colony size and myrmecophyte food (Heil et al. 2001; Itino et al. 2001) and domatia (e.g., Fonseca 1993, 1999; Yu and Pierce 1998) production suggest that the ant colony dynamics may be under host plant control, especially in systems where plant-ants do not forage off of their host trees (Itino et al. 2001). It is possible



that these benefits vary among ant species, potentially having an effect on coexistence within the plant-ant guild.

Heterogeneity in the structural characteristics of host plants may also influence species coexistence within mutualist ant guilds. Morphological traits of some host plant species may act as filters that allow access only by certain plant-ants, thereby providing a competitive refuge to their occupants. Examples of such traits include the slippery stems of some *Macaranga* that can be navigated by only certain ant species (Federle et al. 1997) and uniquely shaped prostomata in *Leonardoxa* spp., which allow access only to apparently coadapted plant-ants (Brouat et al. 2001; see also Fiala and Maschwitz 1992). All else being equal, these traits should shift the competitive balance in favor of specialized mutualist species, but few studies have examined the community-level consequences of these adaptations. Experimental approaches to these questions would contribute to our understanding of the role filters may play in the maintenance of guild diversity.

#### *The Role of Adaptive Responses in Promoting Coexistence among Myrmecophytes*

Observations that plant-ants tend to saturate available domatia (e.g., Fonseca 1999) suggest that mutualistic ants do not limit myrmecophyte population densities. Even so, myrmecophytes are likely to compete, within and among species, for the services of the most beneficial plant-ant symbionts. It is well established that certain species of plant-ants dramatically enhance the fitness of individual host plants through decreases in herbivory and/or increases in growth, survivorship, and reproduction (e.g., Janzen 1966, 1969; Vasconcelos 1991; Fonseca 1994; Yu and Pierce 1998). However, the quality of different plant-ant species as mutualists can vary markedly within a guild, with some ant species providing no net benefits to their host (e.g., Janzen 1975; Fiala et al. 1994), while others actually reduce host-plant growth and/or reproduction (Young et al. 1997; Yu and Pierce 1998).

Strong species-specific variation in the net benefits of ant-plant associations suggests that these interactions may influence both natural selection and competition in myrmecophyte guilds. Myrmecophytes that host more beneficial plant-ants species or that induce more beneficial behaviors from their resident colonies should experience advantages in survival, growth, and reproduction. Three potentially key consequences of variation in ant partner identity to myrmecophytes remain relatively unexplored. First, to what extent can host-plants exert control over the identity of their ant partners through either plastic or adaptive responses? Second, given a particular ant associate, to what extent can host plants influence the quality of services provided (e.g., protection from herbivory)? Fi-

nally, what are the consequences of ant protection of myrmecophytes for plant communities?

Host-plants may show both adaptive and plastic responses to variation in the costs and benefits of ant associates. As previously discussed, coadaptation or ecological sorting among plants and ants over evolutionary time may increase the frequency of particular ant-plant species pairings. Host plants may also show plasticity in the production of nectar (Agrawal and Rutter 1998), domatia (Izzo and Vasconcelos 2002), and food bodies (Letourneau 1990, 1991). If changes in these resources favor certain ant species over others (e.g., see Davidson and McKey 1993; Davidson 1997; Yu and Davidson 1997; Palmer et al. 2002) or even higher levels of activity and aggression within a particular ant species (Davidson 1997), this plasticity may be important in determining fitness variation among plants. Few studies have examined how the quantity, quality, and pattern of food production influence the attractiveness of myrmecophytes to ants (but see Fiala and Maschwitz 1990; Yu and Davidson 1997; Palmer et al. 2002). Within a given ant-plant association, the quantity of mutualist ants in residence on host plants may also influence myrmecophyte fitness. Plant resource production is positively correlated with colony size for several myrmecophyte species (e.g., Heil et al. 2001; Itino et al. 2001), and larger ant colonies may also be better defenders of their hosts (Duarte Rocha and Godoy Bergallo 1992; Heil et al. 2001; Palmer 2001), allowing the possibility that myrmecophytes may exert control over the services provided by their mutualists. The extent to which this control could influence plant fitness and the relative performance of co-occurring myrmecophyte species depends on the balance between costs to the plant of increased resource production and benefits accrued through increased ant services. This balance in turn will depend on relationships between behavioral and demographic responses of ant colonies to variation in host plant resource production, the relationship between ant colony size and services to the host (e.g., herbivore deterrence), and the relationship between ant services and plant reproduction (Bronstein 1998; see also Fonseca 1993). Experimental approaches (e.g., Heil et al. 2001) will help to unravel these complex linkages, clarifying the precise costs and benefits of associations between myrmecophytes and their mutualists.

#### Discussion

Many of the mechanisms that maintain species coexistence in mutualisms appear similar in their nature and diversity to those in other trophic communities. But are there consistent differences between the mechanisms maintaining species diversity within mutualisms and those operating in other guilds? One salient difference is that in mutualist

guilds, the patches for which partners compete are living organisms. Because mutualisms involve coevolutionary processes, there may be selection for species traits or interactions that either oppose or promote coexistence among guilds, depending on whether partner specificity increases or decreases mutualist fitness (see “The Role of Adaptive Responses in Promoting Coexistence among Plants That Share Pollinators” and “The Role of Adaptive Responses in Promoting Coexistence among Myrmecophytes”).

Under certain circumstances, increased mutualist specificity may increase the efficiency of a partnership. In other cases, specificity may be risky if mutualist abundance varies strongly in space or time (Waser et al. 1996; Hoeksema and Bruna 2000). Whether adaptation within mutualist populations will tend to restrict or enhance species coexistence among partner species depends on three factors: variation in the quality of mutualist species, spatial and/or temporal variation in mutualist abundance, and whether less beneficial partners overcome the mechanisms that mutualists evolve to enhance partner specificity. We discuss each of these factors in turn.

#### *Variation in the Quality of Alternative Partner Species*

If all potential partners provide comparable net rewards to their mutualist associates, then selection is less likely to favor increased host specificity within that mutualist population. Conversely, if there is great variation in the degree to which different partners benefit the focal species, or if some are even parasitic, then natural selection should favor traits or behaviors that exclude less beneficial partners from the mutualism. Especially if high-quality mutualists are also good competitors for partners, the evolution of such selective filters will tend to inhibit species coexistence within mutualist guilds. There is a considerable literature discussing the existence of variation in the benefits of mutualist partners, the conditions that may favor some species becoming less mutualistic, and the susceptibility of mutualisms to invasion by parasitic or less faithful species (see Bronstein 1994; Pellmyr and Thompson 1996; Herre et al. 1999; Bronstein 2001). These factors may influence the evolution of partner specificity (Schemske and Horvitz 1984; Thompson and Pellmyr 1992), but we do not yet know how this specificity influences the broader phenomenon of species coexistence.

#### *Reliability of Mutualist Species*

There will only be selection for greater partner specialization if a given mutualist is consistently the most effective mutualist over long timescales. No matter how efficient a partner is when it is present, it may be ineffective overall if its abundance is spatially and/or temporally variable.

How strongly partner unreliability decreases a mutualist's fitness will depend on the consequences of lapses in the relationship. The impact of pollinator unreliability may range from only transient declines in individual fitness to local population extinction, depending on the extent of the missing pollination services, the ability of other pollinators to compensate for their competitors' absence, and life-history traits of the plants. However, a single failed year for either partner in a plant-ant mutualism could be fatal for the other. It may be generally true that the fitness consequences of mutualisms promoting reproduction are more conditional than those with strong impacts on survival.

#### *Effectiveness of Partner Selection Mechanisms*

Traditionally, mechanisms such as morphological filters have been seen as ways of excluding parasites or less beneficial partners from mutualistic systems. Another perspective emerging from this discussion is that these mechanisms may allow mutualists to manipulate competition among different partner species in ways that favor more beneficial partners or that lead to the evolution of mutualistic behavior. Few such mechanisms are foolproof, as evidenced by widespread evidence of cheating in mutualisms (e.g., Inouye 1983; Bronstein 1994, 2001; Young et al. 1997; Irwin and Brody 1998; Golubov et al. 1999; Navarro 2001; Yu 2001).

Pollinators can behaviorally adjust the identities of their mutualist partners on an almost instantaneous timescale, and potentially so can plant-ants, although opportunities for partner choice are likely to be more limited in sessile, symbiotic colonies than for mobile foragers. Evolutionarily, animal partners can evolve behavioral or morphological traits that expand their suite of available mutualists. It is perhaps less clear how (or why) they would evolve fixed traits that exclude certain partners, so long as effective behavioral responses are available.

We might expect plant partners to undergo evolutionary adaptations more than behavioral responses to limit or expand their suite of animal mutualists. However, individual plants can respond on fairly short time frames to changes in their biotic environment (e.g., the extensive literature on induced defenses; reviewed in Karban and Baldwin 1997). It is possible that plants could behaviorally limit access to certain partners, if there are ways in which alternative partner species or the benefits provided by those partners can be distinguished. Plastic responses that influence pollinators may be infeasible, since the association between a plant or flower and any given species of pollinator is typically fleeting. In contrast, plant-ants often remain resident on their hosts for extended periods, opening the door for adaptive plastic responses that encourage

colonization by highly beneficial ant species or that make resident colonies of low-quality mutualists vulnerable to displacement by superior mutualists.

### Conclusion

Interactions with partner species have the potential to strongly influence competitive dynamics within mutualist guilds. Research into the nature and variability of these interactions will provide key insights into how mutualist guild diversity is maintained. Here we list a number of research agendas that deserve empirical attention (in addition to the several research directions mentioned throughout the text):

First, a key issue for species coexistence within mutualist guilds is partner choice. To what extent can mutualists influence the identity of their partners on both evolutionary and ecological timescales? Further, to what extent can mutualists identify which partners are more or less effective?

Second, what is the nature of variation in the effectiveness of different partners? The greater this difference, the greater the potential for selection to favor mutualists that can reduce associations with less beneficial partners.

Third, how does this variation interact with other coexistence mechanisms? Are competitively subordinate species more or less likely to be poor mutualists or antagonists than more persistent competitive dominants? For example, if competitive subordinates persist by fugitive strategies, their more transitory associations may be more likely to devolve into parasitism. Similarly, it is possible that some competitively dominant mutualists may achieve success because partners have evolved mechanisms that favor them.

Fourth, studying mutualisms from a multispecies perspective has the potential to influence our thinking about coevolutionary geographical mosaics (Thompson 1997). For example, is a mutualist that interacts with a partner at the edge of its physiological or geographical distribution less likely to be beneficial than one with a distribution that overlaps more broadly with that partner?

Fifth, how spatially and temporally reliable are different mutualists, and how does this reliability affect the long-term fitness of their partners?

Sixth, are alternative coexistence mechanisms differentially affected by the evolution of partner specificity?

Mutualisms offer excellent opportunities for research into mechanisms of competition and species coexistence and how these processes may be modified by evolutionary adaptation. Traditionally, theoretical and empirical analyses of mutualism have emphasized interactions between associating partners rather than among different species of partners on the same side of the relationship. Expanding

our research focus to account for multispecies guilds of mutualists demands consideration of the forces that maintain diversity in these associations.

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